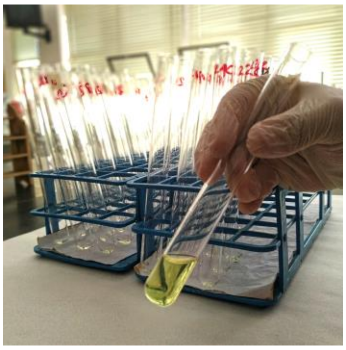
PhD Thesis 2019

EFFECTS OF FIRE RECURRENCE AND BURN SEVERITY IN FIRE-PRONE PINE ECOSYSTEMS

Basis for forest management

Víctor Fernández García





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Pictures on the PhD Thesis cover:

Top left: fire tornado in the 2012 Sierra del Teleno wildfire (José Carlos García).

Top right and back cover: four-year-old *Pinus pinaster* Ait. sapling (GEAT research group).

Bottom: test tubes used in the analysis of soil enzyme activity (GEAT research group).

Departamento de Biodiversidad y Gestión Ambiental

Área de Ecología

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EFECTOS DE LA RECURRENCIA Y DE LA SEVERIDAD DE LOS INCENDIOS FORESTALES EN ECOSISTEMAS DE PINAR PROPENSOS AL FUEGO

Bases para la gestión forestal

Víctor Fernández García

Noviembre, 2019

Departamento de Biodiversidad y Gestión Ambiental

Área de Ecología

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Decicated to my mother

Dedicado a mi madre

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Fotografía en el anverso de esta hoja:

Corzos en la zona afectada por el incendio de la Sierra del Teleno de 2012 (grupo de investigación GEAT).

RESUMEN

Los ecosistemas propensos al fuego dominados por *Pinus pinaster* Ait. y *Pinus halepensis* Mill. son los bosques más afectados por los incendios forestales en la Cuenca Mediterránea. Esto los convierte en ecosistemas prioritarios en los que estudiar las consecuencias ecológicas que pueden tener los cambios en los regímenes de incendios esperables en el actual contexto de cambio global. El objetivo de la presente Tesis Doctoral es analizar los efectos de diferentes regímenes de recurrencia y de severidad de incendios en ecosistemas propensos al fuego dominados por *P. pinaster* y *P. halepensis*.

El primer paso ha sido estudiar la capacidad de imágenes multiespectrales del satélite Landsat para caracterizar la recurrencia (artículo I) y la severidad (artículo II) del fuego en pinares afectados por grandes incendios forestales. Los patrones de variación espacio-temporal de los incendios ocurridos durante el periodo 1978-2014 se determinaron mediante el análisis visual de composiciones en falso color de series temporales de imágenes Landsat 2, 4, 5, 7 y 8 (sensores MSS, TM, ETM+ y OLI respectivamente) y se validaron con los partes oficiales de incendios. Este método permitió cartografiar todos los incendios ocurridos según los registros oficiales, demostrando que la utilización de series temporales de imágenes Landsat es una herramienta eficaz para caracterizar la recurrencia de incendios. De igual modo, para caracterizar la severidad del fuego se calcularon diferentes índices espectrales (métricas térmicas, reflectivas y mixtas) a partir de imágenes Landsat. La habilidad de dichas métricas para determinar la severidad en el suelo, en la vegetación y a nivel global en el conjunto del ecosistema a lo largo de un gradiente climático, se evaluó mediante modelos de regresión lineal utilizando el CBI (*Composite Burn Index*) como verdad terreno. En general, los índices bi-temporales basados en las regiones del espectro del infrarrojo cercano e infrarrojo de onda corta (tipo dNBR; *differenced Normalized Burn Ratio*) mostraron una alta capacidad para determinar la severidad en la vegetación y a nivel global, mientras que la capacidad de Landsat para determinar la

severidad en el suelo fue relativamente baja. También se encontraron diferencias en el rendimiento de los índices a lo largo del gradiente climático, por lo que se propone un nuevo índice espectral de severidad, el dNBR-EVI, que muestra una mayor capacidad para determinar la severidad y una buena transferibilidad a lo largo del gradiente climático.

Para investigar los efectos de la severidad del fuego sobre las propiedades del suelo se llevó a cabo un estudio inmediatamente después del incendio (1 semana) en un pinar de *P. pinaster* con suelos silíceos (artículo III) y otro a medio plazo (3 años) en ecosistemas de *P. pinaster* y *P. halepensis* con suelos silíceos y calcáreos respectivamente (artículo IV). Los resultados mostraron efectos significativos sobre la mayoría de propiedades estudiadas inmediatamente después del incendio (diámetro de los agregados, pH, carbono orgánico, fósforo asimilable, carbono de la biomasa microbiana, y actividades enzimáticas β-glucosidasa y fosfatasa ácida), así como sobre algunos ratios entre dichas propiedades (relación C:N, cociente microbiano y actividad específica de la β-glucosidasa). De entre estas propiedades y ratios, los relacionados con las actividades enzimáticas mostraron la mayor sensibilidad al fuego, decreciendo desde los escenarios de baja severidad. A medio plazo encontramos que algunas propiedades del suelo (fósforo asimilable, carbono de la biomasa microbiana y actividades enzimáticas) siguen mostrando relaciones significativas con la severidad del fuego. El carbono de la biomasa microbiana, la β-glucosidasa y la ureasa disminuyeron con la severidad en los dos ecosistemas estudiados, y podrían ser potenciales indicadores para investigar el legado de la severidad a medio plazo en pinares mediterráneos propensos al fuego.

Los efectos de la recurrencia y de la severidad de incendios sobre la regeneración de la vegetación fueron estudiados mediante técnicas de teledetección (artículo V) y mediante estudios basados en información de campo, focalizados tanto en la población de pinos (artículo VI) como en el conjunto de la comunidad de leñosas (artículo VII). En el estudio basado en técnicas de teledetección se utilizó la diferencia del índice NDVI (*Normalized Difference Vegetation Index*) calculado con Landsat como indicador de la recuperación del vigor vegetal después del incendio. Los resultados indicaron que, durante los años siguientes al incendio (2 y 5 años), las zonas con alta severidad presentan un bajo vigor vegetal. Por otro lado, el vigor vegetal se recuperó mejor en las zonas con alta recurrencia que en las zonas con baja recurrencia. Esto se debe a la dominancia de especies de matorral en los escenarios de alta recurrencia, que requieren menos tiempo que las zonas arboladas para alcanzar la situación pre-incendio. En el estudio de campo encontramos que la densidad y cobertura de las plántulas de *P. pinaster* y *P. halepensis* en las zonas de baja recurrencia y baja severidad es relativamente elevada y suficiente para asegurar la recuperación del dosel arbóreo, mientras que en las zonas afectadas por una alta recurrencia (3 incendios en 34 años) así como recurrencia moderada con alta severidad (2 incendios en 34 años), la regeneración natural de los pinos puede verse amenazada debido a la carencia de un banco de semillas viable. Por otro lado, a nivel de comunidad hemos observado que variaciones en la recurrencia y en la severidad alteran la diversidad de las especies leñosas y la cobertura relativa de las mismas según sus rasgos funcionales, especialmente en aquellas regiones que presentan sequía estival, como son las zonas Mediterráneas. En general, nuestros resultados muestran que la vegetación leñosa con (i) forma de vida no arbórea, (i) alta área foliar específica, (iii) capacidad para fijar nitrógeno, (iv) capacidad para rebrotar, (v) bajo peso de semillas o (vi) germinación estimulada por choque térmico puede ser más resiliente a incrementos en la recurrencia y severidad de los incendios.

Los resultados obtenidos en la presente Tesis doctoral contribuyen al avance del conocimiento en el campo de la ecología del fuego, y constituyen la base científica para una gestión forestal más eficiente en los ecosistemas de pinar de la Cuenca Mediterránea. Así mismo, este trabajo puede ser considerado como referencia a la hora de diseñar estrategias de gestión forestal para afrontar futuros cambios en los regímenes de incendios.

1. INTRODUCCIÓN

Los pinares mediterráneos propensos al fuego

El impacto social de los incendios forestales y sus consecuencias sobre los servicios que ofrecen los ecosistemas han motivado un gran interés en entender mejor los efectos del fuego a nivel ecológico, económico y social. Más de la mitad de la superficie terrestre es susceptible a incendios forestales (Moreno & Oechel, 1994; Keeley *et al.*, 2012). Sin embargo, el papel de los incendios es particularmente relevante en los ecosistemas propensos al fuego (Rundel *et al.*, 2018), que se definen como aquellos ecosistemas donde los incendios constituyen la principal perturbación ecológica, siendo lo suficientemente frecuentes como para actuar como una fuerza selectiva (Pausas & Keeley, 2014).

La Cuenca Mediterránea es una de las regiones más propensas al fuego a nivel mundial (Keeley *et al.*, 2012). En esta región, el clima mediterráneo surgió hace unos 15 millones de años dando lugar a unas condiciones climáticas que favorecen la acumulación de combustible durante el invierno y la primavera, y a una sequía estival que facilita la ocurrencia frecuente y relativamente regular de incendios (Rundel *et al.*, 2018). De este modo, el fuego puede considerarse un factor fundamental en los ecosistemas mediterráneos, que permite explicar la distribución, el funcionamiento y la estructura de los mismos, así como la diversidad y los rasgos funcionales de las especies vegetales que los constituyen (Keeley *et al.*, 2012; Pausas & Keeley, 2014; Rundel *et al.*, 2018).

Los pinares dominados por *Pinus pinaster* Ait. y *Pinus halepensis* Mill. son tradicionalmente los bosques más afectados por incendios en el conjunto de la Cuenca Mediterránea (Le Houerou, 1973) y en la Península Ibérica en particular (ADCIF, 2012; ICFN, 2015). Estos ecosistemas son especialmente relevantes no sólo por la gran extensión que ocupan (Fig. 1) sino también por su importancia ecológica y económica (de las Heras *et al.*, 2012). Ambos tipos de pinar son considerados ecosistemas propensos al fuego, y de hecho se ven favorecidos respecto a otros tipos de vegetación cuando las frecuencias de incendios son intermedias (un incendio cada 10-40 años) (Pausas, 1999; Fernandes & Rigolot, 2007). En general, los bosques de *P. pinaster* crecen sobre suelos pobres en nutrientes, arenosos y ácidos, en zonas con una temperatura media anual comprendida entre 9-16 ºC y una precipitación entre 400-1600 mm. Por otro lado, los ecosistemas de *P. halepensis,* que también se desarrollan sobre suelos pobres en nutrientes, muestran preferencia por suelos básicos, como son los desarrollados sobre margas, calizas o dolomías y resisten condiciones climáticas más térmicas (12-16 ºC) y áridas (300-700 mm) (Richardson, 2000; Serrada *et al.*, 2008; de las Heras *et al.*, 2012). No obstante, ambos ecosistemas comparten características ecológicas similares respecto al fuego, a nivel de la especie dominante y de la comunidad del sotobosque.

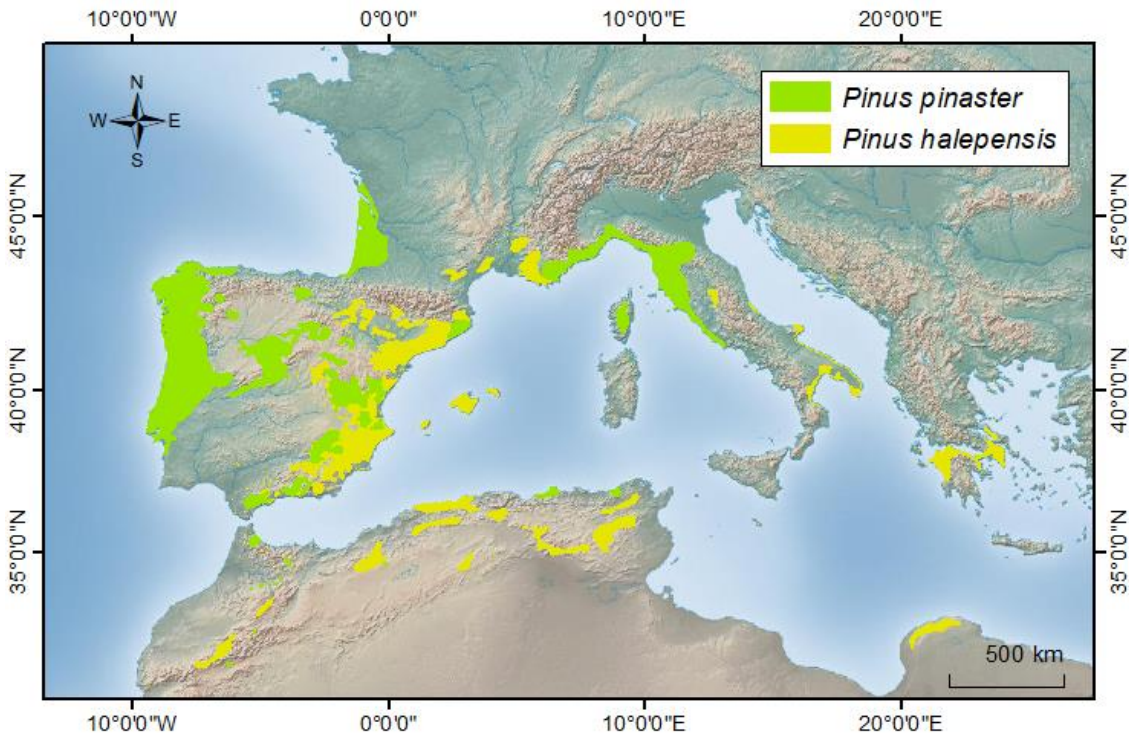

Figura 1. Distribución natural de los pinares de *Pinus pinaster* y *P. halepensis* (EUFORGEN, 2019).

Tanto *P. pinaster* como *P. halepensis* son especies altamente inflamables (Fernandes *et al.*, 2008; Keeley *et al.*, 2012) y originan un mantillo que también es muy inflamable debido a la composición química y las características físicas de sus acículas (Fernandes & Rigolot, 2007; Ormeño *et al.*, 2009). Por lo tanto, en estos ecosistemas es usual que los incendios consuman gran parte de la cubierta vegetal (Fernandes *et al.*, 2008). Después de los incendios, la recuperación de *P. pinaster* y *P. halepensis* se sustenta exclusivamente en la regeneración a partir de semillas, ya que como ocurre con el resto de pinos naturales de la Cuenca Mediterránea, no tienen capacidad para rebrotar (Tapias *et al.*, 2001; Pausas *et al.*, 2008). Para garantizar un banco de semillas abundante y con cierta capacidad para sobrevivir a los incendios forestales, estos pinos (*P. halepensis* y la mayoría de poblaciones de *P. pinaster*) acumulan piñas cerradas con semillas viables durante más de un ciclo reproductivo, lo que se denomina serotinia (Tapias *et al.*, 2001, 2004; Daskalakou & Thanos, 2004; Moya *et al.*, 2018). Las piñas serótinas se abren con las altas temperaturas, liberando las semillas de forma masiva después de los incendios (Tapias *et al.*, 2001; Pausas *et al.*, 2008), encontrando condiciones ambientales propicias para la germinación, establecimiento y crecimiento de las plántulas (Calvo *et al.*, 2008; Moya *et al.*, 2008; Keeley *et al.*, 2011). Generalmente, cuando las plantas de *P. pinaster* y *P. halepensis* tienen entre 4 y 10 años de edad comienzan a producir piñas con semillas viables (Tapias *et al.*, 2004). Esta maduración tan precoz favorece la persistencia de estas poblaciones de pino en ambientes con incendios frecuentes (Moya *et al.*, 2018). Sin embargo, hay que esperar unos 15 años después del incendio para tener un banco de semillas significativo (Pausas *et al.*, 2008; Keeley *et al.*, 2012).

El sotobosque de los pinares de *P. pinaster* y *P. halepensis* suele ser relativamente denso y alto (Fig. 2) (Keeley *et al.*, 2012; Taboada *et al.*, 2018). En general, las especies que conforman el sotobosque son similares a las existentes en los matorrales circundantes, dominando en ellos las familias Fabaceae, Cistaceae y Ericaceae entre otras (de las Heras *et al.*, 2012; Keeley *et al.*, 2012). Algunas de las especies más frecuentes (e.g. *Ulex parviflorus* Pourr., *Cistus albidus* L., *Cistus ladanifer* L., *Ulex europaeus* L., *Pterospartum tridentatum* (L.) Willk.) se caracterizan por acumular una alta proporción (> 20%) de biomasa fina muerta, mientras que otras muchas (fundamentalmente de las familias Lamiaceae y Cistaceae) presentan una alta cantidad de aceites volátiles (Baeza *et al.*, 2011; Keeley *et al.*, 2012).

Todas estas características relativas a la arquitectura y composición del sotobosque lo hacen altamente propenso al fuego (de las Heras *et al.*, 2012). Es por ello que la mayoría de las especies existentes en estos pinares presentan alguna estrategia de regeneración post-incendio como son la capacidad para germinar profusamente después del fuego (germinadoras), o la capacidad de recuperarse a partir de rebrotes vegetativos (rebrotadoras), si bien algunas especies combinan ambas estrategias (facultativas) (Arianoutsou & Ne'eman, 2000; Calvo *et al.*, 2003, 2008; Paula *et al.*, 2009).

Figura 2. Aspecto que presentan los ecosistemas de *P. pinaster* (izquierda) y *de P. halepensis* (derecha) maduros (> 30 años).

Los efectos de los incendios en el suelo y en la vegetación

El estudio de los efectos ecológicos de los incendios en la Cuenca Mediterránea es especialmente relevante teniendo en cuenta el alto riesgo de erosión y desertificación de esta región (Van der Knijff *et al.*, 2000; Prăvălie *et al.*, 2017), así como el alto valor ecológico de sus ecosistemas, que se caracterizan por tener una gran riqueza de especies y endemismos (Cowling *et al.*, 1996; Keeley *et al.*, 2012). Entre los ecosistemas de la Cuenca

Mediterránea, es posiblemente en los pinares propensos al fuego donde los impactos del fuego en el suelo y en la vegetación son más intensos (Pausas *et al.*, 2008).

Los incendios producen cambios inmediatos en las propiedades del suelo que pueden persistir varios años tras el incendio debido al propio efecto de la combustión y al cambio producido por el fuego en las condiciones ambientales (Certini, 2005; Bodí *et al.*, 2012; Caon *et al.*, 2014). A más largo plazo (> 5 años), los efectos del fuego en las propiedades del suelo son menos evidentes (Hedo *et al.*, 2015; Muñoz-Rojas et al, 2016). Tanto a corto como a medio plazo, estudios previos en ecosistemas de pinar han detectado cambios en las propiedades físicas, químicas y biológicas del suelo (Certini, 2005; Cerdá & Jordan 2010). Entre las propiedades físicas que se ven afectadas por el fuego se encuentran las relacionadas con la estructura, como es el tamaño de los agregados (Jordán *et al.* 2011; Mataix-Solera *et al.* 2011), lo que se relaciona con cambios en la capacidad de intercambio gaseoso, cambios en los procesos hídricos y biológicos y cambios en la vulnerabilidad a la erosión (Cerdá & Jordan 2010). El fuego también puede modificar las propiedades químicas del suelo, como el pH, la conductividad eléctrica o la concentración de nutrientes (Marcos *et al.*, 2007; Caon *et al.*, 2014), que muestran una estrecha relación con la productividad del ecosistema y con la diversidad microbiana y vegetal (Roem & Berendse 2000; Arshad & Martin 2002). La concentración de nutrientes en el suelo está controlada además por las propiedades biológicas del suelo, como son la actividad de las enzimas y de la biomasa microbiana (Tabatabai, 1994; Hinojosa *et al.*, 2016), que pueden ser destruidas completamente por el incendio (Vega *et al.* 2013).

Los cambios en las propiedades del suelo después del incendio están fuertemente relacionados con los cambios en la vegetación (Certini, 2005; Hedo *et al.*, 2015). Los efectos inmediatos del fuego en la vegetación son la combustión parcial o total de esta, produciendo un grado variable de mortalidad de las plantas en función de las características del incendio y de las propias especies (Moreno & Oechel, 1994; Paula *et al.*, 2009). La regeneración post-incendio en pinares propensos al fuego puede ser estudiada a nivel poblacional o considerando toda la comunidad vegetal (Arianoutsou & Ne'eman, 2000). En general, tanto la población de la especie dominante como el resto de la comunidad vegetal se recuperan a partir de procesos endógenos (autosucesión), mostrando una resiliencia a los incendios relativamente alta (Moreno & Oechel, 1994; Arianoutsou & Ne'eman, 2000; Calvo *et al.*, 2008). La alta resiliencia de la vegetación mediterránea a los incendios se ha atribuido tradicionalmente a las adaptaciones y exaptaciones de las especies a determinados regímenes de incendios, entre las que se encuentran las distintas estrategias regenerativas, la serotinia o la estimulación de la germinación por las temperaturas propias de los incendios entre otras (Paula *et al.*, 2009; Keeley *et al.*, 2011; de las Heras *et al.*, 2012), por lo que la recuperación puede verse amenazada cuando los regímenes de incendios son alterados (Keeley *et al.*, 2011, 2012; Rundel *et al.*, 2018).

Los atributos del régimen de incendios: recurrencia y severidad

El término régimen de incendios se refiere a los atributos espaciales, de magnitud y temporales de los incendios en un determinado ecosistema (Van Wagtendonk & Lutz, 2007; Bowman *et al.*, 2009; Rundel *et al.*, 2018). Entre los atributos espaciales destacan los patrones de consumo del combustible y el tamaño de los incendios, que es especialmente relevante cuando la recuperación de la vegetación depende de la entrada de semillas desde zonas no quemadas (Bond & Keeley, 2005). Los atributos de magnitud se refieren a la intensidad del fuego, que es la energía liberada por el incendio; y a la severidad del fuego que se entiende como el cambio en la biomasa producido por el incendio (Keeley, 2009). Por otro lado, los atributos temporales incluyen la estacionalidad con respecto a la ocurrencia de incendios, la frecuencia o recurrencia de incendios y periodo libre de incendios, que a su vez pueden ser condicionantes de la severidad del incendio (Steel *et al.*, 2015; García-Llamas *et al.*, 2019a). Los atributos del régimen de incendios son factores importantes para entender la estructura y composición de los ecosistemas propensos al fuego (Fernandes & Rigolot, 2007; Van Wagtendonk & Lutz, 2007), así como los impactos de los incendios y la capacidad de recuperación de los ecosistemas (Espelta *et al.*, 2008; Keeley, 2009). En consecuencia, desarrollar métodos que permitan caracterizar espacialmente los atributos del régimen de incendios es de gran interés para conocer la tolerancia de los ecosistemas y para optimizar la gestión forestal de los mismos (Keeley *et al.*, 2012).

Los cambios en la recurrencia (o frecuencia) de incendios son una importante amenaza para la preservación de los pinares propensos al fuego (Espelta *et al.*, 2008; Taboada *et al.*, 2018). Estudios previos indican que incendios muy frecuentes incrementan el riesgo de degradación del suelo (de las Heras *et al.*, 2012) y perjudican a las especies con tiempos largos de maduración e incapacidad para rebrotar después del fuego (Bond & Keeley, 2005; Rundel *et al.*, 2018), como es el caso de *P. pinaster* y *P. halepensis* (Tapias *et al.*, 2001). La recurrencia de incendios se ha caracterizado tradicionalmente en base a varios métodos, como la utilización de los informes oficiales de incendios elaborados con información de campo, la interpretación de noticias de los medios de comunicación, el uso de técnicas dendrocronológicas basadas en las cicatrices que dejan los incendios en determinados troncos, e incluso mediante el estudio de depósitos de carbón vegetal y polen en los sedimentos lacustres (Keeley *et al.*, 2012). Sin embargo, en la actualidad las imágenes de satélite Landsat ofrecen la posibilidad de identificar zonas quemadas desde la década de 1970 hasta la actualidad (Röder *et al.*, 2008; Meddens *et al.*, 2016) y por tanto podrían ser utilizadas para determinar la recurrencia de incendios para periodos del orden de décadas en cualquier lugar del mundo.

De igual manera, los incendios de alta severidad pueden generar grandes impactos en el suelo (Key & Benson, 2006) y causar una alta mortalidad de plantas y de semillas dificultando la regeneración de la vegetación, incluyendo la de la especie de pino dominante (Fernandes *et al.*, 2008; Fernández *et al.*, 2008; Maia *et al.*, 2012). La severidad del fuego se puede cuantificar en campo utilizando estimaciones o medidas del grado de consumo de la vegetación, la mortalidad de las plantas, los diámetros terminales de las ramas remanentes, la altura de las llamas, el consumo de la hojarasca, el color de las cenizas, los cambios de color del suelo o la profundidad de las cenizas (Key & Benson, 2006; Keeley, 2009; Marcos *et al.*, 2018). Uno de los índices de severidad más utilizados en campo es el *Composite Burn Index* (CBI) (Key & Benson, 2006), que combina varias de estas variables, y puede ser utilizado para dar una valoración global del daño causado por el fuego, o para evaluar la severidad en los compartimentos del ecosistema (suelo y vegetación) de forma independiente. Sin embargo, los métodos de campo son poco eficientes cuando se trata de evaluar severidad en grandes superficies (Chuvieco, 2010; Meng *et al.*, 2017), por lo que actualmente se están desarrollando formas de evaluar severidad basadas en métodos de teledetección como el análisis de mezclas espectrales (Fernández-Manso *et al.*, 2009; Quintano *et al.*, 2017), los modelos de transferencia radiativa (Chuvieco *et al.*, 2006; de Santis *et al.*, 2009) o los índices espectrales (Fernández-Manso *et al.*, 2016; García-Llamas *et al.*, 2019b). Aun así, sigue siendo necesario avanzar en el conocimiento de cómo funcionan estos métodos cuando se trata de determinar la severidad en los distintos compartimentos del ecosistema, así como evaluar su funcionamiento bajo las distintas condiciones ambientales, las cuales pueden modificar la repuesta espectral del suelo y de la vegetación (Chuvieco, 2010).

Justificación del estudio

El éxodo rural y el abandono de las tierras de cultivo ocurrido durante las pasadas décadas en la Cuenca Mediterránea, especialmente en su parte europea, ha dado lugar a un aumento en la cantidad y continuidad de la vegetación (Pausas *et al.*, 2008), lo que unido a un clima cada vez más cálido y seco (Giorgi & Lionello, 2008) está modificando la recurrencia y la severidad de los incendios (Mouillot *et al.*, 2002; Fernandes, 2013; Vázquez *et al.*, 2015). La Cuenca Mediterránea es una zona densamente poblada donde existe una creciente preocupación social por la ocurrencia frecuente de grandes incendios, un fenómeno que es relativamente nuevo y se percibe como catastrófico (Pausas *et al.*, 2008). La problemática social es mayor cuando se trata de ecosistemas cuyo aprovechamiento contribuye a fijar población en el medio rural. Este es el caso de los pinares de *P. pinaster* y *P. halepensis,* cuya gestión es mejorable (de las Heras *et al*., 2012) y en los cuales la ocurrencia de incendios frecuentes y severos podría alterar irreversiblemente algunos de los servicios ecosistémicos que ofrecen, limitando el desarrollo socioeconómico de los pueblos dependientes de los mismos.

En este contexto son pertinentes las siguientes preguntas para avanzar en el campo de la ecología del fuego y de la gestión forestal en los pinares propensos al fuego: ¿Es posible determinar de forma eficiente la recurrencia y la severidad del fuego en zonas afectadas por grandes incendios?; ¿Dependen los efectos de los incendios en el suelo de la severidad del fuego?; ¿Persisten a medio plazo tras el incendio los impactos causados por la severidad en el suelo?; ¿Estará afectada la capacidad de recuperación de la especie arbórea dominante por la recurrencia y la severidad?; ¿Habrá cambios estructurales y funcionales en la comunidad vegetal en función de la recurrencia y de la severidad?; ¿Qué medidas de gestión post-incendio son recomendables en distintos escenarios de recurrencia y severidad? Responder a todos estos interrogantes permitirá conocer en profundidad las consecuencias ecológicas de los incendios en relación con la recurrencia y severidad y establecer las bases científicas para llevar a cabo una gestión forestal eficaz, identificando estrategias que permitan minimizar el impacto ambiental y socioeconómico de los grandes incendios forestales.

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2. OBJETIVOS

El principal objetivo de la presente Tesis Doctoral es analizar los efectos de diferentes regímenes de recurrencia y severidad de incendios en ecosistemas de pinar propensos al fuego. Para alcanzar este objetivo se establecieron los siguientes objetivos específicos:

Objetivo 1. Caracterizar los patrones de variación espacio-temporal de la recurrencia y de la severidad de incendios en pinares propensos al fuego. Para ello se pretende:

- Determinar los patrones de variación espacio-temporal de la recurrencia de incendios utilizando técnicas de teledetección (*artículo I*).
- Evaluar la capacidad de métricas de teledetección obtenidas a partir de imágenes Landsat para determinar la severidad del fuego (*artículo II*).

Objetivo 2. Estudiar los efectos de la severidad del incendio sobre las propiedades del suelo en pinares propensos al fuego. Para ello se pretende:

- Determinar los efectos de la severidad del incendio sobre las propiedades del suelo inmediatamente después del fuego (*artículo III*).
- Identificar qué efectos de la severidad del incendio en las propiedades del suelo persisten a medio plazo después del fuego (*artículo IV*).

Objetivo 3. Analizar los efectos de la recurrencia y severidad de incendios en la regeneración post-incendio de la vegetación en pinares propensos al fuego. Para ello se pretende:

- Examinar la relación entre los atributos del régimen de incendios y la recuperación del vigor vegetal mediante técnicas de teledetección (*artículo V*).
- Estudiar el papel de la recurrencia y de la severidad de incendios en la regeneración post-incendio de pinos mediterráneos con serotinia (*artículo VI*).
- Investigar las consecuencias que tienen los cambios en la recurrencia y severidad sobre la estructura de la comunidad vegetal y sobre sus rasgos funcionales (*artículo VII*).

Objetivo 4. Proporcionar las bases científicas para optimizar la gestión forestal en pinares propensos al fuego (*Discusión*).

3. DIAGRAMA CONCEPTUAL

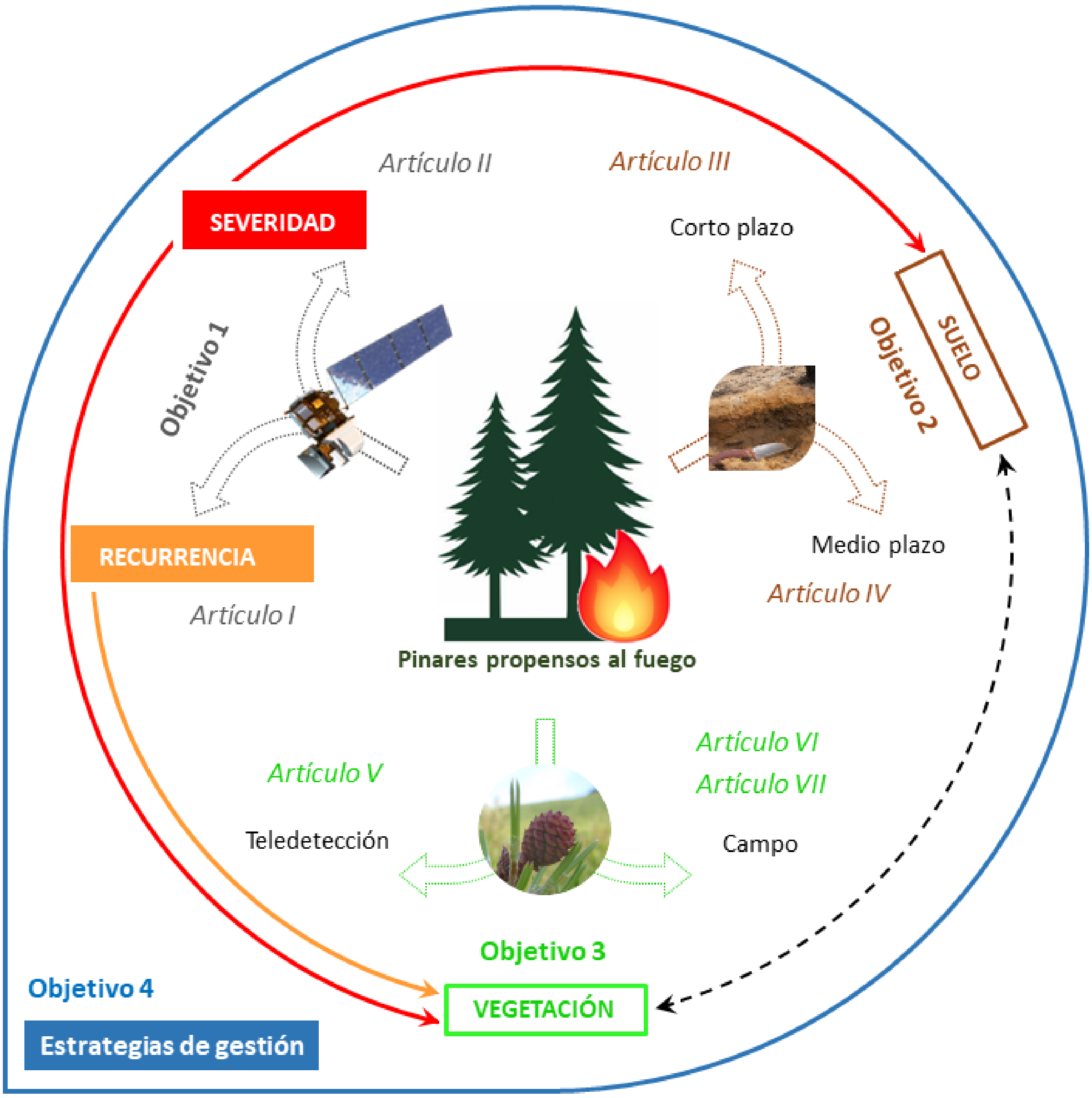

Figura 3. Diagrama conceptual de la Tesis Doctoral.

4. ZONAS DE ESTUDIO

En la presente Tesis Doctoral se han seleccionado siete zonas de estudio, ubicadas en la Península Ibérica (Fig. 4) y ocupadas por ecosistemas de pinar propensos al fuego afectados por incendios forestales entre los años 2012 y 2015.

Figura 4. Localización geográfica de las zonas de estudio.

El gran incendio de Cortes de Pallás (39° 18’ N, 0° 54’ W; provincia de Valencia) se inició el 28 de junio de 2012. La superficie total quemada ascendió a 297 km^2. El clima de esta zona de estudio es típicamente mediterráneo, con una precipitación media anual de 400-600 mm, temperatura media anual de 13-17 °C y veranos cálidos y secos que resultan en cuatro meses de sequía estival (Ninyerola *et al.*, 2005). La orografía es montañosa con una altitud comprendida entre 120-942 m. La litología es calcárea y los suelos de esta zona se clasifican fundamentalmente como Calcisol háplico y Leptosol calcárico-lítico (Jones *et al.*, 2005). Buena parte de la vegetación afectada por el incendio fueron pinares de *P. halepensis* con un sotobosque de matorral mediterráneo compuesto por *Ulex parviflorus*, *Quercus coccifera*

L. y *Rosmarinus officinalis* L. entre otras especies. Esta zona se ha utilizado en los artículos IV, VI y VII de la presente Tesis Doctoral.

El gran incendio de la Sierra del Teleno (42° 15′ N, 6° 11′ W, provincia de León) comenzó el 19 de agosto de 2012, quemando 119 km^2. Se puede considerar como una zona de transición entre el clima mediterráneo y oceánico, al tener una precipitación media anual de 600-800 mm, temperatura media anual de 8-11 °C y dos meses de sequía estival (Ninyerola *et al.*, 2005). La orografía es montañosa con un rango de altitudes entre 836-1493 m. La litología es silícea y los suelos predominantes son del tipo Umbrisol háplico y Regosol dístrico (Jones *et al.*, 2005). La mayor parte de la zona afectada por el incendio estaba ocupada por pinares de *P. pinaster* con una comunidad arbustiva dominada fundamentalmente por *Pterospartum tridentatum*, *Halimium lasianthum* (Lam.) Spach y *Erica australis* L. Esta zona se ha utilizado en los artículos I, II, IV, V, VI y VII de la presente Tesis Doctoral.

En el incendio de Monte Pindo (42° 53′ N, 9° 7′ W; provincia de La Coruña) del 11 de septiembre de 2013 ardieron 25 km^2. La zona afectada se caracteriza por un clima oceánico, con precipitación media anual de 1700-1800 mm, temperatura media anual de 12-15 °C y sin sequía estival (Ninyerola *et al.*, 2005). La orografía es montañosa con una altitud que asciende desde el nivel del mar hasta los 929 m. La litología es silícea, siendo la roca predominante el granito biotítico, con suelos de tipo Umbrisol (Jones *et al.*, 2005). La vegetación afectada por el incendio comprende pinares de *P. pinaster* con una comunidad de sotobosque donde abundan *Rubus* sp., *Ulex europaeus*, *Cytisus scoparius* (L.) Link y *Erica umbellata* Loefl. *ex* L. Esta zona se ha utilizado en el artículo VII de la presente Tesis Doctoral.

El incendio de Quintana del Castillo (42° 42′ N, 6° 0′ W; provincia de León) se declaró el 13 de julio de 2015 y alcanzó una extensión de 26 km^2. Este lugar se encuentra en la zona de transición entre el clima mediterráneo y oceánico, con una precipitación media anual de 700-850 mm, temperatura media anual de 8-10 °C y dos meses de sequía estival (Ninyerola *et al.*, 2005). El terreno es una ladera expuesta al sur con una altitud comprendida entre 1034 y 1531 m. La litología es silícea y los suelos se clasifican como Umbrisol háplico (Jones *et al.*, 2005). La vegetación afectada incluye pinares de *P. pinaster* entre otros, con sotobosque de *E. australis*, *P. tridentatum*, *C. scoparius y Calluna vulgaris* (L.) Hull entre otras especies. Esta zona se ha utilizado en el artículo II de la presente Tesis Doctoral.

En el incendio ocurrido en Tabuyo del Monte (42° 18’ N, 6° 14’ W; provincia de León) se quemaron 0,16 km^2 el 21 de julio de 2015. Esta zona se ubica en las estribaciones de la Sierra del Teleno y por ello presenta un clima de transición entre mediterráneo y oceánico, con una precipitación media anual de 685 mm, temperatura media anual de 10 °C y dos meses de sequía estival (Ninyerola *et al.*, 2005). La topografía es llana con una altitud de 1025 m. La litología es silícea y el suelo es un Umbrisol háplico (Jones *et al.*, 2005). La vegetación arbórea está dominada por *P. pinaster* y entre la comunidad arbustiva destacan *E. australis*, *H. lasianthum* y *P. tridentatum*. Esta zona se ha utilizado en el artículo III de la presente Tesis Doctoral.

Con el incendio iniciado en Tineo (43° 18’ N, 6° 26’ W; Principado de Asturias) el 28 de julio de 2015 ardieron casi 6 km^2. Esta zona tiene un clima oceánico, con una precipitación media anual de 925-1000 mm, una temperatura media anual de 10-13 °C y no presenta sequía estival (Ninyerola *et al.*, 2005). El terreno es muy rugoso, con altitudes comprendidas entre 231 y 768 m. La litología es silícea y los suelos se clasifican como Umbrisoles (Jones *et al.*, 2005). El paisaje de esta zona está dominado por pinares de *P. pinaster* y plantaciones de *P. radiata* D. Don con especies arbustivas como *E. australis* y *Arbutus unedo* L. Esta zona se ha utilizado en el artículo II de la presente Tesis Doctoral.

El gran incendio de Sierra de Gata (40° 12’ N, 6° 43’ W; provincia de Cáceres) comenzó el 6 de agosto de 2015 quemando 89 km^2. Esta zona presenta un clima mediterráneo, con una precipitación media anual de 700-1150 mm, una temperatura media anual de 12-16 °C y 3-4 meses de sequía estival (Ninyerola *et al.*, 2005). El incendio afectó zonas montañosas y zonas llanas, comprendiendo un rango de altitud que va desde los 275 hasta 1449 m. La litología es silícea y los suelos son fundamentalmente Umbrisoles háplicos y Regosoles dístricos (Jones *et al.*, 2005). Entre la vegetación afectada por el incendio se encuentran pinares de *P. pinaster* con distinta vegetación de sotobosque a lo largo del gradiente altitudinal, incluyendo *C. scoparius*, *E. australis* o *Cytisus striatus* (Hill) Rothm. Esta zona se ha utilizado en el artículo II de la presente Tesis Doctoral.

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5. RESULTADOS

La cartografía precisa de los patrones espacio-temporales de la recurrencia de incendios proporciona información esencial para estimar la regeneración post-fuego y puede servir de apoyo al diseño de proyectos de restauración. Los resultados obtenidos en el artículo I mostraron que todos los incendios registrados por la administración regional para el periodo 1978-2014 pudieron ser cartografiados en base a series temporales de imágenes Landsat (Landsat 2, 4, 5, 7 y 8; sensores MSS, TM, ETM+ y OLI respectivamente), demostrando que la teledetección es una herramienta precisa para caracterizar la recurrencia en pinares propensos al fuego. En la Sierra del Teleno, la superficie afectada por el fuego fue de 187,38 km^2 (49% de la zona de estudio), indicando la gran importancia del fuego en esta región. Así mismo, se identificaron extensas áreas afectadas por uno (129,58 km^2) y por dos incendios (50,59 km^2), mientras que la superficie afectada por tres y cuatro incendios fue menor (7,10 km^2 y 0,11 km^2 respectivamente).

Las imágenes multiespectrales son una fuente de información con un alto potencial para determinar la severidad del fuego. Los resultados obtenidos en el artículo II indicaron que, en ecosistemas de pinar, los índices espectrales obtenidos a partir de Landsat tienen una mayor capacidad para determinar la severidad global en el ecosistema y la severidad en la vegetación que la severidad en el suelo. Además, los índices espectrales funcionaron mejor en las zonas de clima mediterráneo y de transición que en la zona oceánica. En general, el dNBR-EVI, un índice espectral propuesto en este trabajo, mostró la mayor capacidad para determinar la severidad (global, en la vegetación y en el suelo) y la mejor transferibilidad entre regiones con distintas condiciones climáticas.

Estudiar los impactos de la severidad en el suelo inmediatamente después de un incendio sirve para conocer la utilidad de este atributo a la hora de identificar áreas prioritarias de actuación post-incendio. En el artículo III se estudiaron los impactos immediatos de la severidad en un ecosistema de *P. pinaster* con suelos silíceos. Los resultados de este trabajo mostraron que el tamaño de los agregados disminuye en las zonas afectadas por una alta severidad. También indicaron que las severidades moderadas y altas se asocian con aumentos en el pH y en la concentración de fósforo asimilable y con disminuciones en la concentración de carbono orgánico. El carbono de la biomasa microbiana se comportó de forma similar al carbono orgánico a lo largo del gradiente de severidad. Las actividades enzimáticas β-glucosidasa y fosfatasa ácida fueron las propiedades más sensibles a la severidad del incendio, disminuyendo drásticamente desde los escenarios de baja severidad. Entre los cocientes de suelo estudiados, la relación C:N, el cociente microbiano y el cociente β-glucosidasa: carbono de la biomasa microbiana disminuyeron con la severidad inmediatamente después del fuego.

Para conocer la resiliencia del suelo a la severidad del fuego es necesario realizar estudios a medio plazo después del incendio. Los resultados del artículo IV mostraron que, tanto en ecosistemas de *P. pinaster* con suelos ácidos como en ecosistemas de *P. halepensis* con suelos silíceos, varias propiedades del suelo siguen afectadas por la severidad tres años después del incendio. En concreto, el fósforo asimilable aumentó con la severidad en el ecosistema de *P. pinaster*, mientras que las actividades enzimáticas β-glucosidasa, la ureasa y fosfatasa ácida, y el carbono de la biomasa microbiana disminuyeron con la severidad en ambos ecosistemas. La β-glucosidasa, la ureasa y el carbono de la biomasa microbiana mostraron patrones comunes en relación con la severidad en los dos ecosistemas (suelos silíceos y calcáreos), y por ello podrían ser considerados potenciales indicadores para estudiar el legado de la severidad a medio plazo después del incendio en pinares mediterráneos. El fósforo asimilable y la fosfatasa ácida podrían ser utilizados como indicadores en el ecosistema de *P. pinaster*.

Los atributos del régimen de incendios como la recurrencia, el periodo de retorno o la severidad, pueden ser factores determinantes en la recuperación de la vegetación después del fuego. En el artículo V se emplearon técnicas de teledetección para estudiar la relación de los atributos del régimen de incendios (utilizados de forma individual y combinados) con la recuperación del vigor vegetal a corto (2 años) y medio plazo (5 años) después del incendio. Los resultados indicaron que todos los atributos, individuales y combinados, afectaron significativamente a la recuperación de la vegetación. Desde el punto de vista individual, la alta recurrencia, los cortos intervalos de retorno y las situaciones de baja severidad alcanzaron la mayor recuperación del vigor vegetal. Analizando los atributos de forma combinada identificamos una mayor variedad de situaciones de recuperación del vigor vegetal. A corto plazo, los escenarios de alta recurrencia con corto intervalo de retorno mostraron la mayor recuperación independientemente de la severidad, mientras que, a medio plazo, la alta recurrencia combinada con baja severidad fue el escenario que alcanzó una mayor recuperación. Este novedoso enfoque combinando atributos del régimen de incendios (temporales y de magnitud) podría ser de gran interés para los gestores forestales para desarrollar estrategias de restauración post-incendio.

Los cambios en la recurrencia y la severidad de incendios podrían comprometer la regeneración post-incendio de los pinos serótinos. Los resultados del artículo VI indicaron que la densidad y cobertura de plántulas de *P. pinaster* y *P. halepensis* es muy baja tras la ocurrencia de dos incendios en un periodo de 34 años combinados con severidades altas, así como después de tres incendios independientemente de la severidad. Así mismo, el reclutamiento de las plántulas después de tres incendios fue escaso, particularmente bajo situaciones climáticas más mediterráneas (0,01 plántulas m^{-2}), lo que resultó en una baja cobertura de plántulas (0,01%). La altura de las plántulas disminuyó tras la ocurrencia de incendios frecuentes debido a los cambios inducidos por los incendios en la fertilidad del suelo y en las condiciones microclimáticas del mismo. Además, se detectó un efecto negativo significativo de la cobertura de especies leñosas del sotobosque sobre el reclutamiento y la cobertura de las plántulas de pino. Estos resultados sugieren que las consecuencias de un incremento en la recurrencia y en severidad de los incendios pueden verse agravadas bajo condiciones climáticas caracterizadas por una prolongada sequía estival.

Los resultados obtenidos en el artículo VII mostraron las consecuencias ecológicas de los cambios en la recurrencia y en la severidad de incendios sobre la estructura de la comunidad de especies leñosas (riqueza de especies, cobertura, uniformidad y diversidad) y sobre sus rasgos funcionales (diferentes formas de vida, rasgos eco-fisiológicos y rasgos regenerativos). La riqueza y la diversidad de las especies aumentaron después de incendios frecuentes, lo que puede atribuirse la reducción del dosel arbóreo tras incendios frecuentes. Por otro lado, los resultados revelaron que la vegetación con ciertos rasgos funcionales (alta área foliar específica, capacidad de fijación de N_2, capacidad de rebrote, baja masa de semillas o germinación estimulada por choque térmico) pueden ser ventajosos en escenarios de alta recurrencia y severidad. En general, los efectos de la recurrencia y de la severidad sobre la estructura y rasgos de la vegetación fueron más significativos bajo condiciones mediterráneas que bajo condiciones oceánicas.

6. DISCUSIÓN

Caracterización del régimen de incendios utilizando técnicas de teledetección

El uso de imágenes de satélite es fundamental para caracterizar el régimen de incendios en grandes superficies utilizando una metodología aplicable a nivel global (Chuvieco, 2010). En concreto, hemos encontrado que el análisis visual de series temporales de imágenes procedentes de los satélites Landsat (sensores MSS, TM, ETM+ y OLI-TIRS) utilizando composiciones en falso color permite identificar zonas quemadas desde que entraron en órbita los primeros satélites Landsat en la década de 1970 (NASA, 2019). La utilización de compuestos en falso color aprovecha la resolución espectral de las imágenes Landsat para identificar los perímetros de los incendios (Röder *et al.*, 2008; Chuvieco, 2010; Bastarrika *et al.*, 2014), aunque es recomendable validar los resultados con información basada en observaciones de campo (Chuvieco, 1999), ya que según Bowman *et al.* (2003) la fiabilidad de este método es variable según las condiciones ambientales y la productividad del ecosistema. La determinación de los perímetros de incendio permite a su vez calcular atributos del régimen de incendios como el tamaño de los incendios, la recurrencia y el periodo libre de fuego, que son de gran relevancia para comprender los efectos del fuego a nivel ecológico y pueden ser útiles para mejorar la gestión forestal (Eugenio *et al.*, 2006; Taboada *et al.*, 2017).

Otro atributo del régimen de incendios con gran interés ecológico (Fernandes & Rigolot, 2007; Pausas & Keeley, 2014) y que se puede determinar utilizando imágenes Landsat (sensores TM, ETM+ y OLI) es la severidad del fuego. Nuestros resultados muestran que los índices espectrales reflectivos de la familia del dNBR, como son el propio dNBR (Key & Benson, 2006), el RdNBR (Miller & Thode, 2007) o el RBR (Parks *et al.*, 2014) son más adecuados para determinar la severidad que los índices térmicos o mixtos. Los índices de tipo dNBR se basan en las regiones del espectro electromagnético correspondientes al infrarrojo cercano e infrarrojo de onda corta que se relacionan con la estructura de las hojas y el contenido de humedad del ecosistema respectivamente (Chuvieco, 2010), dos variables que cambian gradualmente con la severidad del fuego (Key & Benson, 2006). Sin embargo, su funcionamiento muestra una alta variabilidad dependiendo de las condiciones ambientales de la zona afectada por el incendio (Parks *et al.*, 2014), y presentan grandes dificultades a la hora de determinar la severidad en el suelo (Robichaud *et al.*, 2007). Con el fin de solventar estas limitaciones, hemos propuesto un nuevo índice, el dNBR-EVI, que superó al resto de índices espectrales en cuanto a precisión y transferibilidad a lo largo de un gradiente climático. El buen funcionamiento del dNBR-EVI con respecto al resto de índices de tipo dNBR puede atribuirse a la incorporación de la banda del rojo, que presenta una alta sensibilidad a la pigmentación de las hojas; y a la inclusión de la banda del azul, que puede compensar las diferencias debidas a aerosoles atmosféricos (Gao *et al.*, 2000; Chuvieco, 2010). En cualquier caso, los resultados obtenidos ponen de manifiesto que los índices espectrales obtenidos mediante imágenes Landsat tienen una mayor capacidad para cuantificar la severidad global del ecosistema y la severidad en la vegetación que la severidad en el suelo, lo que puede deberse al efecto pantalla de la vegetación y de los restos que quedan de ella (Soverel *et al.*, 2011; Tanase *et al.*, 2011) o a la influencia del tipo de suelo en la respuesta espectral a la severidad (Smith *et al.*, 2010). En este sentido, la caracterización de la severidad en el suelo con una precisión similar a la alcanzada para determinar la severidad en la vegetación sigue siendo un reto, que para ser solventado podría requerir del uso de (i) imágenes con una alta resolución espacial, lo que posibilitaría la eliminación parcial del efecto de sombra de la cubierta vegetal (McKenna *et al.*, 2017); o (ii) el uso de sensores hiperespectrales, que permiten discriminar aspectos muy concretos de la superficie del suelo (Robichaud *et al.*, 2007).

Efectos de la recurrencia y de la severidad

Los efectos de los incendios sobre el suelo y la vegetación son heterogéneos, ya que dependen de múltiples factores como la recurrencia y la severidad del fuego (Bodí *et al.*, 2012). Nuestros resultados han demostrado que la severidad es un factor determinante en el estado de las propiedades del suelo tanto inmediatamente después del fuego como a medio plazo (3 años). Respecto a las propiedades físicas del suelo, hemos encontrado que el tamaño medio de los agregados disminuye a altas severidades, lo que se puede atribuir a los cambios que se producen a temperaturas muy elevadas en los principales agentes aglutinantes (materia orgánica y minerales de arcilla) (Santín & Doerr, 2016). Este resultado recalca la importancia de reducir las situaciones de alta severidad si se pretenden preservar los suelos, ya que la disminución del tamaño medio de los agregados conlleva una pérdida de estructura del suelo (Cerdà & Jordán, 2010) y un aumento de la erosión superficial (Vieira *et al.*, 2015). Por otro lado, a severidades moderadas y altas se producen cambios en las propiedades químicas del suelo, como son los incrementos de pH, la disminución de la concentración de carbono orgánico o el incremento del fósforo asimilable. Los cambios en estas propiedades químicas son consecuencia fundamentalmente de la mineralización de la materia orgánica y de la entrada de cenizas procedentes de la parte aérea (Certini, 2005; Marcos *et al.*, 2007; Caon *et al.*, 2014). A medio plazo, la concentración de fósforo asimilable sigue estando correlacionada positivamente con la severidad del fuego en los suelos silíceos. Este patrón puede deberse a procesos de adsorción-desorción (Serrasoles *et al.*, 2008), ya que la adsorción del fósforo limita su pérdida por percolación y escorrentía a corto plazo, posibilitando su posterior liberación en forma asimilable (Serrasoles *et al.*,2008; Otero *et al.*, 2015). Sin embargo, en los suelos calcáreos parte del fósforo forma apatita, dejando de estar disponible para la biota a medio plazo (Caon *et al.*, 2014; Otero *et al.*, 2015). Es importante señalar que, aunque el fuego puede aumentar la concentración de fósforo asimilable en el suelo, la ocurrencia de un incendio severo siempre causa pérdidas de este nutriente en el conjunto del ecosistema, ya sea por convección de las cenizas durante el incendio o bien por erosión eólica o hídrica (Boerner, 1982). Así mismo, hemos observado que las propiedades biológicas del suelo (actividades enzimáticas y el carbono de la biomasa microbiana) son las más sensibles al fuego, disminuyendo drásticamente a partir de niveles bajos de severidad. Esto se debe a la inactivación y desnaturalización de las proteínas, y la mortalidad de los microorganismos, que ocurren a partir de temperaturas relativamente bajas (50-70 ºC) (Tabatabai, 1994; Vega *et al.*, 2013; Santín & Doerr, 2016). A medio plazo este efecto sobre las propiedades biológicas persiste, ya que el fuego, dependiendo de su severidad, genera impactos sobre sobre las condiciones micro-climáticas del suelo mineral, sobre el mantillo y sobre la cobertura vegetal (Keeley, 2009; Dooley & Treseder, 2012). En base a los resultados obtenidos, podemos considerar que varias propiedades del suelo (pH, fósforo asimilable, actividades enzimáticas β-glucosidasa, ureasa y fosfatasa ácida, y carbono de la biomasa microbiana) pueden ser útiles para monitorear los impactos del fuego a corto plazo en pinares propensos al fuego y para analizar el legado de la severidad del fuego a medio plazo, lo que es fundamental para evaluar la recuperación del suelo (Hedo *et al.*, 2015; Muñoz-Rojas *et al.*, 2016).

La distinta sensibilidad de las propiedades del suelo al fuego hace que los ratios o cocientes entre propiedades se vean modificados con la severidad. En la presente Tesis Doctoral hemos propuesto el estudio de cocientes para comprender mejor el impacto de la severidad en el estado del suelo y en los procesos que en él ocurren (Lagomarsino *et al.*, 2009; Paz-Ferreiro & Fu, 2016). Algunos de los efectos que hemos observado inmediatamente después del fuego han sido (i) descensos del cociente C:N (carbono orgánico: nitrógeno total) con el aumento de la severidad, debido a la mayor estabilidad del nitrógeno total a altas severidades (Vega *et al*., 2013); (ii) una disminución del cociente microbiano (carbono de la biomasa microbiana: carbono orgánico) a severidades moderadas y altas, que se puede atribuir a la mortalidad microbiana y a la falta de una fuente de carbono lábil (Díaz-Raviña *et al*., 2012); (iii) y un fuerte descenso en la actividad específica de la enzima β-glucosidasa (actividad β-glucosidasa por unidad de carbono de la biomasa microbiana) a partir de niveles bajos de severidad, lo que sugiere una disminución en la capacidad fisiológica de la comunidad microbiana (Lagomarsino *et al.*, 2009). Estos cocientes presentan en general, valores más constantes que las propiedades individuales entre suelos de distinto tipo, por lo que pueden ser una herramienta útil y generalizable a la hora de comparar los efectos del fuego entre distintos lugares. No obstante, la persistencia de los cambios generados por el fuego varía según la propiedad del suelo (Certini, 2005; Alcañiz *et al.*, 2016; Muñoz-Rojas *et al.*, 2016), por lo que es recomendable estudiar también la evolución de estos cocientes varios años después del incendio.

Hoy en día, el uso de imágenes de satélite puede ser de gran provecho para identificar los efectos de los incendios en los ecosistemas. En relación con la vegetación, en la presente Tesis Doctoral hemos realizado una aproximación al estudio de los efectos de la recurrencia y severidad de incendios en la regeneración post-fuego utilizando técnicas de teledetección. Los resultados obtenidos indican que ambos atributos del régimen de incendios se relacionan significativamente con la recuperación del vigor vegetal 2 y 5 años tras el incendio. En general, la recuperación del vigor vegetal previo al incendio fue mayor en las zonas con alta recurrencia (3 o más incendios en 40 años) y baja severidad (CBI <2,25). La rápida recuperación en las zonas de alta recurrencia puede deber a la alta velocidad de recuperación de las especies herbáceas y arbustivas, que dominan en las zonas afectadas por incendios frecuentes (Calvo *et al.*, 2008; Tessler *et al.*, 2016). Así mismo, en las zonas con baja severidad, el cambio inicial en el dosel forestal y la mortalidad en la comunidad vegetal es menor que en las situaciones de alta severidad (Key & Benson, 2006), lo que favorece la recuperación de los valores iniciales de vigor vegetal. Nuestros resultados indican que la consideración conjunta de recurrencia y severidad de incendios sirve para aumentar la precisión de las predicciones sobre la recuperación del vigor vegetal, si bien para comprender mejor los mecanismos subyacentes es necesario analizar la regeneración de la población de la especie de pino dominante (Taboada *et al.*, 2017) y del resto de la comunidad (Yang *et al.*, 2017) mediante estudios de campo.

El estudio de la regeneración de las especies de pino (*P. pinaster* y *P. halepensis*) indicó que incrementos conjuntos de recurrencia y severidad disminuyen la densidad y el desarrollo de las plántulas en situación post-incendio hasta valores que pueden dificultar la recuperación del bosque (0,01 plántulas por metro cuadrado) (Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016), especialmente en zonas mediterráneas con una sequía estival prolongada. Una alta frecuencia de incendios puede limitar la regeneración de la población de pino debido a una menor producción de semillas (Eugenio *et al.*, 2006; Santana *et al.*, 2010) y al deterioro de las condiciones del suelo para el establecimiento y desarrollo de las plántulas, lo que comprende una menor protección para las semillas, peores condiciones micro-climáticas y una menor concentración de nutrientes (Pausas *et al.*, 2004; Taboada *et al.*, 2018). Así mismo, incendios severos causan una alta mortalidad en el arbolado, que es fuente de semillas, y mortalidad en el banco de semillas (Habrouk *et al.*, 1999; Fernandes & Rigolot, 2007), lo que contribuye a una menor densidad de plántulas. Estos hallazgos constituyen una referencia para motivar la gestión forestal orientada a una reducción de recurrencia y severidad de los incendios forestales en los pinares mediterráneos propensos al fuego si se pretende mantener el dosel arbóreo.

A nivel de la comunidad de leñosas, hemos encontrado que una recurrencia de incendios relativamente alta puede incrementar la riqueza y la diversidad de especies debido a la reducción de la cobertura del arbolado (Tessler *et al.*, 2016; Meyer *et al.*, 2019), lo que disminuye el riesgo de exclusión competitiva (Beckage & Stout, 2000). Por otro lado, la alta severidad tiende a disminuir la riqueza y la diversidad, posiblemente por ocurrir en zonas con alta densidad de arbolado (Shive *et al.*, 2013; García-Llamas *et al.*, 2019), que son a priori las que presentan una comunidad de matorral menos diversa (Beckage & Stout, 2000; Tessler *et al.*, 2016). También hemos hallado que la recurrencia y la severidad modifican los rasgos funcionales de la vegetación a nivel de comunidad. En concreto, las especies con forma de vida no arbórea, alta área foliar específica, capacidad para fijar nitrógeno atmosférico, capacidad para rebrotar, bajo peso de semillas y germinación estimulada por choque térmico son más resilientes en situaciones de alta recurrencia y severidad, aumentando su abundancia relativa con respecto a las especies que no presentan estos rasgos. Estas diferencias se pueden relacionar con aspectos clave como son la capacidad de colonizar rápidamente zonas quemadas (Calvo *et al.*, 2013; Crotteau *et al.*, 2013), la capacidad para obtener recursos y crecer rápidamente tras los incendios (Dwyer *et al.*, 2014;

Dirks *et al.*, 2017; Sheffer *et al.*, 2015), o la precocidad reproductiva (Pausas, 1999; Santana *et al.*, 2010). Al igual que ocurre con *P. pinaster* y *P. halepensis*, los efectos de la recurrencia y de la severidad sobre la comunidad de leñosas en su conjunto son menos significativos en climas más húmedos, lo que puede atribuirse a una alta velocidad de recuperación y por tanto una madurez más temprana (Pausas & Bradstock, 2007; Enright *et al.*, 2015), así como con una mayor importancia de los efectos competitivos que es típica en ambientes productivos (Clarke *et al.*, 2013; Pausas & Keeley, 2014) y que podría enmascarar los efectos de la recurrencia y de la severidad. Los resultados obtenidos a nivel de comunidad ponen de manifiesto la necesidad de considerar los rasgos funcionales de la vegetación a la hora de gestionar el monte y afrontar cambios en los regímenes de incendios, que son esperables en el actual contexto de cambio global (Enright *et al.*, 2015; Vázquez *et al.*, 2015).

Bases científicas para optimizar la gestión forestal

Durante las últimas décadas la gestión post-incendio de los pinares de *P. pinaster* y *P. halepensis* se ha centrado en la retirada de madera quemada y en la repoblación con la especie de pino dominante en las zonas con escasa regeneración natural (de las Heras *et al.*, 2012). En la actualidad, los avances en el conocimiento científico pretenden optimizar las prácticas forestales para poder alcanzar varios objetivos clave como son mejorar la protección del suelo y la regulación del ciclo del agua, promover la diversidad, madurez y productividad del pinar e incrementar la resistencia y resiliencia del bosque a las perturbaciones (Fernandes & Rigolot, 2007; Valdecantos *et al.*, 2009; de las Heras *et al.*, 2012). En este sentido, los resultados obtenidos en la presente Tesis Doctoral indican que la recurrencia y severidad de los incendios son dos factores fundamentales a considerar en la gestión forestal pre- y post-incendio.

Las primeras actuaciones que han de llevarse a cabo tras la ocurrencia de un incendio son las medidas de emergencia, que han de centrarse en reducir los riesgos para la vida humana, las propiedades y los recursos naturales críticos, como el suelo (de las Heras, 2012). Altas severidades producen la destrucción de los agregados del suelo y la pérdida de estructura

(Cerdà & Jordán, 2010). Esto, acompañado con la pérdida de la litera y de la cubierta vegetal inherentes a la alta severidad (Key & Benson, 2006) y que persiste varios años tras el incendio, facilita la escorrentía superficial y las pérdidas de suelo por erosión (Vieira *et al.*, 2015). Por ello es recomendable que la gestión forestal orientada a reducir la erosión se centre en:

- Limitar la severidad de potenciales incendios forestales. La severidad del fuego en pinares mediterráneos está determinada fundamentalmente por la cantidad de vegetación existente antes del incendio y la continuidad del combustible (García-Llamas *et al.*, 2019). Por lo tanto, las actuaciones encaminadas a reducir la severidad deben realizarse antes del incendio e ir encaminadas a reducir la cantidad de combustible, su continuidad vertical y su continuidad horizontal con actuaciones como podas, entresacas o fuegos prescritos (Fernandes & Rigolot, 2007).
- Una vez ocurrido el incendio, conviene determinar de forma precisa las zonas de alta severidad. Esto se debe realizar mediante trabajo de campo, aunque se puede apoyar en índices espectrales obtenidos de imágenes de satélite de resolución moderada.
- Centrar las actuaciones de emergencia orientadas a la protección del suelo en las zonas con alta severidad, aunque también es necesario considerar otros factores como el clima, la topografía, el tipo de suelo o la hidrología superficial (Renard *et al.*, 1997; Robichaud, 2009). Entre las actuaciones post-incendio que han demostrado ser útiles para prevenir la erosión en pinares propensos al fuego se encuentran la aplicación de mulch, el establecimiento de barreras para la erosión o la protección de los regenerados evitando el pastoreo intensivo (Robichaud, 2009; de las Heras *et al.*, 2012).
- No llevar a cabo actuaciones de preparación del terreno para realizar plantaciones en las zonas con alta severidad en el suelo sin haber evaluado la regeneración natural de la vegetación a medio plazo (1-3 años) tras el incendio, ya que estas

actuaciones pueden agravar el riesgo de erosión (Moreira *et al.*, 2012) y la regeneración natural podría ser suficiente.

Tras implementar las medidas de emergencia y en su caso la extracción de madera (que también puede condicionar la regeneración natural; Taboada *et al.*, 2018), es conveniente identificar a medio plazo aquellos escenarios en los que la regeneración natural es escasa y aquellos en los que la densidad de plántulas es excesiva (de las Heras *et al.*, 2012). Las situaciones de alta recurrencia (3 incendios en 34 años), así como las situaciones de recurrencia moderada combinada alta severidad (2 incendios en 34 años) resultan en una densidad y cobertura de plántulas de pino lo suficientemente bajas como para dificultar la recuperación de la cubierta forestal (Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016). Por otro lado, las zonas quemadas con baja recurrencia y severidad presentaron densidades de plántulas muy elevadas, que también convendría gestionar (Fernandes & Rigolot, 2007; de las Heras *et al.*, 2012). En este sentido, es recomendable:

- Reducir la probabilidad de ocurrencia de incendios muy recurrentes y severos. La supresión de incendios puede facilitarse mediante la creación de cortafuegos (Fernandes & Rigolot, 2007), o un paisaje en mosaico con distintos tipos de vegetación o distintas densidades de arbolado (de las Heras *et al.*, 2012). En este sentido, estudios previos han determinado que con densidades de 100-300 pinos/ha la ocurrencia de incendios de copa es muy limitada (Fernandes & Rigolot, 2007). Realizar tratamientos silvícolas selectivos encaminados a disminuir la cantidad de vegetación altamente inflamable y la cantidad de combustible también puede limitar la ocurrencia y la severidad de los incendios forestales (Baeza & Vallejo, 2008).
- Determinar la recurrencia y severidad del fuego para definir zonas de actuación con respecto a la especie de pino dominante. Para ello, las técnicas de teledetección basadas en imágenes Landsat son herramientas adecuadas para la gestión que

permiten caracterizar de forma precisa la recurrencia de incendios y la severidad en la vegetación.

- Realizar una gestión forestal acorde a cada escenario en relación con su abundancia de pinos. Si se pretende mantener el pinar, en los escenarios con muy baja densidad de plántulas los primeros años tras el incendio (< 0.20 pinos/m^2; Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016) se puede llevar a cabo plantación o siembra, y limitar el pastoreo por ganado ovino y caprino (de las Heras *et al.*, 2012). En las zonas donde la densidad de plántulas es muy elevada se recomienda realizar entresacas, para favorecer el crecimiento del arbolado alcanzar de forma más temprana la madurez reproductiva (de las Heras *et al.*, 2012).

Otro de los objetivos de la gestión forestal es aumentar la diversidad del bosque y su resiliencia a las perturbaciones (Valdecantos *et al.*, 2009). En este sentido, altas recurrencias de incendios incrementan la diversidad de leñosas, pero a expensas de la eliminación del estrato arbóreo, lo que no es deseable (Fernandes & Rigolot, 2007). Así mismo, mantener comunidades vegetales con una alta diversidad de rasgos funcionales puede incrementar su resiliencia ante regímenes de incendios cambiantes. Por ello se recomienda:

- Mantener la diversidad de rasgos funcionales de la vegetación, con especial atención a aquellos que pueden ser clave para mantener la cubierta vegetal ante potenciales escenarios de alta recurrencia y severidad. Entre estos se encuentra la vegetación con forma de vida no arbórea, alta área foliar específica, capacidad para fijar nitrógeno atmosférico, capacidad para rebrotar, bajo peso de semillas y germinación estimulada por choque térmico.

Además de monitorizar los efectos del fuego sobre el suelo y la regeneración de la vegetación para seleccionar las zonas de actuación y llevar a cabo medidas de gestión adecuadas, es importante monitorizar y evaluar la efectividad de las propias medidas de gestión. Este proceso es útil para confirmar la efectividad o re-direccionar las medidas tomadas y aporta conocimiento esencial para optimizar la gestión forestal en el futuro (Moreira *et al.*, 2012).

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7. CONCLUSIONES

Caracterización de los patrones de recurrencia y severidad

El análisis visual de series temporales de imágenes Landsat es un método adecuado para determinar la recurrencia de incendios en ecosistemas de pinar. Aun así, es recomendable validar la información obtenida mediante imágenes Landsat con información de campo.

El uso de índices espectrales basados en imágenes Landsat, calculados tanto desde una perspectiva mono-temporal como bi-temporal, es apropiado para evaluar la severidad del fuego a nivel global y la severidad en la vegetación en ecosistemas de pinar, pero conviene mejorar su capacidad para determinar la severidad en el suelo.

Los índices espectrales de Landsat basados en la región óptica del espectro funcionaron mejor para determinar la severidad del fuego que los índices que incluyen la región térmica del espectro (métricas térmicas e índices mixtos).

El índice propuesto, dNBR-EVI, que combina información de las regiones del espectro correspondientes al azul, rojo, infrarrojo cercano e infrarrojo de onda corta, es el que muestra la mayor capacidad para determinar severidad del fuego en ecosistemas de pinar, así como la mayor capacidad de transferencia entre distintas regiones climáticas.

Efectos de la severidad en las propiedades del suelo

La severidad del fuego afecta significativamente a las propiedades físicas, químicas y biológicas de suelos silíceos inmediatamente después del incendio. Las propiedades biológicas del suelo son más sensibles a la severidad del fuego que las propiedades físicas y químicas. Son particularmente sensibles las actividades enzimáticas β-glucosidasa y fosfatasa ácida, que decrecen desde los escenarios de baja severidad hasta casi desaparecer en las situaciones de máxima severidad.

Los cocientes entre propiedades del suelo que se ven afectados por la severidad son la relación carbono orgánico:nitrógeno total, el cociente microbiano y el cociente β-glucosidasa: carbono de la biomasa microbiana. El uso de cocientes podría ser más generalizable que las propiedades individuales a la hora de comparar los efectos del fuego entre distintos lugares.

Los efectos de la severidad del fuego pueden persistir a medio plazo tras el incendio (tres años) en las propiedades químicas (fósforo asimilable) y biológicas (β-glucosidasa, ureasa, fosfatasa ácida y carbono de la biomasa microbiana) de los suelos en los ecosistemas de pinar. La actividad β-glucosidasa, la actividad ureasa y el carbono de la biomasa microbiana mostraron patrones comunes en relación con la severidad en los pinares de *P. pinaster* (suelos silíceos) y de *P. halepensis* (suelos calcáreos).

El pH, la relación entre el carbono orgánico y el nitrógeno total, las actividades enzimáticas (β-glucosidasa, ureasa y fosfatasa ácida) y el carbono de la biomasa microbiana podrían ser potenciales indicadores para monitorear los efectos de la severidad del fuego en el suelo.

Efectos de la recurrencia y severidad en la regeneración post-incendio de la vegetación

Tanto la recurrencia de incendios como la severidad del fuego afectan de forma significativa la recuperación post-incendio del vigor de la vegetación estimado mediante técnicas de teledetección.

La consideración conjunta de la recurrencia y de la severidad es más efectiva que el uso individual de cada uno de esos atributos para discriminar las distintas situaciones post-incendio de recuperación del vigor vegetal de acuerdo con el índice NDVI. El escenario de alta recurrencia con baja severidad presenta la mayor recuperación del vigor vegetal.

La recurrencia y la severidad afectan significativamente la regeneración post-incendio de las especies de pino con serotinia. Incrementos conjuntos en la recurrencia y la severidad disminuyen la densidad y cobertura de plántulas de pino, que además presentan una menor altura después de incendios recurrentes.

La competencia interespecífica entre las plántulas de pino y el resto de especies leñosas es notoria en los escenarios de recurrencia y severidad más propicios para el establecimiento y desarrollo de las plántulas de pino, particularmente en las zonas con baja recurrencia.

Los incrementos en la recurrencia de incendios ocasionan incrementos en la riqueza y diversidad de especies leñosas en ecosistemas de pinar, que son parcialmente contrarrestados si la severidad del fuego también aumenta. Estos cambios estructurales de la comunidad vegetal se deben a la pérdida del dosel arbóreo y al aumento en la dominancia de las especies de matorral tras incendios recurrentes.

Los efectos de recurrencia y severidad sobre la vegetación leñosa dependen de los rasgos funcionales de la vegetación. En este sentido, las especies con alta área foliar específica, capacidad para fijar N_2, capacidad para rebrotar, bajo peso de semillas o germinación estimulada por altas temperaturas puede ser más resiliente a incrementos conjuntos de recurrencia y severidad.

Los impactos de la recurrencia y de la severidad sobre la regeneración de las especies de pino dominantes y sobre la estructura y composición funcional de la comunidad son más significativos en condiciones climáticas mediterráneas que en climas con una sequía estival menos prolongada.

Bases científicas para optimizar la gestión forestal

Los impactos del fuego en las propiedades del suelo incluyen la destrucción de los agregados a altas severidades, lo que implica un alto riesgo de erosión. Por ello, las zonas de alta severidad deberían ser consideradas prioritarias para aplicar medidas de emergencia de conservación del suelo. Las evaluaciones para identificar los suelos con alta severidad deben realizarse en campo, aunque pueden apoyarse en imágenes multiespectrales de Landsat.

La baja densidad y cobertura de plántulas de pino en las situaciones de alta recurrencia (3 incendios en 34 años), así como en las situaciones de recurrencias moderadas combinadas con alta severidad (2 incendios en 34 años), pueden ser insuficientes para garantizar la recuperación completa del dosel arbóreo. En el resto de escenarios de recurrencia y severidad, la regeneración de pino es abundante y pueden ser necesarias entresacas a medio plazo después del incendio. Los productos obtenidos de Landsat son adecuados para que los gestores clasifiquen estas situaciones de recurrencia y severidad.

Los rasgos funcionales de la vegetación condicionan su respuesta a la recurrencia y a la severidad, y por lo tanto deberían ser considerados en el diseño de estrategias de gestión forestal. Mantener una alta diversidad de rasgos funcionales aumenta la resiliencia de la comunidad vegetal frente a los cambios en el régimen de incendios.

Los mayores impactos del fuego en el suelo y en la vegetación ocurren con altas recurrencias y/o altas severidades, por lo que la gestión forestal pre-incendio debería de centrarse en reducir el riesgo de ocurrencia de incendios frecuentes y severos

EFFECTS OF FIRE RECURRENCE AND BURN SEVERITY IN FIRE-PRONE PINE ECOSYSTEMS

Basis for forest management

Víctor Fernández García

Picture on the front of this page:

Soil with different burn severity levels immediately after fire in Tabuyo del Monte (GEAT research group).

ABSTRACT

Fire prone ecosystems dominated by *Pinus pinaster* Ait. and *Pinus halepensis* Mill. are the forests most affected by fire in the Mediterranean Basin. Consequently, they are priority ecosystems to study the ecological consequences of changes in fire regimes, which are expected in the current context of global change. The objective of this Doctoral Thesis is to analyze the effects of different regimes of fire recurrence and burn severity in fire-prone ecosystems dominated by *P. pinaster* and *P. halepensis*.

The starting point has been to study the ability of multispectral Landsat scenes to characterize fire recurrence (article I) and burn severity (article II) in pine forests affected by large forest fires. The spatio-temporal patterns of wildfires during the period 1978-2014 were determined by visual analysis of Landsat false-color composites, specifically using Landsat 2, 4, 5, 7 and 8 time series (MSS, TM, ETM + and OLI respectively). Then, fire scars were validated with the official wildfire reports. This method allowed mapping all fires documented in the official wildfire reports, demonstrating that the use of Landsat image time series is an effective tool to characterize fire recurrence. Similarly, to characterize burn severity we calculated different spectral indices (thermal, reflective and mixed metrics) using Landsat imagery. The ability of these metrics to determine the soil burn severity, the vegetation burn severity and the site burn severity (soil plus vegetation) along a climatic gradient was evaluated using linear regression models. We calculated the CBI (Composite Burn Index) in field plots to be used as ground truth in the evaluation of the performance of the spectral indices. Overall, bi-temporal indices based on the near-infrared and short-wave infrared regions of the spectrum (dNBR -differenced Normalized Burn Ratio- type indices) showed a high capacity to quantify the vegetation burn severity and site burn severity, whereas the capacity of Landsat spectral indices to determine the soil burn severity was relatively low. Additionally, we found large differences in indices performance along the climatic gradient, so we proposed a new spectral index, the dNBR-EVI, which shows greater

capacity to determine burn severity and better transferability throughout of the different climatic conditions than the previously existing indices.

To investigate the effects of burn severity on soil properties, we conducted a study immediately after the fire (1 week) in a *P. pinaster* forest with siliceous soils (article III) and another study over the medium term after the fire (3 years) in both, *P. pinaster* and *P. halepensis* ecosystems, with siliceous and calcareous soils respectively (article IV). Results showed significant effects of burn severity on most soil properties studied immediately after the fire (aggregate size, pH, organic carbon, available phosphorus, microbial biomass carbon, and enzymatic activities β-glucosidase and acid phosphatase), as well as in some ratios between these properties (C:N ratio, microbial quotient and the specific activity of β-glucosidase). Among these properties and quotients, those related to enzymatic activities showed the highest sensitivity to fire, as they start to decrease at low severities. Over the medium term after the fire, we found that some soil properties (available phosphorus, microbial biomass carbon and enzymatic activities) remained affected by burn severity. The microbial biomass carbon, the β-glucosidase activity and the urease activity decreased with burn severity in the two studied ecosystems, and therefore, they could be used as potential indicators to investigate the burn severity legacy over the medium term after the fire in Mediterranean fire-prone pine forests.

The effects of fire recurrence and burn severity in the natural regeneration of vegetation were studied through remote sensing methods (article V) and through studies based on field information, focused on both the pine population (article VI) and the woody plant community (article VII). In the study based on remote sensing methods, we used the difference of the NDVI (Normalized Difference Vegetation Index) calculated with Landsat to estimate the vegetation greenness recovery after the fire. Results indicated that, following the fire (2 and 5 years), areas affected by high severity showed a low greenness recovery. On the contrary, the areas with high fire recurrence showed higher greenness recovery than low recurrence areas, because of the dominance of shrub species in high recurrence scenarios, which require less time than trees to reach the pre-fire situation. The field study revealed that in low recurrence and low severity areas the density and coverage of *P. pinaster* and *P. halepensis* seedlings was relatively high and enough to ensure the recovery of the tree canopy. As opposed, in the areas affected by high recurrence (3 fires in 34 years), as well as moderate recurrence with high severity (2 fires in 34 years), the natural regeneration of pines was endangered due to the lack of a viable seed bank. At the community level, we found that shifts in fire recurrence and burn severity modified the woody species diversity, as well as the species relative cover depending on their functional traits. The effects were particularly significant in the regions with summer drought such as Mediterranean areas. In general, our results indicated that woody vegetation with (i) non-arboreal life form, (i) high specific leaf area, (iii) nitrogen fixing capacity, (iv) resprouting ability, (v) low seed mass or (vi) heat-stimulated germination may be more resilient to increases in fire recurrence and severity.

The results obtained in this PhD Thesis contribute to the advancement of knowledge in the discipline of fire ecology, and provide the scientific basis for an efficient forest management in fire-prone pine forests of the Mediterranean Basin. Likewise, this work can be considered as a reference to design forest management strategies in the face of future changes in fire regimes.

1. INTRODUCTION

Mediterranean fire-prone pine ecosystems

The social awareness about forest fires and their consequences on ecosystem services have motivated a notable interest in understanding the effects of fire at an ecological, economic and social level. More than half of the Earth's surface is vulnerable to forest fires (Moreno & Oechel, 1994; Keeley *et al.*, 2012). However, the role of wildfires is particularly relevant in fire-prone ecosystems (Rundel *et al.*, 2018), which are defined as the ecosystems where fires constitute the main ecological disturbance, being frequent enough to act as a selective pressure (Pausas & Keeley, 2014).

The Mediterranean Basin is one of the most fire-prone regions worldwide (Keeley *et al.*, 2012). In this region, the Mediterranean climate emerged about 15 million years ago giving rise to climatic conditions that favor the accumulation of fuel during winter and spring, and a summer drought that facilitates relatively regular and frequent wildfires (Rundel *et al.*, 2018). In this way, fire is considered a major factor which explains the distribution, functioning and structure of Mediterranean ecosystems, as well as the diversity and functional traits of its plant species (Keeley et al ., 2012; Pausas & Keeley, 2014; Rundel *et al.*, 2018).

Pine ecosystems dominated by *Pinus pinaster* Ait. and *Pinus halepensis* Mill. are traditionally the forests most affected by fires in the Mediterranean Basin (Le Houerou, 1973) as well as in the Iberian Peninsula (ADCIF, 2012; ICFN, 2015). These ecosystems are especially relevant not only because of their large geographic distribution (Fig. 1) but also because of their ecological and economic importance (de las Heras *et al.*, 2012). Both types of pine forests are prone to fire, and in fact, they are favored over other vegetation types if fire frequencies are intermediate (one fire every 10-40 years) (Pausas, 1999; Fernandes and Rigolot, 2007). In general, *P. pinaster* forests grow on nutrient-poor and sandy acidic soils, in areas with an average annual temperature between 9-16 ºC and precipitation between 400-1600 mm. On the other hand, *P. halepensis* ecosystems, which are also found on nutrient-poor soils, seem to prefer basic soils, such as those developed on marls, limestones or dolomites. *P.*

halepensis also tolerates more thermal (12-16 ºC) and arid climatic conditions (300-700 mm) (Richardson, 2000; Serrada *et al.*, 2008; de las Heras *et al.*, 2012). However, both pine ecosystems had similar ecological features in relation to fire at the dominant species level and at the understory community level.

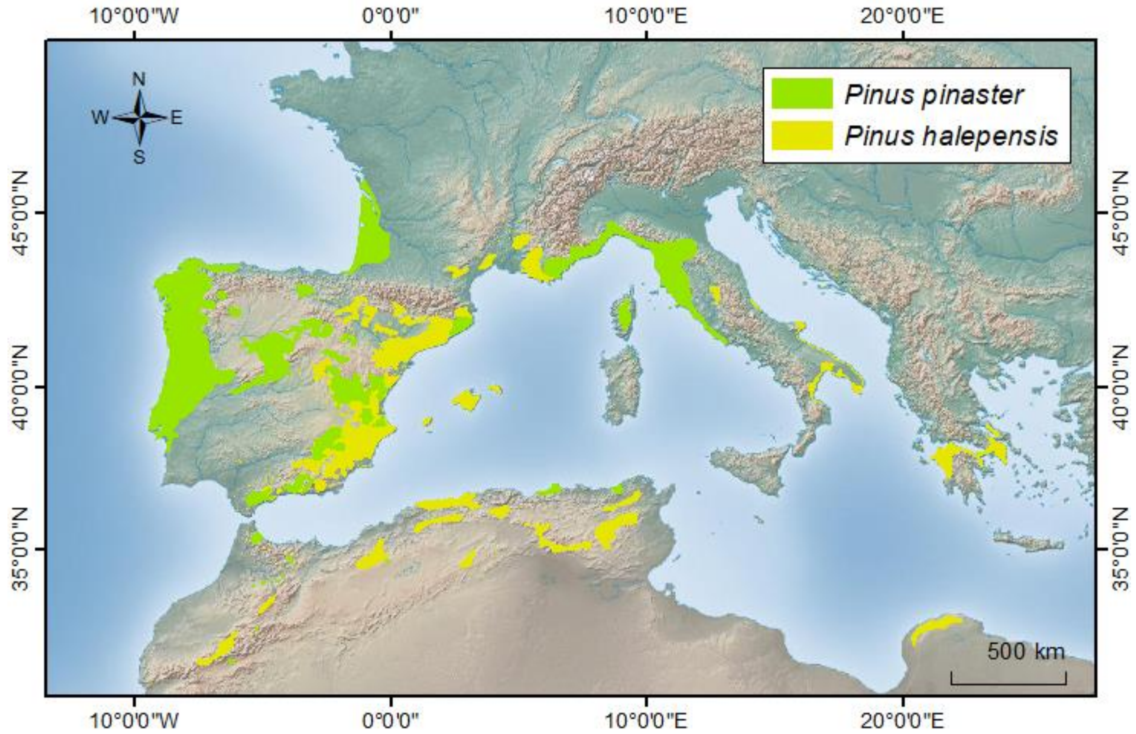

Figure 1. Natural distribution of *Pinus pinaster* and *P. halepensis* ecosystems (EUFORGEN, 2019).

Both *P. pinaster* and *P. halepensis* are highly flammable species (Fernandes *et al.*, 2008; Keeley *et al.*, 2012) and they produce a very flammable litter owing to the chemical composition and physical characteristics of needles (Fernandes & Rigolot, 2007; Ormeño *et al.*, 2009). Therefore, in *P. pinaster* and *P. halepensis* ecosystems, fires usually burn considerably the vegetation cover (Fernandes *et al.*, 2008). As with all pines naturally distributed in the Mediterranean Basin, *P. pinaster* and *P. halepensis* do not resprout after the fire, their post-fire recovery being based exclusively on the regeneration from seeds (Tapias et al ., 2001; Pausas *et al.*, 2008). To ensure an abundant seed bank able to survive wildfires, these pine species (*P. halepensis* and most *P. pinaster* populations) store closed cones with viable seeds for more than one reproductive cycle, a phenomena denominated serotiny (Tapias *et al.*, 2001, 2004; Daskalakou & Thanos, 2004; Moya *et al.*, 2018). Serotinous cones open with the high temperatures of fires, releasing the seeds in bulk (Tapias *et al.*, 2001; Pausas *et al.*, 2008), and thus, finding propitious environmental conditions for germination, and seedling establishment and growth (Calvo *et al.*, 2008; Moya *et al.*, 2008; Keeley *et al.*, 2011). Generally, at the age of 4-10 years old *P. pinaster* and *P. halepensis* plants start to produce cones with viable seeds (Tapias *et al.*, 2004). This early maturation favors the persistence of these pine populations under frequent fire regimes (Moya *et al.*, 2018). However, until 15 years after the fire the seed bank is not significant (Pausas *et al.*, 2008; Keeley *et al.*, 2012).

The understory community of *P. pinaster* and *P. halepensis* ecosystems is usually dense and tall (Fig. 2) (Keeley *et al.*, 2012; Taboada *et al.*, 2018). In general, the understory community is composed by species similar to those in the surrounding shrublands, dominating the species of the Fabaceae, Cistaceae and Ericaceae families among others (de las Heras *et al.*, 2012; Keeley *et al.*, 2012). Some of the most frequent species (e.g. *Ulex parviflorus* Pourr., *Cistus albidus* L., *Cistus ladanifer* L., *Ulex europaeus* L., *Pterospartum tridentatum* (L.) Willk.) are characterized by accumulating a high proportion (> 20%) of fine dead biomass, whereas many others (mainly from the Lamiaceae and Cistaceae families) have a high content of volatile oils (Baeza *et al.*, 2011; Keeley *et al.*, 2012). All these characteristics related to the architecture and composition of the understory community make it highly prone to fire (de las Heras *et al.*, 2012). That is why most of the species in these pine forests have some post-fire regeneration strategy such as the ability to germinate profusely after fire (seeders), or the ability to resprout from vegetative buds (resprouters) , although some species combine both strategies (facultatives) (Arianoutsou & Ne'eman, 2000; Calvo *et al.*, 2003, 2008; Paula *et al.*, 2009).

Figure 2. Photograph of mature (> 30 years) *P. pinaster* (left) and *P. halepensis* (right) ecosystems.

Wildfire effects on soils and vegetation

The knowledge about the ecological consequences of fires in the Mediterranean Basin is of great interest considering the high risk of erosion and desertification in this region (Van der Knijff *et al.*, 2000; Prăvălie *et al.*, 2017), and the high ecological value of its ecosystems, which are characterized by a high endemism and species richness (Cowling *et al.*, 1996; Keeley *et al.*, 2012). Fire-prone pine forests are probably the ecosystems in the Mediterranean Basin where the impacts of fire on soil and vegetation are more intense (Pausas *et al.*, 2008).

Fires cause immediate changes in soil properties that may persist several years after the fire owing to the combustion and to the change in the environmental conditions (Certini, 2005; Bodí *et al.*, 2012; Caon *et al.*, 2014). Over the long term (> 5 years), the effects of fire on soil properties are less evident (Hedo *et al.*, 2015; Muñoz-Rojas et al, 2016). Previous studies in pine ecosystems have noticed fire effects on physical, chemical and biological soil properties over the short and over the medium term (Certini, 2005; Cerdá & Jordan 2010). Among the physical properties affected by fire are those related to soil structure, such as the size of soil aggregates (Jordán *et al.* 2011; Mataix-Solera *et al.* 2011), which is related to the gas exchange capacity, water and biological processes and erosion vulnerability (Cerdá & Jordan 2010). Fire can also modify the soil chemical properties, such as pH, electrical conductivity or nutrient concentration (Marcos *et al.*, 2007; Caon *et al.*, 2014). These properties show a close relationship with ecosystem productivity and with microbial and plant diversity (Roem & Berendse 2000; Arshad & Martin 2002). The nutrients concentration in soils is also controlled by the biological properties, such as the activity of soil enzymes and the microbial biomass (Tabatabai, 1994; Hinojosa *et al.*, 2016), which can be completely depleted by fire (Vega *et al.* 2013).

Changes in soil properties after the fire are closely related to changes in vegetation (Certini, 2005; Hedo *et al.*, 2015). The immediate effects of fire on vegetation are the partial or total combustion of the vegetation, with a variable degree of plant mortality depending on the characteristics of the fire and species tolerance (Moreno and Oechel, 1994; Paula *et al.*, 2009). Post-fire regeneration in fire-prone pine forests can be studied at the pine population level or at the plant community level (Arianoutsou & Ne'eman, 2000). In general, both the dominant pine species and the rest of the plant community recover from endogenous processes (autosucession), showing a relatively high fire resilience (Moreno and Oechel, 1994; Arianoutsou and Ne'eman, 2000; Calvo *et al.*, 2008). The high resilience of Mediterranean vegetation to fires has traditionally been attributed to the adaptations and exaptations of species to certain fire regimes. Among these adaptations are the different regenerative strategies, serotiny or heat-stimulated germination among others (Paula *et al.*, 2009; Keeley *et al.*, 2011; de las Heras *et al.*, 2012), but recovery can be threatened when fire regimes are altered (Keeley *et al.* , 2011, 2012; Rundel *et al.*, 2018).

Fire regime attributes: recurrence and severity

The term fire regime integrates spatial, magnitude and temporal attributes of fire in a given ecosystem (Van Wagtendonk & Lutz, 2007; Bowman *et al.*, 2009; Rundel *et al.*, 2018). Magnitude attributes include fire intensity, which is the energy released by fire; and burn severity, which is defined as the change in ecosystem biomass (Keeley, 2009). Spatial attributes include fuel consumption patterns and fire size, which is especially relevant when vegetation recovery depends on seed dispersal from unburned areas (Bond & Keeley, 2005). Moreover, temporal attributes refer to the seasonality with respect to the occurrence of fires, the frequency or recurrence of fires and fire-free period, which can shape the severity of the fire (Steel *et al.*, 2015; García-Llamas *et al.*, 2019a). Fire regime attributes are determinant factors in fire-prone pine ecosystems structure and composition, fire impacts and ecosystem resilience (Fernandes & Rigolot, 2007; Van Wagtendonk & Lutz, 2007; Espelta *et al.*, 2008; Keeley, 2009). Consequently, developing methods to characterize fire regime attributes is of great interest to understand the ecosystem tolerance to fire and to optimize forest management (Keeley *et al.*, 2012).

Changes in fire recurrence (or fire frequency) are a major threat to the preservation of fire-prone pine forests (Espelta *et al.*, 2008; Taboada *et al.*, 2018). Previous studies indicate that excessively frequent fires increase the risk of soil degradation (de las Heras *et al.*, 2012) and hinder the recovery of obligate seeder species with long maturation times (Bond & Keeley, 2005; Rundel *et al.*, 2018), which is the case of *P. pinaster* and *P. halepensis* (Tapias *et al.*, 2001). Fire recurrence has been traditionally determined by the use of official wildfire reports based on field information, by the interpretation of information from the mass media, the use of dendrochronology-fire scar data, and even through the study of charcoal and pollen deposits in lake sediments (Keeley *et al.*, 2012). However, at present Landsat satellite imagery offer the possibility of identifying burned areas from the 1970s to the present (Röder *et al.*, 2008; Meddens *et al.*, 2016) and could therefore be used to determine the fire recurrence for decades anywhere over the world.

Similarly, high burn severities can lead to large impacts on soils (Key & Benson, 2006) and to high plant and seed mortality rates, hindering the post-fire regeneration of the plant community including the dominant pine species (Fernandes *et al.*, 2008; Fernández *et al.*, 2008; Maia *et al.*, 2012). Burn severity can be quantified in the field using estimates or measures of variables such as the degree of vegetation consumption, the percentage of plants that did not survive fire, terminal diameters of the remaining twigs, flame height, litter consumption, changes in soil color, or color of ashes and their depth (Key & Benson, 2006; Keeley, 2009; Marcos *et al.*, 2018). One of the most commonly used indices for field burn severity assessments is the Composite Burn Index (CBI) (Key & Benson, 2006), which combines several of these variables. This index can be used to estimate the damage caused by fire in the ecosystem (site burn severity), or to assess burn severity by compartments, differentiating the soil burn severity and vegetation burn severity. However, field methods are not efficient to assess burn severity in large areas (Chuvieco, 2010; Meng *et al.*, 2017), so the use of remote sensing methods for burn severity assessments is currently being examined. Among the most popular approaches are those based on spectral mixture analysis (Fernández-Manso *et al.*, 2009; Quintano *et al.*, 2017), radiative transfer models (Chuvieco *et al.*, 2006; de Santis *et al.*, 2009) and spectral indices (Fernández- Manso *et al.*, 2016; García-Llamas *et al.*, 2019b). Even so, it is still necessary further knowledge on the capacity of these methods to determine burn severity in the different compartments of the ecosystem, as well as to evaluate their performance under different environmental conditions, which can modify the spectral response of soil and vegetation (Chuvieco, 2010).

Justification of the study

Last decades, rural exodus and land abandonment in the Mediterranean Basin, especially in its European part, has led to an increase in fuel load and continuity (Pausas *et al.*, 2008). This fact, together with an increasingly warmer and drier climate (Giorgi & Lionello, 2008) is modifying fire recurrence and severity (Mouillot *et al.*, 2002; Fernandes, 2013; Vázquez *et al.*, 2015). The Mediterranean Basin is a densely populated region with a growing social concern about the common occurrence of large fires, a relatively new phenomenon that is perceived as catastrophic (Pausas *et al.*, 2008). The social problem is aggravated when the benefits obtained from these ecosystems contribute to fix population in rural areas. This is the case of *P. pinaster* and *P. halepensis* forests, which have been traditionally poorly managed (de las Heras *et al*., 2012) and whose ecosystem services could be largely constrained if there is an increase in fire frequency and severity, thus, limiting the socio-economic development of rural populations.

In this context, the following questions are timely to advance in the discipline of fire ecology and forest management of fire-prone pine forests: Is it possible to determine efficiently fire recurrence and burn severity in areas affected by large wildfires? Do the fire effects on soils depend on burn severity? Do the impacts caused by burn severity on soils persist over the medium term after the fire? Does fire recurrence and burn severity affect the resilience of the dominant tree species? Are there structural and functional changes in the plant community in relation to fire recurrence and burn severity? Which post-fire management strategies are recommended under different fire recurrence and severity scenarios? Answering all these questions will offer useful knowledge on the ecological consequences of fires in relation to fire recurrence and burn severity, and will help to establish the scientific basis for an effective forest management, identifying strategies to minimize the environmental and socioeconomic impact of large wildfires.

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2. OBJECTIVES

The main objective of the present PhD Thesis is to analyze the effects of different fire recurrence and severity regimes in fire-prone pine ecosystems. To achieve this objective, we established the following specific objectives:

Objective 1. To characterize the spatio-temporal patterns of fire recurrence and burn severity in fire-prone pine ecosystems. Specifically, we aim:

- To determine the spatio-temporal patterns of fire recurrence using remote sensing methods (*article I*).
- To evaluate the ability of remotely sensed indices obtained from Landsat sensors for burn severity assessments (*article II*).

Objective 2. To study the effects of burn severity on soil properties in fire-prone pine ecosystems. Specifically, we aim:

- To determine the effects of burn severity on soil properties immediately after fire (*article III*).
- To identify which effects of burn severity on soil properties persist over the medium term after fire (*article IV*).

Objective 3. To analyze the effects of fire recurrence and burn severity on the post-fire regeneration of vegetation. Specifically, we aim:

- To examine the relationship between fire regime attributes and the post-fire greenness recovery using a remote sensing approach (*article V*).
- To explore the role of fire recurrence and burn severity on the post-fire regeneration of Mediterranean serotinous pines (*article VI*).
- To investigate the consequences of changes in fire recurrence and burn severity on the plant community structure and functional traits (*article VII*).

Objective 4. To provide the scientific basis to optimize Forest management in fire-prone pine ecosystems (*Discussion*).

3. THESIS OUTLINE

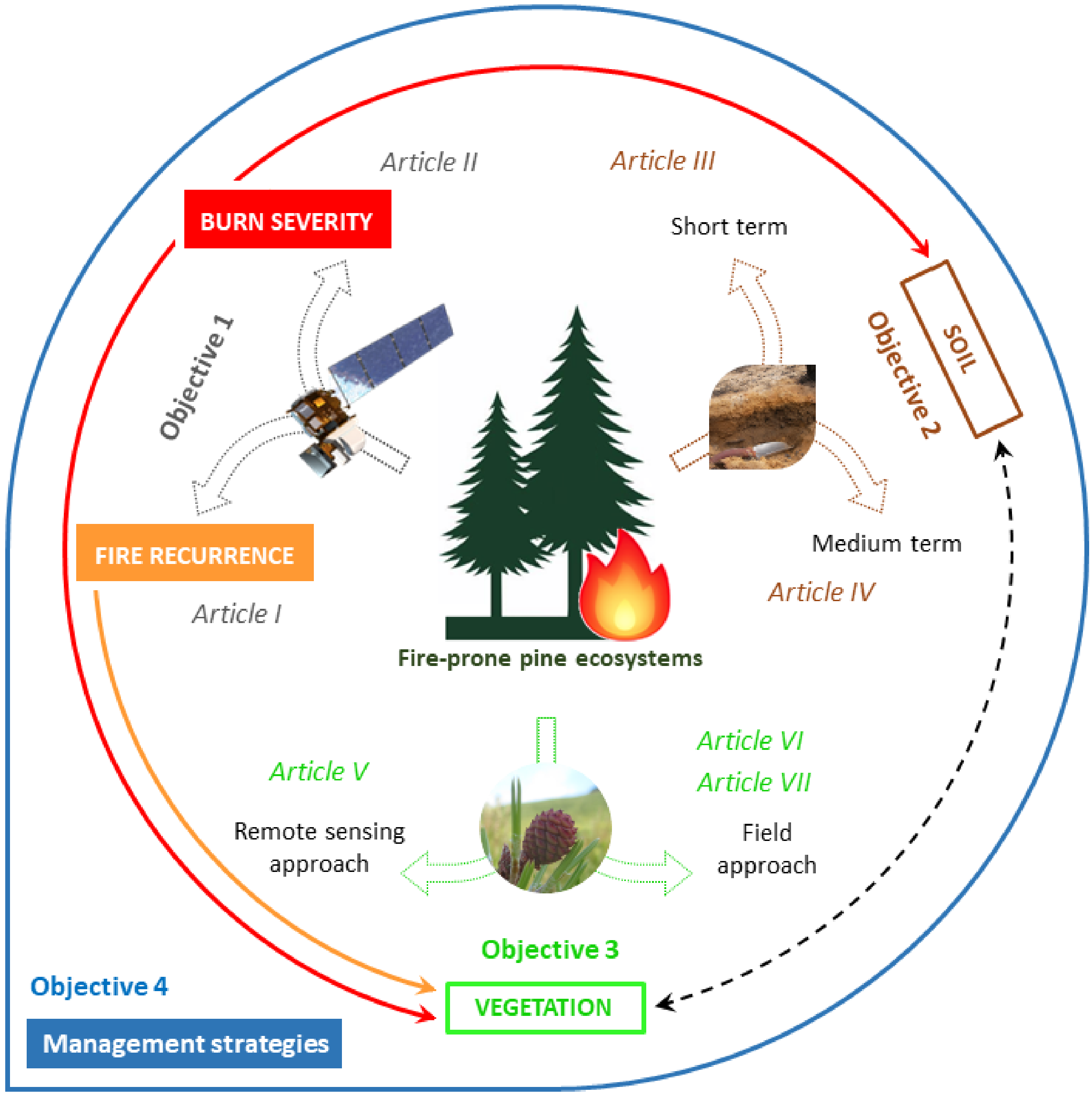

Figure 3. PhD Thesis outline.

4. STUDY SITES

In this PhD Thesis we have selected seven study sites in the Iberian Peninsula (Fig. 4). All the sites were occupied by fire-prone pine ecosystems that burned between 2012 and 2015.

Figure 4. Location of the study sites.

The megafire of Cortes de Pallás (39° 18′ N, 0° 54′ W; province of Valencia) started on June 28, 2012. The final burned area was 297 km^2. The climate in this study site is typically Mediterranean, with a mean annual precipitation of 400-600 mm, mean annual temperature of 13-17 °C and hot and dry summers, resulting in four months of summer drought (Ninyerola *et al.*, 2005). The orography is mountainous with an altitude comprised between 120-942 m. The lithology is calcareous, with soils predominantly classified as Haplic Calcisol and Calcari-lithic Leptosol (Jones *et al.*, 2005). Much of the vegetation affected by the wildfire were *P. halepensis* forests with a Mediterranean scrub undergrowth comprised of *Ulex parviflorus*, *Quercus coccifera* L. and *Rosmarinus officinalis* L. among other species. We have used this study site in the articles IV, VI and VII of the present PhD Thesis.

The megafire of Sierra del Teleno (42° 15′ N, 6° 11′ W, province of León) was declared on August 19, 2012, burning 119 km^2. The climate in this region can be considered as a transition between the Mediterranean and oceanic climates, with a mean annual precipitation of 600-800 mm, mean annual temperature of 8-11°C and two months of summer drought (Ninyerola *et al.*, 2005). The orography is mountainous with an altitudes ranging between 836-1493 m. The lithology is siliceous and the predominant soils are Haplic Umbrisol and Dystric Regosol (Jones *et al.*, 2005). Almost all the area affected by the wildfire was occupied by *P. pinaster* ecosystems with a shrub community dominated by *Pterospartum tridentatum*, *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. We have used this study site in the articles I, II, IV, V, VI and VII of the present PhD Thesis.

The large wildfire of Monte Pindo (42° 53' N, 9° 7' W; province of La Coruña) started on September 11, 2013. The burned area was 25 km^2. This site has an oceanic climate without summer drought. The mean annual precipitation is 1700-1800 mm and the mean annual temperature is 12-15 °C (Ninyerola *et al.*, 2005). The orography is mountainous with an altitude that rises from sea level to 929 m. Soils are Umbrisols (Jones *et al.*, 2005) with frequently exposed bedrock (biotite granite). The vegetation affected by the wildfire includes *P. pinaster* forests with a high abundance of *Rubus* sp., *Ulex europaeus*, *Cytisus scoparius* (L.) Link and *Erica umbellata* Loefl. ex L. We have used this study site in the article VII of the present PhD Thesis.

The large wildfire of Quintana del Castillo (42° 42'N, 6° 0' W; León province) was declared on July 13, 2015 and reached an extension of 26 km^2. This site is located in the transition zone between the Mediterranean and oceanic climates, with a mean annual precipitation of 700-850 mm, mean annual temperature of 8-10 °C and two months of summer drought (Ninyerola *et al.*, 2005). The landscape is a south-exposed hillside with an altitude comprised between 1034 and 1531 m. The lithology is siliceous and soils are classified as Haplic Umbrisol (Jones *et al.*, 2005). The vegetation affected by the fire includes *P. pinaster* forests, with and understory of *E. australis*, *P. tridentatum*, *C. scoparius* and *Calluna vulgaris* (L.) Hull among other species. We have used this study site in the article II of the present PhD Thesis.

The wildfire in Tabuyo del Monte (42° 18' N, 6° 14' W; León province) from July 21, 2015 burned 0.16 km^2. This site is located in the foothills of the Sierra del Teleno, and therefore it has a transition climate between Mediterranean and oceanic climates, with a mean annual precipitation of 685 mm, mean annual temperature of 10 °C and two months of summer drought (Ninyerola *et al.*, 2005). The landscape is flat, with an altitude of 1025 m. The lithology is siliceous and the soil is an Haplic Umbrisol (Jones *et al.*, 2005). Arboreal vegetation is dominated by *P. pinaster* and the shrubby community is dominated by *E. australis*, *H. lasianthum* and *P. tridentatum*. We have used this study site in the article III of the present PhD Thesis.

The large wildfire declared in Tineo (43 ° 18 ’N, 6 ° 26’ W; Principality of Asturias) on July 28, 2015, burned almost 6 km^2. The climate in this site is oceanic, with no summer drought. In this site, the mean annual precipitation is 925-1000 mm, and the mean annual temperature is 10-13 °C and (Ninyerola *et al.*, 2005). The topography is very rough, with altitudes ranging from 231 m to 768 m. The lithology is siliceous and soils are classified as Umbrisols (Jones *et al.*, 2005). The landscape of this area is dominated by *P. pinaster* forests and of *P. radiata* D. Don plantations. The most abundant shrub species are *E. australis* and *Arbutus unedo* L. We have used this study site in the article II of of the present PhD Thesis.

The megafire of Sierra de Gata (40 ° 12 ’N, 6 ° 43’ W; province of Cáceres) was declared on August 6, 2015, and it burned 89 km^2. The climate in this site is Mediterranean, with 3-4 months of summer drought. The mean annual precipitation is 700-1150 mm, and the mean annual temperature is 12-16 °C (Ninyerola *et al.*, 2005). The megafire affected mountainous and flat areas, comprising altitudes between 275 m and 1449 m. The lithology is siliceous and soils are mainly Haplic Umbrisols and Dystric Regosols (Jones *et al.*, 2005). The ecosystems affected by this wildfire include *P. pinaster* forests with different understory species depending on the altitude. The most common shrub species are *C. scoparius*, *E. australis* or *Cytisus striatus* (Hill) Rothm. We have used this study site in the article II of of the present PhD Thesis.

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5. RESULTS

Article I

Mapping fire recurrence in Sierra del Teleno Mountains using Landsat imagery (1978-2014)

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Elena Marcos & Leonor Calvo

Based on the article published in Bustamante J., Díaz-Delgado R., Aragonés D., Afán I., García D. (Eds.), ***Teledetección: Humedales y Espacios Protegidos. XVI Congreso de la Asociación Española de Teledetección*** *(2015), 145-148.*

http://www.aet.org.es/congresos/xvi/XVI_Congreso_AET_actas.pdf

Abstract

The recovery capacity of fire-prone pine ecosystems is closely related to fire recurrence. Accurate mapping of fire recurrence spatio-temporal patterns in forest ecosystems provides essential information to estimate the post-fire regeneration and helps to design restoration projects. In this study we develop an accurate methodology to map fire perimeters and fire recurrence in Teleno Mountains (León) (380 km^2) for the period 1978-2014 using Landsat 2, 4, 5, 7 and 8 scenes (sensors MSS, TM, ETM+ and OLI respectively). Firstly, a visual interpretation of 75 images was performed and potential fires were identified and digitized. Secondly, we validated the digitized fires using the official wildfire reports from the Nature Protection Section of Castilla y León. Results showed that all the wildfires described in the official wildfire reports were mapped using Landsat scenes, demonstrating that Landsat time series are an accurate tool to characterize fire recurrence. In Sierra del Teleno, the area affected by fire was 187.38 km^2 (49% of the study area), showing the high importance of fire in this region. We observed large areas affected by one (129.58 km^2) and two (50.59 km^2) fires, whereas the extension of areas affected by three and four fires was much lower (7.10 km^2 and 0.11 km^2 respectively).

INTRODUCTION

Forest fires are one of the most important ecological disturbances worldwide (Chuvieco, 1999). In the current context of global change, shifts in fire regimes are expected (Mouillot *et al.*, 2002; Vázquez *et al.*, 2015), modifying the impacts of fire on ecosystems as well as their recovery capacity (Fernandes & Rigolot, 2007). Therefore, it is essential to accurately characterize fire regime attributes in order to design the most suitable pre- and post-fire management strategies to maintain the ecosystems functionality. One of the key fire regime attributes conditioning the plant community structure and composition (Eugenio *et al.*, 2006) and soil properties (Certini, 2005) is fire recurrence (Vázquez *et al.*, 2015).

Earth observation satellites are a source of information with high potentiality to identify fire scars and thereby fire recurrence (Chuvieco, 1999). The discrimination of burned areas using remote sensing techniques is based mainly on the changes in surface reflectance owing to two fire effects (Röder *et al.*, 2008): (i) the deposition of ashes and (ii) the change in the structure and abundance of photosynthetic vegetation. Remote sensing methods allow drawing fire perimeters using a single image or by comparing pre- and post-fire images (Chuvieco, 1999).

The aim of the present study is to identify a suitable methodology to elaborate an accurate fire recurrence map in Sierra del Teleno (León), for the period 1978-2014 using remote sensing methods.

MATERIALS AND METHODS

Study site

Sierra del Teleno is located in the southwest of León province (Spain) between the Eria and Duerna rivers. It is a mountainous area with altitudes comprised between 850 and 2183 m. Soils are acidic, predominantly sandy and with low organic matter content. Climate is Mediterranean, with an annual precipitation between 600 and 900 mm and two months of summer drought, in which is common the development of dry storms that cause forest fires (Calvo *et al.*, 2008).

Specifically, the target study area were the municipalities of Castrillo de la Valduerna, Castrocontrigo, Destriana, Luyego, Quintana and Congosto and Truchas matching a 20 x 20 km study framework (Fig. 5). This study area has an extent of 380 km^2, including the entire perimeter of the large fire of August 2012, which burned 119 km^2, mainly forests dominated by *Pinus pinaster* Ait.

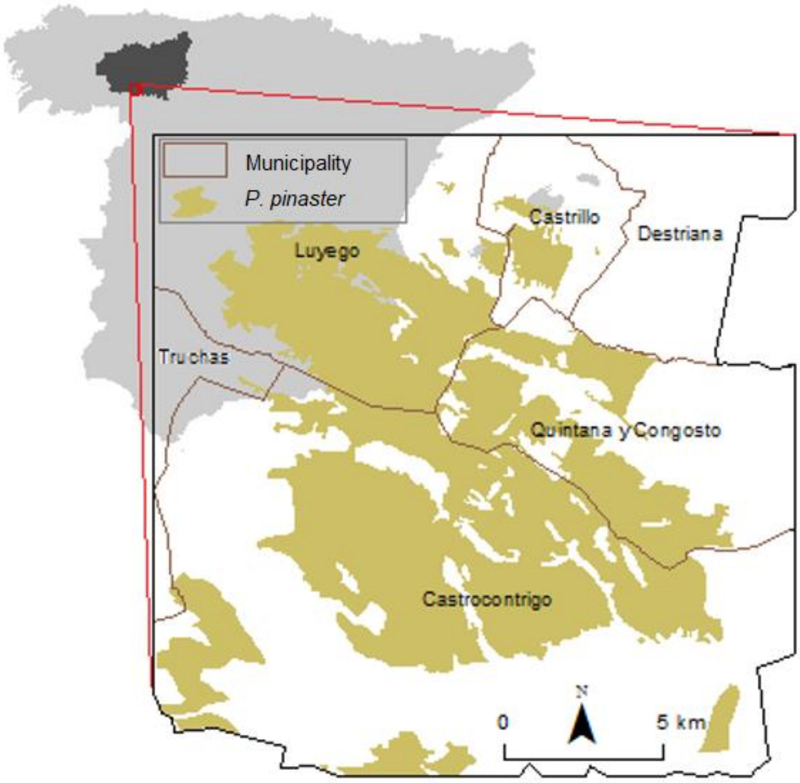

Figure 5. Location of the study area in Spain (light grey) and in León province (dark grey). Location of *P. pinaster* ecosystems was based on the National Forest Inventory (Alberdi *et al.*, 2010).

Material

To identify the forest fires for the period 1978-2014 we set up a database composed of 75 Landsat images (Fig. 6). At least one annual image of the study area was downloaded, representing the phenological state of maximum photosynthetic activity (spring and/or summer). The resulting database was made up of images from Landsat 2 (MSS sensor);

Landsat 4 and 5 (TM sensor); Landsat 7 (ETM+ sensor); and Landsat 8 (OLI sensor). Scenes for the periods 1975-1990 and 1999-2014 were obtained from the Earth Explorer server of the U.S. Geological Survey (USGS) and images from 1991 to 1998 were acquired from the European Space Agency (ESA).

The Landsat series (1975-2014) was complemented with several aerial orthophotos (Fig. 6): (I) images from the IRyDA Interministerial Flight (1977-1983), which flew over the study area in 1980; and (II) orthophotos of the Spanish Plan Nacional de Ortofotografía Aérea (PNOA) until 2014.

To validate the wildfires identified with Landsat imagery we used the official wildfire reports (1978-2007) provided by the Nature Protection Section of the Regional Administration, which included information on the fire date, extent, location (municipality, Monte de Utilidad Pública and toponymy), and the type of vegetation affected for the entire study period. For the period 2007-2014 it was possible to obtain the official information in digital format, which provided equivalent information to the wildfire reports and a geographical representation of the fire perimeter.

Methods

For each year during the period 1978-2014, we identified all the potential fires with an extent larger than 0.02 km^2 (about 20 pixels) by visual analysis of the false color composites performed with each Landsat scene. We also analyzed changes in land use between consecutive scenes to facilitate the identification of fire scars (Fig. 6). The images before 1978 were used as a reference to identify the change caused by potential fires until 1980. For the images obtained by the MSS sensor we used the false color composite RGB 564 (bands 5, 6 and 4), for the images obtained by the TM and ETM+ sensors we used the RGB 541 and for the OLI sensor we used the combination RGB 652. Orthophotos were also used to identify fires by photointerpretation. Once identified, the scars of each fire were digitized. In order to differentiate the burned areas from other silvicultural activities, such as clearing or cutting which may cause similar changes in land surface reflectance (Chuvieco, 1999), each of the digitized fire scars was associated with a wildfire report of the Nature Protection Section. This allowed validating the fire scars detected in the visual analysis. Finally, the fire recurrence for each point of the study area was calculated by overlapping the validated fire scars.

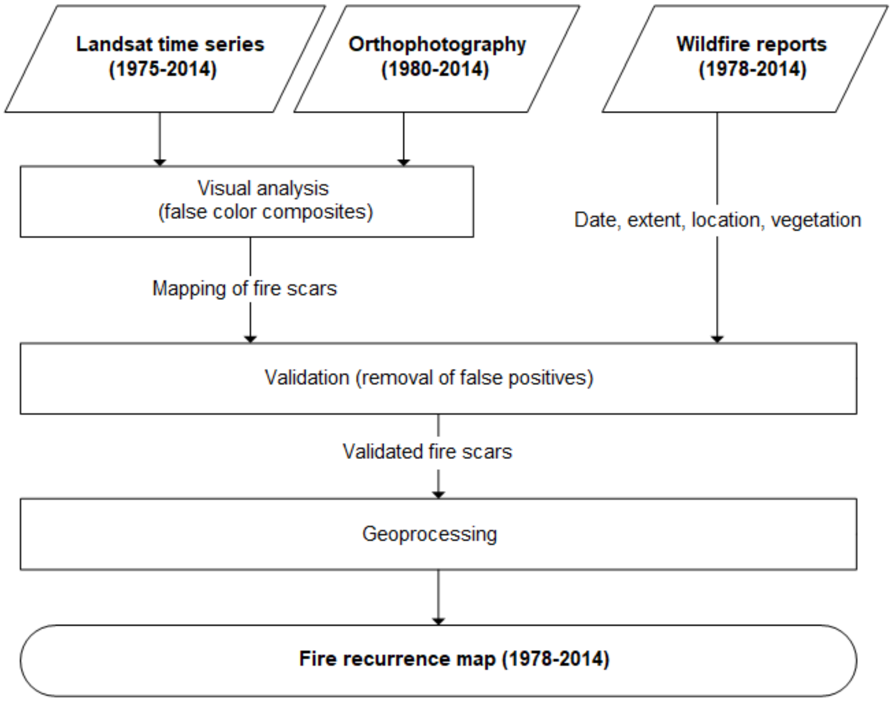

Figure 6. Methodology flowchart.

RESULTS AND DISCUSSION

Forest fires in the period 1978-2014

All the wildfires described in the official wildfire reports were mapped using Landsat scenes. Particularly, the fire scars identified in the study area indicated that the period 1986-1989 concentrated the largest number of wildfires (Fig. 7). Results also showed a decreasing trend in the number of wildfires during last decades. In general, the total area affected by fires is directly related to the occurrence of large forest fires in the study area (1978 and 1981, 1991, 1998 and 2012), which have a return interval of approximately 10 years.

The chronological distribution of the number of fires is similar to that obtained by Santamaría *et al.* (2013) in Sierra del Teleno. According to these authors, the decrease in the number of events can be explained by the contemporary effectiveness of the extinction works. For this reason, most of the fires were extinct at the incipient phase. The peaks corresponding to high number of fires were usually associated with moments of critical climatic conditions (Santamaría *et al.*, 2013).

The adjustment of the results obtained using Landsat imagery with the official reports (unpublished data) demonstrated the validity of using Landsat imagery to map perimeters of forest fires larger than 2 ha over time. However, we encourage validating the information obtained through remote sensing methods with official information when available, since some changes in land use and forest management may result in false colour composites similar to fires. This validation procedure may contribute to avoid errors until cartographers are well trained (Chuvieco, 1999).

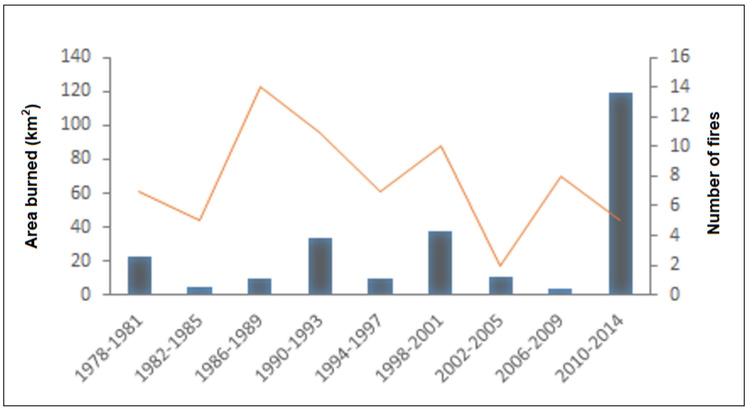

Figure 7. Area burned (bars) and number of wildfires (line) by periods of four years.

Fire recurrence in the period 1978-2014

We observed that the 49% (187.38 km^2) of the study area (380.25 km^2) have burned at least once (Fig. 8; Table 1). Most of this extent corresponded to areas affected by one (34%) and two fires (13%), whereas zones affected by three and four fires showed a much smaller extent, mostly concentrated in the perimeter of the large fire of 2012.

P. pinaster ecosystems occupied the 35% (134.34 km^2) of the study area and comprised the 55% of the area affected by fire (Table 1), indicating that these ecosystems are highly prone to fire. The proportion of area burned among fire recurrence categories was analogous to that of the entire study area, predominating the areas affected by one and two wildfires.

Although three and four fires in 36 years could be considered a high fire recurrence (Eugenio *et al.*, 2006), recent studies in *P. pinaster* forests in northern Portugal (Fernandes *et al.*, 2015) reported higher fire recurrences. These authors obtained a mean recurrence of three fires for the period 1975-2007 in their study areas, their fire recurrence ranging from one to nine fires in 32 years.

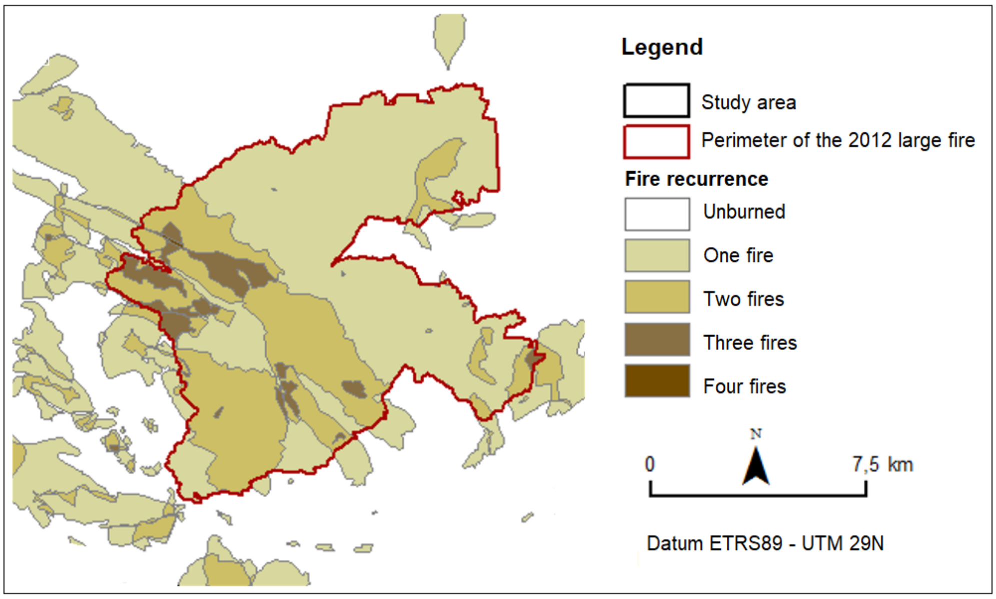

Figure 8. Fire recurrence map.

It is essential to represent the spatio-temporal patterns of fire recurrence in order to analyze the ecological consequences of high fire recurrences, which may hinder the recovery capacity of vegetation, particularly of obligate seeder species (Calvo *et al.*, 2013). The spatio-temporal characterization of fire recurrence and the knowledge of the impact of this fire-regime attribute on the ecosystems may be fundamental for decision makers to optimize forest management.

Table 1. Extent unburned and extent affected by fire (one, two, three and four fires) in the entire study area and in the areas dominated by *P. pinaster* ecosystems.

Fire recurrence	Area (km^2)	Area (%)	Area of pine forest (km^2)	Area of pine forest (%)
Unburned	192.87	50.72	31.75	23.64
One fire	129.58	34.08	62.23	46.33
Two fires	50.59	13.30	34.82	25.92
Three fires	7.10	1.87	5.44	4.05
Four fires	0.11	0.03	0.10	0.07

CONCLUSIONS

This study demonstrates that the identification of fire scars and the elaboration of fire recurrence maps is viable by using Landsat imagery. This remote sensing approach is highly efficient (vs. fieldwork), owing to the accessibility and availability of long time series of Landsat scenes. In order to create a highly reliable cartography it is desirable to validate the information obtained from remote sensing with field information, such as the official fire reports.

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Article II

Burn severity metrics in fire-prone pine ecosystems along a climatic gradient using Landsat imagery

Víctor Fernández-García, Mónica Santamarta, Alfonso Fernández-Manso, Carmen Quintano, Elena Marcos & Leonor Calvo

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Abstract

Multispectral imagery is a widely used source of information to address post-fire ecosystem management. The aim of this study is to evaluate the ability of remotely sensed indices derived from Landsat to assess initial burn severity (overall, on vegetation and on soil) in fire-prone pine forests along the Mediterranean-Transition-Oceanic climatic gradient in the Mediterranean Basin. We selected four large wildfires that affected pine forests in a climatic gradient within the Iberian Peninsula. In each wildfire, we established CBI plots to obtain field values of three burn severity metrics: site, vegetation and soil burn severity. The ability of 13 spectral indices to match these three field burn severity metrics was compared and their transferability along the climatic gradient assessed using linear regression models. Specifically, we analysed the performance of 12 indices previously used for burn severity assessments (8 reflective, 2 thermal, 2 mixed) and a new reflective index (dNBR-EVI). The results showed that Landsat spectral indices have a greater ability to determine site and vegetation burn severity than soil burn severity. We found large differences in indices performance among the three different climatic regions, since most indices performed better in the Mediterranean and Transition regions than in the Oceanic one. In general, the dNBR-EVI showed the best fit to site, vegetation and soil burn severity in the three regions, demonstrating a broad transferability along the entire climatic gradient.

INTRODUCTION

Wildfire is a natural process identified as a serious environmental and socio-economic problem in some regions of the world (Nunes *et al.*, 2016). Indeed, in the European countries of the Mediterranean Basin, wildfires represent the most important abiotic disturbance (Lindner *et al.*, 2008), and they have increased significantly in number since 1980 (San-Miguel-Ayanz *et al.*, 2016). Predictions of future fire regimes forecast an increase in the severity of wildfires in the Mediterranean Basin, under a warmer and drier climate (Lindner *et al.*, 2008; Moreira *et al.*, 2011; Doblas-Miranda *et al.*, 2017). The consequences of fire are highly dependent on burn severity (Pausas *et al.*, 2008; Keeley, 2009; González-de-Vega *et al.*, 2016). This parameter is defined as the change in the burnt area with respect to the pre-fire situation (Key & Benson, 2006; de Santis *et al.*, 2010; Soverel *et al.*, 2011; Meng *et al.*, 2017), and operationally denoted as the aboveground and belowground organic matter consumed by fire (Keeley, 2009).

In Southern Europe, for instance the Iberian Peninsula, forests most affected by wildfires are the fire-prone pine ecosystems (Dimitrakopoulos *et al.*, 2011). In these forests, burn severity plays a key role in the recovery capacity of both vegetation and soil (Calvo *et al.*, 2008; Lindner *et al.*, 2008; Pausas *et al.*, 2008; González-de-Vega *et al.*, 2016). In general, *Pinus* species in the Iberian Peninsula's forests are obligate seeders whose post-fire regeneration relies on seeds stored in serotinous cones within the canopy level (Calvo *et al.*, 2008, 2016). However, their natural regeneration could fail due to severe wildfires, as regeneration from aerial seed banks could be hindered (Calvo *et al.*, 2008; Catry *et al.*, 2013). Depending on burn severity, fire not only affects the regeneration of dominant tree species but also the understory community. Burn severity increases mortality and interacts with regeneration strategies, affecting species with different functional traits in different ways and jeopardizing the recovery of some of them (Céspedes *et al.*, 2014; Pausas & Keeley, 2014; González-de-Vega *et al.*, 2016).

In addition, burn severity has several impacts on soils in fire-prone ecosystems. Whereas low severity has almost negligible or non-negative impacts on soils (Marcos *et al.*, 2009; Alcañiz *et al.*, 2016), high burn severity may cause significant loss of organic matter (Vega *et al.*, 2013), development of hydrophobicity with depth (Rodríguez-Alleres *et al.*, 2012), and deterioration of soil structure (Varela *et al.*, 2015), thus contributing to soil losses (Certini, 2005; Lindner *et al.*, 2008). Soil erosion is probably the most serious ecological threat during the first year after fire in high burn severity areas (Fernández & Vega, 2016), and damage can be significant in regions like the Iberian Peninsula, where the risk of potential erosion is very high (Van der Knijff *et al.*, 2000). Consequently, initial assessments of burn severity are necessary to address the potential post-fire management strategies aimed at maintaining the vegetation community and preserving the soil.

There are several ways to assess burn severity in the field, among which the Composite Burn Index (CBI) (Key & Benson, 2006) has been identified as a standard measurement (e.g. Fernández-Manso & Quintano, 2015; Kong *et al.*, 2015; Quintano *et al.*, 2015; Holden *et al.*, 2016; Meddens *et al.*, 2016; Parks *et al.*, 2016; Day *et al.*, 2017). The CBI has been initially proposed for calibration and validation of remote sensing products of burn severity the first months after fire (initial assessment) or the first growing season after fire (extended assessment) in Western United States (Key & Benson, 1999; Key & Benson, 2006), and it has been adapted for use in different regions (Epting *et al.*, 2005; Kasischke *et al.*, 2008). The CBI approach is more complete than many other classification systems based on single indicators of burn severity (Sikkink, 2015), because it employs several visually estimated metrics of four vegetation strata (vegetation burn severity) and soil (soil burn severity), which can be used together (site burn severity) providing an overall idea of the damage caused by fire, or separately, depending on compartments considered key in post-fire management (Key & Benson, 2006; Zhu *et al.*, 2006; Keeley, 2009). Although several limitations of CBI have been noted, such certain subjectivity on its estimation without knowing the pre-fire situation (Lentile *et al.*, 2009), the CBI is a burn severity index of great interest for land managers and scientists (Holden *et al.*, 2016) due to its integrative nature, rapid application and known relation with many other impacts on the ecosystems and post-fire recovery (e.g. Johnstone *et al.*, 2010; Schwilk & Caprio, 2011; Kong *et al.*, 2015; Holden *et al.*, 2016; Day *et al.*, 2017).

In large forest fires the assessment of burn severity by using only field measurements is not functional, the use of remote sensing methods being necessary (de Santis & Chuvieco, 2007; Wu *et al.*, 2015; Meng *et al.*, 2017). In order to tackle this challenge, various remote sensing methods have been used, including those based on spectral mixture analysis (SMA) (Fernández-Manso *et al.*, 2009; Quintano *et al.*, 2017), radiative transfer models (RTM) (Chuvieco *et al.*, 2006; de Santis *et al.*, 2009) or spectral indices (Chu & Guo, 2014; Wu *et al.*, 2015; Fernández-Manso *et al.*, 2016; Zheng *et al.*, 2016). SMA and RTM have some advantages over spectral indices for burn severity mapping. SMA can be applied to any type of reflective remotely sensed image (multispectral/hyperspectral), independently of their spatial resolution or specific bands, and allows analogous products to some field burn severity measurements to be obtained, having an explicit physical meaning (Lentile *et al.*, 2009). RTM is a physically-based method (Meng *et al.*, 2017), which can model burn severity variables regardless of study site characteristics (de Santis *et al.*, 2009). Furthermore, RTM have successfully achieved higher correlations with field burn severity than spectral indices in temperate and Mediterranean ecosystems (de Santis & Chuvieco, 2007; de Santis *et al.*, 2009; de Santis *et al.*, 2010). However, spectral indices are still the most commonly used method (Key & Benson, 2006; Keeley, 2009; Veraverbeke *et al.*, 2012; Chu & Guo, 2014; Fernández-Manso & Quintano, 2015), because they can be highly accurate when matching field measurements of burn severity using a simple calculation process (Miller & Thode, 2007; Parks *et al.*, 2014; Fernández-Manso *et al.*, 2016; Zheng *et al.*, 2016)., but most studies analysing spectral indices performance have been carried out in North America (Epting *et al.*, 2005; Miller & Thode, 2007; Harris *et al.*, 2011; Cansler & McKenzie, 2012; Parks *et al.*, 2014; Zheng *et al.*, 2016), further evaluations in other regions being advisable.

Among the many factors that can affect the spectral indices performance, climate is one of great interest due to its influence on several proximate factors, which can modify the land surface reflectance and/or thermal emissivity. For instance, along different climates, vegetation may have different leaf pigmentation (Xiao & Moody, 2008), leaf area (Myneni *et al.*, 2002; Zhu *et al.*, 2013), and geometry (Box, 1981); and soils have different moisture content (Reichle & Koster, 2004). Despite this influence, few studies have indicated the relevance of climate-related proximate factors in burn severity assessments (Roy *et al.*, 2006; Picotte & Robertson, 2011; Soverel *et al.*, 2011; Parks *et al.*, 2014).

Landsat 8 satellite allows us to obtain reflective indices, thermal metrics, and mixed indices combining reflective and thermal, so the capacity of these spectral indices to assess burn severity can be compared (Vlassova & Pérez-Cabello, 2016). Most spectral indices can be calculated from a mono-temporal perspective (post-fire situation) or from a bi-temporal perspective (difference between pre-fire and post-fire situations) (Epting *et al.*, 2005; Harris *et al.*, 2011). The main advantage of using mono-temporal indices is the reduction in errors associated with differences in vegetation phenology, which are potentially expected with bi-temporal approaches (Epting *et al.*, 2005) due to imagery acquisition date or because of inter-annual meteorological differences (Veraverbeke *et al.*, 2010). However, the literature usually indicates that bi-temporal indices are more correlated to field burn severity measurements (Key, 2006; Key & Benson, 2006; Miller & Thode, 2007; Zheng *et al.*, 2016).

Spectral indices based on the opposite response of Near Infrared (NIR) and Short Wave Infrared (SWIR) regions, specifically the NBR and its bi-temporal approach called dNBR (Key, 2006), are considered a reference for burn severity mapping (de Santis *et al.*, 2010; Veraverbeke *et al.*, 2012; Parks *et al.*, 2014). Although some authors have found their performance suboptimal (Chuvieco *et al.*, 2006; Roy *et al.*, 2006), other indices based on NBR have been proposed obtaining good results, for instance the RdNBR (Miller & Thode, 2007) and the RBR (Parks *et al.*, 2014), calculated by relativizing the bi-temporal NBR with the pre-fire NBR. Other reflective metrics, such as the typical vegetation indices NDVI (Rouse *et al.*, 1973) and EVI (Gao *et al.*, 2000) have been used in burn severity assessments, both mono and bi-temporal approaches obtaining good results (Wu *et al.*, 2015). Additionally, in recent years, thermal infrared data is starting to be used for burn severity assessments (Vlassova *et al.*, 2014; Quintano *et al.*, 2015, 2017), but there are few studies assessing their bi-temporal approach (Zheng *et al.*, 2016). Thermal remotely sensed information can be easily transformed to land surface temperature (LST), which is a function of soil and air temperature, both of which are positively related to burn severity (Marcos *et al.*, 2009; Vlassova & Pérez-Cabello, 2016). Other authors have sought to improve the functioning of the reflective indices incorporating a thermal component, resulting in mixed burn severity indices that could outperform reference indices such as dNBR (Veraverbeke *et al.*, 2011; Zheng *et al.*, 2016).

Therefore, numerous spectral metrics from Landsat data to quantify burn severity can be found, but there is no consensus about the most appropriate alternative (Cansler & McKenzie, 2012), highlighting the importance of developing more specific research. Thus, there are few studies comparing the capacity of spectral indices to detect site, vegetation and soil burn severity separately (Hudak *et al.*, 2007), and it may be of great interest for a better understanding of indices performance. Differences in spectral indices retrieval of soil and vegetation burn severity can be expected, due to the different sensitivity of each region of the spectrum to each particular change in soil and in vegetation (Key & Benson, 2006; Chuvieco 2010; Veraverbeke *et al.*, 2011; Vlassova *et al.*, 2014). Additionally, finding spectral indices with a great ability to map the site, vegetation and soil burn severity is of great value in defining emergency areas, especially in those ecosystems dominated by obligate seeders or with high vulnerability to soil erosion, such the fire-prone pine forests of the Iberian Peninsula (Van der Knijff *et al.*, 2000; Calvo *et al.*, 2008; Fernández & Vega, 2016; González-de-Vega *et al.*, 2016).

The objective of this study is to evaluate the ability of remotely sensed indices derived from Landsat sensors for initial burn severity assessments in fire-prone ecosystems dominated by

Pinus species along the Mediterranean-Transition-Oceanic climatic gradient. Specifically, we aim to answer the following questions: (i) Which spectral indices (reflective, thermal or mixed) have the best fit to field measurements of burn severity (CBI) along the Mediterranean-Transition-Oceanic climatic gradient? (ii) Do the remotely sensed indices have the same ability in assessing site burn severity (vegetation plus soil) as vegetation burn severity or soil burn severity individually? (iii) Is there any spectral index transferable throughout climatic regions with a high ability to indicate burn severity in the ecosystem (site burn severity) and its compartments (vegetation and soil burn severity)?

METHODS

The followed methodology comprises four steps: study sites selection, field measurements of burn severity, remotely sensed data and data analysis (Fig. 9).

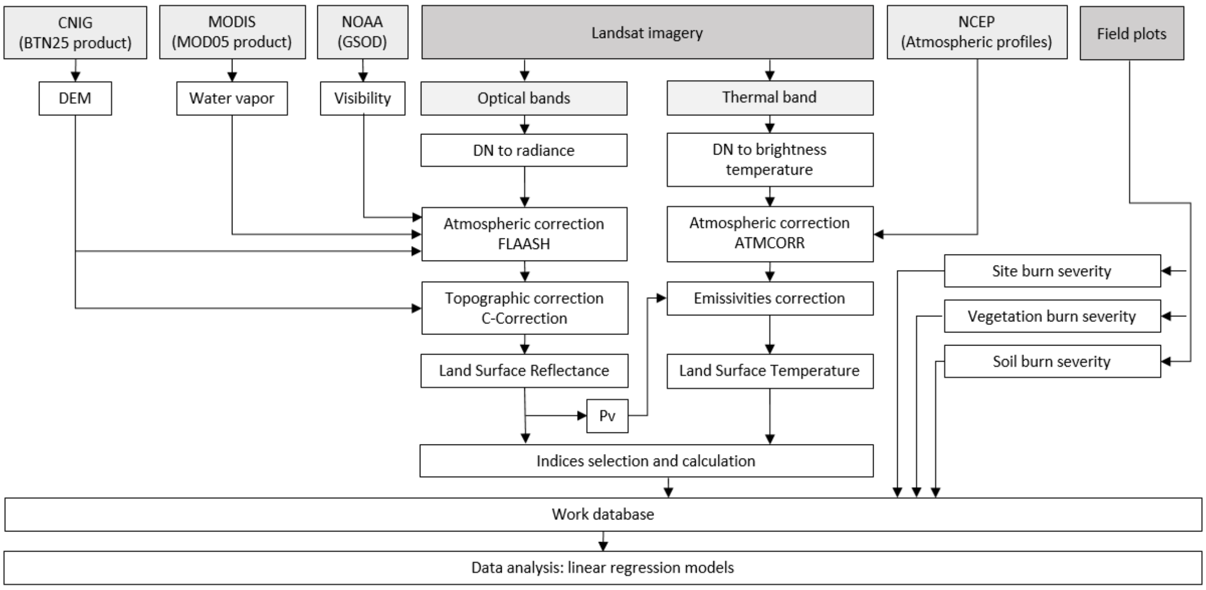

Figure 9. Methodology flowchart. CNIG: Spanish National Centre of Geographic Information; DEM: Digital Elevation Model; NOAA: U.S. National Oceanic and Atmospheric Administration; NCEP: U.S. National Centres for Environmental Prediction; Pv: proportion of vegetation cover.

Study sites

Four wildfires were selected along the Mediterranean-Transition-Oceanic climatic gradient within the Iberian Peninsula (Mediterranean, Transition1, Transition2 and Oceanic sites)

(Table 2). All of them affected closed-canopy forests basically dominated by *Pinus pinaster* Ait., with a similar fuel structure, fuel model number 7 according to Anderson (1982).

The Mediterranean site is located in Cáceres province, Spain (Fig. 10), where 88.90 km^2 burned in summer 2015. The fire regime in this area is characterized by a relatively high number of wildfires (MAGRAMA, 2009) (Table 2). The site combines mountainous terrain with almost no northern exposure with flat areas. Soils are acidic and mainly originated from biotitic-granitic lithologies and slash. The forest is dominated by *P. pinaster*. This region is characterized by typical Mediterranean conditions with 4 months of summer drought.

The Transition1 site is a mega-wildfire occurred in summer 2012 in the south of León province, Spain (Fig. 10), where there are few fires (MAGRAMA, 2009). This wildfire burned 118.91 km^2 of *P. pinaster* stands developed over siliceous lithologies (quartzite, sandstone and slate) in a heterogeneous topography (Table 2).

The Transition2 site is located in the north of León province (Fig. 10), where a wildfire affected 26.00 km^2. In this area, there are few fires (MAGRAMA, 2009) (Table 2). The site is a south-exposed hillside, where soils are acidic, originated from arkosic sands, slash, sandstone and quartzite. The forest is dominated by *P. pinaster* with occasional presence of *P. nigra* Arn. and *P. sylvestris* L. The Transition region is characterized by a summer drought of 2 months, an intermediate period between the Mediterranean climate and Oceanic climates (with no summer drought).

The Oceanic wildfire occurred in Asturias province, Spain (Fig. 10), and burned 5.79 km^2. The rugged terrain topography and patchy landscape (García-Llamas *et al.*, 2016) cause wildfires in this region to be smaller (MAGRAMA, 2009). Soils are acidic, originated from slash, sandstone and conglomerate. The dominant tree species is *P. pinaster* with occasional presence of *P. radiata* D. Don. There is no summer drought in this region.

Table 2. Characteristics of study sites.

	Mediterranean site	Transition1 site	Transition2 site	Oceanic site
Fire alarm date	August 6th, 2015	August 19th, 2012	July 13th, 2015	July 28th, 2015
Wildfire size (km^2)	88.90	118.91	26.00	5.79
Elevation (m)	275 - 1,449	836 - 1,493	1,032 - 1,531	231 - 768
Aspect	S, W, E	N, S, W, E	S	N, S, W, E
Mean annual precipitation (mm) [a]	702	612	703	934
Mean July precipitation (mm) [a]	7	20	30	40
Mean annual temperature (ºC) [a]	14.3	10.7	10.0	10.8
Mean July temperature (ºC) [a]	23.6	19.6	18.3	17.2
Mean summer soil moisture (%) [b]	9.3	22.5	29.2	40.6
Köppen classification [c]	Csa	Csb	Csb	Cfb
Quantity of fires ($N*10\ km^{2\ -1}*10\ years^{-1}$) [d]	12.2	4.7	4.9	12.8
Average size of fires (km^2) [d]	0.18	0.64	0.16	0.08

[a] Precipitation and temperature are 1982 to 2012 averages.

[b] Soil moisture in the summer of the wildfire occurrence, measured as the percentage of soil water with respect to the amount of water that the soil could retain (Data provided by the Spanish meteorological survey - AEMET).

[c] Climatic classifications (1971-2000) are done according to the Spanish meteorological survey (AEMET-IM, 2011). Csa: temperate with hot dry summer (Mediterranean); Csb: temperate with dry temperate summer (Transition); Cfb: temperate without a dry season and temperate summer (Oceanic).

[d] Fire statistics are 1998-2008 averages (MAGRAMA, 2009).

Field measurements of burn severity

Field data to quantify the initial burn severity were collected three months after wildfires in the four study sites. 30 m diameter field plots were randomly distributed in fairly homogeneous patches of at least 100 m diameter throughout each wildfire, and positions were GPS recorded.

According to the sampling intensity reported in other studies (e.g. de Santis *et al.*, 2010; Wu *et al.*, 2015; Zheng *et al.*, 2016), we distributed a total of 183 plots among the four wildfires: 58 in the Mediterranean site, 54 in the Transition1 site, 48 in the Transition2 site, and 23 in the Oceanic site . To ensure that the number of plots was enough in each wildfire we used the following formula (Chuvieco, 2010):

$$n = z^2 s^2 / (L^2 + s^2 z^2 / N)$$

Where n is the minimum sampling size, z is the z-coefficient for a specific confidence level, L is the minimum detectable change or assumable error, s^2 is the variance of the samples, and N is the population size. We assumed an error of 0.5 CBI points and a confidence level of 95%.

Our field protocol to quantify burn severity (Table 3) is an adapted version of the original CBI (Key & Benson, 2006). The sampling procedure consists of rating several variables from 0 points (unburned) to 3 points (maximum burn severity) in 5 strata (Table 3), obtaining an average burn severity value per stratum. The site burn severity score is the average value of all evaluated strata, the vegetation burn severity is the average value of all evaluated strata except substrate, and the soil burn severity only considers the substrate stratum (Fig. 11). In our adapted CBI we did not consider factors that have to be measured in extended assessments (% of living shrubs, colonizers, or change in species composition). In the substrate stratum rating factors we did not use medium and heavy fuel consumption, because they were not significantly present in the study sites.

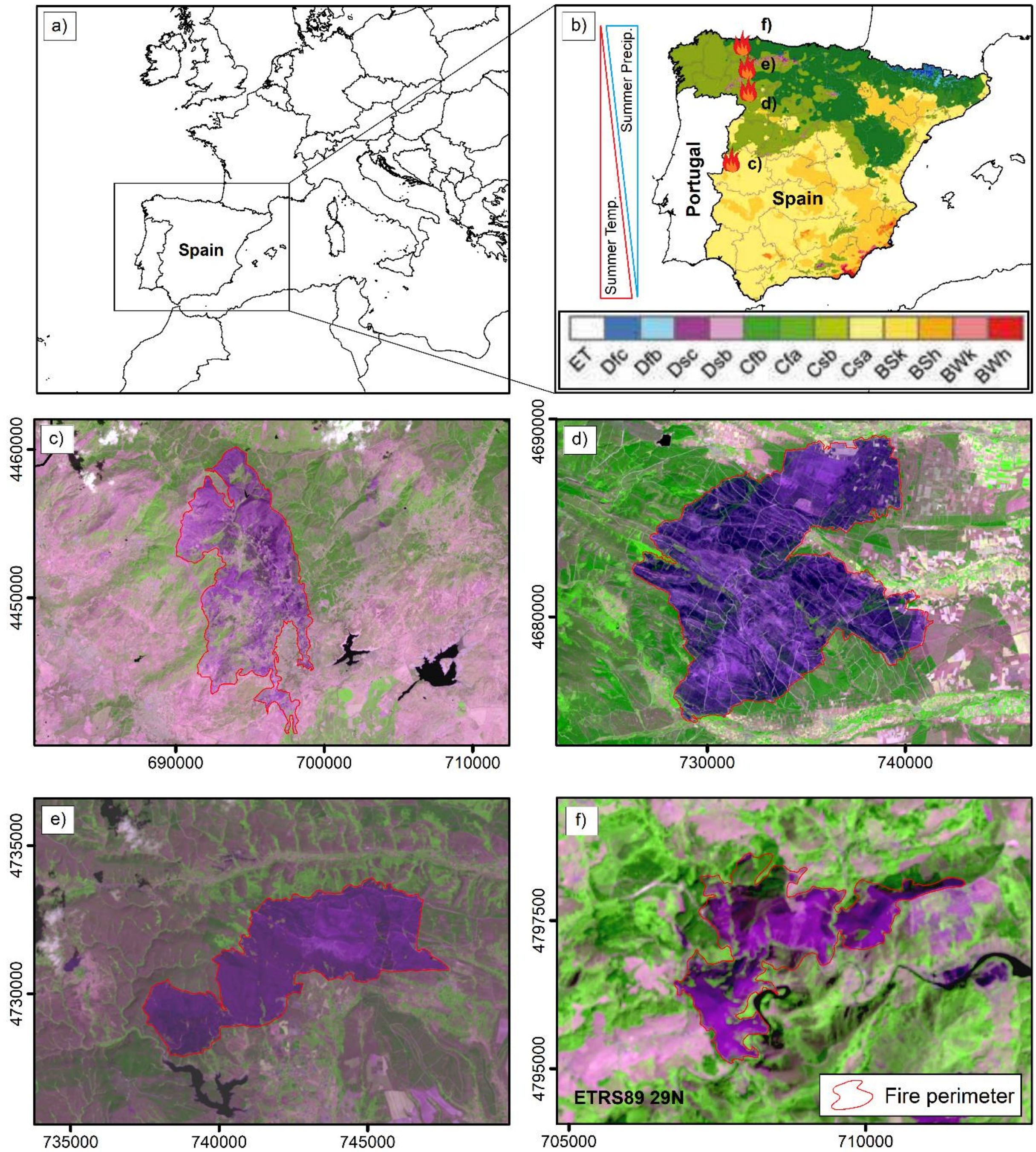

Figure 10. Location of the study sites in Europe a) and in the Iberian Peninsula along the different Köppen climatic regions (AEMET-IM, 2011) b). The study sites are shown using Landsat post-fire false colour composites with burned areas predominantly purple: c) Mediterranean site, d) Transition1 site, e) Transition2 site, f) Oceanic site.

Figure 11. Example of field plots and CBI values of vegetation burn severity (V) and soil burn severity (S).

Table 3. Modified Composite Burn Index used in this study to obtain the field values of burn severity (based on Key & Benson, 2006).

Strata	Burn severity scale						
Rating factors	Unburned	Low		Moderate		High	
	0	0.5	1	1.5	2	2.5	3
Substrate							
Litter/light fuel consumed	None	<10%	10-20%	20-40%	40-80%	80-98%	98%
Char & colour	None	Blackened litter, no changes in soil		Charred remains, recognizable litter		Grey and white ash, grey soil	White ash, reddened soil
Vegetation <1 m							
Foliage consumed	None	<20%	20-40%	40-60%	60-90%	>90%	Branch loss
Vegetation 1-5m							
Foliage consumed	None	<10%	10-30%	30-60%	60-95%	>95%	Branch loss
Vegetation 5-20m							
Green	100%	>90%	70-90%	50-70%	10-50%	<10%	None
Black	None	<5%	5-20%	20-40%	40-85%	>85%	No needles/leaves
Brown	None	<5%	5-20%	20-40%	40-80%	<40 or >80%	None
Tree mortality	None	<5%	5-20%	20-50%	50-80%	>80%	100%
Char height	None	1 m	1.5 m	2 m	2.8 m	4 m	>5 m
Vegetation >20m							
Green	100%	>95%	90-95%	65-90%	10-65%	<10	None
Black	None	<5%	5-10%	10-35%	35-80%	>80%	No needles/leaves
Brown	None	<5%	5-10%	10-30%	30-70%	<30 or >70%	None
Tree mortality	None	<5%	5-20%	20-50%	50-80%	>80%	100%
Char height	None	1 m	1.8 m	3 m	4 m	6 m	>7 m

Remotely sensed data

Remotely sensed information to estimate burn severity was obtained from Landsat imagery (Landsat 8 OLI/TIRS for the Mediterranean, Transition2 and Oceanic fires, and Landsat 7 ETM+ for the Transition1 site). Pre-fire and post-fire scenes were acquired for each fire from the USGS Earth Explorer server (http://earthexplorer.usgs.gov/). We selected imagery without clouds, and as close as possible to the fire date. Scenes in the Mediterranean site were from June 19th, 2015 and September 7th, 2015; in the Transition1 site from September 20th, 2011 and September 6th, 2012; in the Transition2 site from June 19th, 2015 and August 6th, 2015; and in the Oceanic site from June 26th, 2015 and August 29th, 2015.

Landsat imagery provided by the USGS (L1T processing level) is a Digital Numbers (DN) product geometrically rectified and radiometrically corrected (Landsat 8 Users Handbook, 2016; Landsat 7 Science Data Users Handbook, 2017). In this product we can distinguish optical or reflective bands (B1 to B9 in Landsat 8; B1 to B5, B7 and B8 in Landsat 7), and thermal bands (B10 and B11 in Landsat 8; B6L and B6H in Landsat 7), to which we applied different pre-processing treatments.

The reflective bands were spatially subset and pre-processed (Fig. 9). DN were transformed to radiance values (L_λ), which were atmospherically corrected using the Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH) module (Perkins *et al.*, 2012) in ENVI. We used the MODIS water vapor product (MOD05), meteorological data (NOAA) and mean elevation values to set the appropriate atmosphere models, aerosol situations and input parameters. Topographic shadow effects were removed by the C-correction algorithm (Teillet *et al.*, 1982), using a digital elevation model (DEM) generated from the BCN25 product of the National Centre of Geographic Information of Spain (CNIG). We used 10% of the pixels to define the C constant of the algorithm (Quintano *et al.*, 2015). Finally, topographic corrected values were rescaled to land surface reflectance in percentage (ρ). These corrections are convenient due to the relevant effect of atmosphere on some bands and because of the rough terrain in some study sites. The algorithms were chosen based on results by Lin *et al.* (2015) and Hantson & Chuvieco (2011). For each Landsat 7 reflective band, the land surface reflectance was transformed to comparable Landsat 8 surface reflectance values according to the functions proposed by Roy *et al.* (2016).

Thermal band B10 (Landsat 8) or B6L (Landsat 7) was used to obtain the LST product, following the single channel method by the radiative transfer equation according Yu *et al.* (2014). The procedure (Fig. 9) comprises a radiometric calibration of the clipped image to converse DN to radiance with brightness temperature, atmospheric correction with emissivities adjustment, and conversion to temperature in Kelvin. To perform the atmospheric correction we applied the radiative transfer equation:

$$B_x(T_s) = [(B_x(T_x) - I_x^{\uparrow}) / (\varepsilon_x * \tau_x(\Theta))] - [I_x^{\downarrow} (1 - \varepsilon_x) / \varepsilon_x]$$

$B_x(T_s)$ being the ground radiance received by the corresponding thermal band (B_x), $B_x(T_x)$ the radiance received by B_x with brightness temperature T_x, $I^{\uparrow}$ and $I^{\downarrow}$ the upwelling and downwelling radiance respectively to B_x. $\tau_x(\Theta)$ is the atmospheric transmittance when the view zenith angle is Θ, and ε_x is surface emissivities for channel x. $B_x(T_x)$ is obtained from B_x radiance, $I_x^{\uparrow}$, $I_x^{\downarrow}$ and $\tau_x(\Theta)$ were obtained from the National Centres for Environmental Prediction (NCEP) profiles provided by Barsi *et al.* (2005) in the ATMCORR tool (http://atmcorr.gsfc.nasa.gov/). ε_x was calculated using an NDVI thresholds method as follows:

$$\varepsilon_x = \begin{cases} 0.973 - (0.047\rho_{red}) & NDVI < 0.2 \\ 0.986Pv + 0.967(1 - Pv) + 0.018(1 - Pv) & 0.2 \leq NDVI \leq 0.5 \\ 0.991 & NDVI > 0.5 \end{cases}$$

Where ρ_{red} is the reflectance of corrected B4 in Landsat 8 or B3 in Landsat 7, and Pv is calculated as follows:

$$Pv = \begin{cases} 0 & [(NDVI - 0.2) / 0.3]^2 < 0.2 \\ [(NDVI - 0.2) / 0.3]^2 & 0.2 \leq [(NDVI - 0.2) / 0.3]^2 \leq 0.5 \\ 1 & [(NDVI - 0.2) / 0.3]^2 > 0.5 \end{cases}$$

Lastly, $B_x(T_s)$ radiance is transformed into LST (Kelvin) based on Planck's law using the following equation:

$$LST = K2_x / (\ln((K1_x / B_x(T_s)) + 1))$$

Where $K1_x$ and $K2_x$ are thermal constants obtained from each image metadata for Landsat 8, and 666.09 W m^{-2} sr^{-1} μm^{-1} and 1282.71 K for Landsat 7 ETM+, respectively.

In order to find the most suitable spectral indices to quantify burn severity in pine forests throughout the Mediterranean-Transition-Oceanic climatic gradient, we evaluated reflective, thermal and mixed (combining reflective and thermal) metrics sensitive to changes caused by fires. Indices were obtained from land surface reflectance (ρ) or/and LST products of Landsat pre-processed bands following the algorithms included in Table 4. Specifically, we checked 13 spectral indices: 9 reflective indices (NBR, dNBR, RdNBR, RBR, NDVI, dNDVI, EVI, dEVI and dNBR-EVI), 2 thermal metrics (LST and dLST), and 2 mixed indices ((LST/EVI) and d(LST/EVI)).

We proposed the dNBR-EVI index as a potential improvement of traditional NBR-based indices for initial assessments of burn severity along climatic gradients, because its expected enhanced sensitivity to physical or bio-physical parameters such as: (i) the reflectance related to the internal structure of the leaves and the canopy density, retrieved by the NIR band (Key, 2006; Chuvieco, 2010; Veraverbeke *et al.*, 2011), on which both components of the new index (dNBR and EVI) are supported; (ii) the reflectance related to the moisture content of both vegetation and soil, retrieved by the SWIR band (Key, 2006; Chuvieco, 2010; Vlassova *et al.*, 2014) of the dNBR component, but attenuated by the inclusion of the post-fire EVI for better transferability among climates; and (iii) the reflectance related to the post-fire photosynthetic pigments, by the inclusion of Red and Blue bands (Gao *et al.*, 2000; Chuvieco, 2010) from the EVI index, for better detection of senescent leaves in initial assessments. Furthermore, the dNBR-EVI combination attempts to solve the saturation problem of traditional NBR-based indices when estimating severely burned areas (e.g. Parks *et al.*, 2014; Holden *et al.*, 2010; Chen *et al.*, 2011), by including the EVI index that has demonstrated not to saturate (Holden *et al.*, 2010; Chen *et al.*, 2011).

Spectral indices values corresponding to each field plot were extracted by averaging the values of 175 sample points systematically distributed within each 30 m diameter plot, following the procedure of Picotte & Robertson (2011). We ensure that the number of points was representative according to accumulative adjustment curves.

Data analysis

The relationships between the field burn severity measurements (site burn severity, vegetation burn severity and soil burn severity) and the 13 remotely sensed metrics of burn severity were analysed along the climatic gradient (Mediterranean, Transition1, Transition2 and Oceanic sites) using ordinary least squares models. Although it is common to find non-linear relationships between CBI-based measurements and some remotely sensed metrics in the literature (Miller & Thode, 2007; Soverel, 2011; Cansler & McKenzie, 2012), we found a marginal improvement in the performance of models. Then, we graphically checked the assumptions of homoscedasticity and normality of model residuals, and we decided to work with linear regression models, as other authors have done (e.g. Epting *et al.*, 2005; de Santis & Chuvieco, 2009; Quintano *et al.*, 2015). We considered the field burn severity measurements from each study site (Mediterranean, Transition and Oceanic) as dependent variables and the spectral indices as explanatory variables. The coefficient of determination (R^2) and statistical significance (*P*) of the regression models obtained fitting all the available plots were used to compare the performance of the spectral indices to each other in the same climatic region, and each index among the different climatic regions.

Table 4. Selected indices and calculation algorithm, using Landsat 8 OLI/TIRS bands or Landsat 7 ETM+ bands.

Spectral index		Landsat 8 OLI/TIRS formula	Landsat 7 ETM+ formula	Reference
Reflective	NBR	$(\rho_5 - \rho_7) / (\rho_5 + \rho_7)$	$(\rho_4 - \rho_7) / (\rho_4 + \rho_7)$	López-García & Caselles (1991)
	dNBR	$1000\ (NBR_{pre} - NBR_{post})$ - offset*	$1000\ (NBR_{pre} - NBR_{post})$ - offset*	Key (2006)
	RdNBR	$dNBR / (\lvert NBR_{pre}\rvert^{0.5})$	$dNBR / (\lvert NBR_{pre}\rvert^{0.5})$	Miller & Thode (2007)
	RBR	$dNBR / (NBR_{pre} + 1.001)$	$dNBR / (NBR_{pre} + 1.001)$	Parks *et al.* (2014)
	NDVI	$(\rho_5 - \rho_4) / (\rho_5 + \rho_4)$	$(\rho_4 - \rho_3) / (\rho_4 + \rho_3)$	Rouse *et al.* (1973)
	dNDVI	$NDVI_{pre} - NDVI_{post}$	$NDVI_{pre} - NDVI_{post}$	Zhu *et al.* (2006)
	EVI	$2.5\ [(\rho_5 - \rho_4) / (\rho_5 + 6\rho_4 - 7.5\rho_2 + 1)]$	$2.5\ [(\rho_4 - \rho_3) / (\rho_4 + 6\rho_3 - 7.5\rho_1 + 1)]$	Gao *et al.* (2000)
	dEVI	$EVI_{pre} - EVI_{post}$	$EVI_{pre} - EVI_{post}$	Zhu *et al.* (2006)
	dNBR-EVI	(dNBR-EVI*1000) - offset*	(dNBR-EVI*1000) - offset*	Proposed by the authors
Thermal	LST	LST in Kelvin from $B_{10}(T_s)$	LST in Kelvin from $B_{6L}(T_s)$	Yu *et al.* (2014)
	dLST	$LST_{post} - LST_{pre}$	$LST_{post} - LST_{pre}$	Zheng *et al.* (2016)
Mixed	LST/EVI	(LST - 273.15)/EVI	(LST - 273.15)/EVI	Zheng *et al.* (2016)
	d(LST/EVI)	$(LST/EVI)_{post} - (LST/EVI)_{pre}$	$(LST/EVI)_{post} - (LST/EVI)_{pre}$	Zheng *et al.* (2016)

* Offset is the average index value from pixels in homogeneous and unchanged areas.

We analysed the transferability of the spectral indices-derived models using a cross validation “leave-one out” approach. Iteratively, models were trained using all the available plots of three wildfires, and validated using the plots of the remaining wildfire. The predictive accuracy of the models was assessed in each iteration by calculating the root mean squared error (RMSE) between observed and predicted values. RMSE values higher than 25% of the total range of the CBI (0.75 CBI points) were considered not acceptable (de Santis & Chuvieco, 2007).

In order to determine whether the coefficients of determination R^2 and the RMSE values were statistically different among the analysed spectral indices, we performed analysis of variance of linear mixed models (LMMs) including the study site as random factor. Fisher’s LSD test was applied to specify which of the means were significantly different.

All statistical analyses were performed using R (R Core Team, 2016). nlme (Pinheiro *et al.*, 2017) and multcomp (Hothorn *et al.*, 2017) packages were used.

RESULTS

Relationship between field burn severity and spectral indices

We found a common trend in the behaviour of the spectral indices that were, in general, highly suitable to correlate site (Table 5) and vegetation (Table 6) burn severity, but not so able to match soil burn severity (Table 7).

The results of the site burn severity (Table 5) indicated that the proposed new index dNBR-EVI and the other differenced reflective indices based on NBR (dNBR, RdNBR and RBR), showed significantly better correlations than thermal and mixed metrics along the climatic gradient. The new index showed the best fit in the Mediterranean (R^2 = 0.82) and Oceanic (R^2 = 0.78) sites. The rest of the indices showed a significantly worse performance to match site burn severity along the entire gradient. In particular, NDVI and dNDVI did not work well in the Mediterranean region ($R^2 \leq 0.28$), and thermal metrics (LST and dLST) did not work in the Oceanic region ($R^2 \leq 0.24$). Mixed indices [LST/EVI and d(LST/EVI)], were outperformed along the climatic gradient by reflective indices based on NBR and by EVI.

Focusing on vegetation burn severity (Table 6), there were similar fits and patterns as on site burn severity along the climatic gradient. Therefore, reflective NBR based indices (NBR, dNBR, RdNBR and RBR) and EVI were the best fitted along the entire climatic gradient, although the dNBR-EVI index was the best fitted ($R^2 \geq 0.82$).

The analysed spectral indices did not correlate soil burn severity as well as site or vegetation burn severity (Table 7). Reflective indices based on NBR reached the highest R^2 values, being significantly better than thermal and mixed indices, dNBR-EVI being the best one. Thermal metrics reached relatively high values of the coefficient of determination in the Transition region ($R^2 \geq 0.54$), but a non-significant relation was found in the Oceanic region. Mixed indices did not reach high values in any climatic region ($R^2 \leq 0.45$).

The dNBR-EVI outperformed the previously existing indices in most situations, and was the only index whose coefficients of determination were significantly higher than vegetation reflective indices (NDVI, dNDVI, EVI and dEVI), thermal metrics and mixed indices when matching the site, vegetation and soil burn severity. Furthermore, regressions between dNBR-EVI and field measurements of burn severity (Fig. 12) showed that dNBR-EVI index did not have saturation-related problems in high severity scenarios, as occurs with the other NBR-based indices.

Table 5. Coefficients of determination (R^2) and significance (P) of the linear regression models between spectral indices and site burn severity in the four study sites. Models were performed fitting all the available plots from each study site.

Spectral index		Site burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.82···	0.87···	0.87···	0.78···	0.84 ± 0.04 a
	NBR	0.62···	0.75···	0.88···	0.62···	0.72 ± 0.12 ac
	dNBR	0.79···	0.88···	0.86···	0.69···	0.81 ± 0.09 ab
	RdNBR	0.76···	0.83···	0.89···	0.68···	0.79 ± 0.09 ab
	RBR	0.77···	0.88···	0.88···	0.68···	0.80 ± 0.10 ab
	NDVI	0.02	0.69···	0.54···	0.51···	0.44 ± 0.29 e
	dNDVI	0.28···	0.76···	0.69···	0.58···	0.58 ± 0.21 ce
	EVI	0.59···	0.68···	0.63···	0.69···	0.65 ± 0.05 bcd
	dEVI	0.53···	0.66···	0.37···	0.69···	0.56 ± 0.15 ce
Thermal	LST	0.31···	0.66···	0.65···	0.21··	0.46 ± 0.23 e
	dLST	0.54···	0.80···	0.77···	0.24··	0.59 ± 0.26 ce
Mixed	LST/EVI	0.56···	0.51···	0.50···	0.44···	0.50 ± 0.05 de
	d(LST/EVI)	0.59···	0.53···	0.51···	0.43···	0.52 ± 0.07 de

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Significances of the correlations are represented as ·, ·· and ··· ($P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively).

Letters (a, b, c, d, e) indicate significant differences among mean R^2 values of the spectral indices.

Table 6. Coefficients of determination (R^2) and significance (*P*) of the linear regression models between spectral indices and vegetation burn severity in the four study sites. Models were performed fitting all the available plots from each study site.

Spectral index		Vegetation burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.85$^{\cdots}$	0.87$^{\cdots}$	0.85$^{\cdots}$	0.82$^{\cdots}$	0.85 ± 0.02 a
	NBR	0.67$^{\cdots}$	0.77$^{\cdots}$	0.86$^{\cdots}$	0.69$^{\cdots}$	0.75 ± 0.09 ac
	dNBR	0.81$^{\cdots}$	0.89$^{\cdots}$	0.84$^{\cdots}$	0.75$^{\cdots}$	0.82 ± 0.06 ab
	RdNBR	0.80$^{\cdots}$	0.84$^{\cdots}$	0.86$^{\cdots}$	0.74$^{\cdots}$	0.81 ± 0.05 ab
	RBR	0.81$^{\cdots}$	0.89$^{\cdots}$	0.86$^{\cdots}$	0.74$^{\cdots}$	0.83 ± 0.07 a
	NDVI	0.04	0.70$^{\cdots}$	0.52$^{\cdots}$	0.56$^{\cdots}$	0.46 ± 0.29 e
	dNDVI	0.31$^{\cdots}$	0.76$^{\cdots}$	0.69$^{\cdots}$	0.63$^{\cdots}$	0.60 ± 0.20 ce
	EVI	0.60$^{\cdots}$	0.69$^{\cdots}$	0.61$^{\cdots}$	0.67$^{\cdots}$	0.64 ± 0.04 bcd
	dEVI	0.50$^{\cdots}$	0.67$^{\cdots}$	0.35$^{\cdots}$	0.74$^{\cdots}$	0.57 ± 0.18 de
Thermal	LST	0.37$^{\cdots}$	0.67$^{\cdots}$	0.65$^{\cdots}$	0.28$^{\cdot\cdot}$	0.49 ± 0.20 de
	dLST	0.61$^{\cdots}$	0.81$^{\cdots}$	0.77$^{\cdots}$	0.30$^{\cdot\cdot}$	0.62 ± 0.23 ce
Mixed	LST/EVI	0.58$^{\cdots}$	0.52$^{\cdots}$	0.49$^{\cdots}$	0.48$^{\cdots}$	0.52 ± 0.05 de
	d(LST/EVI)	0.60$^{\cdots}$	0.53$^{\cdots}$	0.49$^{\cdots}$	0.48$^{\cdots}$	0.53 ± 0.05 de

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Significances of the correlations are represented as ·, ·· and ··· ($P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively).

Letters (a, b, c, d, e) indicate significant differences among mean R^2 values of the spectral indices.

Table 7. Coefficients of determination (R^2) and significance (*P*) of the linear regression models between spectral indices and soil burn severity in the four study sites. Models were performed fitting all the available plots from each study site.

Spectral index		Soil burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.54···	0.74···	0.63···	0.47···	0.60 ± 0.12 a
	NBR	0.34···	0.65···	0.67···	0.28··	0.49 ± 0.20 ae
	dNBR	0.51···	0.77···	0.57···	0.34··	0.55 ± 0.18 ab
	RdNBR	0.47···	0.69···	0.63···	0.32··	0.53 ± 0.17 ab
	RBR	0.47···	0.77···	0.63···	0.32··	0.55 ± 0.20 abc
	NDVI	0.00	0.58···	0.60···	0.26·	0.36 ± 0.29 ce
	dNDVI	0.13··	0.67···	0.53···	0.34··	0.42 ± 0.23 be
	EVI	0.41···	0.57···	0.55···	0.55···	0.52 ± 0.07 abcd
	dEVI	0.41···	0.56···	0.25···	0.34··	0.29 ± 0.13 be
Thermal	LST	0.13··	0.54···	0.66···	0.05	0.35 ± 0.30 e
	dLST	0.24···	0.66···	0.66···	0.07	0.41 ± 0.30 be
Mixed	LST/EVI	0.34···	0.43···	0.36···	0.21·	0.34 ± 0.09 de
	d(LST/EVI)	0.37···	0.45···	0.35···	0.21·	0.35 ± 0.10 e

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Significances of the correlations are represented as ·, ·· and ··· (*P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively).

Letters (a, b, c, d, e) indicate significant differences among mean R^2 values of the spectral indices.

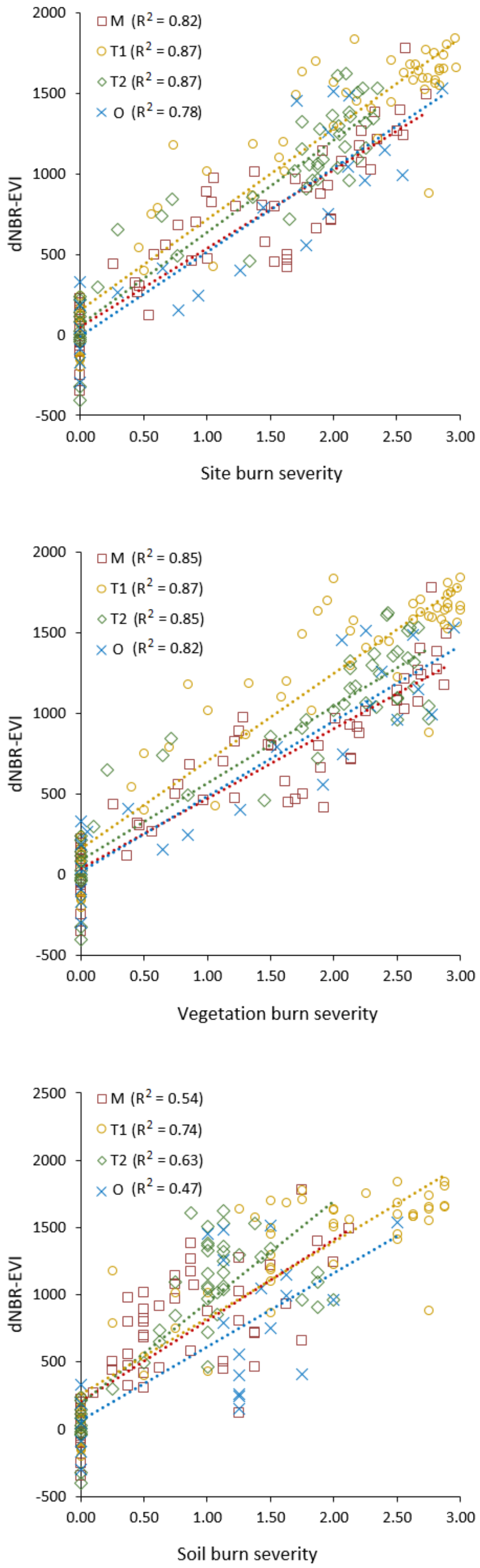

Figure 12. Linear relationships between spectral index dNBR-EVI and each field measurement of burn severity (site, vegetation and soil burn severity). Study sites are represented as M (Mediterranean), T1 (Transition1), T2 (Transition2) and O (Oceanic).

Transferability of spectral indices-derived models to predict burn severity

Cross-validation showed the highest accuracies when predicting the site burn severity (Table 8), little differences with vegetation (Table 9) and soil burn severity (Table 10) being observed. Broadly, errors were higher when predicting burn severity in the Transition1 and Oceanic sites.

Analysing the transferability of spectral indices-derived models to predict the site burn severity (Table 8) along the entire climatic gradient, we found that the dNBR-EVI-based models reached the lowest RMSE values (RMSE ≤ 0.47), being significantly better than vegetation (RMSE ≥ 0.60), thermal (RMSE ≥ 0.70) and mixed (RMSE ≥ 0.63) indices. Only models based on differenced NBR-type indices reached admissible RMSE values (≤ 25% of the CBI range) along the entire gradient. Focusing on the rest of the metrics, predictions of models based on vegetation indices worked better on the humid side of the gradient, particularly in the Oceanic site.

Focusing on vegetation burn severity (Table 9), models showed very similar patterns to site burn severity, being the dNBR-EVI the most transferable index along the climatic gradient. RMSE values of vegetation, thermal and mixed indices were inadmissible (> 25% of the CBI range) in most scenarios.

Predictions of soil burn severity (Table 10) indicated that the dNBR-EVI-derived models were the most accurate and transferable along the climatic gradient. RMSE values of predictions based on the other indices were not acceptable (RMSE > 0.75) in at least one study site, except for dEVI. The EVI-based model showed a good ability when predicting the soil burn severity in the Oceanic site.

Table 8. RMSE in CBI units of the spectral indices-derived models trained with a set of plots from three wildfires, when predicting the site burn severity in the remaining wildfire (noted in the heading of the table).

Spectral index		Site burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.41	0.41	0.34	0.47	0.41 ± 0.05 a
	NBR	0.59	0.85	0.37	0.83	0.66 ± 0.23 bc
	dNBR	0.43	0.51	0.49	0.58	0.50 ± 0.06 ab
	RdNBR	0.46	0.52	0.32	0.67	0.49 ± 0.15 ab
	RBR	0.44	0.38	0.35	0.65	0.46 ± 0.14 ab
	NDVI	0.97	0.83	0.64	0.81	0.81 ± 0.14 cde
	dNDVI	0.79	0.71	0.60	0.67	0.69 ± 0.08 bd
	EVI	0.87	1.45	0.72	0.60	0.91 ± 0.38 de
	dEVI	0.71	1.29	0.76	0.69	0.86 ± 0.29 cde
Thermal	LST	0.79	0.98	0.90	0.94	0.90 ± 0.08 de
	dLST	0.91	0.70	0.84	0.84	0.82 ± 0.09 cde
Mixed	LST/EVI	0.80	1.39	1.01	0.78	1.00 ± 0.28 e
	d(LST/EVI)	0.63	0.85	0.96	0.74	0.80 ± 0.14 cde

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Letters (a, b, c, d, e) indicate significant differences among mean RMSE values of the spectral indices.

Table 9. RMSE in CBI units of the spectral indices-derived models trained with a set of plots from three wildfires, when predicting the vegetation burn severity in the remaining wildfire (noted in the heading of the table).

Spectral index		Vegetation burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.47	0.53	0.42	0.49	0.48 ± 0.05 a
	NBR	0.66	1.07	0.52	0.86	0.78 ± 0.24 bc
	dNBR	0.45	0.42	0.51	0.59	0.49 ± 0.08 a
	RdNBR	0.52	0.71	0.43	0.70	0.59 ± 0.14 ab
	RBR	0.48	0.45	0.41	0.66	0.50 ± 0.11 a
	NDVI	1.09	0.85	0.77	0.85	0.89 ± 0.14 cd
	dNDVI	0.89	0.64	0.66	0.71	0.73 ± 0.11 ac
	EVI	0.94	1.50	0.81	0.70	0.99 ± 0.36 cd
	dEVI	0.85	1.62	0.95	0.80	1.06 ± 0.38 d
Thermal	LST	0.85	0.91	0.96	1.02	0.94 ± 0.07 cd
	dLST	1.07	0.64	0.84	0.92	0.87 ± 0.18 cd
Mixed	LST/EVI	0.86	1.39	1.16	0.86	1.07 ± 0.26 d
	d(LST/EVI)	0.72	0.81	1.01	0.81	0.84 ± 0.12 bcd

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Letters (a, b, c, d) indicate significant differences among mean RMSE values of the spectral indices.

Table 10. RMSE in CBI units of the spectral indices-derived models trained with a set of plots from three wildfires, when predicting the soil burn severity in the remaining wildfire (noted in the heading of the table).

Spectral index		Soil burn severity				
		M	T1	T2	O	Mean ± SD
Reflective	dNBR-EVI	0.45	0.71	0.48	0.61	0.56 ± 0.12 a
	NBR	0.52	0.80	0.37	0.89	0.65 ± 0.24 acd
	dNBR	0.54	0.90	0.62	0.68	0.69 ± 0.15 ae
	RdNBR	0.49	0.71	0.51	0.76	0.62 ± 0.14 ac
	RBR	0.51	0.76	0.45	0.74	0.62 ± 0.16 ac
	NDVI	0.77	1.01	0.45	0.86	0.77 ± 0.24 bce
	dNDVI	0.65	0.98	0.61	0.67	0.73 ± 0.17 ae
	EVI	0.82	1.35	0.60	0.52	0.82 ± 0.37 de
	dEVI	0.49	0.67	0.52	0.65	0.58 ± 0.09 ab
Thermal	LST	0.71	1.15	0.73	0.81	0.85 ± 0.20 e
	dLST	0.57	0.96	0.85	0.72	0.78 ± 0.17 bce
Mixed	LST/EVI	0.75	1.36	0.69	0.66	0.87 ± 0.33 e
	d(LST/EVI)	0.56	1.04	0.91	0.68	0.80 ± 0.22 ce

M: Mediterranean site, T1: Transition1 site, T2: Transition2 site, O: Oceanic site.

Letters (a, b, c, d, e) indicate significant differences among mean RMSE values of the spectral indices.

DISCUSSION

Reflective spectral indices were the best matched to field measurements of burn severity based on CBI in pine forests in the three climatic regions. Specifically, indices using NIR and SWIR or indices combining Red and Blue worked better than thermal and mixed metrics, on the one hand correlating better the field burn severity measurements, and on the other hand being more transferable among climatic regions. Both thermal and mixed indices showed worse performance and greater variability among regions. Another feature confirmed in this study is the limitation of remotely sensed indices to correlate soil burn severity, probably due to the shielding effect of vegetation or its remains (Soverel *et al.*, 2011; Tanase *et al.*, 2011), corroborating results found by other authors when analysing the remote sensing of burn severity on understory (Key, 2006; Cansler & McKenzie, 2012; Wu *et al.*, 2015).

Reflective indices based on NBR (NBR, dNBR, RdNBR and RBR) showed good behaviour in Mediterranean and Transition environments, reaching good relationships with field measurements of burn severity similar to, or even better, than those reported in other wildfires (Zhu *et al.*, 2006; Miller & Thode, 2007; Veraverbeke *et al.*, 2010; Tanase *et al.*, 2011; Parks *et al.*, 2014) and their models showed a high transferability for site burn severity predictions as other authors found (Soverel *et al.*, 2011). The sensitivity of these indices to burn severity is widely recognized (e.g. Miller *et al.*, 2009; Chu & Guo, 2014; Fernández-Manso & Quintano, 2015), and it is due to the decrease in NIR reflectance, sensitive to the cellular structure of the leaves, and the simultaneous increase in SWIR reflectance primarily related to decreases in moisture content (Key, 2006; de Santis & Chuvieco, 2007; Miller & Thode, 2007; Robichaud *et al.*, 2007; Chuvieco, 2010; Veraverbeke *et al.*, 2011; Harris *et al.*, 2011; Cansler & McKenzie, 2012). The dNBR and the relativized indices RdNBR and RBR produced similar regression fits and predictive errors, a result that can be attributed to the high homogeneity of the studied ecosystems (Miller & Thode, 2007). Analysing the models along the climatic gradient, despite the good performance of reflective indices based on

NBR in Mediterranean and Transition regions, our results demonstrate more difficulties in correlating and predicting CBI in the Oceanic region. Other studies can support the idea that climate-related factors have an important effect on the performance of these indices. Thus, Zhu *et al.* (2006) found the worst fit for dNBR in the Northern Rockies, with a humid climate (R^2 = 0.65), and much better results in Mediterranean and arid zones (R^2 from 0.72 to 0.79). Also Parks *et al.* (2014) found the best performance of dNBR-based indices in the Southwestern US, with a relatively dry climate. Soverel *et al.* (2011) related the lower R^2 values (0.40 to 0.50) in some of their study regions to the high soil moisture content, which is a potential facilitator of decoupled fires (fires with different burn severity levels per strata). A single index does not capture this decoupling among strata because it provides an overall value not segregated by strata, leading in worse correspondences (Tanase *et al.*, 2011). Another potential cause of the worse performance in the Oceanic region related to soil moisture is its high absorbance of SWIR radiation (Chuvieco, 2010; Vlassova *et al.*, 2014). Consequently, the expected increase in SWIR reflectance after fire may be attenuated in Oceanic sites, especially in the highest burn severity areas, where soils can play a major role in the satellite received reflectance because of the depletion of the vegetation layer (Robichaud *et al.*, 2007; Chuvieco, 2010). These hypotheses are supported by the mean SWIR reflectance values obtained within the fire perimeters in the post-fire image, being lower in the Oceanic study site (3.14 ± 1.64) than in the other wildfires (≥ 4.50). Furthermore, areas with a humid climate can have faster post-fire green-up (Soverel *et al.*, 2011; Liu, 2016; Rother & Veblen, 2017), rapidly reducing the change in reflectance values caused by burn severity. This influence of climate could be greatest in extended assessments, when the apparent magnitude of the initial burn severity is decreased (Key & Benson, 2006).

The analysed reflective vegetation indices (NDVI, dNDVI, EVI and dEVI) showed very different results when correlating burn severity, as they did when extrapolating their models to new study sites. Their response is based on the reflectance of the Red band, which is higher when the vegetation is stressed, and also in the NIR reflectance, which has an opposite response to Red (Gao *et al.*, 2000; Huete *et al.*, 2002; Chuvieco, 2010). However, although both kinds of indices (NDVI and EVI) are highly sensitive to chlorophyll levels, EVI is more related to structural characteristics of vegetation, such as leaf area, plant canopy and architecture of the vegetation (Huete *et al.*, 2002). NDVI and dNDVI showed a great variability along the climatic gradient, and they did not work in the Mediterranean region, maybe due to the higher effect of summer drought on chlorophyll levels than in other indices like EVI (Mänd *et al.*, 2010) and because, in general, the pigment content per leaf area decreases with climate aridity (Madani *et al.*, 2017; Yudina *et al.*, 2017) as the NDVI of the fire scars revealed in the pre-fire images (from 0.38 ± 0.09 in the Oceanic site to 0.31 ± 0.09 in the Mediterranean site). Thus, it is very likely that the NDVI and dNDVI indices confused severity levels and burned areas with low activity zones in Mediterranean regions, where the drought period is usually coincident to the fire occurrence period (Steel *et al.*, 2015). For this reason, greenness immediately before the fire could be lower than values from the pre-fire images. This possibility was previously reported by Picotte & Robertson, (2011). Conversely, EVI relationships with field burn severity were relatively as good as could be expected (Harris *et al.*, 2011; Wu *et al.*, 2015; Zheng *et al.*, 2016), principally in the Oceanic region. EVI is a robust index against changes of soil type and atmosphere because it includes the Blue band and two coefficients, unlike the NDVI, which is also less consistent in time (Gao *et al.*, 2000; Chuvieco, 2010). Furthermore, the Red band can detect senescent leaves (Chuvieco, 2010; Mänd *et al.*, 2010), which is advantageous information for initial burn severity assessments, when the delayed tree mortality detection is challenging (Key & Benson, 2006). The worse transferability of the EVI-based models to the Transition1 site (Landsat 7 imagery) could be due to the lower correlation between Blue bands than between the other reflective bands from ETM+ and OLI sensors (Roy *et al.*, 2016).

Thermal metrics (LST and dLST) did not work in the same way along the climatic gradient. The highest coefficients of determination of the thermal metrics were reached in the

Transition region, obtaining similar results to those reported in other wildfires (Quintano *et al.*, 2015, Zheng *et al.*, 2016). However, these indices did not work as well in the other two regions. The variable performance of thermal metrics in the different study sites could lead to unacceptable predictions (RMSE > 0.75) in most scenarios when extrapolating LST-based models along the climatic gradient, suggesting that models have to be performed in each single fire. These differences may be due to the influence of topographic factors in the LST generating changes not related to burn severity. Aspect and altitudinal differences strongly affect LST (Vlassova *et al.*, 2014; Quintano *et al.*, 2015), and these topographic parameters have a larger variation in the Mediterranean and Oceanic sites than in the Transition one. Another factor that could affect the operation of thermal metrics along the climatic gradient could be moisture, which is higher in the Oceanic region. Chuvieco (2010) indicates that moisture content is one of the most outstanding factors in the thermal behaviour of soils. Thus, higher moisture content in soil and above the surface could soften the LST differences caused by the burn severity. Besides, assorted aspects lead to differences in moisture (Wu *et al.*, 2013). In brief, homogeneity in topography and moisture in the Transition site, where thermal metrics are some of the best to assess soil burn severity, can explain the widely better results obtained in this site in comparison to the other study areas. For extended assessments, it is necessary to take into account that differences in LST due to burn severity rapidly decrease with the time-lapse after fire (Quintano *et al.*, 2015).

Indices that combine thermal and optical bands (LST/EVI and dLST/EVI) performed better than thermal metrics at the ends of the gradient, and worse in the Transition region. They did not exceed optical indices such as mono-temporal or bi-temporal NBR, and they showed little transferability since they exceeded the assumable error in many scenarios. Our coefficients of determination coincided with those obtained in previous research works in Western United States (Zheng *et al.*, 2016), although these authors obtained higher R^2 using mixed indices than using reflective and thermal indices. Similarly, Harris *et al.* (2011)

proposed the use of indices based on reflective and thermal bands that were well correlated to ground measured burn severity.

The new proposed index, dNBR-EVI, showed the best performance along the climatic gradient. First, the dNBR-EVI reached the highest R^2 values when matching the three field measurements of burn severity (site, vegetation and soil burn severity). Additionally, its models showed the highest transferability along the climatic gradient, being the only analysed index with admissible predictions in all studied scenarios (RMSE ≤ 0.75). Particularly, the new index has proven to be a large improvement in the assessment of soil burn severity, which was the most difficult variable to be detected by spectral indices. The new index also constituted an enhancement in burn severity detection in the Oceanic region (site, vegetation and soil burn severity), the study site where the other NBR-based indices performed the worst. The better performance of the new index in comparison with the others analysed may be due to several reasons: (i) The dNBR-EVI regression did not show signal saturation at high severities, a common problem when using dNBR, RdNBR or RBR (de Santis *et al.*, 2010; Veraverbeke *et al.*, 2012; Parks *et al.*, 2014). This is a significant improvement when predicting high burn severity patches, because those are the areas where the recovery of vegetation and soil may be endangered (Calvo et al, 2008; Fernández & Vega, 2016; González-de-Vega *et al.*, 2016), and consequently, they are target for forest managers (Miller & Thode, 2007). (ii) dNBR-EVI uses more spectral information than the other NBR type indices, combining Red, Blue, NIR and SWIR bands, which are meaningful for initial burn severity assessments along climatic gradients due to their respective sensitivity to atmospheric aerosols, chlorophyll levels, cellular structure of the leaves and canopy density, and soil and vegetation moisture (Huete *et al.*, 2002; Key, 2006; Chuvieco, 2010; Cansler & McKenzie, 2012). (iii) In the calculation of the dNBR-EVI, the contribution of the SWIR band is less important than in the other NBR type indices. As SWIR reflectance is closely related to moisture content (Veraverbeke *et al.*, 2011; Harris *et al.*, 2011; Cansler & McKenzie, 2012), the dNBR-EVI index could be more robust dealing with moisture variability, typical in climatic gradients. (iv) The dNBR-EVI index combines the bi-temporal approach by including the dNBR, and the mono-temporal perspective provided by the post-fire EVI. Thus, the new index has the advantage of a high model fit, characteristic of bi-temporal NBR-based indices, with the influence of a mono-temporal index that can lead to more scatter in the unburned areas. However, the mono-temporal component compensates for differences in vegetation phenology (Veraverbeke *et al.*, 2010) or hydrological fluctuations (Picotte & Robertson, 2011) between the pre and post-fire scenes.

Our results demonstrate that the new dNBR-EVI index is very suitable for use in initial burn severity assessments of pine forests across different climatic regions. Thus, several issues should be taken into account when applying it under different circumstances, such as extended assessments, different ecosystems or different geographical regions. In this study we analysed the performance of spectral indices for initial burn severity assessments, because in the Mediterranean countries interventions are usually carried out within the first year after fire, extended assessments being less appropriate (Tanase *et al.*, 2011). However, extended assessments are widely used in other regions of the world (Miller & Thode 2007; Miller *et al.*, 2009; Parks *et al.*, 2014; Zheng *et al.*, 2016), so the dNBR-EVI performance should be analysed considering that spectral response is highly dependent on the time lapse after fire (Chen *et al.*, 2011; Quintano *et al.*, 2015; Meddens *et al.*, 2016). Further validations are also recommended when extrapolating the new index to ecosystems with different species composition, since the spectral signature of each kind of forest is different (Lehmann *et al.*, 2015). We also highlight the importance of further research in different geographic regions, because they are linked to different climates and ecosystems, and these variables have an influence on spectral indices performance (Roy *et al.*, 2006; Parks *et al.*, 2014).

The convenience of validations in different scenarios is characteristic of empirical models (de Santis & Chuvieco, 2007). Future research to avoid this time-consuming process may be focused on the development of accurate models supported on more generalizable physically-based methods such as RTM or SMA.

CONCLUSIONS

The results found in our study constitute a novelty in the field of burn severity initial assessment using remote sensing imagery. This is the first evaluation of the performance of different spectral indices (reflective, thermal and mixed) as suitable tools to match field burn severity (site, vegetation and soil burn severities) throughout climatic regions in the Mediterranean Basin. Moreover, we proposed and evaluated a new spectral index, the dNBR-EVI, for increasing the transferability along climatic regions (Mediterranean, Transition and Oceanic).

Specifically, our results demonstrated that reflective indices based on dNBR fitted field values of burn severity better than thermal metrics and mixed ones (combining thermal and optical information).

Besides, in fire-prone pine forests in the Mediterranean Basin, remotely sensed indices indicated better site and vegetation burn severity than soil burn severity.

Most spectral indices used, such as dNBR, showed variable behaviour along the climatic gradient to match burn severity. In order to solve this problem, we proposed an alternative index for initial burn severity assessments using Landsat reflective bands: the dNBR-EVI. We concluded that this index performs better than the other studied indices, showing the best fit to burn severity field data and the best transferability throughout the climatic gradient (Mediterranean-Transition-Oceanic).

Finally, we recommended further evaluations of the performance and suitability of the new dNBR-EVI index for extended assessments of burn severity, as well as in other types of ecosystems, and different geographical regions or climatic situations. Likewise, we highlight the necessity to enhance the current capacity of remotely sensed methods to detect soil burn severity, a crucial factor in areas with high post-fire erosion vulnerability, such as fire prone ecosystems in the Mediterranean Basin.

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Article III

Impact of burn severity on soil properties in a *Pinus pinaster* ecosystem immediately after fire

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Abstract

We analyze the effects of burn severity on individual soil properties and soil quotients in Mediterranean fire-prone pine forests immediately after a wildfire. Burn severity was measured in the field through the substrate stratum of the Composite Burn Index and soil samples were taken 7-9 days after a wildfire occurred in a *Pinus pinaster* Ait. ecosystem. In each soil sample, we analyzed physical (size of soil aggregates), chemical (pH, organic C, total N, and available P), and biological properties (microbial biomass C, β-glucosidase, urease, and acid phosphatase activities). Size of soil aggregates decreased in the areas affected by high burn severity. Additionally, moderate and high severities were associated with increases in pH and available P concentration and with decreases in organic C concentration. Microbial biomass C showed similar patterns to organic C along the burn severity gradient. The enzymatic activities of phosphatase and β-glucosidase showed the highest sensitivity to burn severity, as they strongly decreased from the low severity scenarios. Among the studied soil quotients, the C:N ratio, microbial quotient and β-glucosidase:microbial biomass C quotient decreased with burn severity. This work provides valuable information on the impact of burn severity on the functioning of sandy siliceous soils in fire-prone pine ecosystems.

INTRODUCTION

Wildfires are a determining factor in the functioning and structure of fire-prone forests (Keeley *et al.*, 2012). In general, these forests are adapted to natural fire regimes, recovering under a relatively wide range of fire frequencies and severities (Noss *et al.*, 2006). However, burn severity is increasing in many parts of the world because of changes in land-use and climatic conditions (Lindner *et al.*, 2008; Moreira *et al.*, 2011; Doblas-Miranda *et al.*, 2017). This is the case in the Mediterranean Basin, where there is major concern about the ecological consequences of high severity fires on soils in fire-prone pine ecosystems (Pausas *et al.*, 2008), which are the forests most affected by fire in this region (Moreira *et al.*, 2012).

Burn severity is used to describe the loss of or change in biomass caused by fire in the ecosystem (Key & Benson, 2006; Keeley, 2009; Fernández-García *et al.*, 2018a). The most common approach for estimating burn severity in forest soils is through visual evidence of the loss of litter and changes in soil upper layers, such as alterations in soil color and structure, soil char or ash depth (Parsons *et al.*, 2010). This evidence is highly valuable for managers because it is related to other physical, chemical and biological changes in soils (Vega *et al.*, 2013) and to some extent, to ecosystem responses after fire, such as soil erosion (Shakesby, 2008; Vieira *et al.*, 2015) or vegetation recovery (Fernández-García *et al.*, 2018b). However, other factors such as vegetation and soil type mediate changes caused by fire in ecosystems as well as potential responses after fire, thus limiting the predictive capacity of burn severity measurements (Keeley, 2009). It is therefore necessary to study the relationships between burn severity and changes in soil status and processes in different types of ecosystems and especially in those prone to fire. A better understanding of the impact of burn severity on ecosystems may help to clarify its value as a tool to identify target areas in which to implement emergency stabilization strategies (Merino *et al.*, 2018). Some studies have analyzed changes in soils related to burn severity (Jordán *et al.*, 2011; Jain *et al.*, 2012; Pingree *et al.*, 2012; Miesel *et al.*, 2015; Dzwonko *et al.*, 2015; Moody *et al.*, 2016), but relatively few analyze the effects of burn severity on soil properties immediately after a wildfire (Vega *et al.*, 2013).

Several physical, chemical and biological soil properties provide relevant information on soil status and functioning in relation to fire (Certini, 2005). Among physical properties that have shown to be affected by fire there are those related to soil structure (e.g. aggregate size) (Jordán *et al.*, 2011; Mataix-Solera *et al.*, 2011). Changes in soil structure can play an important role in hydrological, biological and gas-exchange processes (Neary *et al.*, 1999; Puglisi *et al.*, 2006). Soil structure also provides information on soil resistance to external factors, and could thus be indicative of soil vulnerability to erosion (Cerdá & Jordan, 2010). Additionally, several soil chemical properties such as pH and nutrient-supplying capacity [carbon (C), nitrogen (N) and phosphorus (P)], are usually affected by fire (Certini, 2005). These soil properties show a close relationship with ecosystem productivity (Arshad & Martin, 2002), as well as plant and microbial diversity (Roem & Berendse, 2000). Nevertheless, biological properties tend to be affected at lower intensity disturbances than chemical parameters (Paz-Ferreiro & Fu, 2016; Alcañiz *et al.*, 2018). Fire-induced changes in microbial biomass also involve impacts on nutrient cycling and soil detoxification capacity as microorganisms are both a source and a sink of nutrients, and they participate in the degradation of xenobiotics and in the immobilization of heavy metals (Gil-Sotres *et al.*, 2005; Lagomarsino *et al.*, 2009). Likewise, the microbial biomass, with plant and animal residues, are the main sources of soil enzymes, responsible for the catalysis of soil biochemical reactions (Tabatabai, 1994; Li *et al.*, 2009). As proteins, soil enzymes are denatured by fairly low temperatures (60-70 ºC) (Tabatabai, 1994), and can therefore be significantly affected immediately after the fire, depending on burn severity (Vega *et al.*, 2013). Among soil enzymes, those involved in C, N and P cycles are considered especially relevant in ecosystem functioning, because they allow soil biota to obtain the major nutrients from complex organic substrates (Lagomarsino *et al.*, 2009; Li *et al.*, 2009; Adetunji *et al.*, 2017).

According to Bastida *et al.* (2008) and Lagomarsino *et al.* (2009), the study of changes in soil quotients (ratios between two different soil properties) can provide additional information on impacts on soil status and functioning. Fire impacts on soil quotients may be more consistent among different soils because they are relativized. One of the most used soil quotients is the C:N ratio (Badía *et al.*, 2014; Schnecker *et al.*, 2015), which controls organic matter mineralization and the development of microorganisms (Wild, 1992). This quotient, which is sensitive to fire (Vega *et al.*, 2013), shows low variability in undisturbed forest soils (Wild, 1992), and is therefore likely to be highly generalizable. Another soil quotient commonly analyzed after disturbances is the microbial quotient (Q_{mic}), a ratio of microbial biomass C and soil organic C. This quotient could be more informative about changes in organic matter than the single assessment of soil organic C and microbial biomass C, separately (Piao *et al.*, 2001). Thus, Q_{mic} provides an idea of substrate availability for microorganisms (Lagomarsino *et al.*, 2009; Paz-Ferreiro & Fu, 2016) and organic matter stabilization (Piao *et al.*, 2001). Additionally, specific activities of soil enzymes (enzyme activity per unit of microbial biomass C) have been proposed as indicators of the physiological capacity of the microbial community (Waldrop *et al.*, 2000; Bastida *et al.*, 2008; Lagomarsino *et al.*, 2009).

The objective of the present study is to analyze the effects of field-estimated burn severity on individual soil properties, as well on as soil quotients indicative of soil status and processes in a *Pinus pinaster* forest immediately after fire. Specifically, we aim to analyse the effects of burn severity on (i) physical (mean weight diameter), chemical (pH, organic C, total N, available P) and biological (microbial biomass C, β-glucosidase, urease and acid phosphatase activities) soil properties, as well as on (ii) soil quotients (C:N, Q_{mic} and the activity of β-glucosidase, urease and acid phosphatase per microbial biomass C unit), incorporating the study of the specific activity of soil enzymes into the fire ecology discipline. According to prior studies focused on the effects of fire on soils, we hypothesized that physical (Jordán *et al.*, 2011; Mataix-Solera *et al.*, 2011), chemical (Marcos *et al.*, 2007; Badía *et al.*, 2014), and biological properties (Neary *et al.*, 2008; Vega *et al.*, 2013) and soil quotients (Vega *et al.*, 2013), would be affected at different severities. We expect biological properties to be affected at lower severities than physical and chemical properties (Santín & Doerr, 2016). Besides, as soil quotients combine the information of two different soil properties (Bastida *et al.*, 2008; Lagomarsino *et al.*, 2009) we expect them to be more sensitive to burn severity than single soil properties.

MATERIAL AND METHODS

Study site

The study was conducted within a fire scar that burned on 21st July 2015 in Sierra del Teleno (León Province, north-west Iberian Peninsula) (Fig. 13). This wildfire affected a *Pinus pinaster* Ait. (maritime pine) ecosystem, which is the type of forest most affected by fire in the Iberian Peninsula (ADCIF, 2012; ICNF, 2015).

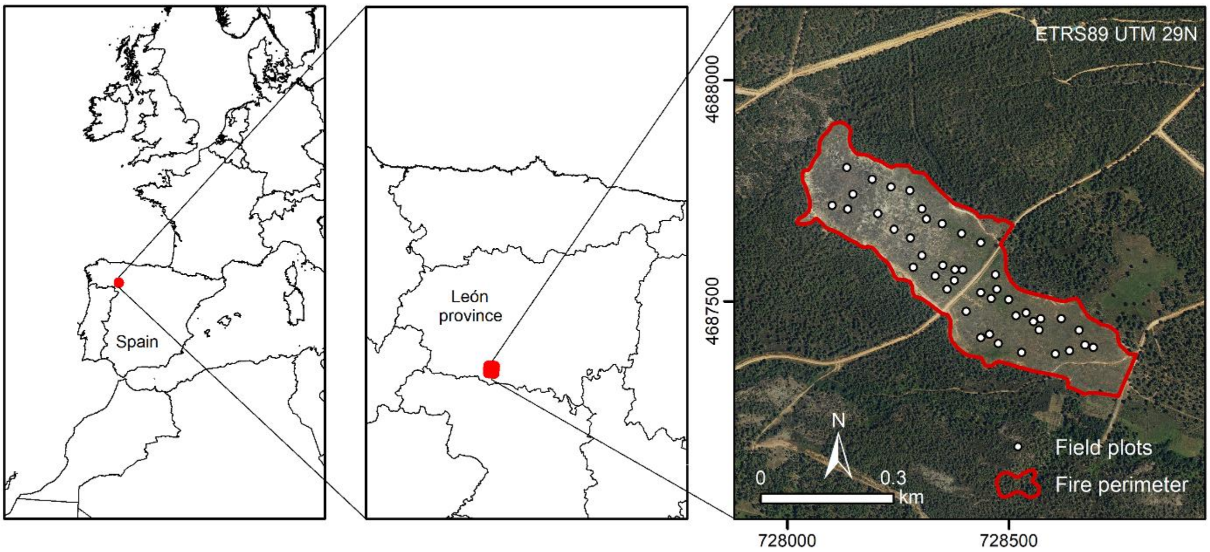

Figure 13. Location of the study area on the Iberian Peninsula (left) and in León province (centre). The image on the right shows the fire perimeter and the spatial distribution of the field plots in an orthophotography taken in 2017.

The wildfire scar is an area of 16 ha located on a south-east-facing hillside with a slight slope (5%) and an average altitude of 1,025 m.a.s.l. The soils are characterized by a dark acid surface horizon rich in organic matter, weakly developed subsurface horizons, free-draining conditions and absence of carbonates. These soils are classified as Haplic Umbrisols according to the World Reference Base for Soil Resources (WRB) system (Jones *et al.*, 2005). The soil textural class in the study area is sandy-loam. The parent material is silt, clay, sand, boulders and conglomerates from the Neogene period (GEODE, 2018). The climate is Mediterranean, Csb type according to Köppen, and classified by the Spanish meteorological survey as temperate with dry temperate summers (AEMET-IM, 2011). Mean annual precipitation is around 685 mm and mean annual temperature is 10 ºC (Ninyerola *et al.*, 2005). The understorey of the *P. pinaster* forest is dominated by *Erica australis* L., *Halimium lasianthum* (Lam.) Spach. and *Pterospartum tridentatum* (L.) Willk.

Data collection

Field sampling

Field sampling was carried out on the 7th, 8th and 9th day after the wildfire. In the period between the wildfire and field sampling there was no precipitation in the study area, and the atmospheric conditions were warm (mean temperature of 20.65 ºC), dry (mean relative humidity of 49.62 %) and not windy (mean wind speed of 11.75 km h^{-1}) (NOAA, 2018). Additionally, soils were dry, as there was no precipitation for 34 days prior to field sampling.

We established a total of 44 (1 m x 1 m) plots randomly distributed within the burned area (Fig.13). In each plot, we estimated soil burn severity using the substrate stratum of the Composite Burn Index-based protocol (CBI) proposed by Fernández-García *et al.* (2018a) for *P. pinaster* ecosystems in the Iberian Peninsula (Table 11; Fig. 14). Visual evidences used in this index were: (i) the proportion of litter and light fuel (leaves, needles, and woody material less than 2 cm in diameter located on the ground surface) consumed by fire, and (ii) char depth (considering litter and mineral soil), and colour of ash and mineral soil. Char depth and colour of ash and mineral soil were closely linked, and therefore, considered together (see characterization in Table 11).

To analyze the relationships between soil burn severity and soil properties, we collected a soil sample in each field plot. Each sample was composed of four subsamples collected along two perpendicular transects using an auger (5 cm diameter x 3 cm depth), after removing the litter and post-burn residues (ash and scorched debris). The soil samples were air-dried, sieved (< 2 mm) and stored until laboratory analysis (20 ºC).

Table 11. Factors and scores used as reference to quantify soil burn severity (substrates stratum of the Composite Burn Index) according to Fernández-García *et al.* (2018a). Scores shown in the table were assigned to each rating factor, as well as mean values when the situation was considered intermediate (i.e. a value of 0.75 was assigned for litter/light fuel consumed when it was 10%). UB = unburned. n indicates the number of plots distributed in each severity category. Note that both, UB and low severity categories correspond to no apparent changes in mineral soil.

Rating factors	Burn severity scale						
	UB (n=0)	Low (n= 2)		Moderate (n=24)		High (n=18)	
	0	0.5	1	1.5	2	2.5	3
Litter/light fuel consumed	No changes	0-10%	10-20%	20-40%	40-80%	80-98%	98%
Char & colour	No changes	Blackened litter, no changes in soil		Charred remains, recognizable litter		Grey and white ash, grey soil	White ash, reddened soil

Figure 14. Examples of plots with different soil burn severity values in CBI units. The panel on the left shows a field plot burned at low severity (10% of litter and light fuel were consumed and litter blackened with, in general, no changes in mineral soil). The panel in the middle shows a field plot burned at moderate severity (60% of the litter and light fuel were consumed and there were charred remains with recognizable litter in some areas). The panel on the right shows soil burned at high severity (98% of litter and light fuel were consumed, all ash was white and the soil was completely reddened). See Table 11 for further information.

Soil analyses

From each soil sample, we analyzed soil physical [mean weight diameter (MWD)], chemical [pH, organic C, total N and available P] and biological [microbial biomass C, β-glucosidase, urease and acid phosphatase] properties.

Aggregate size distribution was determined by dry-sieving the soil samples through 1, 0.25, 0.1 and 0.05 mm sieves for 120 s in an electromechanical shaker (Kemper & Rosenau, 1986). The results were expressed as MWD, which reflects the average size of the stable aggregates (Cerdà & Jordán, 2010; Mataix-Solera *et al.*, 2011). MWD was calculated using the following equation:

$$\mathrm{MWD} = \sum_{i=1}^{n} X_i\, W_i$$

where X is the mean particle size in mm, and W the percentage weight of each soil fraction.

Soil pH was determined at 25 ºC in a suspension of soil:deionized water (1:2.5, w/v). To analyze the soil organic C we ground the soils to < 0.15 mm particle size using a pestle and mortar, and we applied Walkley-Black dichromate digestion (Nelson and Sommers, 1982). As the soil in the study site is non-calcareous, values obtained for soil organic C and total C are very similar (Nelson and Sommers, 1982; Vega *et al.*, 2013). Total N (sum of organic N, NO_3^-, NO_2^- and NH_4^+) was determined by the Kjeldahl method (Bremner and Mulvaney, 1982) using a DK 20 digestion unit (VELP Scientifica, Italy). Available P was analyzed following the procedure of Olsen *et al.* (1954), at 882 nm wavelength on an UV Mini 1240 spectrophotometer (Shimadzu Corporation, Japan).

We analyzed microbial biomass C (MBC) by the fumigation-extraction method (Vance *et al.*, 1987). This procedure uses the difference (E_C) in organic C (analyzed by Walkley-Black dichromate oxidation) between filtered soil extracts of chloroform fumigated ($CHCl_3$, 24 h) and non-fumigated samples. Then, we used an extraction efficiency coefficient (K_{EC}) of 0.38 (Vance *et al.*, 1987; Joergensen, 1996) to calculate microbial biomass C using the following equation:

$MBC = E_C / K_{EC}$

Three soil enzymatic activities corresponding to the biogeochemical cycles of C, N and P were determined. Specifically, we selected β-glucosidase (enzyme nomenclature: EC 3.2.1.21; β-D-glucoside glucohydrolase), urease (EC 3.5.1.5; urea amidohydrolase) and acid phosphatase (EC 3.1.3.2; phosphate-monoester phosphohydrolase). To analyze the β-glucosidase and acid phosphatase we followed the procedure described by Tabatabai (1994), whereas urease activity was analyzed according to Kandeler & Gerber (1988). For the analysis of the three enzymatic activities, the soils were incubated with their corresponding enzyme substrates (*p*-nitrophenyl-β-d-glucopyranoside, urea and *p*-nitrophenyl-phosphate respectively). The products released by the enzymatic activity were determined colorimetrically with a UV-1700 PharmaSpec spectrophotometer (Shimadzu Corporation, Japan). We measured the absorbance of the *p*-nitrophenol (*p*NP) produced by β-glucosidase and acid phosphatase activities at 400 nm wavelength, whereas absorbance of the NH_4^+ released by urease activity was measured at 690 nm.

From the analyzed soil properties, we calculated several soil quotients: (i) C:N quotient calculated as µg of soil organic C to µg of total N; (ii) the microbial quotient (Q_{mic}) as µg of microbial biomass C to µg of soil organic C; and (iii) the specific activity of soil enzymes (β-glucosidase, urease and acid phosphatase) expressed as the µg of product released (*p*NP for β-glucosidase and acid phosphatase, and NH_4^+ for urease) per µg of microbial biomass C.

Data analysis

We evaluated the relationship between burn severity (explanatory variable) and each single soil property and each quotient (response variables) by fitting linear regression models (LMs). Models including single soil properties and quotients were calibrated using linear and quadratic terms to account for potential non-linear relationships, and the most parsimonious model was selected following Akaike's information criterion (AIC). The normality and homogeneity of model residuals were checked using diagnostic plots. The goodness of fit of the models to the data was assessed by the coefficient of determination

(R^2) and statistical significance of the relationships (*P*) obtained from the model summary outputs.

All data analyses were carried out with R (R Core Team, 2017).

RESULTS

Soil properties

The relationships between most soil properties (MWD, pH, organic C, available P, microbial biomass C and β-glucosidase) and field-estimated soil burn severity were quadratic (Table 12; Fig. 15). All soil properties, except total N and urease activity, were significantly affected by soil burn severity immediately after fire ($P < 0.05$) (Fig. 15).

MWD showed a non-linear relationship with burn severity ($R^2 = 0.284$; $P < 0.001$) (Fig 15), increasing at low to moderate severities (≤ 1.75 CBI units) and decreasing at high severities (> 2.25 CBI units).

Soil pH had a strong significant relationship with burn severity (Fig. 15), and was the soil property with the highest proportion of variance explained by burn severity ($R^2 = 0.802$). pH values ranged from 3-5 in the areas burned at low severity to 7-9 in the most severely burned areas. The most pronounced change in pH was observed at moderate and high severities (CBI > 1.25 CBI units).

Focusing on soil major nutrients, we found a significant relationship between organic C ($R^2 = 0.594$; $P < 0.001$) and available P ($R^2 = 0.666$; $P < 0.001$) with burn severity (Fig. 15). Nevertheless, the patterns of change in both nutrients were opposed. Organic C decreased with burn severity, whereas available P increased with burn severity, mainly at moderate and high severities (CBI > 1.25 CBI units). We did not find significant effects of burn severity on total N ($R^2 = 0.059$; $P > 0.05$).

Microbial biomass C showed an inverse relationship with burn severity ($R^2 = 0.504$; $P < 0.001$) (Fig. 15) following the same pattern of change as organic C. The highest microbial biomass C contents (> 1000 µg g^{-1} dry soil) were obtained in soils that did not burn with high severity (≤ 2.25 CBI units).

Table 12. Akaike's information criterion (AIC) values of models calculations performed between soil properties (response variables) and soil burn severity measured as the substrate stratum of the Composite Burn Index (CBI) (explanatory variable) using a linear ('CBI') and a quadratic function ('poly(CBI,2)'). The lowest AIC values for each soil property, which indicate the most adequate model, are in bold face. MWD = Mean weight diameter, MBC = microbial biomass C.

Soil property	CBI	AIC
MWD	Linear	-50.226
	Quadratic	**-59.248**
pH	Linear	114.122
	Quadratic	**104.907**
Organic C	Linear	382.682
	Quadratic	**381.924**
Total N	Linear	**140.792**
	Quadratic	142.847
Available P	Linear	302.148
	Quadratic	**299.502**
MBC	Linear	650.972
	Quadratic	**649.480**
β-glucosidase	Linear	33.336
	Quadratic	**14.853**
Urease	Linear	**120.225**
	Quadratic	122.219
Phosphatase	Linear	**121.942**
	Quadratic	122.725

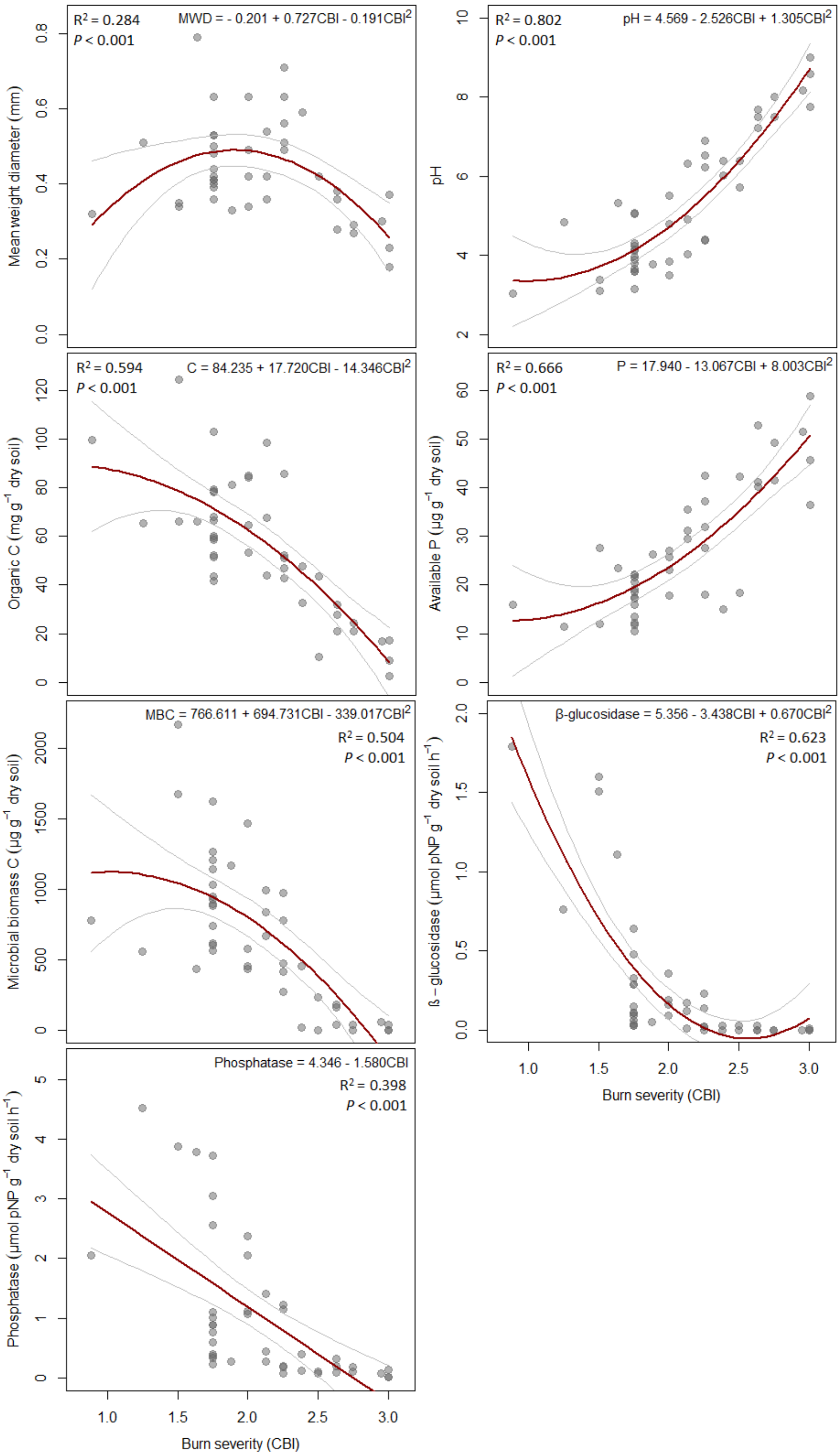

Figure 15. Relationships between soil properties (response variables) and soil burn severity measured as the substrate stratum of the Composite Burn Index (CBI) (explanatory variable). The lines represent model-predicted values (mean ± 95% confidence intervals) for each soil property along the burn severity gradient.

Similarly, the activities of soil enzymes β-glucosidase and acid phosphatase were inversely related to burn severity. β-glucosidase had a quadratic response to burn severity (R^2 = 0.623; *P* < 0.001), stronger than the linear relationship exhibited by acid phosphatase activity (R^2 = 0.398; *P* < 0.001). Both activities decreased from the low severity scenario and showed values corresponding to no activity in the severely burned areas, thus being the studied soil properties most sensitive to burn severity. We did not find significant effects of burn severity on urease activity (R^2 = 0.005; *P* > 0.05).

Soil quotients

Several soil quotients showed significant linear (C:N) and quadratic (Q_{mic} and β-glucosidase:microbial biomass C) inverse relationships with burn severity (Table 13; Fig. 16).

Burn severity had a significant effect on the C:N ratio, explaining a high percentage of variance on that quotient (R^2 = 0.740; *P* < 0.001) (Fig. 16). The C:N ratio strongly decreased from values of 30 µg organic C µg^{-1} total N in the lowest severities to values around 5 µg organic C µg^{-1} total N in the highest severities.

The Q_{mic} showed a significant decrease with burn severity (R^2 = 0.443; *P* < 0.001) (Fig. 16). The quadratic relationship between Q_{mic} and burn severity suggested that changes in Q_{mic} appeared at moderate to high severities (CBI > 1.75).

Among the specific activities of soil enzymes, only the β-glucosidase:microbial biomass C quotient significantly decreased with burn severity (R^2 = 0.497; *P* < 0.001). As occurred with β-glucosidase activity, the β-glucosidase:microbial biomass C quotient was very sensitive to fire, showing notable decreases even at low severities with the same pattern in relation with burn severity as β-glucosidase (Figs. 15, 16).

Table 13. Akaike's information criterion (AIC) values of models calculations performed between soil properties (response variables) and soil burn severity measured as the substrate stratum of the Composite Burn Index (CBI) (explanatory variable) using a linear ('CBI') and a quadratic function ('poly(CBI, 2)'). The lowest AIC values for each soil property, which indicate the most adequate model, are in bold face. Q_{mic} = microbial quotient, MBC = microbial biomass C.

Soil quotient	Explanatory variable	AIC
C:N	Linear	**246.773**
	Quadratic	247.696
Q_{mic}	Linear	76.414
	Quadratic	**71.997**
β-glucosidase:MBC	Linear	-101.162
	Quadratic	**-111.828**
Urease:MBC	Linear	**47.694**
	Quadratic	49.612
Phosphatase:MBC	Linear	**52.281**
	Quadratic	54.105

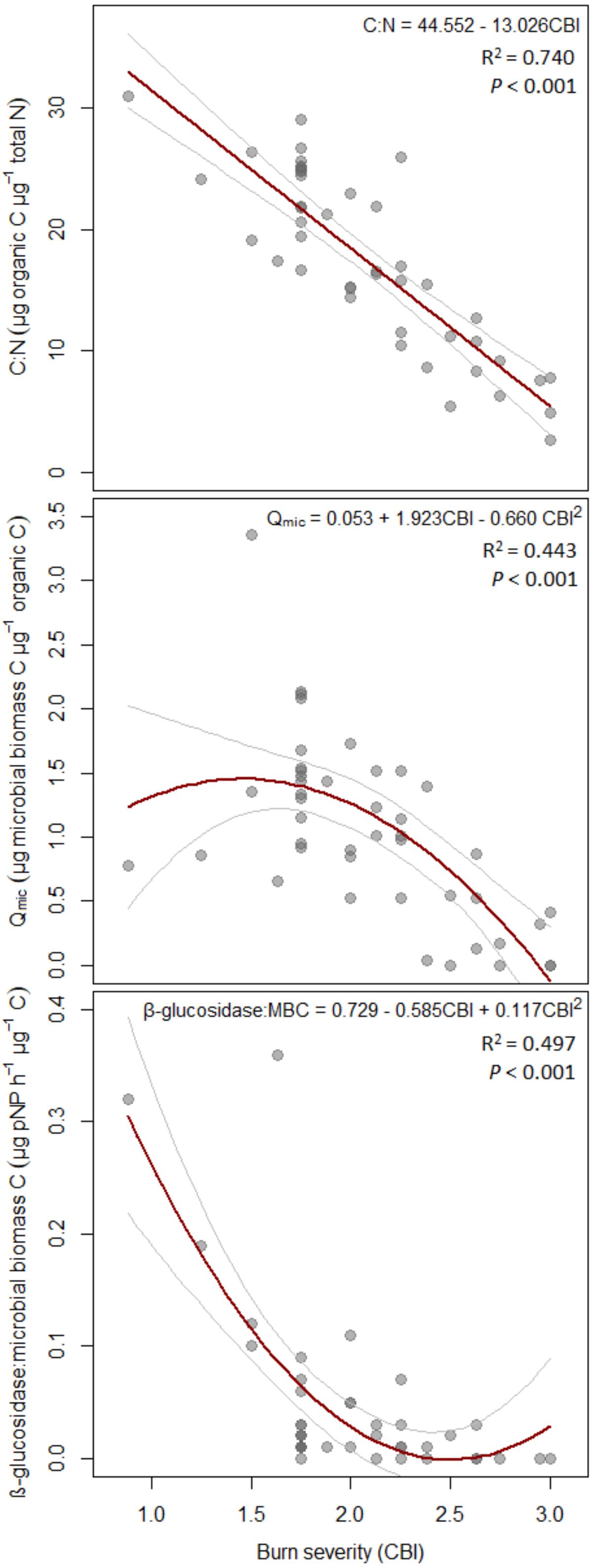

Figure 16. Relationships between soil quotients (response variables) and soil burn severity measured as the substrate stratum of the Composite Burn Index (CBI) (explanatory variable). The lines represent model-predicted values (mean ± 95% confidence intervals) for each soil property along the burn severity gradient. MBC = microbial biomass C.

DISCUSSION

We developed a study to analyze fire effects on acidic soils along a burn severity gradient in a *Pinus pinaster* ecosystem immediately after fire (7-9 days). Our results revealed significant relationships between burn severity and physical, chemical and biological soil properties [mean weight diameter (MWD), pH, organic C, available P, microbial biomass C, β-glucosidase activity and acid phosphatase activity].

In the present study, we observed that the physical property MWD increased at low to moderate severities and decreased mainly at high severities. The increase in MWD may be related to the enhancement of aggregate stability that typically occurs at moderate severities in hydrophilic soils with organic matter as the main binding agent (Mataix-Solera *et al.*, 2011). Laboratory heating experiments have clarified that aggregate stability can be enhanced at low temperatures (75-200 ºC) (Santín & Doerr, 2016) due to the volatilization of some organic matter, which then condenses on the aggregates, contributing to their stability (Mataix-Solera *et al.*, 2011). However, at higher temperatures stable aggregates can be dispersed (Benito *et al.*, 2009; Varela *et al.*, 2015; Santín & Doerr, 2016) due to major alterations in the main binding agents: the organic matter, which is depleted at high severities; and clay minerals, which are modified at extreme severities (Neary *et al.*, 1999; Santín & Doerr, 2016). The decrease in MWD at high severities involves other negative effects on ecosystems, such as loss of structure (Cerdá & Jordan, 2010), and consequently a decrease in infiltration capacity and an increase in erosion rates (Vieira *et al.*, 2015). Therefore, the burn severity impact on MWD has significant ecological consequences, especially in areas where potential erosion risk is very high, such as Southern Europe (Van der Knijff *et al.*, 2000).

The soil chemical properties pH, soil organic C and available P, were also affected by burn severity immediately (7-9 days) after fire. We found proportional decreases in organic C concentration at moderate and high severity, our results being consistent with those found in previous research on fire ecology (Nave *et al.*, 2011; Vega *et al.*, 2013). Loss of organic C in the mineral soil starts at moderate severities (Key & Benson, 2006; Keeley, 2009) and is a consequence of organic matter mineralization and volatilization caused by fire (Caon *et al.*, 2014). Laboratory heating experiments indicated that organic C concentration in Mediterranean *P. pinaster* ecosystems with acidic soils decreases at temperatures higher than 220 ºC (Varela *et al.*, 2015). The opposite trend was found for pH and available P. pH showed a large increase (almost 6 pH units) with burn severity, exceeding figures reported in other field studies (Certini, 2005; Marcos *et al.*, 2007; Vega *et al.*, 2013) and similar to increases found in acidic soils from *P. pinaster* ecosystems heated to 800 ºC under laboratory conditions (Fuertes, 2015), suggesting that temperatures reached in the study site were relatively high. Increases in pH are due to denaturation of organic acids and release of bases from organic matter mineralization (Neary *et al.*, 2008; Alcañiz *et al.*, 2018). Similarly, the mineralization of organic matter converts organic P into available P (Certini, 2005; Marcos, 2007), which is frequently limiting in forest soils (Neary *et al.*, 2008), especially in those developed from highly siliceous lithologies (Binkler & Fisher, 2013), which is the case in our study area. Additionally, burn severity may have a significant effect on the concentration of available P in acidic soils through the increase in pH, as maximum P availability is between pH 6 and 7.5 (Neary *et al.*, 2008). Therefore, changes caused by burn severity in both soil properties, pH and available P content, are particularly relevant in acidic soils in *P. pinaster* ecosystems, because they have notable implications in soil fertility. In this study, we did not find significant effects of burn severity on total N concentration, which can be attributed to low N losses by volatilization (Caon *et al.*, 2014). Other studies have not found changes in total N in Mediterranean soils after fire (Caon *et al.*, 2014), or in soils heated in laboratory at 350 ºC for 1 hour (Tecimen and Sevgi, 2011).

The biological soil properties significantly affected by burn severity (microbial biomass C, β-glucosidase activity and acid phosphatase activity) strongly decreased (to zero) in the highest severity scenario. Declines in microbial biomass C with burn severity were found by Vega *et al.* (2013) in *P. pinaster* ecosystems. The decrease in microbial biomass C is attributed to the mortality of microorganisms occurring between 50 and 160 ºC (Neary *et al.*, 2008; Vega *et al.*, 2013). Additionally, changes caused by fire in soil nutrients, moisture and temperature may affect the abundance of microorganisms (Dooley & Treseder, 2012). Similarly, temperatures above 60-70 ºC bring about the inactivation and denaturation of soil enzymes (Tabatabai, 1994). These temperatures are lower than necessary to produce significant effects on the other soil properties analyzed in this study (Neary *et al.*, 2008). Therefore, the soil enzymes β-glucosidase and acid phosphatase are the soil properties most sensitive to burn severity in the present study, understood to be the first properties affected, decreasing from severities of 1.25 CBI units (considered the severity threshold between visible changes and no visible changes in the mineral soil; see table 11; Key & Benson, 2006) to 2.5 CBI units, where no activity was found. In contrast, we did not find significant effects of burn severity on urease activity. We hypothesize that the high NH_4^+ concentration, which is expected in soils immediately after fire (Certini, 2005; Caon *et al.*, 2014), may inhibit the enzyme reaction (Goberna *et al.*, 2012), as well as mask the enzyme activity determination, as it is quantified by the NH_4^+ released (Kandeler & Gerber, 1988).

Among the soil quotients, we found a significant relationship between burn severity and the C:N ratio, Q_{mic} and β-glucosidase:microbial biomass C quotient. The decrease in C:N ratio with fire (González-Pérez *et al.*, 2004; Santín *et al.*, 2008), and particularly, the inverse relationship between C:N ratio and burn severity has been noted in previous studies (Vega *et al.*, 2013). Thus, burn severity can transform oligotrophic soils into eutrophic soils (from C:N > 20 to C:N < 12; Porta *et al.*, 1999), conditioning the composition of the future plant community (Pöyry *et al.*, 2017). This result can be attributed to higher losses caused by fire in soil organic C than in N, which is volatilized at higher temperatures (Neary *et al.*, 2008), and to the increase in recalcitrant organic N forms in charred remains (Santín *et al.*, 2008). Apart from the sensitivity to fire, the quite constant values of the C:N ratio among undisturbed forest soils (Wild, 1992) suggests that this quotient may be a generalizable tool to analyze fire impact on soils. Similarly, we found decreases in Q_{mic} with burn severity, which can be attributed to a higher impact on microbial biomass C than on organic C (Bastida *et al.*, 2008). Several authors have noted that Q_{mic} values of 2.2 reflect a good equilibrium between both C fractions (Bastida *et al.*, 2008), whereas Q_{mic} values lower than 2 are indicative of organic matter depletion (Lagomarsino *et al.*, 2009; Paz-Ferreiro & Fu, 2016). This suggests a large decrease in organic matter in the highest severity scenarios (> 2.5 CBI units) of our study, where Q_{mic} values were always lower than 1. Among the specific activities of soil enzymes, β-glucosidase:microbial biomass C decreased with burn severity. Other studies carried out by Lagomarsino *et al.* (2009) in agrarian ecosystems have pointed out the β-glucosidase:microbial biomass ratio as the most sensitive specific enzyme activity to indicate land use impacts. The inverse relationship between this ratio and burn severity could be explained by (i) a decrease in β-glucosidase activity per microbial biomass unit (Waldrop *et al.*, 2000); (ii) β-glucosidase immobilization in clays or humic colloids; and (iii) a decrease in the concentration of glucopyranosides (Bastida *et al.*, 2008).

The present study contributes to advancing knowledge of what soil burn severity means for the soil status and functioning immediately after fire in *P. pinaster* ecosystems with acidic soils. Additionally, our results revealed several soil properties that could be considered key for monitoring fire impacts on soils, due to their high sensitivity to burn severity and their relationship with relevant soil ecological processes. Among them, (i) pH showed the strongest relationship with burn severity, with a large increase at moderate and high severities; (ii) the activity of soil enzymes acid phosphatase and particularly β-glucosidase (both, the single soil property and the soil quotient as specific enzyme activity) showed the highest sensitivity to fire, decreasing from the low severity scenario; and (iii) the C:N quotient, whose results could be more generalizable, showing a progressive decrease with burn severity. However, it has been recognized that not all changes caused by fire in soil parameters persist for a long time, depending on the magnitude of the fire impact and the recovery of vegetation, among other factors (Certini, 2005; Alcañiz *et al.*, 2016; Muñoz-Rojas *et al.*, 2016). Therefore, we recommend monitoring the evolution of soil properties in relation to burn severity over the medium and long term after a wildfire in fire-prone pine ecosystems.

Research on how burn severity affects soil properties is particularly relevant in the European countries of the Mediterranean Basin, since land use changes occurring during recent decades have led to an increase in fuel amount and continuity (Pausas *et al.*, 2008; Doblas-Miranda *et al.*, 2017), thus constituting landscapes prone to large high severity fires (San-Miguel-Ayanz *et al.*, 2016; García-Llamas *et al.*, 2019). This new fire-regime pattern could be enhanced in the current context of climate change due to climate-driven increases in burn severity and the area affected by fire because of the drier and warmer climate expected in many regions of the world (Azpeleta *et al.*, 2014; San-Miguel-Ayanz *et al.*, 2016). Consequently, the present study not only contributes to a better understanding of changes occurring in a particular situation, but can also inform on fire impacts in *P. pinaster* forests under in future scenarios of increasing burn severity.

CONCLUSIONS

This study adds to the knowledge on how field-estimated burn severity is related to changes in single soil properties (physical, chemical and biological) as well as in soil quotients indicative of soil status and processes in *Pinus pinaster* ecosystems with acidic soils immediately (7-9 days) after fire. Specifically, our results showed that decreases in the size of stable aggregates (mean weight diameter) occurred mainly at high burn severities, whereas changes in chemical properties (pH, organic C and available P) were associated with moderate and high severities. We also demonstrated that biological properties, and particularly the activity of soil enzymes (β-glucosidase and acid phosphatase), are one of the most sensitive properties to burn severity as they largely decrease from the low-severity scenarios, becoming depleted at the highest severities. Furthermore, burn severity affected the C:N ratio, microbial quotient and the specific activity of β-glucosidase. In view of our results, we propose pH, β-glucosidase and C:N ratio as key properties in surveying fire impacts on soils immediately after fire in *P. pinaster* ecosystems, because of their sensitivity and potential generalization.

This research constitutes a benchmark for monitoring longer-term relationships between burn severity and soil properties in *P. pinaster* ecosystems, as well as forecasting how the effects of fire will be in the future, considering the predictions of more severe wildfires in the Mediterranean region.

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Article IV

Wildfire effects on soil properties in fire-prone pine ecosystems: indicators of burn severity legacy over the medium term after fire

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Abstract

The aim of this study was to determine the effects of burn severity on soil properties (chemical, biochemical and microbiological) in fire-prone pine ecosystems three years after fire. To achieve these goals, we selected two large wildfires that occurred in summer 2012 within the Iberian Peninsula: the Sierra del Teleno wildfire, which burned 119 km^2 dominated by *Pinus pinaster* forests developed over acidic soils, and the Cortes de Pallás wildfire, which burned 297 km^2, part of them dominated by *Pinus halepensis* ecosystems with calcareous soils. We classified the burned areas into low or high burn severity categories using spectral indices. Three years after the wildfires, we distributed 56 field plots proportionally to the extent of each severity category. In each field plot, we collected samples of mineral soil from a depth of 0-3 cm. We analysed soil chemical (pH, electrical conductivity, organic carbon, total nitrogen, available phosphorus) biochemical (β-glucosidase, urease and acid phosphatase enzymatic activities) and microbiological (microbial biomass carbon) properties in each soil sample. The relationship between burn severity and soil properties was analysed by a Permutational Multivariate Analysis of Variance and Generalized Linear Models. The results showed a significant influence of the original ecosystem and of burn severity on the overall soil status over the medium term after fire. Available P content increased with burn severity in the acidic soils of the *P. pinaster* ecosystem. However, the three enzymatic activities and microbial biomass carbon decreased with burn severity in both types of pine ecosystems. β-glucosidase, urease and microbial biomass carbon showed common patterns in relation to burn severity in the two different *Pinus* ecosystems (acidic and calcareous soils), and therefore we suggest that they could be potential indicators of the burn severity legacy on soils over the medium term after fire in fire-prone pine Mediterranean forests. Available P and acid phosphatase could be potential indicators in the *P. pinaster* ecosystem. This study provides useful knowledge for developing hazard reduction and restoration strategies after large wildfires.

INTRODUCTION

Wildfires are one of the recurrent ecological disturbances in forest ecosystems (Fultz *et al.*, 2016; Heydari *et al.*, 2017; Taboada *et al.*, 2017). During recent decades, wildfires in the Mediterranean Basin can be perceived as disasters due to increased numbers of large fires and area burned (Pausas *et al.*, 2008). Besides, wildfire-related problems are more pronounced in Southern Europe, where there is an increase in burn severity associated with land use change and climate change (Hinojosa *et al.*, 2016; Catalanotti *et al.*, 2017). For these reasons, the effects of burn severity on the recovery of Mediterranean ecosystems is one of the main current issues in scientific research into fire ecology (e.g. Fernández-Manso *et al.*, 2016; Francos *et al.*, 2016; Fernández-García *et al.*, 2017).

Burn severity is defined as the loss of or change in ecosystem biomass, caused by fire (Keeley, 2009). It is related to fire intensity, which denotes the energy released from fire. Both parameters, burn severity and fire intensity, may determine the impacts of fire on ecosystems, and therefore, may help predict post-fire recovery (Keeley, 2009; Dzwonko *et al.*, 2015; Pereira *et al.*, 2017). However, most studies use burn severity instead of fire intensity, because it can be measured after fire (Zavala *et al.*, 2014) over extended time frames ranging from days to decades (Heward *et al.*, 2013). There are two different approximations to assessing burn severity: using remote sensing methods (Fernández-Manso *et al.*, 2016; Fernández-García *et al.*, 2018a) or field data (Fernández-García *et al.*, 2017). Among field methods to estimate burn severity, one of the most straightforward and widespread procedures in Mediterranean ecosystems is to measure the minimum diameter of remaining twigs (Keeley, 2009), as it indicates the magnitude of impacts caused by fire aboveground (Fernández-García *et al.*, 2017) and belowground (Keeley *et al.*, 2008; Maia *et al.*, 2012). Fire, and hence burn severity, plays an essential role in the mineral soil status of forest ecosystems (Certini, 2005; Zavala *et al.*, 2014; Knelman *et al.*, 2015) by modifying soil properties, chiefly in the uppermost 2-3 cm (Badía *et al.*, 2014; Caon *et al.*, 2014). Thus, to assess the influence of burn severity on overall soil status after fire, some authors have used a combination of fire-sensitive soil properties, such as chemical, biochemical and microbiological properties (Vega *et al.*, 2013; Pourreza *et al.*, 2014; Hedo *et al.*, 2015; Muñoz-Rojas *et al.*, 2016).

In general, soil chemical properties show significant changes after fire, such as increased pH and electrical conductivity (EC) (Certini, 2005; Notario *et al.*, 2008; Fontúrbel *et al.*, 2016; Pereira *et al.*, 2017). The modification of soil pH, and high temperatures reached during a fire may induce relevant changes in major soil nutrients such as organic carbon (C), nitrogen (N) and phosphorus (P), essential for the post-fire recovery of soil microbiota and vegetation (Serrasoles *et al.*, 2008; Caon *et al.*, 2014; Otero *et al.*, 2015; Ferreira *et al.*, 2016). Nutrient concentrations and bioavailability are also controlled by the activity of soil enzymes (Tabatabai, 1994; Fultz *et al.*, 2016; Hinojosa *et al.*, 2016). Due to their relevance in the cycles of major nutrients and high sensitivity to disturbances, enzyme activities such as glucosidase, urease and phosphatase have been considered as indicators of the degree of impact on soils (Pourreza *et al.*, 2014; Hedo *et al.*, 2015; Hinojosa *et al.*, 2016). Soil enzymes can originate from plant and animal residues, but mainly from microbial biomass (Tabatabai, 1994). Consequently, both soil enzyme activities and microbial biomass content usually show similar patterns after fire (Vega *et al.*, 2013; Pourreza *et al.*, 2014), and decrease with burn severity (Lombao *et al.*, 2015; Fontúrbel *et al.*, 2016; Holden *et al.*, 2016). There are many examples of short-term fire effects on soil properties (e.g. Vega *et al.*, 2013; Badía *et al.*, 2014; Fultz *et al.*, 2016; Heydari *et al.*, 2017; Prendergast-Miller *et al.*, 2017), but data on how fire affects soils over the medium term (2-5 years after fire) are scarce (Muñoz-Rojas *et al.*, 2016), and most studies do not consider burn severity (Certini, 2005; Caon *et al.*, 2014), highlighting the importance of further research to better understand soil resilience across gradients of burn severity. Therefore, identifying appropriate indicators of ecosystem resilience in relation to burn severity remains an important challenge for distinguishing recovered soils from those that are still affected by fire.

However, the impacts of burn severity on soil can also vary depending on plant communities and soil types (Certini, 2005; Knicker, 2007; Badía *et al.*, 2014; Keesstra *et al.*, 2017; Prendergast-Miller *et al.*, 2017). In the Mediterranean Basin, *Pinus pinaster* Ait. and *Pinus halepensis* Mill. ecosystems are two of the fire-prone forests most frequently affected by fire (Pausas *et al.*, 2008). Both plant communities are fire-sensitive and have common structural characteristics (de las Heras *et al.*, 2012), since the dominant tree species in both is a highly flammable obligate seeder, the post-fire regeneration of which relies mainly on seeds stored in serotinous cones (Pausas *et al.*, 2008). However, the two communities have preference for different types of soils. *P. pinaster* usually grows on sandy-acidic soils, whereas *P. halepensis* communities prefer basic soils developed from lithologies such as marls, limestones or dolomites (Richardson, 2000; de las Heras *et al.*, 2012). This niche preference can influence the magnitude and direction of fire impacts on soil properties (Terefe *et al.*, 2008; Martin *et al.*, 2012; Caon *et al.*, 2014; Ferreira *et al.*, 2016).

In the present study we aimed to characterize the medium-term effects of burn severity on soils affected by fire in two fire-prone, pine-dominated Mediterranean forest types. Specifically, we addressed the following questions: (i) Are soil properties (chemical, biochemical and microbiological) affected by burn severity over the medium term after fire in the same way in *P. pinaster* and *P. halepensis* ecosystems? (ii) Can we identify potential indicators of burn severity impact on soils over the medium term after fire in Mediterranean fire-prone pine ecosystems? We hypothesise that burn severity effects on soil chemical properties will be unnoticeable in both ecosystems over the medium term after the fire, since fire impacts on soil pH, EC and nutrients are, in general, ephemeral (Certini, 2005; Zavala *et al.*, 2014). Conversely, we expect that the effect of burn severity will be noticeable on soil properties that are largely modified by high severities (Martin *et al.*, 2012) and that need long periods to recover from the burn severity impact. This may be the case of biochemical and microbiological properties (Dumonet *et al.*, 1996; Dooley and Treseder, 2012), whose response to burn severity over the medium term can be modulated by the recovery of the plant community (Hedo *et al.*, 2015; Pérez-Varela *et al.*, 2018) and by the different edaphic conditions in the studied ecosystems (Terefe *et al.*, 2008; Martin *et al.*, 2012; Ferreira *et al.*, 2016). Therefore, we predict that soil biochemical and microbiological properties will be potential indicators of burn severity over the medium term after fire.

MATERIAL AND METHODS

Study sites

The study was conducted on two large wildfires in the Iberian Peninsula: the Sierra del Teleno wildfire and the Cortes de Pallás wildfire (Fig. 17).

The Sierra del Teleno wildfire occurred in León province (NW Iberian Peninsula). It burned 119 km^2 in August 2012 (Table 14), 103 km^2 being occupied by *P. pinaster* forests, with the understorey community dominated by *Pterospartum tridentatum* (L.) Willk., *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. In this site, the climate is temperate with dry temperate summers (AEMET-IM, 2011). The orography is heterogeneous, ranging from flat to mountainous areas. Soils are developed over siliceous lithologies, predominantly Haplic Umbrisols and Dystric Regosols, according to the World Reference Base for Soil Resources (WRB) classification (Jones *et al.*, 2005).

The Cortes de Pallás wildfire occurred in Valencia province (Eastern Iberian Peninsula) in June 2012. In this fire, an area of 297 km^2 was affected, burning 66 km^2 of *P. halepensis* ecosystems (Table 14) with presence of *P. pinaster*. The understory of these ecosystems was dominated by *Ulex parviflorus* Pourr., *Quercus coccifera* L. and *Rosmarinus officinalis* L. Its climate is temperate, with hot dry summers (AEMET-IM, 2011). This study site is mountainous with calcareous lithologies. In general, its soils are classified as Haplic Calcisols and Calcari-lithic Leptosols (Jones *et al.*, 2005).

Table 14. Characteristics of the study sites.

	Sierra del Teleno wildfire	Cortes de Pallás wildfire
Fire alarm date	August 19th, 2012	June 28th, 2012
Wildfire size (km^2)	118.91	297.52
Dominant pine species	*P. pinaster*	*P. halepensis*
Pine ecosystem burned (km^2)	102.65	65.69
Elevation (m)	836 - 1,493	120 - 942
Aspect	N, S, W, E	N, S, W, E
[1] Mean annual precipitation (mm)	600 - 800	400 - 600
[1] Mean annual temperature (K)	281 - 284	286 - 290
[2] Lithology	Quartzite, conglomerate, sandstone, sand, slate, silt	Limestone, dolomite, sandstone, marl
[3] Soil WRB classification	Haplic Umbrisol, Dystric Regosol	Haplic Calcisol, Calcari-lithic Leptosol
[4] Soil textural class	sandy loam	loamy sand, sandy loam
[5] Soil $CaCO_3$ (mg/g)	-	193.2 ± 116.9
[6] Soil pH	4.86 ± 0.14	8.14 ± 0.06
[6] Soil electrical conductivity (dS m^{-1})	0.04 ± 0.01	0.15 ± 0.02
[7] Soil organic matter (mg/g)	75.5 ± 1.26	70.2 ± 12.8

[1] Precipitation and temperature were obtained from Ninyerola *et al.* (2005).

[2] Lithologies were determined according to the geological map of Spain (GEODE, 2017).

[3] World Reference Base for Soil Resources classification according to Jones *et al.* (2005).

[4] Soil textures are USDA classes. Particle-sizes were obtained according to Bouyoucos (1936).

[5] $CaCO_3$ was determined using a Bernard calcimeter (M.A.P.A., 1986).

[6] A suspension of soil:deionized water was used to determine pH (1:2.5, w/v) and conductivity (1:5, w/v).

[7] Organic matter was quantified according to Nelson and Sommers (1982).

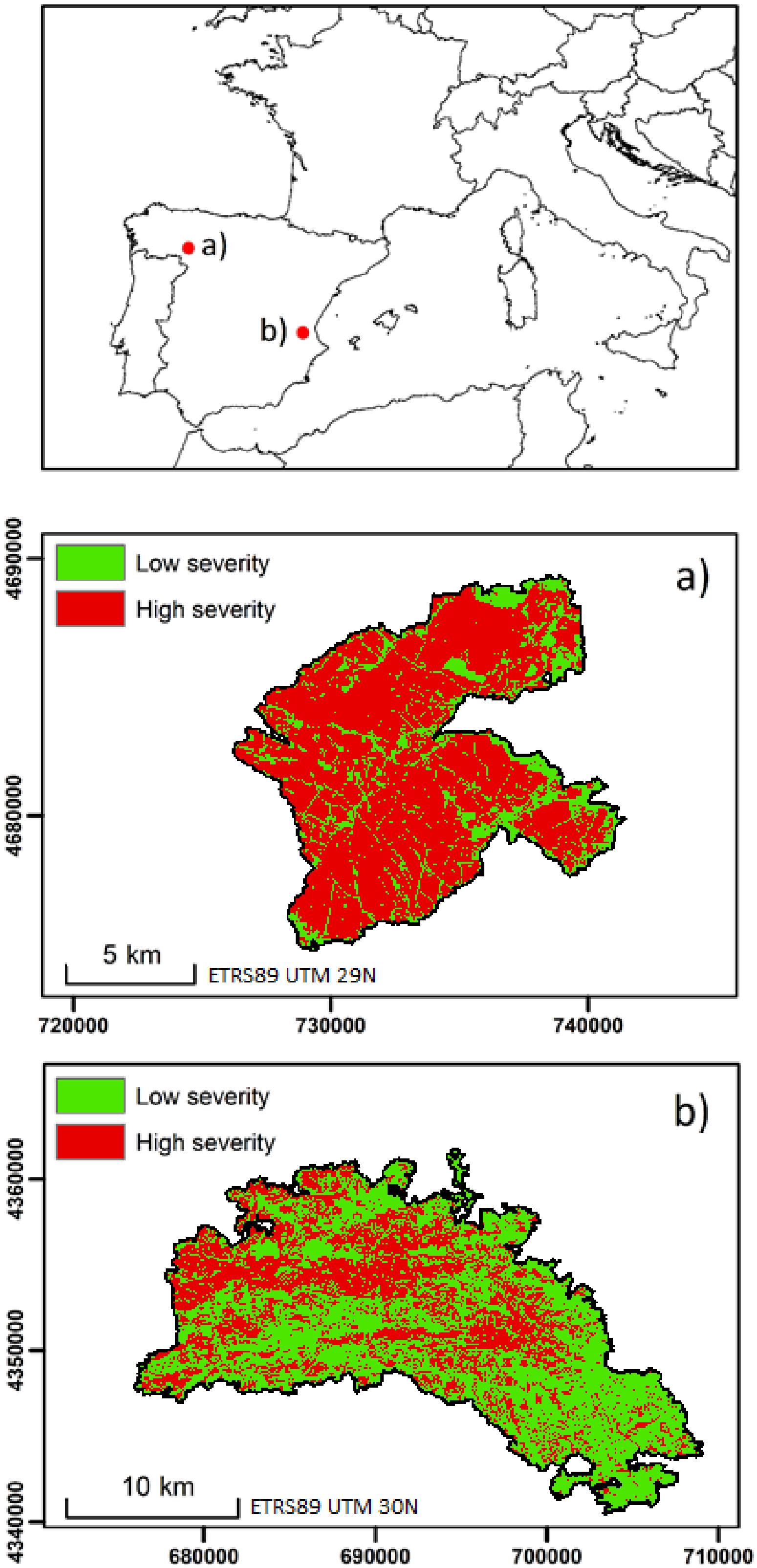

Figure 17. Location of the Sierra del Teleno wildfire (a) and the Cortes de Pallás wildfire (b) in SW Europe, and burn severity maps (a and b study sites) differentiating low and high burn severity areas through the dNBR index.

Field sampling

In each study site we mapped burn severity using the differenced Normalized Burn Ratio (dNBR) (Key, 2006) spectral index in order to design the field sampling. The dNBR, which is usually calculated from Landsat imagery, is considered a reference for burn severity mapping (Fernández-García *et al.*, 2018a; Fernández-García *et al.*, 2018b). This index uses the difference between the pre- and post-fire reflectance of Near Infrarred and Short Wave Infrarred regions to estimate the degree of change caused by fire in ecosystems (see Key, 2006). The dNBR maps of the study sites (30 m spatial resolution) were classified into low and high severity, using the value of 550 as threshold (Fernández-Manso *et al.*, 2015). Sierra del Teleno dNBR was obtained using the Landsat 7 ETM+ scenes from September 20th, 2011 (pre-fire) and from September 6th, 2012 (post-fire); Cortes de Pallás dNBR was obtained using the Landsat 7 ETM+ scenes from August 22nd, 2011 (pre-fire) and from August 25th, 2012 (post-fire). Three years after the wildfires, a total of 56 field plots (30 m x 30 m) were established in the study sites following a stratified random design with proportionate allocation in the severity categories defined by the dNBR: 26 plots in the *P. pinaster* ecosystem in Sierra del Teleno (5 at low severity, 21 at high severity) and 30 in the *P. halepensis* ecosystem in Cortes de Pallás (12 at low severity, 18 at high severity).

In each plot, we calculated field burn severity by measuring the minimum twig diameter remaining of characteristic shrub species in each community (Keeley *et al.*, 2008; Keeley, 2009; Maia *et al.*, 2012). Shrub skeletons of *Erica australis* L. were used in the *P. pinaster* ecosystem, whereas *Quercus coccifera* L. was used in the *P. halepensis* ecosystem. Within each 30 m x 30 m plot, four shrub skeletons were randomly selected, and four of the thinnest burned terminal branches were measured in each skeleton. Values were averaged obtaining a twig diameter remaining value per plot (d). We then calculated the Twig Diameter Index of burn severity (TDI) for each plot according to the model proposed by Maia *et al.* (2012): TDI = d / dmax, where dmax is the maximum diameter measured in the study site. TDI values ranged from near zero (low burn severity) to one (maximum burn severity).

To analyse the effects of burn severity on soil properties, in spring 2015 we collected two soil samples from each 30 m x 30 m plot (Fig. 18). Each sample was composed of four subsamples. Each subsample corresponded to the volume of an auger of 5 cm diameter x 3 cm depth. Herbs, woody debris and litter were removed before collecting the soil subsamples. The soil samples were air-dried, sieved (<2 mm) and stored at 20 ºC for 2-3 months until laboratory analysis.

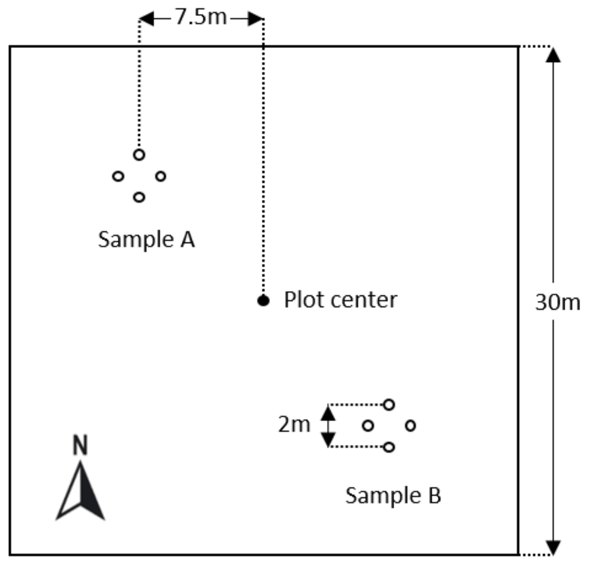

Figure 18. Soil sampling design within each 30 m x 30 m plot. Hollow circles represent the subsamples with which each sample (sample A and sample B) was composed.

Soil analysis

We analysed soil chemical [pH, electrical conductivity (EC), organic C, total N and available P], biochemical (β-glucosidase, urease and acid phosphatase) and microbiological (microbial biomass C) properties of the soil. The two samples taken in each plot were analysed independently for all soil properties. For each soil sample, two laboratory replicates were analysed. Average values were calculated to obtain a single value per 30 m x 30 m plot, for each measured property.

Soil pH was determined in a suspension of soil:deionized water (1:2.5, w/v) and EC was determined in a suspension of soil:deionized water (1:5, w/v) at 25 ºC. Soil organic C was obtained by Walkley-Black dichromate oxidation (Nelson and Sommers, 1982) after grinding the soils to <0.15 mm particle size. Total N was determined by the Kjeldahl method (Bremner and Mulvaney, 1982) using a DK 20 digestion unit (VELP Scientifica, Italy) and available P was analysed following the Olsen *et al.* (1954) procedure, at 882nm wavelength on a UV Mini 1240 spectrophotometer (Shimadzu Corporation, Japan).

We analysed three soil extracellular enzymatic activities corresponding to the biogeochemical cycles of C, N and P. Specifically, we selected β-glucosidase (EC 3.2.1.21; β-D-glucoside glucohydrolase), urease (EC 3.5.1.5; urea amidohydrolase) and acid phosphatase (EC 3.1.3.2; phosphate-monoester phosphohydrolase). We analysed β-glucosidase and acid phosphatase activities following the procedure described by Tabatabai (1994), and the urease activity according to Kandeler and Gerber (1988). Thus, soils were incubated with correspondent enzyme substrates and the product released was determined colorimetrically. Two sample blanks were used for each soil sample. The *p*-nitrophenol (*p*NP) produced by the activities of β-glucosidase and acid phosphatase was measured at 400nm wavelength, and the NH_4^+ released by urease activity was measured at 690nm with a UV-1700 PharmaSpec spectrophotometer (Shimadzu Corporation, Japan).

Microbial biomass C was determined by the fumigation-extraction method (Vance *et al.*, 1987). This procedure is based on Walkley-Black dichromate digestion to calculate the difference (E_C) in organic C between filtered extracts of chloroform fumigated ($CHCl_3$, 24h) and non-fumigated soil samples. We then used an extraction efficiency coefficient (k_{EC}) of 0.38 (Vance *et al.*, 1987; Joergensen, 1996) to calculate microbial biomass C following the formula: microbial biomass C = E_C/ k_{EC}.

Statistical analysis

A Permutational Multivariate Analysis of Variance (PERMANOVA) using the *adonis* function implemented with 1000 permutations was carried out in order to identify the effects of the ecosystem type and burn severity on soil properties considered together. We included in the analysis all the soil properties as response variables; and as predictors (i) the type of ecosystem (*P. pinaster* and *P. halepensis*) and (ii) field burn severity (continuous TDI values).

To display overall similarity among soil samples for the full dataset, we performed a non-metric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity among the analysed soil properties, using values relativized (from 0 to 1) within variables. To facilitate visualization of the associations between soil samples and burn severity, the NMDS solution was rotated, matching the first axis to the external variable burn severity (continuous TDI values). Vectors of soil properties were fitted in the NMDS ordination using the *envfit* function implemented with 1000 random permutations, obtaining the directions of the vectors, the strength of the gradients (R^2) and their significances (*P*).

In order to identify which soil properties are affected by burn severity (potential indicators), and to investigate whether the effects are similar between *P. pinaster* and *P. halepensis* ecosystems, we performed an ANOVA of the Generalised Linear Models (GLMs). GLMs were fitted using Gamma error distribution with the "log" link function to predict the EC, available P, acid phosphatase and soil microbial C. We used Gaussian error distribution with the "identity" link function to model the other analysed soil properties (pH, organic C, total N, β-glucosidase and urease). The goodness of fit of the models was assessed by visual analysis of homoscedasticity and normality of residuals.

All data analyses were carried out with R (R Core Team, 2016), using the *vegan* package (Oksanen *et al.*, 2016).

RESULTS

The results of the PERMANOVA (Table 15) showed that the type of ecosystem had a significant effect on the overall soil status of fire-prone pine forests three years after fire (P <0.01). Furthermore, the analysis revealed a significant influence of burn severity on soil properties (P <0.05), but no significant interaction was found between ecosystem type and burn severity.

Table 15. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) [‘adonis()’ outputs], showing the effects of the factor pine ecosystem (*P. pinaster* and *P. halepensis*), and the effects of the variable burn severity (Twig Diameter Index), and the interaction (Pine ecosystem x Burn severity), on soil properties (pH, EC, organic C, total N, available P, β-glucosidase, urease, acid phosphatase and microbial biomass C). Df are degrees of freedom. Significant P-values are in bold face.

Model term	Df	Sums of Squares	Mean of Squares	Pseudo-F	*P*
Pine ecosystem	1	0.58	0.58	7.98	<**0.01**
Burn severity	1	0.31	0.31	4.26	**0.03**
Pine ecosystem x Burn severity	1	0.04	0.04	0.49	0.59
Residuals	52	3.79	0.07		
Total	55	4.71			

The final NMDS ordination resulted in a two-dimensional solution with low stress (stress = 0.14; Fig. 19). The external parameters type of pine ecosystem (*P. pinaster* and *P. halepensis*) and burn severity (continuous TDI values) showed significant correlations with the NMDS ordination (Table 16). All the analysed soil properties had a significant role in the ordination (Table 16). Soil samples formed clearly separated clusters by ecosystem type along NMDS axis 2 (Fig. 19). In general, soils of the *P. halepensis* ecosystem were characterized by higher pH, electrical conductivity (EC), total N, and available P content, and higher β-glucosidase and urease activity than the soils of the *P. pinaster* ecosystem. Furthermore, NMDS significantly ordinated soil samples according to burn severity, which increased with the axis 1 (Fig. 19; Table 16), showing that burn severity was inversely related to the activity of enzymes, especially acid phosphatase and urease.

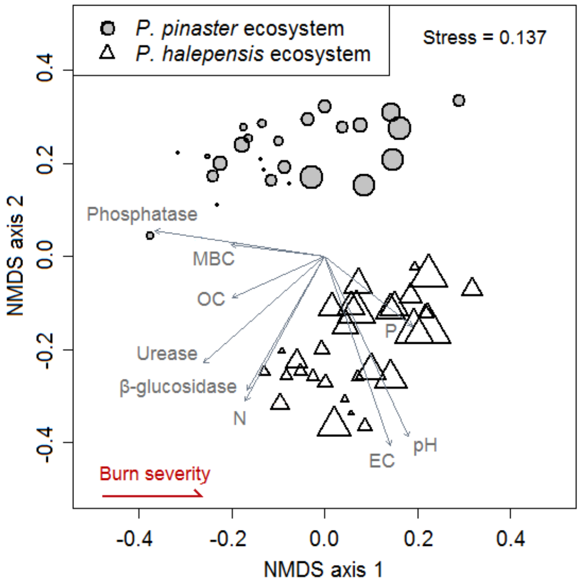

Figure 19. NMDS ordination of soil samples from the two studied pine ecosystems (*P. pinaster* and *P. halepensis*). NMDS was performed using 9 soil properties: pH, EC (electrical conductivity), OC (organic C), N (total N), P (available P), β-glucosidase, urease, acid phosphatase and MBC (microbial biomass C). Vectors of each soil property were included to represent the direction and strength of the gradients. Shape sizes are directly proportional to burn severity (Twig Diameter Index).

Table 16. Determination coefficients (R^2) and significance (P) of vectors determined by the NMDS ordination (nine soil parameters in a two-dimensional ordination space). The table includes the relation of the NMDS ordination with the external parameters burn severity (Twig Diameter Index) and type of ecosystem (*P. pinaster* and *P. halepensis*). R^2 and P were obtained using 1000 random permutations.

NMDS term	R^2	*P*
Ordination vectors		
pH	0.92	<0.01
EC	0.93	<0.01
Organic C	0.24	<0.01
Total N	0.63	<0.01
Available P	0.29	<0.01
β-glucosidase	0.55	<0.01
Urease	0.61	<0.01
Acid phosphatase	0.69	<0.01
Microbial biomass C	0.21	<0.01
Pine ecosystem	0.66	<0.01
Burn severity	0.34	<0.01

The GLMs (Fig. 20; Table 17) showed that all the analysed soil properties were affected by the type of pine ecosystem (*P* <0.01) except organic C and microbial biomass C. Soil pH, EC, total N, available P, glucosidase and urease were higher in the *P. halepensis* ecosystem, whereas acid phosphatase was higher in the *P. pinaster* forest soils (Fig. 20).

We found that burn severity (continuous TDI values) had no significant effects on most chemical properties, such as pH, EC (marginally significant), total N and organic C (Table 17). However, the EC showed a different response in the two ecosystems (*P* <0.01), increasing with burn severity in the *P. pinaster* ecosystem and with no changes in the *P. halepensis* ecosystem (Fig. 20). Available P content was significantly affected by burn severity (*P* <0.05) (Table 17), with different behaviour in the two ecosystems, since it only increased with severity in the *P. pinaster* ecosystem (Fig. 20).

In relation to soil biochemical properties, we observed that burn severity significantly decreased the activity of the three enzymes (Table 17; Fig. 20). Among them, soil urease activity showed the greatest decrease with burn severity, with an analogous response in both ecosystems. In fact, burn severity explained much more of variance in urease activity (21.88%) than in the other analysed soil properties (≤8.59%). β-glucosidase activity decreased with burn severity in both ecosystems. We found a significant decrease in the acid phosphatase activity with burn severity, showing a significant interaction with the type of ecosystem (Table 17, Fig. 20) because of the greater effect of burn severity on the *P. pinaster* than in the *P. halepensis* ecosystem.

Microbial biomass C showed a significant reduction with burn severity in both pine ecosystems without any interaction between them.

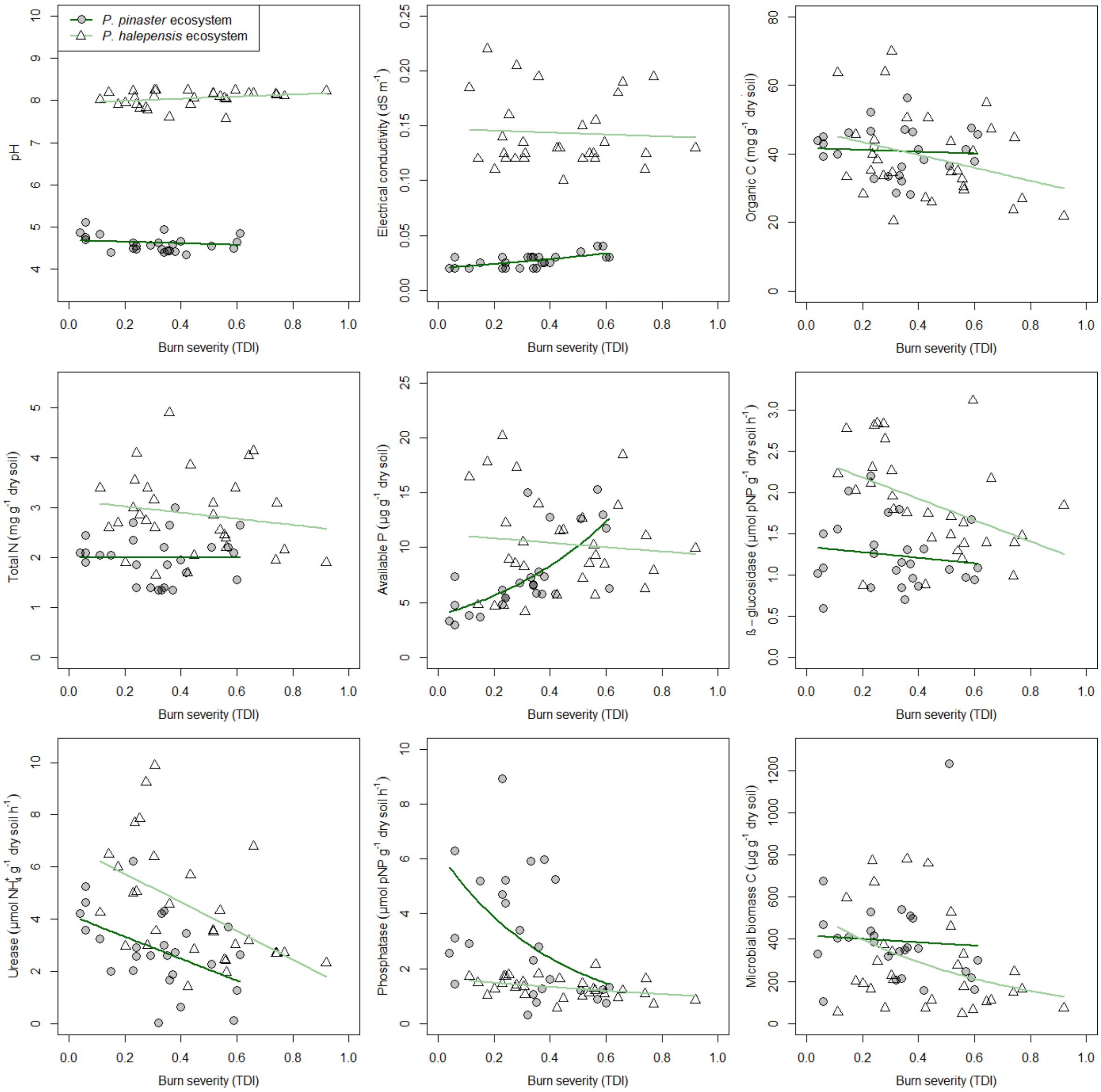

Figure 20. Relationship between each soil property and burn severity (measured as Twig Diameter Index) over the medium term after fire in the two studied ecosystems (*P. pinaster* and *P. halepensis*). The lowest TDI values correspond to the lowest burn severities whereas the highest TDI values correspond to the highest burn severities.

Table 17. Results of the Generalized Linear Models (GLMs) [‘anova()’ outputs] showing the effects of the factor Pine ecosystem (*P. pinaster* and *P. halepensis*), the effects of the variable Burn severity (Twig Diameter Index), and interaction (Pine ecosystem x Burn severity), on each soil property. Df are degrees of freedom. Significant P-values are in bold face.

Response variable	Model term	Df	Deviance explained	Residual deviance	F	*P*
pH	Null			165.04		
	Pine ecosystem	1	162.95	2.08	4286.52	<**0.01**
	Burn severity	1	0.02	2.07	0.45	0.51
	Pine ecosystem x Burn severity	1	0.09	1.98	2.36	0.13
Electrical conductivity	Null			37.10		
	Pine ecosystem	1	34.47	2.64	814.12	<**0.01**
	Burn severity	1	0.16	2.48	3.81	0.06
	Pine ecosystem x Burn severity	1	0.41	2.06	9.75	<**0.01**
Organic C	Null			59.51		
	Pine ecosystem	1	0.45	59.06	0.43	0.52
	Burn severity	1	3.36	55.70	3.21	0.08
	Pine ecosystem x Burn severity	1	1.22	54.49	1.16	0.29
Total N	Null			0.36		
	Pine ecosystem	1	0.11	0.25	23.62	<**0.01**
	Burn severity	1	0.00	0.24	0.69	0.41
	Pine ecosystem x Burn severity	1	0.00	0.24	0.39	0.54
Available P	Null			12.31		
	Pine ecosystem	1	1.48	10.83	9.46	<**0.01**
	Burn severity	1	0.66	10.17	4.25	**0.04**
	Pine ecosystem x Burn severity	1	2.19	7.98	14.01	<**0.01**
β-glucosidase	Null			21.14		
	Pine ecosystem	1	5.80	15.35	23.02	<**0.01**
	Burn severity	1	1.82	13.53	7.22	<**0.01**
	Pine ecosystem x Burn severity	1	0.43	13.10	1.72	0.20
Urease	Null			234.61		
	Pine ecosystem	1	36.18	198.42	12.86	<**0.01**
	Burn severity	1	51.33	147.10	18.24	<**0.01**

	Pine ecosystem x Burn severity	1	0.78	146.32	0.28	0.60
Acid phosphatase	Null			28.109		
	Pine ecosystem	1	10.32	17.79	40.13	<**0.01**
	Burn severity	1	2.22	15.57	8.62	<**0.01**
	Pine ecosystem x Burn severity	1	1.34	14.23	5.20	**0.03**
Soil microbial C	Null			27.09		
	Pine ecosystem	1	1.34	25.76	2.98	0.09
	Burn severity	1	1.76	24.00	3.91	**0.05**
	Pine ecosystem x Burn severity	1	0.78	23.22	1.73	0.19

DISCUSSION

Our results demonstrate that the type of ecosystem and burn severity determined the overall soil status over the medium term (three years after fire) in two contrasting Mediterranean fire-prone pine forest types. Burn severity effects on soils were exerted on all the biochemical and microbiological properties and available P. Conversely, burn severity did not alter other soil parameters three years after the fire, such as pH, electrical conductivity (EC), organic C or total N.

Different studies have shown a clear increase in soil alkalinity and EC for short-term post-fire measurement events (Notario *et al.*, 2008; Knelman *et al.*, 2015; Heydari *et al.*, 2017), and some of them have related this effect to burn severity, in both *P. pinaster* (Vega *et al.*, 2013; Martin *et al.*, 2012) and *P. halepensis* (Henig-Sever *et al.*, 2001; Bárcenas-Moreno and Bååth, 2009) ecosystems. However, it has been noted that these changes in pH and in EC are not persistent for a long time (Certini, 2005; Zavala *et al.*, 2014; Pereira *et al.*, 2017), coinciding with our results over the medium term after fire, where no effect of burn severity was found. The lack of burn severity effects over the medium term after the fire on soil pH may be associated with the removal of ash bases, which are expected to be higher in the severely burned areas, by water and wind (Certini, 2005; Notario *et al.*, 2008), and the formation of new humus at longer term (Zavala *et al.*, 2014). Similar processes may result in the uniformity of EC values within the burned area over the medium term after fire, since soluble salts are quickly leached or transported by runoff (Zavala *et al.*, 2014). However, we found different trends for EC between *P. pinaster* and *P. halepensis* ecosystems that can be attributed to the different behaviour of available P in the studied ecosystems, since a higher available P content contributes to increases in EC (Bolan *et al.*, 1996).

Among the soil major nutrients, available P content was affected by burn severity over the medium term after fire. We found a large increase in available P with burn severity in the *P. pinaster* ecosystem. These results agree with those obtained by Dzwonko *et al.* (2015) in acidic soils in a *P. sylvestris* forest three years after fire, and with other shorter-term (0-12 months post-fire) studies in *P. pinaster* ecosystems (Martin *et al.*, 2012; Vega *et al.*, 2013). Available P in soil can increase after fire proportionally to burn severity (Vega *et al.*, 2013; Pourreza *et al.*, 2014; Dzwonko *et al.*, 2015; Heydari *et al.*, 2017) because burning transforms organic P from litter, soil organisms and vegetation into orthophosphate (Knicker, 2007; Serrasoles *et al.*, 2008). In the longer term, available P content can continue to increase through sorption-desorption processes (Serrasoles *et al.*, 2008). In this way, Romanyà *et al.* (1994) revealed that large ash inputs, typical in high-severity fires, facilitate P sorption to the solid phase. This sorption process hinders P losses by percolation or runoff over the short term, and consequently P can be released over the medium term after fire, thereby increasing the available P content in soils (Serrasoles *et al.*, 2008; Otero *et al.*, 2015). However, fire effects on available P are highly dependent on the type of ecosystem (Certini, 2005; Ferreira *et al.*, 2016) mainly due to differences in soil type (Martin *et al.*, 2012). For example, in calcareous soils, P retention is dominated by precipitation reactions, which forms apatite - a long-term P sequestration form - several months after fire, thereby keeping P unavailable for use by biota (Caon *et al.*, 2014; Otero *et al.*, 2015). This effect may explain the different response obtained in the *P. halepensis* ecosystem, with calcareous soils, where we did not find a positive effect of burn severity on available P.

Soil organic C and total N were not significantly affected by burn severity three years after fire. Contrasting results can be found in the literature about the effects of wildfire on soil C and N concentration on mineral soils (Johnson and Curtis, 2001; Certini, 2005; Neary *et al.*, 2008; Badía *et al.*, 2014), indicating a high dependence on factors that are variable among and within fires, such as the depth of burning, litter inputs, post-fire vegetation or the modification of decomposition rates (Johnson and Curtis, 2001; Caon *et al.*, 2014). Some specific studies focused on burn severity effects on Mediterranean soils have shown significant decreases in soil organic C concentration with burn severity (Vega *et al.*, 2013), whereas others have found increases (Maestrini *et al.*, 2017) or no effects (Mataix-Solera and Doerr, 2004), which is in agreement with the results obtained in this study. In the same way, some studies have found decreases in total N with fire lasting for several years (Alcañiz *et al.*, 2016; Pérez-Varela *et al.*, 2018), whereas other works have suggested that the effects of fire on total N concentration in the mineral soil are not significant or highly variable (Wan *et al.*, 2001; Caon *et al.*, 2014). Furthermore, Tecimen and Sevgi (2011) confirmed in a heating experiment that fire intensity is not a relevant factor on total N in Mediterranean soils, even at temperatures of 350 ºC sustained for four hours.

In relation to soil biochemical properties, we found that soil extracellular enzyme activity rates (for β-glucosidase, urease and acid phosphatase) decreased with burn severity over the medium term after fire. In general, these results are in agreement with those obtained by most studies analysing fire effects on enzymatic activities over the short (Fontúrbel *et al.*, 2012; Vega *et al.*, 2013; Pourreza *et al.*, 2014; Knelman *et al.*, 2015) and medium term post-fire (Gutknecht *et al.*, 2010; Miesel *et al.*, 2011). The negative effects of burn severity on soil extracellular enzyme activities over the short and medium term after fire could be explained by (i) direct enzyme denaturation (Knicker, 2007; Vega *et al.*, 2013; Fultz *et al.*, 2016) occurring when the temperature reached during fire exceeds 60-70 ºC, and the complete destruction of soil enzymes at 180 ºC (Mataix-Solera *et al.*, 2009); (i) the removal of vegetation - which increases with burn severity (Keeley, 2009) and requires longer times to be completely recovered- and consequent changes in the composition of soil microbiota (Knicker, 2007; Mataix-Solera *et al.*, 2009), because they are the main sources of soil enzymes (Tabatabai, 1994); and (iii) the increase in nutrients after burning, such as available N and available P, which often persist over the medium term after fire (Lezberg *et al.*, 2008; Dzwonko *et al.*, 2015). Several authors have indicated the influence of soil nutrients on soil extracellular enzyme activity (Mataix-Solera *et al.*, 2009; Miesel *et al.*, 2011; Pourreza *et al.*, 2014), because organisms generate enzymes to catalyse the release of nutrients. When concentrations of nutrients are high, organisms do not need to produce these extracellular enzymes (Bünemann, 2008), which are energetically costly for biota (Pourreza *et al.*, 2014). Additionally, the release of elevated concentrations of the end reaction products caused by fire may inhibit enzyme activities (Schmidt *et al.*, 1983; Goberna *et al.*, 2012). These reasons could explain the different response of acid phosphatase activity found in the two studied ecosystems, which was inversely related to the concentration of available P in both.

The decreases we found in soil enzyme activities can also be related to the loss of microbial biomass C (Knelman *et al.*, 2015). Although some studies have shown transient increases in microbial biomass C immediately after low severe fires attributed to increases in the concentration of oxidisable C and nutrients (Bárcenas-Moreno and Bååth, 2009; Goberna *et al.*, 2012), decreases in soil microbial C have been largely reported in the literature over the short term after fire (e.g. Miesel *et al.*, 2012; Vega *et al.*, 2013; Lombao *et al.*, 2015; Muñoz-Rojas *et al.*, 2016; Prendergast-Miller *et al.*, 2017), and even up to 11 (Dumonet *et al.*, 1996) or 15 years post-fire (Dooley and Treseder, 2012). The decrease in microbial biomass C content with burn severity can be explained by the direct mortality of microorganisms due to lethal temperatures (50-160 ºC according to Neary *et al.*, 2008) reached during fire (Holden and Treseder, 2013; Muñoz-Rojas *et al.*, 2016), as well as by indirect effects due to changes in the soil environment and vegetation abundance and composition (Hedo *et al.*, 2015). For example, decreases in the availability of organic resources in soils (Pérez-Varela *et al.*, 2015), or the incorporation of organic pollutants and heavy metals during combustion can limit post-fire development of microorganisms (Certini, 2005; Vega *et al.*, 2013). Additionally, decreases in soil microbial C have been related to modifications in substrates such as soil drying or depletion and recovery of litter following fire, depending on burn severity (Dooley and Treseder, 2012).

Our results indicated that burn severity left an important legacy on soil biochemical and microbiological properties over the medium term after fire. We identified that enzymatic activities β-glucosidase and urease, and microbial biomass C may be informative as indicators of burn severity legacy on soils over the medium term after fire in both *P. pinaster* and *P. halepensis* ecosystems. Furthermore, available P content and acid phosphatase activity were identified as potential indicators in the *P. pinaster* ecosystem, which has acidic soils. Biochemical and microbiological properties have been proposed as indicators of soil status after wildfires by other authors (Hedo *et al.*, 2015; Lombao *et al.*, 2015; Muñoz-Rojas *et al.*, 2016), not only because they are affected by fire, but also because of their relevance in the functioning of the ecosystem, since they are involved in processes related to soil conservation through stabilization of soil structure, nutrient cycling and many other physico-chemical properties (Pourreza *et al.*, 2014; Hinojosa *et al.*, 2016).

CONCLUSIONS

Soil chemical (available P), biochemical (β-glucosidase, urease and acid phosphatase) and microbiological (microbial biomass C) properties were affected by burn severity over the medium term after fire in fire-prone pine ecosystems.

In general, soil biochemical (β-glucosidase, urease) and microbiological (microbial biomass C) properties were negatively affected by burn severity, showing similar patterns in the *P. pinaster* and *P. halepensis* ecosystems. Soil available P increased with burn severity in the *P. pinaster* ecosystem (acidic soils), the only ecosystem where acid phosphatase activity was reduced.

We identified β-glucosidase, urease and microbial biomass C as potential indicators of the burn severity legacy on soils in both type of ecosystems (*P. pinaster* and *P. halepensis*) over the medium term after fire. Available P content and acid phosphatase activity were potential indicators in the *P. pinaster* ecosystem.

This study provides a reference for monitoring fire effects in fire-prone pine ecosystems in the Mediterranean Basin. We encourage managers to take into account burn severity when developing hazard reduction and restoration strategies over the medium term after large wildfires.

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APPENDIX

Table 18. Location, environmental description (lithology, elevation, slope, aspect) and burn severity measurements (differenced Normalized Burn Ratio, dNBR; and Twig Diameter Index, TDI) of the studied plots. Reference system for coordinates is ETRS89, Zone 29N for plots of the *Pinus pinaster* ecosystem and Zone 30N for plots of the *Pinus halepensis* ecosystem. Lithological information was obtained from GEODE (2017).

Plot ID	Ecosystem	X UTM	Y UTM	Lithology	Elevation (m)	Slope (°)	Aspect (°)	dNBR	TDI
L002	*P. pinaster*	732437	4682073	Quartzite, sandstone and slate	1104	17	104	254	0.51
L005	*P. pinaster*	729862	4679334	Alluvium, slate, quartzite and silt	1086	11	183	865	0.06
L011	*P. pinaster*	732845	4682626	Alluvium, slate, quartzite and silt	1028	19	195	383	0.57
L013	*P. pinaster*	733489	4683203	Quartzite, sandstone and slate	1029	13	209	453	0.40
L015	*P. pinaster*	729538	4679480	Alluvium, slate, quartzite and silt	1113	12	177	682	0.35
L024	*P. pinaster*	730644	4678809	Conglomerate, sandstone and silt	1004	3	129	901	0.34
L043	*P. pinaster*	730750	4684346	Conglomerate, sandstone and silt	1002	5	97	1039	0.60
L045	*P. pinaster*	732374	4682926	Quartzite, sandstone and slate	1065	16	192	898	0.59
L049	*P. pinaster*	733121	4683445	Quartzite, sandstone and slate	990	6	15	915	0.32
L060	*P. pinaster*	730747	4682832	Quartzite, sandstone and slate	1111	8	211	780	0.06
L061	*P. pinaster*	732123	4682403	Quartzite, sandstone and slate	1103	18	71	691	0.29
L065	*P. pinaster*	731963	4682227	Quartzite, sandstone and slate	1114	10	190	870	0.24
L067	*P. pinaster*	731619	4681427	Conglomerate, sandstone and silt	1067	8	240	864	0.33
L075	*P. pinaster*	732433	4680308	Quartzite, sandstone and slate	1072	12	270	816	0.61
L080	*P. pinaster*	730176	4683983	Quartzite, sandstone and slate	1069	13	49	713	0.42
L082	*P. pinaster*	729524	4683232	Quartzite, sandstone and slate	1204	12	157	794	0.23
L084	*P. pinaster*	730506	4683178	Quartzite, sandstone and slate	1184	15	207	514	0.15
L09	*P. pinaster*	732542	4682393	Quartzite, sandstone and slate	1045	14	31	535	0.34
L091	*P. pinaster*	729557	4683719	Quartzite, sandstone and slate	1122	13	22	699	0.24
L092	*P. pinaster*	730141	4683813	Quartzite, sandstone and slate	1091	10	44	1016	0.36
L093	*P. pinaster*	730453	4683678	Quartzite, sandstone and slate	1082	13	26	876	0.23

L094	*P. pinaster*	732089	4682535	Quartzite, sandstone and slate	1097	17	84	815	0.37
L095	*P. pinaster*	730970	4683617	Quartzite, sandstone and slate	1079	16	3	1113	0.38
L130	*P. pinaster*	732189	4681005	Quartzite, sandstone and slate	1098	17	197	619	0.11
L131	*P. pinaster*	730403	4682268	Alluvium, slate, quartzite and silt	1119	17	185	749	0.04
L133	*P. pinaster*	732601	4681549	Quartzite, sandstone and slate	1031	7	77	828	0.06
V001	*P. halepensis*	682735	4356504	Clay, conglomerate, sand and calcarenite	401	6	287	385	0.45
V002	*P. halepensis*	678772	4351460	Dolomite	491	16	226	516	0.17
V005	*P. halepensis*	682031	4353228	Undifferentiated alluvial	621	2	15	778	0.28
V006	*P. halepensis*	678648	4351972	Sand, sandstone, loam and red clay	586	18	223	546	0.23
V007	*P. halepensis*	682507	4356301	Clay, conglomerate, sand and calcarenite	397	14	292	298	0.11
V008	*P. halepensis*	683026	4356323	Clay, conglomerate, sand and calcarenite	396	5	85	811	0.92
V009	*P. halepensis*	678891	4352043	Red calcareous conglomerate with clay matrix	567	18	184	768	0.77
V011	*P. halepensis*	679739	4353245	Dolomite	708	12	245	806	0.64
V012	*P. halepensis*	680012	4353036	Dolomite	696	7	168	693	0.66
V016	*P. halepensis*	680663	4353374	Limestone and marl	663	7	88	788	0.59
V017	*P. halepensis*	678883	4353931	Sand, sandstone, marls and limestone	759	21	178	394	0.30
V018	*P. halepensis*	681667	4351666	Limestone and marl	651	4	347	634	0.36
V019	*P. halepensis*	679125	4350611	Red calcareous conglomerate with clay matrix	443	18	349	464	0.20
V021	*P. halepensis*	680651	4350852	Versicolor gypsum	378	14	294	787	0.31
V024	*P. halepensis*	678904	4351030	Red calcareous conglomerate with clay matrix	452	15	54	272	0.31
V027	*P. halepensis*	682274	4351895	Limestone and marl	577	19	47	812	0.52
V028	*P. halepensis*	682560	4354588	Undifferentiated alluvial	601	4	32	895	0.74
V029	*P. halepensis*	681820	4355223	Clay, conglomerate, sand and calcarenite	433	14	315	778	0.42
V035	*P. halepensis*	682995	4352953	Sand, sandstone, marl and limestone	615	11	229	702	0.51
V038	*P. halepensis*	681691	4354068	Undifferentiated alluvial	610	15	317	781	0.56
V039	*P. halepensis*	683294	4352553	Limestone, marl and calcarenite	550	7	23	376	0.23
V040	*P. halepensis*	682994	4352339	Sand, sandstone, marl and limestone	515	17	164	398	0.14
V041	*P. halepensis*	680944	4355204	Clay, conglomerate, sand and calcarenite	521	11	95	461	0.25
V042	*P. halepensis*	679589	4354259	Dolomite	713	13	125	450	0.27
V044	*P. halepensis*	678706	4354681	Dolomite	843	12	194	404	0.24

V048	*P. halepensis*	681091	4355938	Clay, conglomerate, sand and calcarenite	442	14	18	697	0.56
V050	*P. halepensis*	681167	4355048	Sand, sandstone, marl and limestone	461	13	157	644	0.54
V051	*P. halepensis*	683047	4352416	Sand, sandstone, marl and limestone	504	23	51	659	0.43
V052	*P. halepensis*	682958	4355088	Sand, sandstone, marl and limestone	463	12	50	751	0.74
V058	*P. halepensis*	681235	4353660	Undifferentiated alluvial	626	3	95	580	0.56

Article V

Remote sensing applied to the study of fire regime attributes and their influence on post-fire greenness recovery in pine ecosystems

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Abstract

We aimed to analyze the relationship between fire regime attributes and the post-fire greenness recovery of fire-prone pine ecosystems over the short (2-year) and medium (5-year) term after a large wildfire, using both a single and a combined fire regime attribute approach. We characterized the spatial (fire size), temporal (number of fires, fire recurrence, and return interval), and magnitude (burn severity of the last fire) fire regime attributes throughout a 40-year period with a long-time series of Landsat imagery and ancillary data. The burn severity was measured by the dNBR (difference of the Normalized Burn Ratio) spectral index, and classified according to the ground reference values of the CBI (Composite Burn Index). Post-fire greenness recovery was obtained through the difference of the NDVI (Normalized Difference Vegetation Index) between pre- and post-fire Landsat scenes. The relationship between fire regime attributes (single attributes: fire recurrence, fire return interval, and burn severity; combined attributes: fire recurrence-burn severity and fire return interval-burn severity) and post-fire greenness recovery was evaluated using linear models. The results indicated that all the single and combined attributes significantly affected greenness recovery. The single attribute approach showed that high recurrence, short return interval and low severity situations had the highest vegetation greenness recovery. The combined attribute approach allowed us to identify a wider variety of post-fire greenness recovery situations than the single attribute one. Over the short term, high recurrence as well as short return interval scenarios showed the best post-fire greenness recovery independently of burn severity, while over the medium term, high recurrence combined with low severity was the most recovered scenario. This novel combined attribute approach (temporal plus magnitude) could be of great value to forest managers in the development of post-fire restoration strategies to promote vegetation recovery in fire-prone pine ecosystems in the Mediterranean Basin under complex fire regime scenarios.

INTRODUCTION

Forest fires are the predominant disturbance in many regions of the world (Thonicke *et al.*, 2001; Bond & Keeley, 2005). This is the case in the Mediterranean Basin, where fire has a significant effect on the functioning and structure of ecosystems (Chuvieco, 1999; Pausas *et al.*, 2008). In this area, forests most affected by fire are the fire-prone pine ecosystems (Moreira *et al.*, 2012), whose species have developed different fire-adaptive strategies to facilitate post-fire survival or reproduction (Richardson, 2000; Tapias *et al.*, 2004; Röder *et al.*, 2008).

The role of fire in fire-prone pine ecosystems can be characterized by describing the fire regime (Richardson, 2000). The term fire regime integrates spatial, temporal, and magnitude attributes (Bergeron *et al.*, 2002; Van Wagtendonk *et al.*, 2007; Turner, 2010). Among the spatial attributes, fire size can hinder the regeneration of vegetation, especially in those ecosystems whose regeneration is not completely dependent on endogenous processes, and therefore depends on seed dispersal from nearby unburned areas (Bond & Keeley, 2005). Temporal attributes include fire recurrence and fire return interval, which are important driving factors of the structure and composition of Mediterranean ecosystems (Eugenio *et al.*, 2006; Espelta *et al.*, 2008; Fernandes & Rigolot, 2007), as well as of their post-fire regeneration capacity. Fire recurrence, is considered as the number of fires that occurred in a given period (Röder *et al.*, 2008). High fire recurrences can reduce the ability of some species to recover, especially obligate seeders (Keeley, 1986; Bond & Keeley, 2005), such as the endemic pine species of the Mediterranean Basin (Richardson, 2000; Tapias *et al.*, 2004), whereas other species, including resprouter shrubs, can be promoted by recurrent fires (Chuvieco, 1999; Calvo *et al.*, 2012). On the contrary, the fire return interval is defined as the time lapse between fires (Van Wagtendonk *et al.*, 2007). In most fire-prone Mediterranean ecosystems, auto-succession is expected when fire return intervals are longer than the period required by plants for regeneration or maturation (Röder *et al.*, 2008). Therefore, the fire return interval can be a determinant parameter in the recovery of ecosystems that need long periods to achieve maturity. This is the case of many pine ecosystems in the Mediterranean Basin, whose dominant tree species need up to 15 years to achieve maturity or to produce a large seed bank ensuring post-fire recruitment (Tapias *et al.*, 2001, 2004; González-De-Vega *et al.*, 2016). The magnitude attributes include burn severity (Van Wagtendonk *et al.*, 2007), considered as the loss of or change in ecosystem biomass (Keeley, 2009), and linked to the ecosystem response after disturbances (Fernandes & Rigolot, 2007; Francos *et al.*, 2016; González-De-Vega *et al.*, 2016). Burn severity is a frequently used metric because it can be quantified after fire (Zavala *et al.*, 2014). Therefore, the knowledge of the spatial patterns of fire regime attributes in large wildfires can contribute to understanding the ecosystem structure (Van Wagtendonk *et al.*, 2007) and post-fire dynamics (Francos *et al.*, 2016; Taboada *et al.*, 2017; Yang *et al.*, 2017). Consequently, this information is of great interest for managers to promote ecosystem resiliency (Krasnow *et al.*, 2017), and to design adequate post-fire restoration strategies.

In the Mediterranean Basin, land use changes that occurred during the last decades have resulted in increases of fuel continuity, which are facilitating the occurrence of a high number of large wildfires (> 500 ha) [Pausas *et al.*, 2008; Pausas & Fernández-Muñoz, 2012). As a consequence, burned areas are increasingly larger and highly heterogeneous, making it difficult to study the spatial patterns of fire regime attributes through field work, and therefore remote sensing methods are essential (Chuvieco, 1999). The starting point to define the spatial and temporal attributes of a fire regime, such as fire size, fire recurrence, and fire-return interval, is the mapping of fire scars (Van Wagtendonk *et al.*, 2007; Krasnow *et al.*, 2017). The moderate-resolution sensors on board Landsat satellites have been largely employed for fire scar mapping (Meddens *et al.*, 2016; Soulard *et al.*, 2016; Hawbaker *et al.*, 2017). Landsat missions have the advantage of providing multispectral imagery for a long historical period (since 1972) (USGS, 2018). An easy and reliable way to discriminate burned areas using Landsat imagery is through a visual analysis of subsequent Landsat scenes (Bowman *et al.*, 2003; Bastarrika *et al.*, 2014; Hawbaker *et al.*, 2017). In addition, Landsat imagery is the most used source of information to map burn severity (Keeley, 2009) through the standard spectral index dNBR (difference of the Normalized Burn Ratio) (Key, 2006). The dNBR uses pre- and post-fire information provided by the Near Infrared, which is sensitive to changes in canopy density and the cellular structure of plant leaves, and the information provided by the Short Wave Infrared, which is primarily related to moisture content (Fernández-García *et al.*, 2018). Although the performance of dNBR has been validated repeatedly in the literature (Chu & Guo, 2014; Parks *et al.*, 2014; Fernández-García *et al.*, 2018), it is convenient to calibrate its thresholds in each specific fire to generate meaningful categorical maps (Key & Benson, 2006; Miller & Thode, 2007). The validation and thresholds calibration of dNBR is traditionally done through the CBI (Composite Burn Index) (Key & Benson, 2006), a field index that integrates several burn severity metrics visually estimated of five vertical strata.

To date, there are many studies determining the influence of a single fire regime attribute on post-fire recovery (e.g., Díaz-Delgado *et al.*, 2003; Viana-Soto *et al.*, 2017), but we did not find studies accomplishing a full approach integrating the spatial, temporal, and magnitude fire regime attributes using remote sensing methods. This integrated approach is of great interest in fire-prone ecosystems, because some fire regime attributes can interact among them and produce synergistic effects on ecosystems (Donato *et al.*, 2009; Stephens *et al.*, 2013). For instance, field studies have suggested that high severities might hinder post-fire recovery, especially in forest systems adapted to recurrent, low severity fires (Broncano & Retana, 2004; Stephens *et al.*, 2013). Conversely, other authors have suggested that the most harmful fires could be those with a long-return interval affecting forests prone to high severity fires (Yang *et al.*, 2017). The expected influence of the joint effect of temporal (fire recurrence and fire return interval) and magnitude (burn severity) fire regime attributes on post-fire vegetation recovery suggests the need to merge these parameters in more realistic combined fire regime attribute categories. Using this novel combined attribute approach could therefore be very useful in studies on post-fire recovery capacity under different real-world fire regime scenarios, allowing the identification of critical burned areas where regeneration could be endangered and require post-fire management actions.

Beyond the fire regime characterization, Landsat imagery can be used to assess post-fire vegetation recovery (Röder *et al.*, 2008; Wittemberg *et al.*, 2007; Fernández-Manso *et al.*, 2016), which is defined as the ecological process aimed at reverting to pre-fire status (Yang *et al.*, 2017). Remote sensing methods to quantify post-fire regeneration include the analysis of vegetation greenness through spectral indices. In this case, the Normalized Difference Vegetation Index (NDVI), proposed by Rouse *et al.* (1973), has become accepted as the standard index (Díaz-Delgado *et al.*, 2003; Chuvieco, 2010; Soulard *et al.*, 2016; Viana-Soto *et al.*, 2017; Yang *et al.*, 2017). The NDVI index is highly sensitive to canopy cover and photosynthetic activity by combining Near Infrared reflectance and the Red reflectance (Chuvieco, 2010). Thus, on the landscape scale, the NDVI is a reasonable proxy for green biomass, providing an overall idea of the vegetation greenness recovery independently of the plant species (Malak *et al.*, 2006).

The aim of this study is to analyze how vegetation greenness responded to fire regime attributes in pine ecosystems in an area where wildfires are very frequent, both over the short (2 years) and medium (5 years) term after the most recent large wildfire, using a remote sensing approach. Specifically, we intend to (i) characterize the spatial, temporal, and magnitude fire regime attributes affecting the fire-prone pine ecosystems in the study area over a 40-year period, (ii) determine the post-fire recovery of vegetation greenness in pine ecosystems, and (iii) analyze the relationship between the characterized fire regime attributes and greenness recovery over the short and medium term after fire, using both a single and a combined fire regime attribute approach. We expected that, relative to the single attribute analysis, the novel combined attribute approach would enable the identification of the most favorable situations for vegetation greenness recovery under complex fire regime scenarios.

MATERIAL AND METHODS

Study Area

The study was conducted within the perimeter of the large wildfire that occurred on 19 August 2012 in Sierra del Teleno (León Province, NW Iberian Peninsula) (Fig. 21), a mountain range largely affected by wildfires (Santamaría, 2015).

The wildfire scar is an area of 119 km^2, 103 km^2 of which were formerly occupied by *Pinus pinaster* Ait. ecosystems (Fig. 21). The *P. pinaster* population of Sierra del Teleno is adapted to a severe crown fire regime, bearing a high percentage of serotinous cones (Tapias *et al.*, 2004). However, due to increased fire recurrence in recent decades (Santamaría, 2015), *P. pinaster* forests are turning into successional shrublands dominated by *Pterospartum tridentatum* (L.) Willk., *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. (Taboada *et al.*, 2017), as in many areas in the Western Mediterranean Basin (Fernandes & Rigolot, 2007). The orography is heterogeneous, ranging from 836 to 1493 m.a.s.l. Soils are acidic (4.86 ± 0.14; mean ± standard error pH), developed over siliceous lithologies such as quartzite, conglomerate, sandstone, and slate (GEODE, 2018). The study area is on the limit of the Mediterranean region, whose climate is classified as temperate with dry and temperate summers (AEMET-IM, 2011), and characterized by a mean annual precipitation of between 600 and 800 mm and a mean annual temperature of 8-11 °C (Ninyerola *et al.*, 2005).

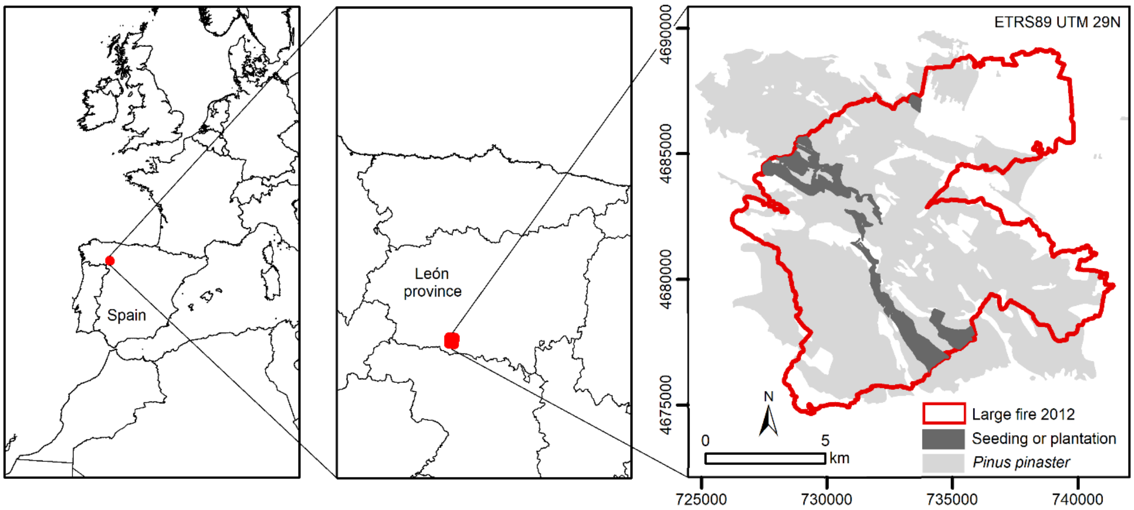

Figure 21. Location of the study area. The perimeter of the large wildfire that occurred in 2012, the natural occurrence of *Pinus pinaster*, and post-fire management actions applied after the large fire of 2012 are indicated.

Methodology

Landsat Database

In order to characterize (a) the spatial (average fire size), temporal (number of fires, fire recurrence, and fire return interval), and magnitude (burn severity) attributes of the fire regime, and (b) the post-fire recovery of vegetation greenness 2 (short term) and 5 (medium term) years after the 2012 large wildfire, we built a database composed of 80 Landsat images, covering the period 1975-2017 (Fig. 22). The scenes before 1978 were used as a reference to identify the wildfires that occurred between 1978 and 1980. When available, at least one annual image of the study area without clouds was included in the database, with preference for those taken in late summer. The database encompassed images from the Landsat 2 (MSS sensor), Landsat 4 (TM sensor), Landsat 5 (TM sensor), Landsat 7 (ETM + sensor), and Landsat 8 (OLI sensor) satellites. The images for 1975-1990 and 1999-2017 were obtained from the Earth Explorer server of the U.S. Geological Survey (https://earthexplorer.usgs.gov), whereas those for 1991-1998 were acquired from the European Space Agency (https://earth.esa.int).

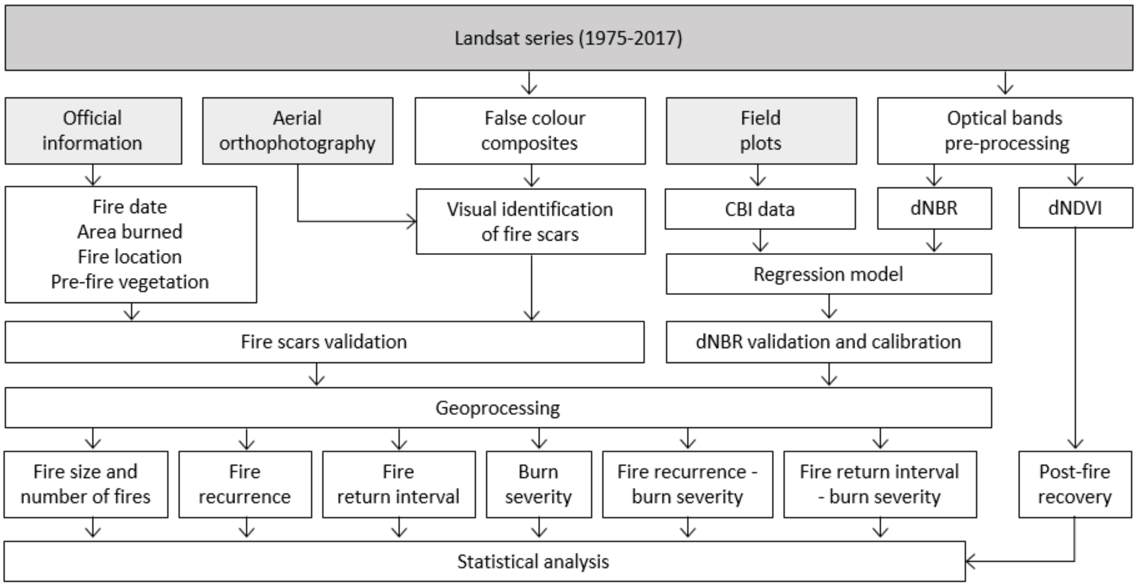

Figure 22. Methodology flowchart.

Fire Regime Characterization

Fire scars from the wildfires that occurred between 1978 and 2017 were identified by visual analysis of consecutive Landsat false color composites (Fig. 22). We displayed the false color composite RGB 564 for the images obtained by the MSS sensor, RGB 541 for the TM and ETM + sensors, and RGB 652 for the OLI sensor. Orthophotography from 1980 taken by the National Institute for Agrarian Reform and Development flight (1977-1983) was used as ancillary data to identify fire scars during a period with low availability of Landsat images, as well as to support the MSS imagery, which has a lower spatial resolution (60 m). The perimeters of every wildfire were manually digitized using a scale of 1:5000 in ArcMAP 10.6 (Esri España, 2018). The minimum mapping unit used for hand drawing was 0.01 km^2, as this is the limit between an incipient fire and a wildfire according to the Spanish Administration classification (MAPAMA, 2018), and because it surpasses the minimum identifiable fire size using imagery from TM sensors and later (Miller *et al.*, 2002). In order to ensure that the digitized scars were the consequence of wildfires, and not the result of other potential land uses (e.g., ploughing, cutting, clearcutting, etc.), we linked every digitized perimeter to an official wildfire report (1978-2017) provided by the Nature Protection Section of the Regional Administration, which included information on the fire date, location, extent, and burned vegetation for the entire study period, and also fire perimeters after 2007. All wildfires recorded by the official reports were matched with the fire perimeters mapped by the authors. The validated map of the fire scars from 1978 to 2017 was the source of information to determine the following: (i) the total number and average size of the wildfires in each decade (1978-1987, 1988-1997, 1998-2007, and 2008-2017), (ii) wildfire recurrence during the study period by classifying the study area into low (1 fire), moderate (2 fires), and high (≥ 3 fires) recurrence, and (iii) the fire return interval as the number of years between the 2012 large wildfire and the preceding fire, by classifying the study area into short (years ≤ 15), intermediate (15 < years ≤ 30) and long (years > 30) return intervals.

In order to characterize the burn severity of the 2012 large wildfire that occurred in 19 August, we calculated the dNBR spectral index (Key, 2006) from the Landsat 7 ETM+ scenes of 20 September 2011 (pre-fire situation) and 6 September 2012 (post-fire). The Landsat 7 ETM+ scenes obtained are a Digital Numbers (DN) product geometrically rectified and radiometrically corrected (Landsat L1T processing level). The scenes were subset and optical bands were pre-processed (Fig. 22). Pre-processing included a conversion of DN to radiance values. Then, radiance images were atmospherically corrected by using the Fast Line-of-sight Atmospheric Analysis (FLAASH) module. To select the appropriate atmosphere model and input parameters in FLAASH, we used the MODIS water vapor product (MOD05), meteorological data (NOAA), and mean elevation values according to Fernández-García *et al.* (2018). A Delaunay interpolation was applied to fill the gaps of the Scan Line Corrector (SLC) (Ali & Salman, 2015). Corrected bands were used to calculate the dNBR index according to the following formulas:

$$NBR = (\rho 4 - \rho 7)/(\rho 4 + \rho 7)$$

$$dNBR = (1000\ (NBRpre - NBRpost)) - offset$$

where “ρ” is the reflectance of each specific corrected band and “offset” is the average index value in unchanged areas outside the fire perimeter, to account for differences in phenology between Landsat scenes (Key, 2006). For the offset calculation, we selected *P. pinaster* ecosystems unburned for the last 40 years, and less than 1.5 km from the fire scar, in which we randomly sampled 78 pixels (1% of the area that met these specifications).

The performance of the burn severity spectral index (dNBR) was field-validated with the ground reference CBI by performing linear regression models and examining the statistical significance and coefficient of determination (R^2) of the relationship. To determine burn severity in the field we randomly established 54 30 m × 30 m plots in the *P. pinaster* ecosystem within the first three months after the 2012 large wildfire. The positions of all field plots were GPS recorded. In each field plot we calculated burn severity following a CBI-based protocol described in Fernández-García *et al.* (2018), in which several variables of five vertical strata are rated, obtaining a final ground burn severity value ranging from 0 (unburned) to 3 (high severity). Following Quintano *et al.* (2015), we established two burn severity categories: low-moderate (hereafter low severity) (CBI ≤ 2.25) and high (CBI > 2.25), and used the linear models to calibrate the dNBR thresholds according to the CBI values obtained in the field.

We then combined the temporal (fire recurrence and fire return interval) and magnitude (burn severity of the 2012 large wildfire) fire regime attributes and spatially analyzed the extent of each of the following combinations: (i) fire recurrence (3 classes) and burn severity (2 classes), and (ii) fire return interval (3 classes) and burn severity (2 classes).

Post-Fire Greenness Characterization

The post-fire recovery of vegetation greenness after the 2012 large wildfire was evaluated as the difference of the Normalized Difference Vegetation Index (dNDVI) (Díaz-Delgado *et al.*, 2003; Hope *et al.*, 2007) 2 (short term) and 5 (medium term) years after the fire (Fig. 22). We selected the Landsat 7 ETM+ scenes from 20 September 2011 (pre-fire situation), 27 August 2014 (short term) and 20 September 2017 (medium term). Optical bands were subset and pre-processed equally as for dNBR calculation. Corrected bands were used to calculate the dNDVI index according to the following formulas:

$$NDVI = (\rho 4 - \rho 3)/(\rho 4 + \rho 3)$$

$$dNDVI = (NDVIpre - NDVIpost) - offset$$

where "ρ" is the reflectance of each specific band, and "offset" is the average index value in unchanged areas outside the fire perimeter to account for differences in phenology between Landsat scenes (Key, 2006). For the offset calculation, we selected *P. pinaster* ecosystems unburned for the last 40 years, and less than 1.5 km from the fire scar, in which we randomly sampled 78 pixels (1% of the area that met these specifications). dNDVI values ≤ 0 indicate the full recovery of vegetation greenness.

Sampling

The categories of fire regime attributes and values of post-fire greenness recovery were extracted using a random sampling design with a minimum distance between sample points of 60 m (two Landsat 7 ETM+ pixels). We distributed 932 sample points within the 2012 fire scar, in the area formerly dominated by *P. pinaster* ecosystems where no post-fire management actions were accomplished (Fig. 21), excluding paths and the Landsat SLC failure zones. The same procedure was repeated in unburned areas adjacent (< 1.5 km) to the fire perimeter (i.e., unburned *P. pinaster* ecosystems for at least 40 years), distributing 78 sample points. The number of sampling points corresponds to 1% of Landsat pixels of the burned and unburned areas with the specified characteristics (Quintano *et al.*, 2015).

Data Analysis

In order to analyze the effects of the single and combined fire regime attributes (fire recurrence, fire return interval, burn severity, fire recurrence-burn severity, and fire return interval-burn severity; categorical explanatory variables) on vegetation greenness (dNDVI 2 and 5 years after the fire; continuous response variables), we performed linear models (LMs) on which we conducted an Analysis of Variance (ANOVA) with pairwise multiple comparison of means (Tukey HSD). The goodness of fit of the models was assessed by visual analysis of homoscedasticity and normality of the residuals. Global spatial autocorrelation in the model residuals was checked using Moran's index (I), indicating that it had no effect on the study results (Moran's I < |0.1|) (Diniz-Filho *et al.*, 2011).

All data analyses were carried out with R software, version 3.4.0 (R Core Team, 2017), using the "spdep" package (Bivand & Piras, 2015).

RESULTS

Fire Regime Attributes

We identified a total of 28 wildfires (size ≥ 0.01 km^2) between 1978 and 2017 combining Landsat imagery and ancillary data (Fig. 23). There were no fires subsequent to the 2012 large wildfire. In the last two decades (1998-2007 and 2008-2017), there was a decrease in the number of fires, and an increase in fire extent, reaching an average fire size of 29.74 km^2 during 2008-2017 (Fig. 24).

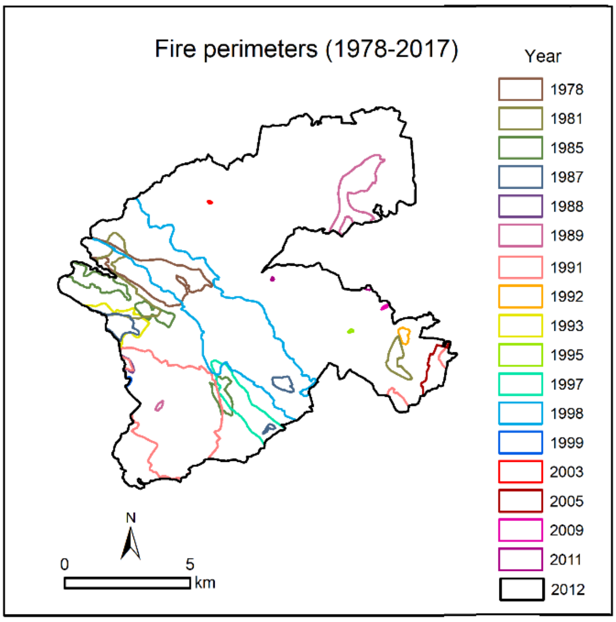

Figure 23. Fire perimeters and year of wildfire occurrence from 1978 to 2017.

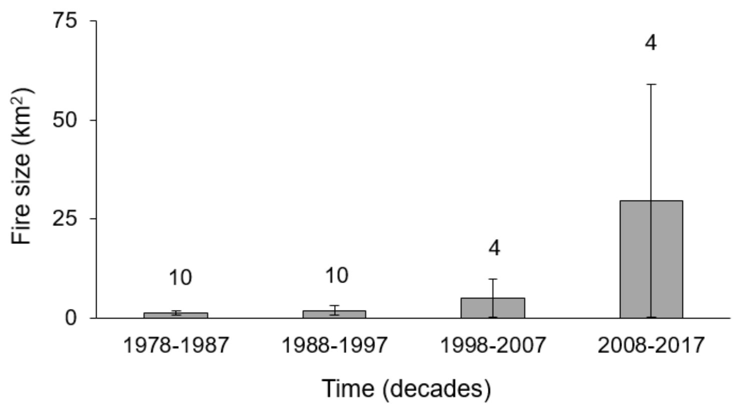

Figure 24. Average (± standard error) size of wildfires by decade from 1978 to 2017 within the study area (the fire scar of the 2012 large wildfire). Numbers above bars indicate the total number of wildfires in each period.

The majority of the study area (70.95 km^2) has not experienced any other fire prior to the large wildfire that occurred in 2012, and therefore was classified in the low fire recurrence category (1 wildfire from 1978 to 2017) (Fig. 25a) and long fire return interval (> 30 years) (Fig. 25b).

The correlation between the values of the spectral burn severity index (dNBR) and the ground burn severity index (CBI) was statistically significant ($P < 0.05$), with a high coefficient of determination ($R^2 = 0.88$). For the most part (61.02 km^2), the burn severity of the 2012 large wildfire was high (Fig. 25c).

The combined fire regime attribute approach differentiated six fire recurrence-burn severity scenarios, with the low recurrence-low severity (38.38 km^2) and low recurrence-high severity (32.57 km^2) scenarios being the most extensive (Fig. 26a). Correspondingly, there were six fire return interval-burn severity scenarios, with a spatial dominance of the areas with a long time-period between the 2012 large wildfire and the preceding fire, independently of burn severity (Fig. 26b).

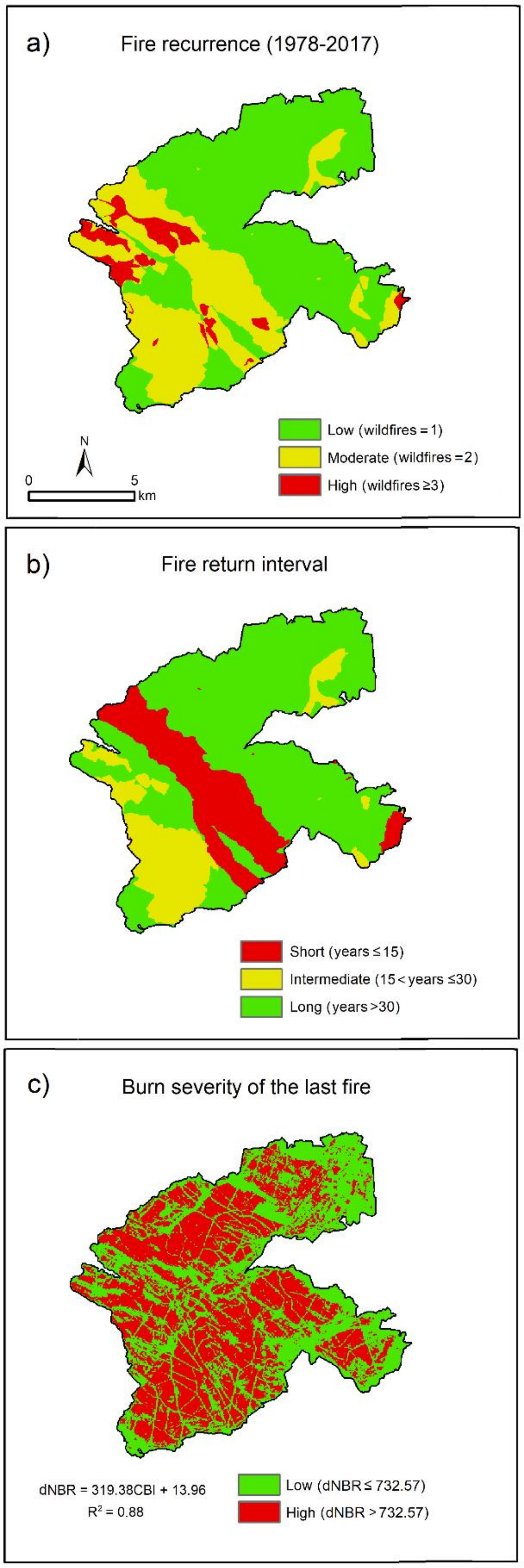

Figure 25. Spatial patterns of fire recurrence (total number of wildfires from 1978 to 2017) (a), fire return interval (number of years between the 2012 large wildfire and the preceding fire) (b), and burn severity of the 2012 large wildfire, measured by the difference of the Normalized Burn Ratio (dNBR) and classified according to the ground reference values of the Composite Burn Index (CBI) (c). The results of the linear regression between dNBR and CBI values for the 2012 large wildfire are also indicated.

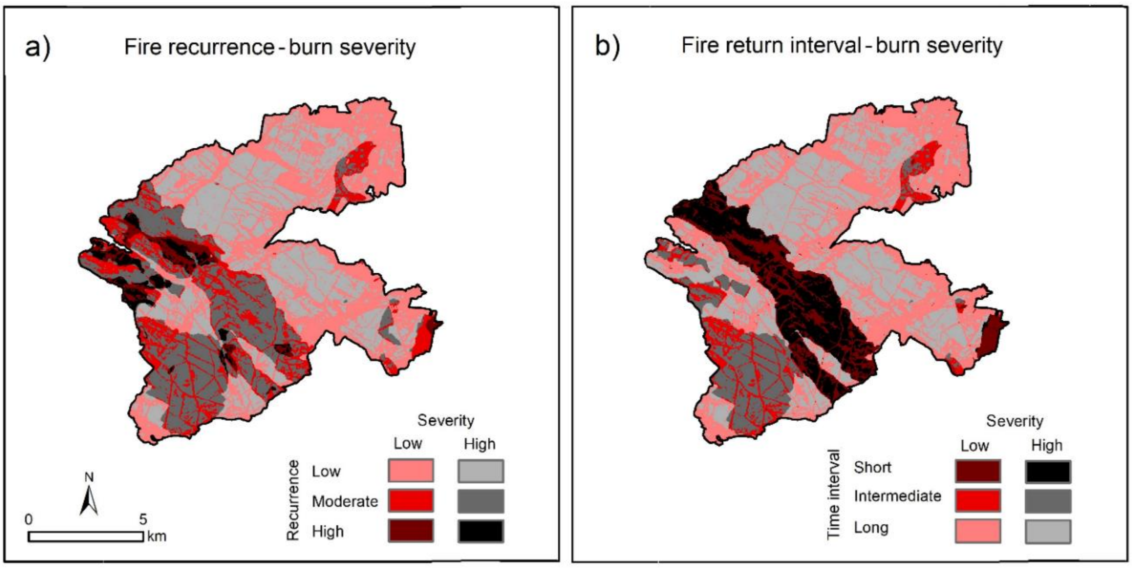

Figure 26. Combined fire regime attribute approach identifying the spatial patterns of the different fire recurrence-burn severity (a) and fire return interval-burn severity (b) scenarios. See Fig. 25 for further information.

Post-Fire Greenness Recovery

The vegetation greenness over the short term (2 years after the 2012 large wildfire) was not recovered in any fire regime scenario (i.e., all dNDVI values > 0) (Fig. 27a). On average, the short-term dNDVI value of the fire scar was 0.59 ± 0.11 (mean ± standard deviation), indicating low vegetation recovery 2 years after fire.

However, the post-fire recovery of vegetation greenness over the medium term (5 years after the 2012 large wildfire) was greater than over the short term (0.10 ± 0.08). It was found that 10.25% of the burned surface attained the greenness values of the pre-fire situation (dNDVI ≤ 0.00) (Fig. 27b) nonetheless, the remaining 89.75% of the surface had lower greenness values than the pre-fire situation (dNDVI > 0).

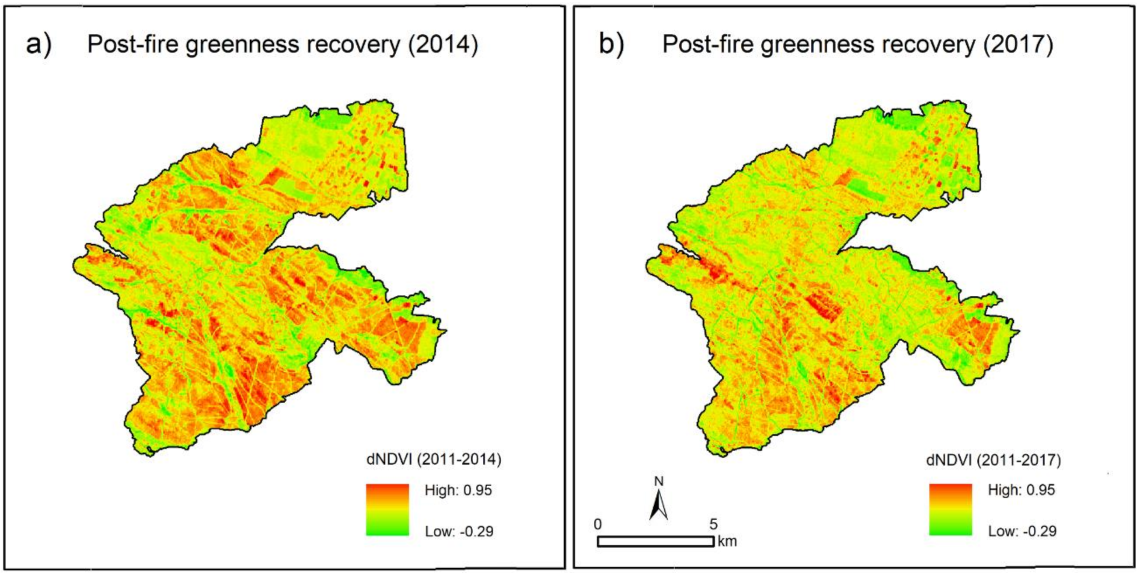

Figure 27. Spatial patterns of post-fire recovery of vegetation greenness over the short term (2 years) (a) and medium term (5 years) (b) after the 2012 large wildfire.

Effects of Fire Regime Attributes on Post-Fire Greenness Recovery

Every single and combined fire regime attribute had a statistically significant effect ($P < 0.001$) on the recovery of vegetation greenness (dNDVI), both over the short and medium term after the 2012 large wildfire (Table 19). The combined fire regime attributes always showed higher R^2 values than the single ones, indicating a higher explanatory capacity. In general, greenness recovery was greater (i.e., lower dNDVI values) over the medium than short term for the single and combined fire regime attributes (Figs. 28, 29).

Table 19. Results of the linear models [‘anova()’ outputs] showing the effects of the single and combined fire regime attributes (fire recurrence, fire return interval, burn severity, fire recurrence-burn severity and fire return interval-burn severity) on post-fire greenness recovery over the short [dNDVI (2011-2014)] and medium [dNDVI (2011-2017)] term after the 2012 fire. dNDVI = difference of the Normalized Difference Vegetation Index. Df = degrees of freedom. Significant p-values are in bold face.

Response variable	Predictor variable	Df	R^2	F-value	*P*-value
dNDVI (2011-2014)	Fire recurrence	3	0.348	177.522	<**0.001**
	Fire return interval	3	0.352	180.058	<**0.001**
	Burn severity	2	0.338	254.305	<**0.001**
	Fire recurrence-burn severity	6	0.380	101.405	<**0.001**
	Fire return interval-burn severity	6	0.394	107.361	<**0.001**
dNDVI (2011-2017)	Fire recurrence	3	0.193	79.529	<**0.001**
	Fire return interval	3	0.142	55.070	<**0.001**
	Burn severity	2	0.272	186.045	<**0.001**
	Fire recurrence-burn severity	6	0.313	75.279	<**0.001**
	Fire return interval-burn severity	6	0.287	66.604	<**0.001**

The recovery of vegetation greenness was significantly greater in the high fire recurrence scenario both over the short (Fig. 28a) and medium (Fig. 28b) term. Nevertheless, during the study period, none of the fire recurrence categories was completely recovered.

Correspondingly, the short fire-return interval scenario had significantly higher vegetation greenness recovery over the short term (Fig. 28c). This difference among fire-return interval categories was attenuated over the medium term, as both the short and long fire-return situations had similar values for greenness recovery (Fig. 28d). However, none of the fire return interval categories attained the dNDVI values of the unburned situation.

The burn severity of the 2012 large wildfire showed an inverse relationship with the recovery of vegetation greenness over the short (Fig. 28e) and medium (Fig. 28f) term after fire (i.e., the low burn severity category had the greatest greenness recovery). Even so, the dNDVI values of both low and high burn severity classes were significantly higher than those of the unburned situation.

Generally, the combination of temporal (fire recurrence and fire return interval) and magnitude (burn severity) fire regime attributes resulted in wider ranges of greenness recovery values (Fig. 29) than those obtained with single fire regime attributes (Fig. 28). Also, the differences in greenness recovery between low and high burn severity categories over the short term were lessened when combined with either the high fire recurrence or short fire return interval (Fig. 29a,c). Consequently, there were no statistically significant differences ($P \geq 0.05$) in greenness recovery between (i) high recurrence-low severity and high recurrence-high severity combinations (Fig. 29a), and (ii) short return interval-low severity and short return interval-high severity combinations (Fig. 29c) 2 years after fire.

Focusing on fire recurrence-burn severity, the highest recovery of the vegetation greenness was attained at the high recurrence scenarios (high recurrence-low severity and high recurrence-high severity) over the short term (Fig. 29a), and at the high recurrence-low severity scenario over the medium term (Fig. 29b), which reached the closest dNDVI value to the unburned situation among all the analyzed single and combined fire regime scenarios (Figs. 28, 29).

Similarly, on analysis of the fire return interval-burn severity, the greatest greenness recovery corresponded to the short fire-return interval scenarios (short interval-low severity and short interval-high severity) over the short term (Fig. 29c), and to the three low severity combinations (short interval-low severity, intermediate interval-low severity, and long interval-low severity) over the medium term (Fig. 29d).

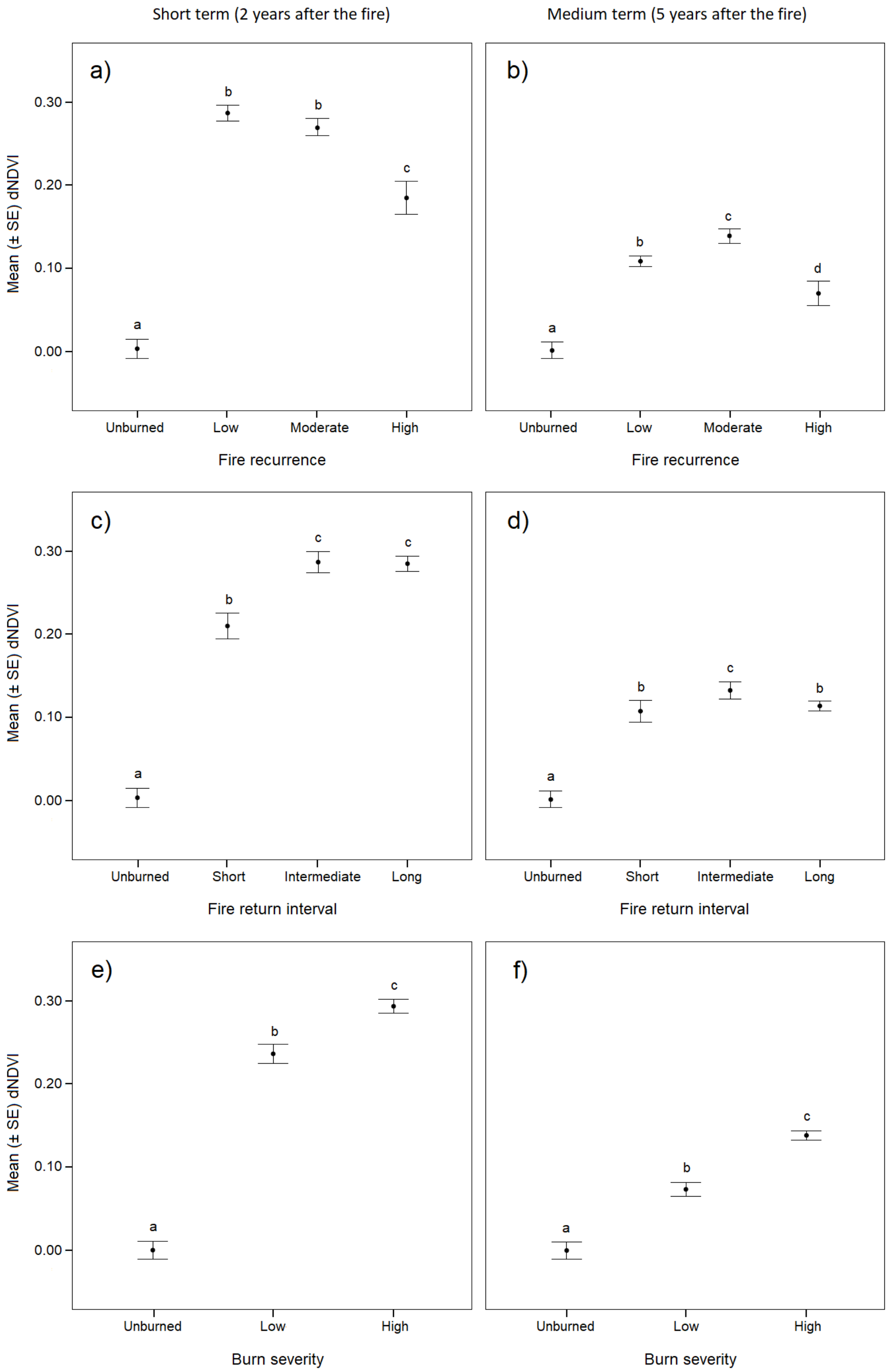

Figure 28. Mean (± standard error) vegetation greenness values measured by the difference of the Normalized Difference Vegetation Index (dNDVI) over the short (2 years) and medium (5 years) term after the 2012 large wildfire for the different scenarios of fire recurrence (total number of wildfires from 1978 to 2017) (a,b), fire return interval (number of years between the 2012 large wildfire and the preceding fire) (c,d), and burn severity of the 2012 large wildfire as the difference of the Normalized Burn Ratio (dNBR) (e,f). Different letters above the error bars (a, b, c, d) denote statistically significant differences between mean values ($P < 0.05$).

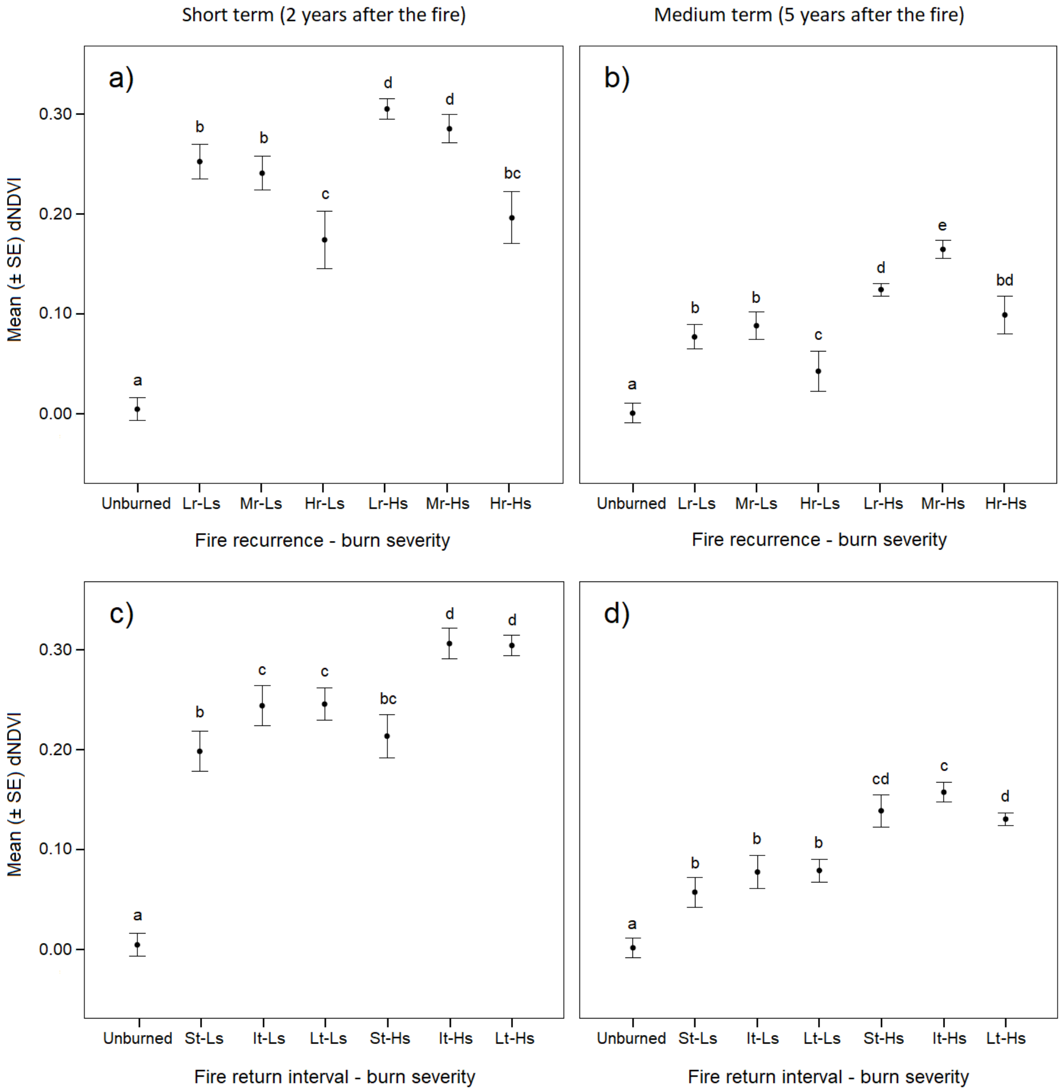

Figure 29. Mean (± standard error) vegetation greenness values measured by the difference of the Normalized Difference Vegetation Index (dNDVI) over the short (2 years) and medium (5 years) term after the 2012 large wildfire for the different scenarios identified by the combined fire attribute approach: fire recurrence-burn severity (a,b), and fire return interval-burn severity (c,d). Lr, Mr, and Hr indicate low, moderate and high fire recurrence, respectively. Ls and Hs indicate low and high burn severity, respectively. St, It, and Lt indicate short, intermediate and long fire return interval. Different letters above the error bars (a, b, c, d, e) denote statistically significant differences between mean values ($P < 0.05$). See Fig. 28 for further information.

DISCUSSION

In this work, we have shown the utility of remote sensing tools to analyze fire regime attributes and their effects on vegetation greenness recovery after large wildfires. Landsat imagery and ancillary data were used to identify the 28 wildfires that occurred in a 40-year period (1978-2017) in Sierra del Teleno within the perimeter of the 2012 large fire, resulting in a spatially heterogeneous fire history and a wide range of post-fire greenness recovery. Our results demonstrated that all the fire regime attributes that were spatially characterized, whether they followed a single (fire recurrence, fire return interval, burn severity) or combined approach (fire recurrence-burn severity and fire return interval-burn severity), were significantly related to the post-fire recovery of vegetation greenness. However, the combination of fire recurrence or fire return interval with burn severity was able to identify a larger variety of scenarios of post-fire greenness recovery than the single approach, the combined attributes being the best predictors of post-fire recovery of vegetation greenness.

The fire scars analysis allowed us to identify the temporal evolution of fire size and number throughout the four studied decades in our specific study site. The results, which have to be interpreted considering the limited extent of the studied area and period, indicated a decrease in the number of fires and an increase in the extent of the burned area during the studied period. This is an opposite trend to that reported for Southern European countries and for Spain, where, in general, the average fire size has decreased and the number of fires has increased since the 1980s (San-Miguel-Ayanz *et al.*, 2016). However, other authors have found different trends in particular regions within the Iberian Peninsula. For instance, Pausas *et al.* (2004) indicated an unclear trend for the size of the area burned in the Eastern Iberian Peninsula between 1968 and 2000, which was closely related to summer rainfall. The patterns of the increasing average size of fires in our study area could be explained by the contribution of the large wildfires that occurred in 1998 and 2012, which burned 31% and 100% of the study area, respectively. Furthermore, the fuel depletion caused by these two large fires could prevent subsequent wildfires during the following years, as fire occurrence in Mediterranean ecosystems is fuel-limited (Pausas & Paula, 2012). The occurrence of such large wildfires is increasing in some regions in the world (Turner, 2010; Bowman *et al.*, 2017) and is relatively recent in Spain (Pausas *et al.*, 2008; Pausas & Fernández-Muñoz, 2012), the study area being a good example.

The fire recurrences found in this study were consistent with those in other fire-prone pine forests within the Iberian Peninsula (Röder *et al.*, 2008; Lucas-Borja *et al.*, 2016) for a 25-year period or longer. Fire recurrence affected post-fire greenness recovery over the short and medium term post-fire, the high recurrence scenario being the most recovered. Recovery in the different fire recurrence scenarios can be explained by the vegetation composition in the pre-fire situation, because post-fire regeneration in *P. pinaster* ecosystems is via auto-succession (Fernandes & Rigolot, 2007; Tessler *et al.*, 2016). In this sense, the areas classified as high recurrence were occupied mainly by shrubs and herbaceous species (4.53% pines, 36.89% shrubs, 38.13% grasses) (SIOSE, 2011), which are promoted by high recurrences and additionally, are rapidly recovered after fire (Calvo *et al.*, 2008; Tessler *et al.*, 2016; Taboada *et al.*, 2017). Conversely, the low recurrence areas were predominantly covered by pines (57.53% pines, 13.25% shrubs, 19.16% grasses) (SIOSE, 2011), which require more time than shrubs to completely recover (Rodrigo *et al.*, 2004).

The fire return intervals in the study area ranged from < 15 years to > 30 years, being within the typical intervals reported for Mediterranean ecosystems (varying from 10 to up to more than 120 years) (Thonicke *et al.*, 2001). The areas burned in a short-return interval were more rapidly recovered than those burned in an intermediate and long interval, probably due to the dominance of shrubs (6.72% pines, 38.80% shrubs, 32.11% grasses) (SIOSE, 2011). In this sense, it is expected that shrubs such as those present in our study area (Ericaceae and Cistaceae) increase their dominance in short fire interval scenarios, optimal at fire intervals of 5 and 10 years, respectively (Pausas, 1999). Conversely, Mediterranean fire-prone pine forests have their optimum conditions at fire return intervals over 40 years, and only disappear when intervals are shorter than 5 years (Pausas, 1999).

The burn severity obtained through the dNBR spectral index indicated that the large wildfire of 2012 was predominantly severe, with the low severity class confined to valleys, areas close to paths, and limits of the fire scar as previous studies pointed out (Quintano *et al.*, 2015, 2017). *P. pinaster* forest ecosystems are frequently subjected to high severity fires, because they are highly flammable and prone to crown fires (Calvo *et al.*, 2008; Fernandes & Rigolot, 2007; Pausas & Fernández-Muñoz, 2012). The relationships between burn severity and post-fire greenness recovery indicated that this fire regime attribute was a crucial factor over the short (2 years) and medium (5 years) term after the fire (Maia *et al.*, 2012; Fernández-Manso *et al.*, 2016; Viana-Soto *et al.*, 2017). In low burn severity areas, greenness recovery was higher, because some pines (between 0 and 80%) remained alive (Fernández-García *et al.*, 2018), and additionally, their canopy seed bank guaranteed seed dispersal over the medium term after fire (Calvo *et al.*, 2008). The understory shrub community is also less affected in low severity scenarios, with a general survival rate of up to 80% (Key & Benson, 2006). Conversely, in severely burned areas, pine and shrub mortality involves a significant canopy change (Fernández-García *et al.*, 2018; Key & Benson, 2006). This results in considerable changes in vegetation greenness after the fire. However, over that span of time (2-5 years), the ecosystem has shown a large recovery in both low and high severities, as other researchers have found (Fernández-Manso *et al.*, 2016). This could be related to the high pine seedling establishment that follows crown fires in Mediterranean fire-prone forests such as those dominated by *P. pinaster* (Pausas *et al.*, 2008; Calvo *et al.*, 2008), and to the high resiliency of the present understory community, which can be completely recovered in 9 years even after severe disturbances (Calvo *et al.*, 2002).

The combined approach merging fire temporal (fire recurrence and fire return interval) and magnitude (burn severity) attributes represented a large variety of scenarios, being more representative than the other analyzed products of the high spatial heterogeneity, which is typical after large wildfires (Turner, 2010). Among the identified scenarios, the two burn severity classes were well represented in the three fire recurrence and fire return interval scenarios. This result suggests that under the Mediterranean climatic conditions of the study site, even the high recurrence (3 or 4 fires in 40 years) and short fire interval (< 15 years) scenarios had fuel loads enough to originate high burn severity scenarios (Bond & Keeley, 2005). Moreover, the combined fire regime attributes were the best predictors of post-fire greenness recovery, and they differentiate more extreme situations than the single approach over the short and medium term after the fire, apparently due to the cumulative effect of the fire temporal and magnitude fire regime attributes. Thus, the fire recurrence-burn severity and fire return interval-burn severity classification showed the most affected scenarios and the closest scenarios to the unburned situation.

Our study shows the possibility of carrying out integral assessments of fire regime attributes (spatial, temporal and magnitude) using remote sensing methods, and indicates a high predictive capacity of fire regime attributes (temporal, magnitude and combined) for post-fire greenness recovery after large wildfires in fire-prone pine ecosystems. This information can help managers to predict the post-fire greenness recovery capacity of fire-prone *P. pinaster* forests according to their specific fire regime, and therefore could be used to adopt the appropriate management strategies aimed at reverting to the pre-fire status in each scenario (Moreira *et al.*, 2012).

In order to generalize our results, we encourage conducting future studies analyzing the relationship between fire regime attributes and post-fire greenness recovery in other wildfires and in different regions. Studies in other types of ecosystems are also recommendable, because the resilience of the communities can vary considerably (Johnstone *et al.*, 2016). We also highlight the importance of differentiating the structure and composition of the vegetation (Yang *et al.*, 2017) for a better understanding of greenness recovery after different fire regime scenarios in fire-prone pine forests in the Mediterranean Basin.

CONCLUSIONS

The spatial, temporal and magnitude attributes of a fire regime are important driving factors in the post-fire recovery of Mediterranean pine ecosystems, especially in areas subjected to increasingly more extensive recurrent fires (Fernandes & Rigolot, 2007; González-De-Vega *et al.*, 2016; Moreira *et al.*, 2011). Under the growing complexity of wildfire regimes, our findings demonstrated that integrating temporal (fire recurrence and return interval) and magnitude (burn severity) attributes using remote sensing methods allows for a more realistic identification of the most favorable scenarios for vegetation greenness recovery after fire, relative to the typical single fire regime attribute analysis of most research. This novel combined attribute approach evidenced that high fire recurrence and short fire return interval combinations with any category of burn severity (low or high) attained the greatest recovery of vegetation greenness over the short term [2 years after the most recent large (> 500 ha) fire]. Whereas the high fire recurrence-low burn severity situation, and the low severity combinations with any category of fire return interval (short, intermediate or long) were the most propitious scenarios for greenness recovery over the medium term (5 years after fire). Moreover, the results of the spatial analysis of the different combined scenarios using remote sensing methods highlighted the outstanding heterogeneity in the post-fire greenness recovery of pine ecosystems subjected to an intricate reality of fire regimes with varying attributes over vast burned areas. This information will be highly valuable to forest managers facing the consequences of even more acute fire regimes, as it will aid the implementation of effective restoration actions in extensively burned areas when the main restoration goal is the full recovery of vegetation greenness. Nonetheless, we encourage future remote sensing studies aimed at a better understanding of the impact of combined fire regime attributes on post-fire greenness recovery in fire-prone pine ecosystems that further integrate the spatial variation of pre-fire vegetation (Yang *et al.*, 2017).

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Article VI

The role of fire frequency and severity on the regeneration of Mediterranean serotinous pines under different environmental conditions

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Abstract

Fire frequency and burn severity may increase in pine forests in the Mediterranean Basin under the warmer and drier climate projected for this region. Our study aims to evaluate the role of fire frequency and burn severity in the post-fire recruitment and development of Mediterranean serotinous pines under different environmental conditions. Two pine forests representing contrasting climatic conditions and soil types that support serotinous pines in the Iberian Peninsula and affected by large wildfires in summer 2012, were selected. In these two study sites, we determined the number of wildfires between 1978 and 2012 and the burn severity of the last fire (2012 at both sites) through the dNBR spectral index. Three and four years after the wildfires, we sampled the density, cover and height of pine seedlings and the cover of woody understory species in 1296 1-m^2 plots. The results indicated that the density and cover of pine seedlings were low after two fires combined with high severities, as well as after three fires, regardless of burn severity. Seedling recruitment after three fires was particularly threatened in the most arid study site (0.01 seedlings m^{-2}), resulting in low seedling cover (0.01%). Seedling height decreased with fire frequency in both study sites, and with burn severity owing to fire-induced shifts in soil fertility and microclimatic conditions. There was a significant negative effect of the cover of woody understory species on the recruitment and cover of pine seedlings. Our results suggest that the effects of increasing fire frequency and severity on pine regeneration may be aggravated under arid conditions. Additionally, this study encourages forest managers to avoid the occurrence of frequent crown fires in order to prevent the loss of serotinous pine forest, and provides useful information to predict the scenarios in which post-fire restoration actions would be helpful.

INTRODUCTION

Fire plays a critical role in many ecosystems worldwide (Pausas & Vallejo, 1999), particularly in the Mediterranean Basin, determining the distribution, composition and structure of vegetation, and acting as a selective force for plant traits (Keeley *et al.*, 2012). The vegetation in Mediterranean ecosystems recovers after fires mainly from endogenous sources (Moreno & Oechel, 2012). In general, plant species in this region can regenerate after wildfires by resprouting from tissues that survive fire (resprouters), by seedling recruitment (obligate seeders), or by the combination of both mechanisms (facultatives) (Calvo *et al.*, 1998, 2002a, 2002b; Pausas & Vallejo, 1999; Pausas & Keeley, 2014).

All the pine species naturally distributed across the Mediterranean Basin are obligate seeders (Tapias *et al.*, 2001; Pausas *et al.*, 2008). *Pinus pinaster* Ait. and *Pinus halepensis* Mill. are two of the most widespread species (Richardson, 2000; Tapias *et al.*, 2004). Both pines are highly flammable (Fernandes *et al.*, 2008), and dominate forest ecosystems with a continuous and high (up to 1.5 m) woody understory layer. This fuel profile facilitates the occurrence of crown fires that cause a high mortality rate (Daskalakou & Thanos, 2004; Fernandes *et al.*, 2008; Calvo *et al.*, 2008). As an adaption to this fire regime (Keeley *et al.*, 2011; He *et al.*, 2012; Hernández-Serrano *et al.*, 2013), *P. halepensis* and most *P. pinaster* populations are able to store seeds in closed cones (serotinous cones) within the canopy for longer than one reproductive cycle (Tapias *et al.*, 2001, 2004; Daskalakou & Thanos, 2004; Moya *et al.*, 2018). The seeds in serotinous cones are protected from fire and massively released after the disturbance, finding proper conditions for germination, seedling establishment and growth (Calvo *et al.*, 2008; Moya *et al.*, 2008; Keeley *et al.*, 2011). In general, this mechanism ensures the regeneration of *P. pinaster* and *P. halepensis* forests after a fairly wide range of burn severities, but many studies have indicated that very high burn severity can cause significant seed mortality (Fernandes *et al.*, 2008; Fernández *et al.*, 2008; Maia *et al.*, 2012; García-Llamas *et al.*, 2019a).

Another characteristic of the fire regime in Mediterranean pine ecosystems is the repeated occurrence of fires at short intervals, with *P. pinaster* and *P. halepensis* being the tree species most affected by fire in the Iberian Peninsula (ADCIF, 2012; ICFN, 2015). Simulation studies have indicated that intermediate fire return intervals (40-100 years) are optimal for maintaining Mediterranean pine forests (Pausas, 1999). In fact, the reproductive precocity of *P. pinaster* (4-10 years) and *P. halepensis* (4-8 years) is considered an adaptation to a relatively frequent fire regime (Tapias *et al.*, 2004; González-de-Vega *et al.*, 2016 Moya *et al.*, 2018). However, when fire frequency is out of the natural range, regeneration may be endangered because these pines need at least 15 or 20 years to develop a fully productive canopy seed bank (Pausas *et al.*, 2008).

Thus, previous research indicated that fire frequency and burn severity directly affect pine regeneration, but additional indirect effects may be expected through changes in the abundance and composition of the woody understory community (Pausas, 1999; Pausas & Keeley, 2014; Fernández-García *et al.*, 2017). Frequent fires (fire intervals ≤ 20 years) may facilitate the development of woody understory species (Pausas, 1999; Fernández-García *et al.*, 2018a), which compete with pines for light (*P. pinaster* and *P. halepensis* seedlings are heliophilous; Richardson, 2000), space, and nutrients (de las Heras *et al.*, 2002; Calvo *et al.*, 2005, 2008, 2013; Taboada *et al.*, 2017). Additionally, previous studies have indicated that high burn severity can favor the recovery of seeders at the expense of resprouters (Pausas & Keeley, 2014). This potential change in understory community composition can also interact with pine regeneration, as the competition exerted by woody species on pines can vary depending on the vegetation functional type (Taboada *et al.*, 2017).

Although Mediterranean serotinous pine forests are adapted to certain fire regimes (Pausas *et al.*, 2008), rural abandonment in the European countries of the Mediterranean Basin has led to an increase in fuel loads and continuity (Lindner *et al.*, 2008; Moreira *et al.*, 2011; Doblas-Miranda *et al.*, 2017; García-Llamas *et al.*, 2019a). Fuel accumulation coupled with an expected warmer and drier climate, particularly during summer (Giorgi & Lionello, 2008), could lead to increases in fire frequency (Vázquez *et al.*, 2015) and burn severity that can hinder pine regeneration (Fernandes *et al.*, 2008; Flatley & Fulé, 2016). Knowledge of the effects of fire frequency and severity on pines is crucial for land-managers to predict post-fire regeneration and develop post-fire restoration strategies aimed at maintaining the forest ecosystem (Moreira *et al.*, 2012; García-Llamas *et al.*, 2019a). Previous studies have analyzed separately the effects of fire frequency (Eugenio & Lloret, 2004; Baeza *et al.*, 2007) and burn severity (Fernández *et al.*, 2008; Moya *et al.*, 2018) on the regeneration of Mediterranean serotinous pines. However, the pine regeneration results are inconsistent, particularly in relation to burn severity (Pausas *et al.*, 2003; Vega *et al.*, 2008; González-de-Vega *et al.*, 2016). Therefore, the study of seedling recruitment and development of serotinous pines after different frequencies and severities in different environmental conditions (e.g. soil and climate) may help to clarify the situation. Additionally, we have not found any studies analyzing the interacting effects of fire frequency and burn severity on seedling recruitment and development. Such an approach may provide realistic insights into the post-fire regeneration capacity of the ecosystem, since both variables overlap under natural conditions (Fernández-García *et al.*, 2018a).

The objective of the present study is to analyze the role of fire frequency and burn severity in post-fire regeneration of serotinous pines in Mediterranean ecosystems over the medium term (three and four years) after fire. In particular, we aim to answer the following questions: (i) Does the combination of frequent fires and high severities constrain the post-fire recruitment (density) and development (cover and height) of pine seedlings? (ii) Does competition between woody understory species and pine regeneration vary depending on fire frequency and burn severity? (iii) Does the impact of fire frequency and burn severity on pine regeneration vary depending on the environmental conditions? According to previous research, we would expect a decrease in pine seedling recruitment after frequent fires (Eugenio & Lloret, 2004; Baeza *et al.*, 2007; Taboada *et al.*, 2017), as well as in high severity patches (Fernandes & Rigolot, 2007; González-de-Vega *et al.*, 2016). Thus, natural regeneration of pines would be particularly limited when combining high fire frequency and extreme severity situations. Additionally, we hypothesize that increases in fire frequency and burn severity would negatively affect the development of pines (cover and height) through changes in seedling growth conditioning factors, such as microclimatic conditions (Pausas *et al.*, 2004a) and soil properties (Fernández-García *et al.* 2019). We also expect competition between woody understory species and pine regeneration (Calvo *et al.*, 2005, 2008) to be mediated by fire frequency and severity, as changes in these fire regime attributes entail changes in community structure and composition (Pausas & Keeley, 2014; Taboada *et al.*, 2017). Finally, we expect the impact of frequent and severe fires to be stronger in warmer and drier areas (Flatley & Fulé, 2016), because droughts constrain seedling establishment and growth (Padilla & Pugnaire, 2007; Rodríguez-García *et al.*, 2011; Calvo *et al.*, 2013; Lucas-Borja, 2016).

MATERIAL AND METHODS

Study sites

We selected two study sites burned in summer 2012, representing contrasting climatic conditions and soil types that support serotinous pine forests in the Iberian Peninsula. The first site is Sierra del Teleno (42°15’N 6°11’W), dominated by *P. pinaster* ecosystems, with two months of summer drought and acidic soils. The second site is Cortes de Pallás (39°18’N 0°54’W), dominated by *P. halepensis* ecosystems, with four months of summer drought and calcareous soils (Figs. 30, 31; Table 20).

Figure 30. Photos of the study sites (Sierra del Teleno on the left and Cortes de Pallás on the right) immediately after the fire (top) and three years after the fire (bottom).

The Sierra del Teleno wildfire was a high-intensity crown fire that burned 119 km^2 in the northwestern Iberian Peninsula (León province, Spain). The study site is located in a mountain range with a heterogeneous fire history (large wildfires also occurred in 1978, 1991 and 1998, among others) (Fig. 31). Sierra del Teleno is dominated by natural *P. pinaster* forests (103 km^2) with 97% serotinous trees (Tapias *et al.*, 2004). Tree density in old stands (no wildfires recorded since 1978) in Sierra del Teleno is 765 plants ha^{-1}. The shrubby understorey community is mostly comprised of *Pterospartum tridentatum* (L.) Willk., *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. The climate is temperate with dry temperate summers (AEMET-IM, 2011), averaging two months of summer drought (transition between Mediterranean and Oceanic climates). Soils are siliceous, with sandy loam texture and relatively poor in nutrients (4 µg available P g^{-1} dry soil and 2 mg total N g^{-1} dry soil; Fernández-García *et al.*, 2019). Pine mortality caused by the wildfires was almost total (Fig. 30) and salvage logging was conducted following the fires. After the 2012 wildfire, only unmerchantable trees (<10 cm diameter) were left on the site (Taboada *et al.*, 2018).

The Cortes de Pallás wildfire burned an area of 297 km^2 in the eastern Iberian Peninsula (Valencia province, Spain). Part of the area had been burned by previous wildfires in 1978, 1991 and 1994. The Cortes de Pallás wildfire burned 66 km^2 occupied by *P. halepensis* natural forests (100% of serotinous trees, Tapias *et al.*, 2001; Hernández-Serrano *et al.*, 2013), with localized presence of *P. pinaster*. Tree density in stands unburned since 1978 in Cortes de Pallás was 283 plants ha^{-1}. The understory of these fire-prone pine ecosystems was dominated by *Ulex parviflorus* Pourr., *Quercus coccifera* L. and *Rosmarinus officinalis* L. The climate is temperate, with warm dry summers (AEMET-IM, 2011) resulting in four months of summer drought (typical Mediterranean conditions). Soils are calcareous, with loamy sand or sandy loam texture, and higher nutrient concentrations than soils in Sierra del Teleno (12 µg available P g^{-1} dry soil and 3 mg total N g^{-1} dry soil; Fernández-García *et al.*, 2019). The Cortes de Pallás wildfire was, in general, a stand replacing fire in the areas dominated by pine forests (Fig. 30), and salvage logging was conducted in a small portion of the affected area.

Table 20. Characteristics of the study sites.

	Sierra del Teleno wildfire	Cortes de Pallás wildfire
Fire alarm date	August 19th, 2012	June 28th, 2012
Wildfire size (km^2)	118.91	297.52
Previous large wildfires	1978, 1991, 1998	1978, 1991, 1994
Dominant pine species	*P. pinaster*	*P. halepensis*
Pine ecosystem burned (km^2)	102.65	65.69
Elevation (m)	836 - 1,493	120 - 942
Aspect	N, S, W, E	N, S, W, E
[1] Mean annual precipitation (mm)	600 - 800	400 - 600
[1] Mean annual temperature (ºC)	8 - 11	13 - 17
[2] Lithology	Quartzite, conglomerate, sandstone, sand, slate, silt	Limestone, dolomite, sandstone, marl
[3] Soil WRB classification	Haplic Umbrisol, Dystric Regosol	Haplic Calcisol, Calcari-lithic Leptosol
[4] Soil pH	4.86 ± 0.14	8.14 ± 0.06

[1] Precipitation and temperature were obtained from Ninyerola *et al.* (2005).
[2] Lithologies were determined according to the geological map of Spain (GEODE, 2019).
[3] World Reference Base for Soil Resources classification according to Jones *et al.* (2005).
[4] A suspension of soil:deionized water was used to determine pH (1:2.5, w/v).

Fire frequency and burn severity

We characterized the fire frequency (number of wildfires between 1978 and 2012) and burn severity of the last wildfire (wildfires occurred in 2012) in the two study sites. The fire perimeters of the wildfires occurred in Sierra del Teleno since 1978 were mapped using Landsat imagery false colour composites and aerial orthophotography, and validated with official information according to Fernández-García *et al.* (2018a). In Cortes de Pallás, official fire perimeters were available for the entire study period (Alloza *et al.*, 2012). We obtained a fire frequency map (1978-2012) for the two study sites by overlaying the fire scars.

Burn severity was obtained as a continuous variable by calculating the differenced Normalized Burn Ratio (dNBR) (Key, 2006). This index is a standard burn severity metric and has shown a high accuracy for assessing burn severity in forest ecosystems within the Iberian Peninsula (Fernández-García *et al.*, 2018a, 2018b; García-Llamas *et al.*, 2019b). Landsat 7 ETM+ scenes from September 20th, 2011 (pre-fire) and from September 6th, 2012 (post-fire) were used to calculate the dNBR in the Sierra del Teleno wildfire, and Landsat 7 ETM+ scenes from August 22nd, 2011 (pre-fire) and from August 25th, 2012 (post-fire) in the Cortes de Pallás wildfire. Images were atmospherically corrected using the FLAASH module (Perkins *et al.*, 2012) and topographically corrected by applying the C-correction (Teillet *et al.*, 1982) (see Fernández-García *et al.*, 2018b for a detailed description on the imagery pre-processing). Then, dNBR was calculated using the following equations:

$NBR = (\rho_4 - \rho_7) / (\rho_4 + \rho_7);$

$dNBR = (NBR_{pre} - NBR_{post}) - offset$

where NBR is the Normalized Burn Ratio, calculated in the pre-fire situation (NBR_{pre}) and in the post-fire situation (NBR_{post}), ρ is the land surface reflectance in percentage for each specific Landsat 7 ETM+ band, dNBR is the differenced Normalized Burn Ratio ranging from -2 to 2, and offset is the average index value from pixels in homogeneous and unchanged areas near the fire scar.

Field sampling

In each study site, we focused the field sampling in a frame of 3000 ha established in areas dominated by pine ecosystems, with three fire frequency scenarios and heterogeneous burn severity (Fig. 31). Aiming to design a field sampling representative of the different fire frequency and severity situations, we developed a fire frequency-severity map for each study site (Fig. 31). In these maps we obtained six frequency-severity categories by combining the fire frequency (one to three fires) and burn severity classified into low and high (using the dNBR value 550 as threshold, which can be considered moderate burn severity; Fernández-García *et al.*, 2018a, 2018b, 2019). We distributed 30 m x 30 m field plots (corresponding to the spatial resolution of Landsat ETM+ reflective bands) proportionally to the area of each frequency-severity category, with a minimum of 30 plots per study site and ensuring that all the fire frequency-severity scenarios were represented. The minimum distance between plots was 200 m. A total of 108 field plots of 30 m x 30 m was established: 78 plots in Sierra del Teleno and 30 in Cortes de Pallás. In each 30 m x 30 m plot, we located three 2 m x 2 m subplots, divided into four 1 m x 1 m quadrats. Plot and subplot centres were fixed in field for successive monitoring and geo-referenced with high precision GPS ($RMSE_{X,Y} < 0.5$ m).

To analyze the post-fire regeneration of pines over the medium term after the fire, we surveyed the 1296 (1 m x 1 m) quadrats distributed in the two wildfires in May-June 2015 (three years after fire), and again in May-June 2016 (four years after fire). In each quadrat (i) we measured the number of pine seedlings, (ii) we visually estimated the percentage cover of pine seedlings, and (iii) we calculated the mean height of pine seedlings by averaging the height of 10 randomly selected individuals. Additionally, to evaluate the potential competition effects of woody understory species on pine recruitment and development, we estimated the percent cover of each woody species in each 1 m x 1 m quadrat, and calculated the global cover of woody understory species as the sum of the individual cover of all species.

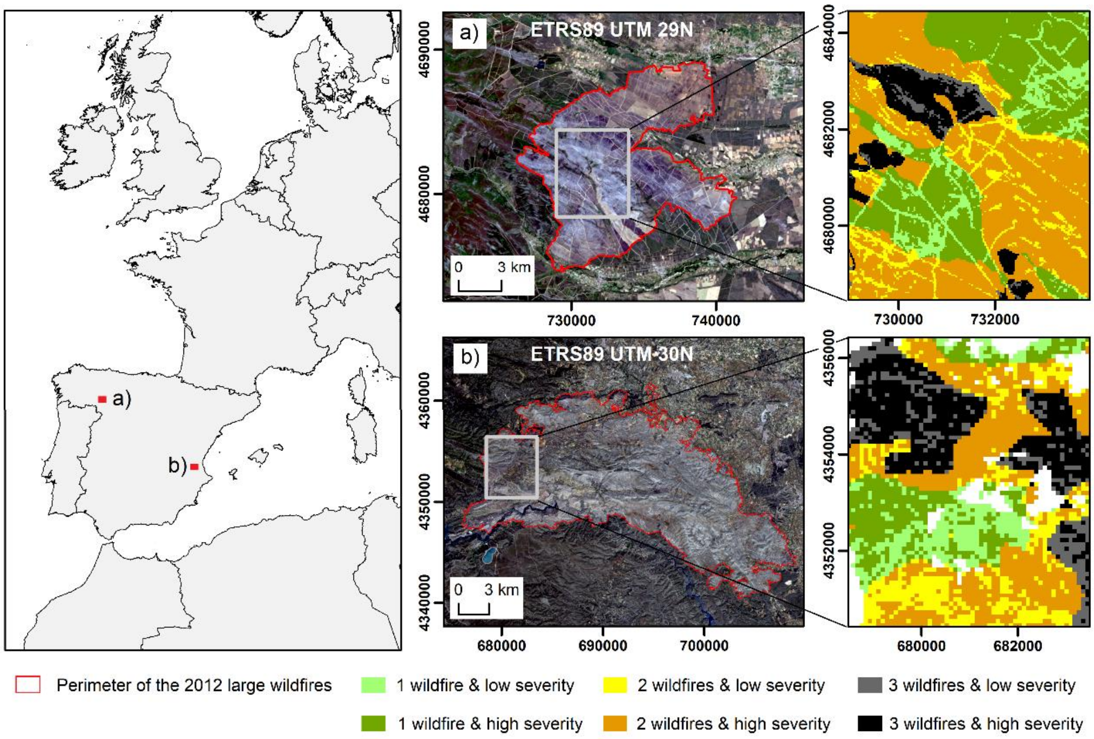

Figure 31. Location of the study sites: Sierra del Teleno (a) and Cortes de Pallás (b) in SW Europe (panel on the left). The panel in the centre shows the fire perimeters of the large wildfires. Panels on the right show the 3000 ha study frame with the different scenarios of fire frequency (one to three wildfires in 34 years) and burn severity (classified in low and high according to the dNBR index).

Data analysis

To analyze the effects of time since the wildfire (three and four years), fire frequency (number of wildfires between 1978 and 2012), burn severity (continuous value of the dNBR spectral index), and the competition of woody understory species (percentage cover) on pine regeneration, we fit generalized linear mixed models (GLMMs) for each study site. We used penalized quasi-likelihood (*glmmPQL* function) to account for overdispersion. We studied three response variables: number of pine seedlings (density), percentage cover of pine seedlings, and mean height of pine seedlings. The density and cover of pine seedlings were fitted following a quasi-Poisson error distribution using the *log* link function, whereas a Gaussian error distribution with the *identity* function was used to model the mean height of pine seedlings. The identities of the 30 m x 30 m and 2 m x 2 m field plots were included in the models as a nested random factor. We retained the interaction terms in the models only when they were significant ($P < 0.05$).

All data analyses were carried out with R (R Core Team, 2017), using the *MASS* (Venables & Ripley, 2002) and *nlme* (Pinheiro *et al.*, 2017) packages.

RESULTS

All the explanatory variables (time, fire frequency, burn severity and total cover of woody understory species) had significant effects on the recruitment of pine seedlings in *P. pinaster* and *P. halepensis* ecosystems over the medium term after fire (Table 21). Results showed a significant decrease in the number of pine seedlings per m^2 in time (from the third to the fourth year) in both *Pinus pinaster* (2.25 ± 0.15 to 1.77 ± 0.11; mean ± standard error) and *Pinus halepensis* ecosystems (2.85 ± 0.17 to 2.68 ± 0.54). Focusing on the fire regime attributes, we found that increases in both fire frequency and burn severity had a negative impact on the recruitment of pine seedlings in the *P. pinaster* ecosystem (Table 21; Fig. 32). Similarly, there was a clear negative effect of the cover of woody understory species on seedling recruitment (Table 21; Fig. 33). In the case of *P. halepensis*, the effects of fire frequency, severity and competition on the density of pine seedlings showed similar trends (Figs. 32, 33). However, the triple interaction found in the *P. halepensis* ecosystem means that the strong effect of each single predictor on pine recruitment obscured the effect of the other two in the less favourable scenarios (two or three wildfires, high severity and/or high cover of woody species), because pine density had already decreased to very low values. In both ecosystems, the lowest pine seedling density occurred in areas affected by two wildfires combined with high severity (< 0.40 seedlings m^{-2}), and in the areas affected by three wildfires, regardless of burn severity and cover of woody species (0.34 ± 0.07 seedlings m^{-2} in the *P. pinaster* ecosystem; 0.01 ± 0.01 seedlings m^{-2} in the *P. halepensis* ecosystem) (Figs. 32, 33).

Table 21. Results of the fixed effects of the Generalized Linear Mixed Models (GLMMs) indicating the effects of the time factor (three years and four years after the fire), fire frequency (number of wildfires 1978-2012), burn severity (dNBR of the 2012 wildfires) and woody cover (cover of woody understory species excluding pines), and their interactions, on pine seedlings (density, cover and height) in the two studied ecosystems (*Pinus pinaster* and *Pinus halepensis*). Only significant interactions were retained. The intercept represents 3 years of the time factor. SE = standard error. Significant *P*-values are in bold face.

Response variable	Predictor Variable	*Pinus pinaster* ecosystem			*Pinus halepensis* ecosystem		
		Estimate	SE	*P* value	Estimate	SE	*P* value
Density of seedlings (pines/m^2)	Intercept	3.532	0.528	<**0.001**	6.101	3.007	**0.043**
	Time	-0.189	0.043	<**0.001**	-0.111	0.044	**0.012**
	Frequency	-1.425	0.152	<**0.001**	-2.489	1.934	0.209
	Severity	-1.442	0.565	**0.013**	-3.580	5.162	0.494
	Woody cover	-0.003	0.001	**0.014**	0.030	0.029	0.306
	Frequency * Severity	-	-	-	-1.914	3.469	0.586
	Frequency * Woody cover	-	-	-	-0.031	0.028	0.274
	Severity * Woody cover	-	-	-	-0.107	0.047	**0.023**
	Frequency * Severity * Woody cover	-	-	-	0.094	0.045	**0.039**
Cover of seedlings (%)	Intercept	3.792	0.448	<**0.001**	5.595	1.335	<**0.001**
	Time	0.461	0.042	<**0.001**	0.342	0.046	<**0.001**
	Frequency	-1.436	0.132	<**0.001**	-2.819	0.456	<**0.001**
	Severity	-0.603	0.479	0.212	-3.894	1.643	**0.025**
	Woody	-0.007	0.001	<**0.001**	-0.004	0.002	**0.018**
Height of seedlings (cm)	Intercept	12.055	7.248	0.097	3.646	0.287	<**0.001**
	Time	8.602	0.758	<**0.001**	0.367	0.050	<**0.001**
	Frequency	-4.723	1.994	**0.021**	-0.363	0.131	**0.013**
	Severity	25.055	7.983	**0.003**	-0.540	0.380	0.173
	Woody cover	0.054	0.057	0.341	0.002	0.002	0.254
	Severity * Woody cover	-0.144	0.070	**0.042**	-	-	-

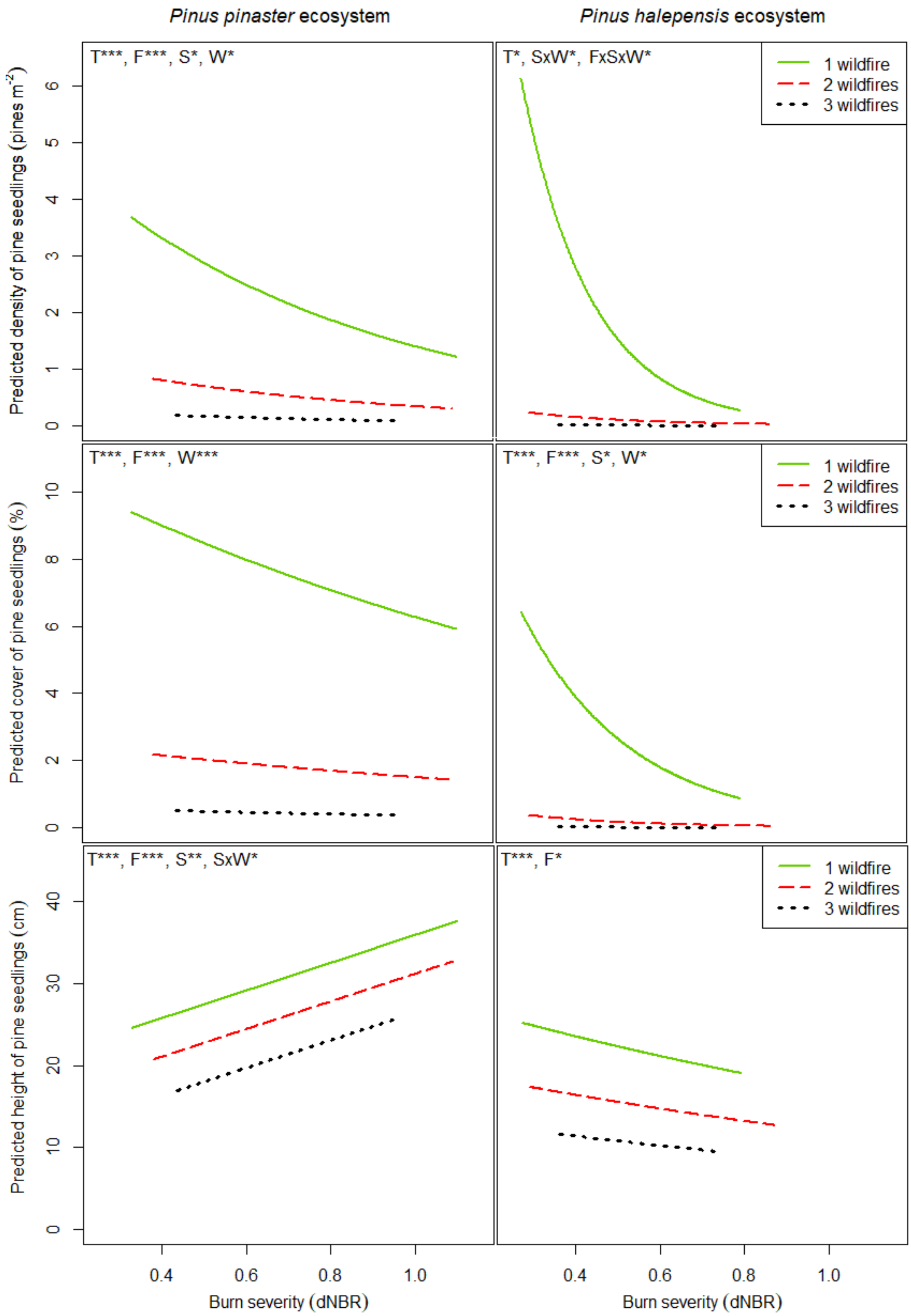

Figure 32. Mean predicted density, cover and height of pine seedlings in the two studied pine ecosystems (on the left: *Pinus pinaster* ecosystem, on the right: *Pinus halepensis* ecosystem) four years after the fire in relation to fire frequency and burn severity (cover of woody understory species was fixed to the mean). The significance of model predictors time (T), fire frequency (F), burn severity (S), cover of woody understory species (W) and their interactions are represented as * (*P* <0.05), ** (*P* <0.01) and *** (*P* <0.001).

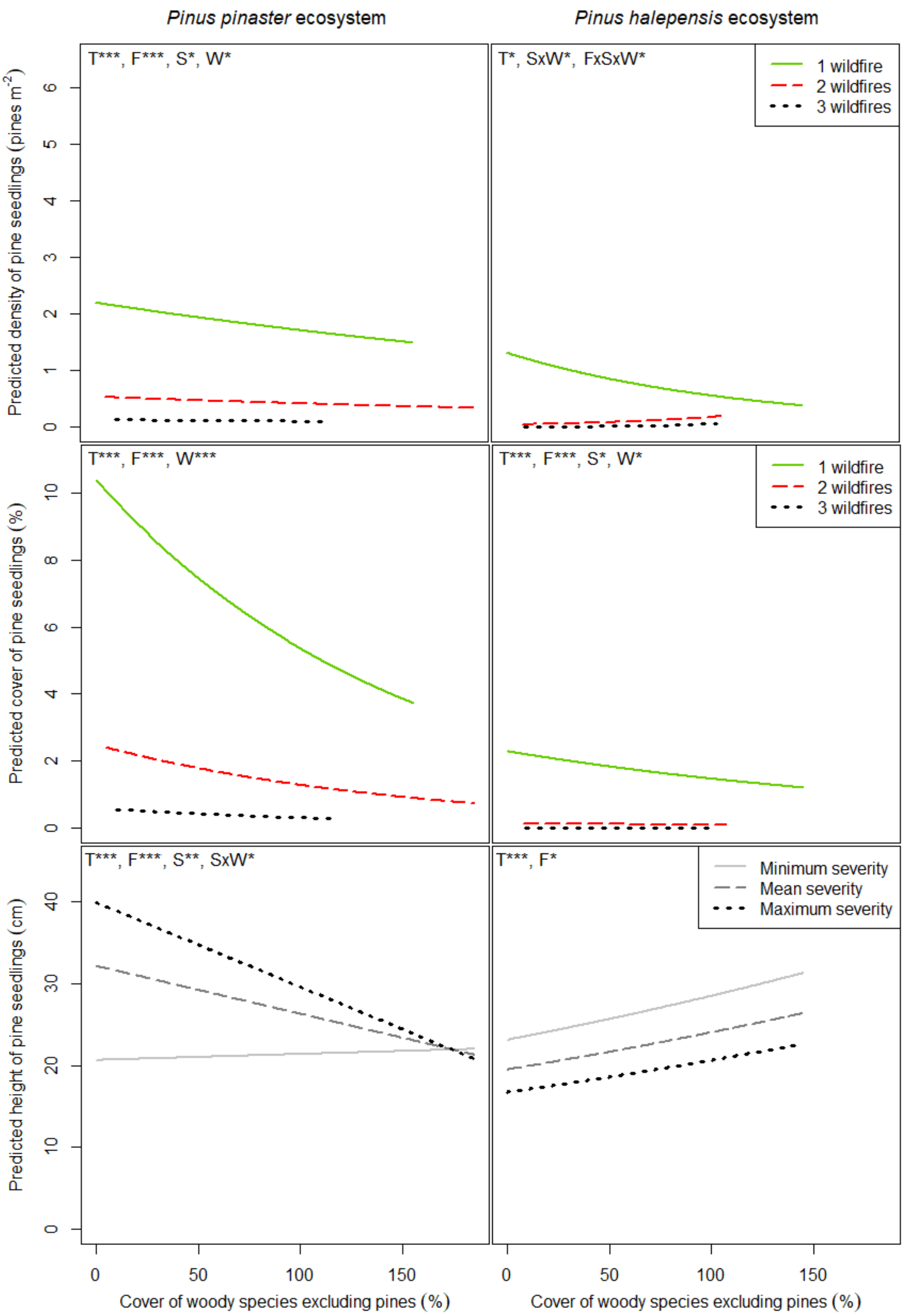

Figure 33. Mean predicted density and cover of pine seedlings in relation to the cover of woody understory species in the different fire frequency scenarios (in the panels on the top and in the middle, burn severity was fixed to the mean); and mean predicted height of pine seedlings in relation to the cover of woody understory species along the burn severity gradient (in the panels on the bottom, fire frequency was fixed to the mean). Results are presented for the two studied pine ecosystems (on the left: *Pinus pinaster* ecosystem, on the right: *Pinus halepensis* ecosystem) four years after the fire. The significance of model predictors time (T), fire frequency (F), burn severity (S), cover of woody understory species (W) and their interactions are represented as * (P <0.05), ** (P <0.01) and *** (P <0.001).

The percent cover of pine seedlings increased from the third to the fourth year after the fire (Table 22) (4.30 ± 0.26 to 6.05 ± 0.36 in the *P. pinaster* ecosystem; 2.45 ± 0.39 to 3.41 ± 0.42 in the *P. halepensis* ecosystem). However, as with pine density, the cover of pine seedlings significantly decreased with fire frequency in both ecosystems (Fig. 32). Burn severity had significant effects on cover of pine seedlings only in the *P. halepensis* ecosystem, although both forests showed the same pattern (Fig. 32). The cover of pine seedlings significantly decreased with the cover of woody understory species in both ecosystems, especially in the areas affected by one wildfire (Fig. 33). In general, the areas with the lowest cover of pine seedlings corresponded with those with the lowest density of pine seedlings, showing a significant correlation even four years after the fire ($R^2 = 0.45$, $P < 0.01$ in *P. pinaster*; $R^2 = 0.66$, $P = 0.01$ in *P. halepensis*).

The height of pine seedlings significantly increased in time (Table 22) (22.71 cm ± 0.71 to 30.24 cm ± 0.93 in the *P. pinaster* ecosystem; 22.12 cm ± 1.26 to 33.03 cm ± 1.70 in the *P. halepensis* ecosystem) and decreased with fire frequency in both ecosystems (Table 22; Fig. 32). In the *P. pinaster* ecosystem, we found a significant interaction effect of burn severity and cover of woody species on the height of pine seedlings (Fig. 33). This result suggests that higher burn severity facilitated the development in height of pine seedlings only when the cover of woody species was not very high. We did not find significant effects of burn severity or cover of woody understory species on seedling height in the *P. halepensis* ecosystem (Table 22, Figs. 32, 33).

DISCUSSION

We found that the post-fire recruitment and development of Mediterranean serotinous pine seedlings is influenced by fire frequency (number of wildfires in 34 years) and severity (dNBR spectral index), as well as by the inter-specific competition with woody species (cover of woody understory species). The influence of these variables on the regeneration of *P. pinaster* and *P. halepensis* can be attributed to effects on: (i) the canopy seed bank existing prior to the fire (Daskalakou & Thanos, 1996; Fernández *et al.*, 2008), (ii) seed survival and germination (Daskalakou & Thanos, 2004; Fernandes & Rigolot, 2007), and (iii) post-fire establishment and dynamics of pine seedlings, which are highly dependent on environmental conditions such as climate (Padilla & Pugnaire, 2007; Calvo *et al.*, 2008; Fernandez *et al.*, 2008; Taboada *et al.*, 2017).

Fire frequency effects on pine regeneration

Our results indicated that increased fire frequency reduced seedling density over the medium term after the fire (three and four years). Previous studies have found decreases in the density of seedlings after frequent fires in both *P. pinaster* (Torres *et al.*, 2016; Taboada *et al.*, 2017) and *P. halepensis* ecosystems (Eugenio *et al.*, 2006; Santana *et al.*, 2010; Arnan *et al.*, 2013). Presumably, community replacement would be expected if two consecutive fires occur in a period shorter than necessary for pines to reach reproductive maturity (4-10 years *P. pinaster*, 4-8 years *P. halepensis*; Tapias *et al.*, 2004, Baeza *et al.*, 2007). However, large decreases in pine recruitment would also be expected when fire intervals are shorter than the time necessary to accumulate a critical seed store for guaranteeing self-replacement (Eugenio & Lloret, 2004). Several authors have stated that the minimum fire intervals in Mediterranean fire-prone pines are around 15-20 years (Eugenio *et al.*, 2006; Santana *et al.*, 2010), coinciding with the scenarios of two and three wildfires in this study. Additionally, changes in environmental conditions owing to fire frequency may affect the density of pine seedlings. For example, it has been demonstrated that the amount of both light fuel and coarse woody debris on the forest floor, which is lower after frequent fires, provide seed protection from predation (Taboada *et al.*, 2018) and appropriate microclimatic conditions for seedling establishment (Pausas *et al.*, 2004a). In this study, we observed that the percentage of soil covered by plant debris is still higher four years after the fire in the areas burned once than in those affected by two or three wildfires (17.32%, 10.72% and 7.04% in the *P. pinaster* ecosystem; 48.20%, 28.92% and 27.36% in the *P. halepensis* ecosystem in the areas burned once, twice and three times, respectively). Therefore, the lowest fire frequency provides the best microclimatic conditions for seedling establishment. Fire frequency also showed a significant impact on the variables related to the development of pine seedlings: cover of pine seedlings, which was dependent on the density of pine seedlings ($R^2 \geq 0.45$, $P < 0.05$ 4 years after the fire), and height of pine seedlings. The negative effects of high fire frequencies on the development of seedlings could be explained by the decrease in soil nutrient concentrations after recurrent fires (Eugenio & Lloret, 2004, Eugenio *et al.* 2006). In fact, the available P concentration, which can be a limiting nutrient in forest soils (Binkler & Fisher, 2013), largely decreased with fire frequency even four years after the fire in our two study sites (12.60ppm, 5.07ppm, 3.07ppm in the *P. pinaster* ecosystem; 13.77ppm, 8.92ppm and 8.03 ppm in the *P. halepensis* ecosystem in the areas burned once, twice and three times, respectively). The plant debris covering the forest floor, which decreased with fire frequency, is another factor that may be related to the decreased development of pines after two and three fires (Taboada *et al.*, 2018). The plant debris may contribute to the growth of seedlings by reducing water stress (Fernandez *et al.*, 2008), increasing protection from adverse climatic conditions, and providing nutrients over the medium term (Taboada *et al.*, 2018).

Burn severity effects on pine regeneration

The other fire regime attribute we studied, burn severity, also decreased the recruitment of pine seedlings, mainly in the single fire occurrence scenarios. Serotinous cones are an extraordinary mechanism to protect seeds from fire, maintaining their viability at temperatures up to 400 ºC for 1 min (Habrouk *et al.*, 1999; Fernandes & Rigolot, 2007). However, higher temperatures or longer exposure time cause high mortality rates of seeds encased in serotinous cones as well as total mortality of non-protected seeds (Habrouk *et al.*, 1999; Fernandes & Rigolot, 2007). Considering that these temperatures are exceeded in the flame zone, as well as in the first meters above flames (Trabaud, 1989), it is logical to expect a negative effect of crown severe fires on seed survival and consequently on the post-fire density of pine seedlings. Burn severity also played a significant role in the development of pine seedlings. Thus, in the *P. pinaster* ecosystem we found that growth of regenerating seedlings was stimulated in the severely burned areas (reflected in the non-significant effect on seedling cover despite the decrease in density, as well as the increase in seedling height), but no effects were detected in the *P. halepensis* ecosystem. This difference might be explained by the differences in soil fertility (mainly P) (Pausas *et al.*, 2003), which was enhanced by burn severity in the *P. pinaster* ecosystem we studied, but not in the *P. halepensis* ecosystem (see Fernández-García *et al.*, 2019).

Influence of fire frequency and severity on the competition between pines and woody understory species

The cover of woody understory species showed an inverse relationship with the regeneration of pines, which has been explained in the literature by the competition for light, water and nutrients (de las Heras *et al.*, 2002; Calvo *et al.*, 2008; Arnan *et al.*, 2013; Taboada *et al.*, 2018). However, we observed shifts in competition in relation to the fire regime. Thus, the effects of the cover of woody understory species were relevant mostly in areas burned once, probably because this is the situation with the highest densities of both pines and shrubs, facilitating the manifestation of inter-specific competitive effects (Calvo *et al.*, 2008). Additionally, the tallest pine seedlings in the *P. pinaster* ecosystem were found in the scenario of high severity with low cover of woody species, probably due to the high availability of resources for pine growth in these areas (Pausas *et al.*, 2003; Fernández-García *et al.*, 2019). In contrast, no significant effects of woody cover on *P. halepensis* height were found, but we note that in the *P. halepensis* ecosystem the cover of woody species is lower than in the *P. pinaster* ecosystem. Moreover, other factors could mask the impact of woody cover on seedling growth in the *P. halepensis* ecosystem, such as intra-specific competition (Pausas *et al.*, 2003) or the prolonged summer drought under the Mediterranean climate regime, which could be a limiting factor in the growth of seedlings (Rodríguez-García *et al.*, 2011; Calvo *et al.*, 2013; Lucas-Borja, 2016).

Consequences of combined increases in fire frequency and severity under a warming climate

This study confirms the negative ecological consequences of a potential future regime of higher fire frequency and severity (Fernandes *et al.*, 2008; Vázquez *et al.*, 2015) on the post-fire regeneration of serotinous pine species in the Mediterranean Basin. Our findings indicate that two fires in 34 years combined with high severity resulted in low density and cover of pine seedlings in the *P. pinaster* (0.40 seedlings m^{-2}) ecosystem, and especially in the *P. halepensis* (0.03 seedling m^{-2}) ecosystem. The situation was aggravated if three fires occurred, decreasing the density of seedlings in the *P. pinaster* ecosystem (≤ 0.34 seedling m^{-2}), and showing almost no seedling recruitment in the *P. halepensis* ecosystem (0.01 seedlings m^{-2}). The seedling densities obtained in these scenarios (two wildfires with high severity, and three wildfires) in the *P. halepensis* ecosystem are below the minimum necessary for successful natural recovery of these pine forests, which has been estimated at 0.20 seedlings m^{-2} (2,000 seedlings ha^{-1}) (Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016). Furthermore, our results indicated that the number of seedlings significantly decreased between the third and fourth year after fire, so we can expect further seedling mortality over the medium term (Daskalakou & Thanos, 2004). Therefore, low natural regeneration after two fires plus high severity, or after three fires in a short period (34 years) may lead to low density *P. pinaster* stands and to the replacement of the *P. halepensis* forest, requiring post-fire restoration actions to preserve the pine ecosystem (Pausas *et al.*, 2004a).

Considering that the life history traits of *P. pinaster* and *P. halepensis* are quite similar (Richardson, 2000; Tapias *et al.*, 2004; Santana *et al.*, 2010), the notably lower seedling recruitment after high frequencies and/or severities in Cortes de Pallás could be attributed to differences in climatic conditions, even though *P. halepensis* is adapted to drier and warmer conditions than *P. pinaster* (Richardson, 2000). The summer drought, which is two months longer in the *P. halepensis* than in the *P. pinaster* ecosystem, can limit seedling emergence and survival (Pausas *et al.*, 2004b; Padilla & Pugnaire, 2007; Rodríguez-García *et al.*, 2011; Calvo *et al.*, 2013; Lucas-Borja, 2016), potentially aggravating the impact of frequent fires. An additional aggravating factor of high fire frequencies and high severities under a dry climate is the depletion of litter and woody debris (Key, 2006; Fernandez-García *et al.*, 2018b Taboada *et al.*, 2018), which are key elements in reducing hydric stress in seedlings against drought (Fernandez *et al.*, 2008). Accordingly, we would expect the effects of fire frequency and burn severity to be magnified in the future in dry forested areas of the Iberian Peninsula, because of the lengthening and intensification of the summer drought projected for the Mediterranean Basin (Giorgi & Lionello, 2008; Lucas-Borja, 2016).

CONCLUSIONS

The fire-prone forests of the Mediterranean Basin are ecosystems of particular concern considering the warmer and drier climate projected for this region, particularly during the fire season (Giorgi & Lionello, 2008), which would lead to changes in the fire regime by increasing fire frequency and burn severity (Fernandes *et al.*, 2008; Vázquez *et al.*, 2015). In the present study, we demonstrated that these fire regime attributes are important drivers of the recruitment and development of *P. pinaster* and *P. halepensis* seedlings over the medium term after the fire (three and four years), as well as on the competition between pine seedlings and woody understory species.

Fire frequency (1978-2012) largely decreased the density, cover and height of pine seedlings in *P. pinaster* and *P. halepensis* ecosystems. The burn severity of the last wildfire reduced the density of pine seedlings in the two studied ecosystems. Pine cover was reduced mainly in the *P. halepensis* ecosystem, because the growth of *Pinus pinaster* was enhanced in the severely burned areas. The interactions between the cover of woody understory species and pine regeneration revealed that inter-specific competition was more noticeable in the scenarios of fire frequency and severity most favorable for seedling establishment and growth.

As a consequence of the additive impacts of both fire frequency and burn severity, the natural recovery of serotinous pines is likely to be insufficient to restore full forest cover after two wildfires in 34 years combined with high severity as well as in the areas affected by three wildfires in 34 years, particularly in a climate characterized by pronounced summer drought. This information is of considerable relevance for land managers, as it highlights the importance of minimizing the occurrence of frequent severe fires to preserve serotinous pine forests. Management strategies to reduce the risk of frequent and severe fires could be focused on breaking up fuel continuity, decreasing surface fuel accumulation, reducing canopy bulk density by selective thinning, fostering multi-species forest composition, and the enhancement of tree growth to the detriment of the shrubby understory community (Corona *et al.*, 2014; García-Llamas *et al.*, 2019a). The present study provides ecological clues to identify the impact of potential future fire regimes on the regeneration of serotinous pines in the Mediterranean Basin.

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Article VII

Fire regimes shape diversity and traits of vegetation under different environmental conditions

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Abstract

Changes in climate and land use are altering fire-regimes in many regions across the globe. This work aims to study the influence of fire recurrence and severity on woody community structure and traits under different environmental conditions. We selected three study sites along a Mediterranean-Oceanic climatic gradient, where we studied the fire history and severity of the last wildfire. Four years after the last wildfire, we established 1,776 1-m^2 plots where the percentage cover of each woody species was sampled. We calculated structural parameters of the community such as total cover and alpha diversity (including species richness, evenness, and Shannon diversity index), and vegetation cover corresponding to each functional group (different life forms, eco-physiological traits and regenerative traits). Focusing on community structure, results showed increases in species richness and Shannon diversity index as fire recurrence increased, but this effect was partially counterweighted in high severity situations. In relation to plant traits, we found that increases in fire recurrence and severity fostered transition from tree- to shrub-dominated ecosystems. Non-arboreal life form, high specific leaf area, N_2-fixing capacity, resprouting ability, low seed mass and heat-stimulated germination may be advantageous traits under high fire recurrences and severities. We found that the strength of the effects of fire recurrence and severity on vegetation structure and traits might vary with climate, as it increased from the Oceanic to the Mediterranean site. Under Mediterranean conditions, fire recurrence and burn severity explained the highest proportion of variance on traits related to germination (seed mass and heat-stimulated germination), whereas in the Oceanic climate the highest explained variance was related to a resprouting-related trait (bud location). Our study anticipate changes in vegetation structure and composition owing to shifts in fire regimes, and provides useful information about plant traits that could be key to enhance vegetation resilience after recurrent and severe wildfires.

INTRODUCTION

Fire regimes determine vegetation structure and composition in many biomes worldwide (Pausas & Vallejo, 1999). Fire recurrence (number of fires in a given period) and burn severity (loss of or change in ecosystem biomass) are two of the most important fire-regime attributes in shaping plant communities (Keeley *et al.*, 2011; Fernández-García *et al.*, 2018a; Hart *et al.*, 2019). Generally, vegetation is adapted to certain patterns of fire recurrence and burn severity, but shifts in these variables might result in changes in plant communities (Keeley *et al.*, 2011). There is thus a growing concern about the possible ecological consequences of expected increases in fire recurrence and burn severity arising from warmer and drier climate conditions and increases in fuel load and continuity in many regions of the world (Mouillot *et al.*, 2002; Stephens *et al.*, 2013; Fréjaville & Curt, 2015).

Southern Europe is one of the most vulnerable regions to global change (Giorgi & Gionello, 2008). In this region, climate warming is expected to alter vegetation structure from decreasing diversity, particularly in the transition areas between Mediterranean and continental climates and in mountain ranges (Thuiller *et al.*, 2005). Additionally, rural exodus and land abandonment has led to increases in fuel load and continuity in this region (Pausas *et al*., 2008). Understanding the vulnerability of plant community structure to changes in climate and land use is essential to predict modifications in ecosystem functioning (Guiot & Cramer, 2016). However, the indirect effects of climate and land-use change on vegetation through increases in both fire recurrence and burn severity are not well understood. Previous studies have focused primarily on the effects of fire-regime attributes on vegetation structure, and they showed highly variable results (Beckage & Stout, 2000; Blair *et al.*, 2016; Tessler *et al.*, 2016; Meyer *et al.*, 2019), further studies being advisable.

Changes in fire regimes can also modify the composition of plant communities because of differences in species fitness (Keeley *et al.*, 2011; Lamont *et al.*, 2018). Several functional traits have been considered key in determining plant fitness in relation to fire recurrence and burn severity, including life form (Pekin *et al.*, 2011; Blair *et al.*, 2016), eco-physiological traits (Anacker *et al.*, 2011; Hart *et al.*, 2019) and regenerative traits (Ojeda *et al.*, 2005; Wright *et al.*, 2016). In relation to life form, fire recurrence has been shown to increase the cover of shrubs to the detriment of trees (Tessler *et al.*, 2016; Fernández-García *et al.*, 2018a; Kowaljow *et al.*, 2018), and an analogous pattern has been found with burn severity (Crotteau *et al.*, 2013). However, little is known about the consistency of the relationship between life form and fire regimes under different environmental conditions (Pausas & Bradstock, 2007).

Among plant eco-physiological traits, specific leaf area (leaf area per unit dry mass; SLA) could be affected by changes in fire-regimes and environmental conditions in several ways (Macfarlane *et al.*, 2004; Dwyer *et al.*, 2014). Low SLA species invest more dry matter per leaf area, exhibit longer life spans, and have lower growth rates than high SLA species, which are associated with productive habitats (wet and fertile) (Dwyer *et al.*, 2014; Greenwood *et al.*, 2017). Anacker *et al.* (2011) found that SLA decreases at the community level after the fire, explaining this result by complex interdependences between fire regimes, climate, and reproductive strategies. Another eco-physiological trait that may be relevant in the post-fire regeneration is the atmospheric nitrogen (N_2) fixing capacity (Lajeunesse *et al.*, 2006). Legumes and actinorhizal plants have this ability through symbiosis with *Rhizobia* and *Frankia* bacteria respectively; it is particularly advantageous in N-deficient areas (Lajeunesse *et al.*, 2006), which can be the case for systems affected by recurrent fires or extreme severities (Certini, 2005). However, the potential relationship between N_2-fixing capacity and fire regime parameters could be modulated by climate, since aridity and low temperatures largely decreases nitrogen fixation (Poth, 1982; Lajeunesse *et al.*, 2006). Consequently, research concerning fire recurrence and severity effects on SLA and N_2-fixing capacity should consider the potential influence of environmental conditions, particularly climate.

Plant regenerative traits are key to post-fire recovery capacity (Calvo *et al.*, 2003; Keeley *et al.*, 2011; Clarke *et al.*, 2013). Many studies in fire ecology differentiate among obligate resprouters (plants whose post-fire regeneration relies on resprouting), obligate seeders (plants whose post-fire regeneration relies on seeding), and facultatives (plants with both mechanisms) (Anacker *et al.*, 2011; Pausas & Keeley, 2014; Pausas *et al.*, 2015). On one hand, it has been proposed that seeders could be better adapted than resprouters to severe fires, where most of the vegetative buds don't survive, particularly those aboveground (Clarke *et al*., 2013). On the other hand, resprouters can take advantage over seeders in situations of high recurrence, because they are not subjected to immaturity risk (Calvo *et al.*, 2003; Lloret *et al.*, 2005; Pausas & Keeley, 2014). There is evidence indicating that environmental conditions influence the regenerative strategies in Mediterranean biomes, with resprouters being more abundant in the most humid areas, as resprouting facilitates rapid regeneration particularly in highly competitive environments (Lloret *et al.*, 2005; Reyes *et al.*, 2009; Pausas & Bradstock, 2007; Pausas *et al.*, 2015). In addition, simulation models suggest that climate can shape the relationship between fire regime attributes and the regenerative strategy (Ojeda *et al.*, 2005), field studies being timely to corroborate this outcome.

Although the regenerative strategy helps to broadly predict vegetation responses to fire regimes (Pausas *et al.*, 2004; Pausas *et al.*, 2015), differences within the community of resprouters as well as within the community of seeders are expected. For instance, Clarke *et al.* (2013) indicate that among resprouters, those with buds located belowground are the most protected from recurrent and severe fires. With respect to seeders, some studies suggest that large seeds can be more resistant to fire and produce more vigorous seedlings (Bond *et al.*, 1999; Delgado *et al.*, 2008; Calvo *et al.*, 2015). Apart from seed allometry, the germination of many obligate seeders is heat-stimulated (Baskin & Baskin, 2014; Tavsanoglu & Pausas, 2018), and the establishment of heat-stimulated species has been positively related with fire recurrence (Lamont *et al.*, 2018) and burn severity (Wright *et al.*, 2016). Heat-stimulated germination is consequence of the rupture of physical seed dormancy by the high temperatures reached during the fire (Baskin & Baskin, 2014) and can be advantageous in fire-prone environments because it promotes germination when conditions for seedling establishment and growth are optimal (Pausas & Keeley, 2014; Lamont *et al.*, 2018). However, potential interaction effects of fire and climate on stimulating germination could be expected, as laboratory studies have indicated that moist heat could promote germination more than dry heat in some species (i.e. hard-seeded legumes) (Wiggers *et al.*, 2017). Consequently, to study the influence of fire regimes on plant traits along a climatic gradient will contribute to better understanding the potential impacts of fire on vegetation as well as to identifying which traits are key for the resilience of the community.

As far as we know, there are no studies analyzing the combined effects of fire recurrence and burn severity on functional traits under different environmental conditions. Advances in this knowledge are particularly relevant in the current context of expected increases in fire recurrence (Mouillot *et al.*, 2002; Enright *et al.*, 2015; Vázquez *et al.*, 2015) and burn severity (Parks *et al.*, 2016; Stephens *et al.*, 2013). The aim of this work is to study the effects of fire recurrence and burn severity on woody community structure and traits along a Mediterranean-Oceanic climatic gradient. Specifically, we aim to answer the following questions (i) Is the woody community structure (species richness, total cover, evenness and diversity) related with fire recurrence and burn severity over the medium term (four years) after fire? (ii) Are plant functional traits (life form, eco-physiological traits, and regenerative traits) related with fire recurrence and burn severity over the medium term (four years) after fire? We hypothesize that combined high fire recurrence and severity would result in a decrease in species richness, total cover and diversity. Furthermore, the effects of fire recurrence and burn severity on vegetation would depend on plant functional traits, which may be intercorrelated (Anacker *et al.*, 2011). In general, we assume the effects of fire recurrence and severity to be aggravated under Mediterranean as compared to Oceanic conditions, as fire impacts in humid climates are, in general, less persistent because of the rapid post-fire regeneration (Pausas & Bradstock, 2007; Fernández-García *et al.*, 2018b).

MATERIALS AND METHODS

Study sites

We selected three study sites within the Iberian Peninsula (Fig. 34) representing the Mediterranean-Oceanic gradient, which is the most representative climatic gradient of Southern Europe (Rivas-Martinez & Rivas-Saenz, 2017): the area affected by wildfire in Cortes de Pallás in summer 2012 (297 km^2), hereafter Mediterranean site; the area affected by wildfire in Sierra del Teleno in summer 2012 (119 km^2), hereafter Transition site; and the area affected by wildfire in Monte Pindo in summer 2013 (25 km^2), hereafter Oceanic site. The three wildfires were largely stand-replacing that affected serotinous pine forests, the type of forest most affected by fire in the Iberian Peninsula (Pausas & Vallejo, 1999; Fernández-García *et al.*, 2019). No subsequent fires were detected prior to field sampling.

The Mediterranean site is located in a mountainous area (120-942 m.a.s.l.) in the eastern Iberian Peninsula. This site is characterized by hot and dry summers, averaging four months of summer drought (typical Mediterranean conditions), annual precipitation of 400-600 mm and mean annual temperature of 13-17 ºC (Ninyerola *et al.*, 2005). Apart from the large wildfire of June 2012, the Mediterranean site was affected by wildfires in 1978, 1991 and 1994, repeatedly burning *Pinus halepensis* Mill. ecosystems with localized presence of *Pinus pinaster* Ait. and an understory dominated by *Ulex parviflorus* Pourr., *Quercus coccifera* L. and *Rosmarinus officinalis* L. among other Mediterranean shrubs (see Tables 24, 25, 26 in the Appendix for further information on the community composition of the three study sites). Soils are calcareous (8.14 ± 0.06; mean pH ± standard error), with loamy sand and sandy loam texture.

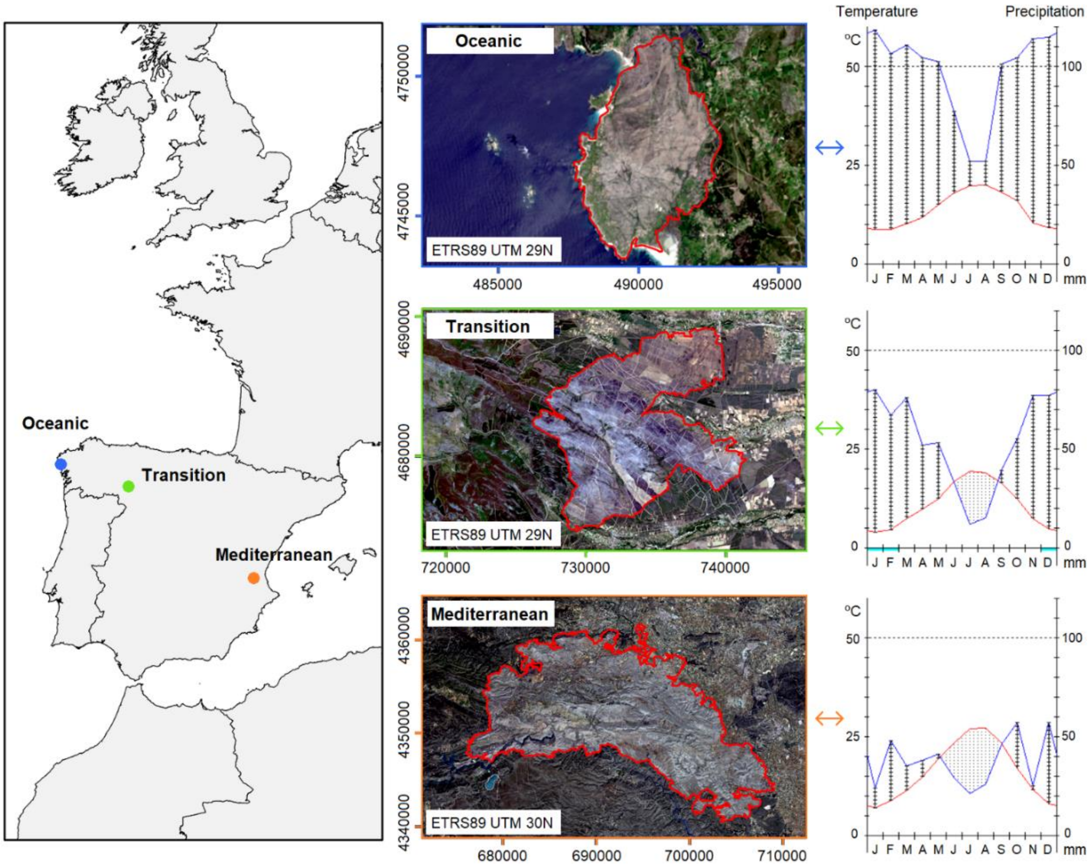

Figure 34. Location of the study sites in the Iberian Peninsula (panel on the left) and perimeters of the last wildfire in each study site (panel in the centre). Panels on the right show the climate diagrams of the closest meteorological stations based on Rivas-Martinez & Rivas-Saenz (2017).

The Transition site is located in the foothills of a mountain range (836-1,493 m.a.s.l.) in the northwestern Iberian Peninsula. This site is characterized by temperate and dry summers with two months of summer drought, annual precipitation of 600-800 mm and mean annual temperature of 8-11 ºC (Ninyerola *et al.*, 2005). Part of the area that burned in August, 2012, was previously affected by large wildfires in 1978, 1991 and 1998. The Transition site is occupied by *Pinus pinaster* ecosystems with a shrubby understorey community dominated by *Pterospartum tridentatum* (L.) Willk., *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. Soils are siliceous (pH 4.86 ± 0.14), with sandy loam texture.

The Oceanic site is located in Mount Pindo (0-929 m.a.s.l.) in the northwestern Iberian Peninsula. This site is characterized by temperate summers with no drought, annual precipitation of 1700-1800 mm and mean annual temperature of 12-15 ºC (Ninyerola *et al.*, 2005). The area affected by the wildfire of September 2013 was partially affected by fires occurred in 2005, 2004, 2000 and 1995 among others. The vegetation is dominated by *P. pinaster* and *Eucalyptus globulus* Labill. as invader species from nearby plantations. The understorey community is mostly comprised of *Rubus* sp., *Ulex europaeus* L., *Cytisus scoparius* (L.) Link and *Erica umbellata* Loefl. *ex* L. Soils are siliceous (pH 5.08 ± 0.10) with frequently exposed bedrock (biotite granite). The land uses in this site are more heterogeneous than in the Mediterranean and Transition sites, comprising natural forests highly variable in tree density, some of them developed over abandoned cropfields, and plantations.

Fire regime parameters: recurrence and severity

We mapped the fire recurrence by geoprocessing the fire perimeters in the Mediterranean and Transition sites for the period 1978-2012 and in the Oceanic site for the period 1990-2013. In the Mediterranean site, official cartography of fires was available for the entire study period (Alloza *et al.* 2012). In the Transition and Oceanic sites we digitized the fire perimeters using false colour composites from satellite imagery (Landsat 2, 4, 5, 7 and 8) (Earth Explorer, 2019) and aerial orthophotography (see Fernández-García *et al.*, 2018a).

The burn severity was obtained in the three study sites as a continuous variable, by calculating the differenced Normalized Burn Ratio (dNBR) of the last wildfire from Landsat imagery. Landsat 7 scenes from August 22nd, 2011 (pre-fire) and from August 25th, 2012 (post-fire) were used in the Mediterranean site; Landsat 7 scenes from September 20th, 2011 (pre-fire) and from September 6th, 2012 (post-fire) were used in the Transition site; and Landsat 8 scenes from August 30th 2013 and September 15th 2013 were used in the Oceanic site. Images were atmospherically and topographically corrected and dNBR was calculated, with values ranging from -2 to 2 (see Fernández-García *et al.*, 2018b for a detailed description on the imagery pre-processing and dNBR calculation).

Woody vegetation: sampling, structural parameters and traits

We focused the field sampling in a study frame of 3000 ha in the Mediterranean and Transition sites, and in 2500 ha in the Oceanic site (corresponding to the entire wildfire). These areas were selected because they were formerly dominated by pine ecosystems, with three different fire recurrences (one, two and three wildfires) and heterogeneous burn severity. In order to distribute the field plots proportionally to the area of each fire recurrence and along the burn severity gradient, we created a fire recurrence-severity map for each study site with six recurrence-severity categories, by combining the recurrence (one to three fires) and the burn severity classified into low and high severity (using the dNBR value 0.55 as threshold, which is considered moderate burn severity; Fernández-García *et al.*, 2018a, 2018b, 2019). We distributed 30 m x 30 m field plots (corresponding to the spatial resolution of Landsat ETM+ and OLI reflective bands) proportionally to the area of each frequency-severity category, with a minimum of 30 plots per study site, thereby ensuring that all the fire frequency-severity situations were represented. A total of 148 field plots of 30 m x 30 m were established: 30 plots in the Mediterranean site, 78 plots in the Transition site and 40 plots in the Oceanic site. The minimum distance between plots was 200 m. In each 30 m x 30 m plot we located three 2 m x 2 m subplots, divided in four 1 m x 1 m quadrats. Plot and subplot centres were georeferenced with a high precision GPS (RMSE X,Y < 0.5m). Four years after the wildfires (May-June 2016 in the Mediterranean and Transition, May-June 2017 in the Oceanic site), in each 1 m^2 quadrat we visually estimated the percentage cover of each woody species.

Several structural parameters of the woody plant community were studied in each 1-m^2 quadrat. Specifically, we determined the total cover and alpha diversity, including the species richness (S), Shannon diversity index (H) and species evenness (J) according to the following equations:

$$H = -\sum_{i=1}^{S} pi \ln pi$$

Where H is the Shannon diversity index (Shannon & Weaver, 1949), S is the species richness and pi is the relative cover of each species i.

J = H / Hmax

Where J is the Pielou's evenness index (Pielou, 1966), ranging from 0 to 1; H is the Shannon diversity index and Hmax is the maximum possible value for H for the existing species richness (ln S).

We classified each woody species according to their life form (tree or not tree), ecophysiological traits (low or high SLA -specific leaf area-; with N_2-fixing capacity or without N_2-fixing capacity) and regenerative traits (seeder, facultative or resprouter; presence of underground buds or absence of underground buds; low or high seed mass; with heat-stimulated germination or without heat-stimulated germination) when there was information available (Tables 24, 25, 26 in the Appendix). The information of plant traits was obtained from the BROT 2.0 database (Tavsanoglu & Pausas, 2018), bibliographic review (Cornelissen, 1996; Macfarlane *et al.*, 2004; Reyes *et al.*, 2009; Proença *et al.*, 2010), and field observations in the study sites. SLA and seed mass categories based on the median value from all the species used in the present study.

We calculated the relative cover (RC) of vegetation in relation to the functional traits in each 1-m^2 quadrat as follows. (i) RC of tree species: sum of the cover of tree species/sum of the cover of all species. (ii) RC of species with high SLA: sum of the cover of species with high SLA/sum of the cover of the cover of all species classified according to the SLA; (iii) RC of species with N_2-fixing capacity (sum of the cover of all Fabaceae species /sum of the cover of all species. (iv) RC of species with resprouting ability: sum of the cover of resprouters and facultatives/sum of the cover of all species classified according to the regenerative strategy; (v) RC of species with underground buds: sum of the cover of resprouters and facultatives with underground buds/sum of the cover of resprouters and facultatives classified according their bud location; (vi) RC of species with high seed mass: sum of the cover of seeders and facultatives with high mass/sum of the cover of seeders and facultatives classified according their seed mass; (vii) RC of species with heat-stimulated germination: sum of the cover of seeders and facultatives with heat-stimulated germination/sum of the cover of seeders and facultatives classified according their germinative response to heat-treatments.

Data analysis

To study the overall similarity of the samples from the three study sites (n = 1776) in relation to the structural parameters and traits, we performed non-metric multidimensional scaling ordinations (NMDSs) using the *metaMDS* function. A Wisconsin double standardization was applied to the data and Bray-Curtis dissimilarity was used to ordinate the samples. The *envfit* function performed with 1000 random permutations was used to calculate the correlation of the ordination with the external factor study site (Mediterranean, Transition and Oceanic) and with the external variables fire recurrence (number of fires) and burn severity (dNBR spectral index), obtaining the strength (R^2) and significance (*P*) of the correlations. In the same way, we calculated the correlation of the NMDSs with the structural parameters and vegetation traits with which the ordination was performed, and vectors were fitted in the NMDSs.

To analyze the effects of fire recurrence (number of fires) and burn severity (continuous dNBR spectral index) on the woody community structure and traits we performed generalized linear mixed models (GLMMs) for each study site (n = 360 in the Mediterranean; n = 936 in the Transition; n = 480 in the Oceanic) via penalized quasi-likelihood (*glmmPQL* function) to account for overdispersion. The response variables related with the community structure were: woody species richness, total cover, evenness and Shannon diversity index. The response variables related with the woody vegetation traits were: the relative cover (RC) of trees, of species with high SLA, of species with N_2-fixing capacity, of resprouters, of resprouters and facultatives with underground buds, of seeders and facultatives with high seed mass, and of seeders and facultatives with heat-stimulated germination. Following Zuur *et al.*´s (2009) recommendations, a Gaussian error distribution was used in the GLMMs to fit the continuous response variables (Shannon diversity index), a quasi-Poisson error distribution for count data and cover (richness and cover), and a quasi-binomial error distribution for the response variables expressed as percentage data ranging from 0 to 1 (species evenness, and relative covers). We used the canonical links for each error distribution family: *identity* for Gaussian, *log* for Poisson and *logit* for binomial. The identities of the 30 m x 30 m and 2 m x 2 m field plots/subplots were included into the models as a nested random factor. The interaction term (Recurrence x Severity) was retained in the models only when it was significant (P < 0.05). The generalized R^2 of the GLMMs was obtained via the standardized generalized variance approach.

We tested the significance of the association between the different traits at the species level in each study site (n = 49 in the Mediterranean; n = 11 in the Transition; n = 28 in the Oceanic) using the Fisher´s exact test.

All data analyses were carried out with R (R Core Team, 2017), using the packages *vegan* (Oksanen *et al.*, 2019) *MASS* (Venables & Ripley, 2002), *nlme* (Pinheiro *et al.*, 2017) and *r2glmm* (Jaeger, 2017).

RESULTS

Effects of fire recurrence and burn severity on plant community structure

The NMDS ordination (Fig. 35) separated the samples from the three study sites (R^2 = 0.43; P <0.01), indicating differences in the woody community structure among the three climatic conditions. Both fire-regime parameters, recurrence and severity, were significantly related with the ordination (P <0.01). Species evenness (J) increased from the Oceanic to the Transition and Mediterranean sites, whereas both species richness (S) and Shannon diversity index (H) increased towards the Mediterranean site.

Overall, the GLMMs indicated that the variance explained from fire recurrence and burn severity on structural parameters was higher in the Mediterranean site (0.17 ± 0.06; average

R^2 of models ± standard error) than in the Transition (0.04 ± 0.01) and Oceanic site (0.05 ± 0.01) (see R^2 in Fig. 36).

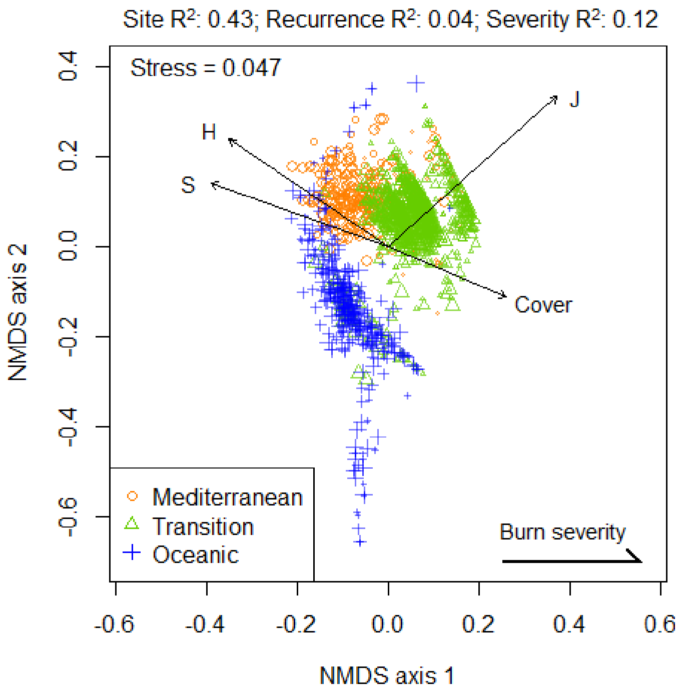

Figure 35. NMDS ordination of the samples from the three study sites (Mediterranean, Transition and Oceanic) according to the structure (total cover, alpha species richness, alpha evenness, and alpha diversity calculated with the Shannon diversity index) of the woody community. R^2 values show the goodness of fit of the ordination to the external parameters study site, fire recurrence (number of fires) and burn severity (dNBR) whereas the length of vectors in the panels indicate the goodness of fit of the ordination to the structural parameters. The ordination was rotated, matching burn severity with the axis 1. Shape sizes are proportional to the number of fires. S: alpha species richness; J: alpha evenness; H: alpha diversity calculated with the Shannon diversity index.

Focusing on each structural parameter, we observed that species richness, cover and Shannon diversity index increased from the less disturbed (i.e. one fire and the lowest severity) to the most disturbed scenario (i.e. three fires and the highest severity) in the three study sites (see arrows in Fig. 36). Analyzing the effects of fire recurrence and burn severity separately, we found that fire recurrence significantly increased species richness (Fig. 36a) and Shannon diversity index (Fig. 36d) in the Mediterranean and Transition sites, with the Oceanic site showing the same pattern. The cover of woody species also increased with fire recurrence in the Transition site (Fig. 36b). The effects of burn severity on the structural parameters were not significant, but a common trend was found in the three study sites, decreasing richness, evenness and Shannon diversity index (Fig. 36a, c, d; Table 27 in the Appendix).

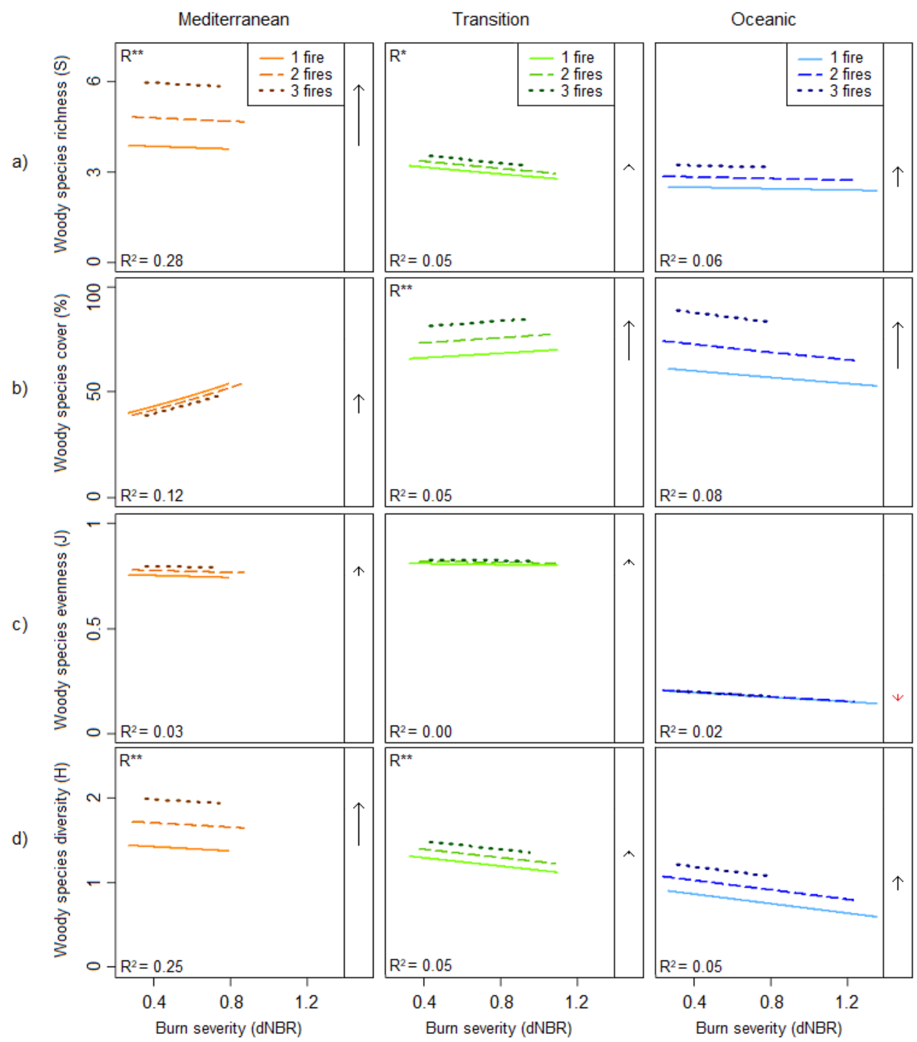

Figure 36. Mean predicted (a) alpha species richness (S), (b) total cover (%), (c) alpha evenness (J), and (d) alpha diversity calculated with the Shannon diversity index (H) of the woody community in relation to fire recurrence (number of fires) and burn severity (dNBR). Arrows on the right of the panels indicate the magnitude of change (positive in black, negative in red) in the mean predicted response variable from the least (one fire and the lowest severity) to the most (three fires and the highest severity) disturbed scenario. R^2 values indicate the standardized generalized variance (mean generalized R^2) explained by the GLMMs. The significance of model predictors (recurrence: R, severity: S) is represented as * (*P* <0.05) and ** (*P* <0.01).

Effects of fire recurrence and burn severity on plant traits

The NMDS ordination based on functional traits (Fig. 37) did not show a clear clustering of samples. The study site, fire recurrence, and burn severity were significantly related with the ordination ($P < 0.01$).

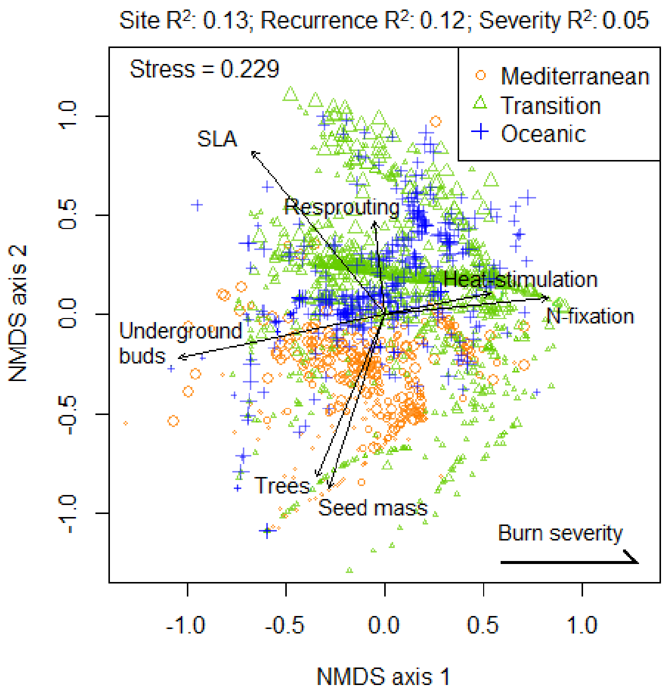

Figure 37. NMDS ordination of the samples from the three study sites (Mediterranean, Transition and Oceanic) according to the functional traits of the woody community. R^2 values show the goodness of fit of the ordination to the external parameters study site, fire recurrence (number of fires) and burn severity (dNBR) whereas the length of vectors in the panels indicate the goodness of fit of the ordination to the functional traits. The ordination was rotated, matching burn severity with the axis 1. Shape sizes are proportional to the number of fires. SLA = specific leaf area.

In general, we did not find significant correlations among plant traits at the species level (Table 23), except in the Mediterranean site where we found a significant correlation between N_2-fixing capacity and seed mass, and in the Oceanic site where we found a significant correlation between N_2-fixing capacity and heat-stimulated germination.

Table 23. Correlation matrix showing the Fisher's significance of the relationships between traits at species level in the woody community. SLA = Specific leaf area; Underg. Buds = Underground buds; Heat-stim. = Heat-stimulated germination. Significant correlations between traits for each study site (M = Mediterranean, T = Transition, O = Oceanic) are represented as * (*P* <0.05) and ** (*P* <0.01). n.s.= non-significant in any study site.

	Trees	SLA	N_2-fixation	Resprouting	Underg. buds	Seed mass
SLA	n.s.					
N_2-fixation	n.s.	n.s.				
Resprouting	n.s.	n.s.	n.s.			
Underg. buds	n.s.	n.s.	n.s.	n.s.		
Seed mass	n.s.	n.s.	**M***	n.s.	n.s.	
Heat-stim.	n.s.	n.s.	**O***	n.s.	n.s.	n.s.

The GLMMs performed to analyze the effects of fire recurrence and burn severity on plant functional traits indicated that the variance explained by the models (R^2) decreased from the Mediterranean (0.33 ± 0.06; average R^2 of models ± standard error) to the Oceanic site (0.12 ± 0.05), being intermediate in the Transition site (0.21 ± 0.04) (Fig. 38). Results also showed that variances explained on the traits related with germination (relative cover -RC- of species with high seed mass and RC of species with heat-stimulated germination) were higher in the Mediterranean end of the gradient, whereas the variance explained on the resprouting-related trait (RC of resprouters and facultatives with underground buds) was more relevant in the Oceanic site. In the Transition site, models performed with the traits related with the life form (RC of trees) and the reproductive strategy (RC of species with resprouting ability) reached the highest R^2.

Analyzing the effects of fire recurrence and burn severity on each trait along the climatic gradient we found that all of them were significantly affected four years after fire in the Mediterranean and Transition sites, whereas only two traits were affected in the Oceanic site (Fig. 39; Table 28 in the Appendix).

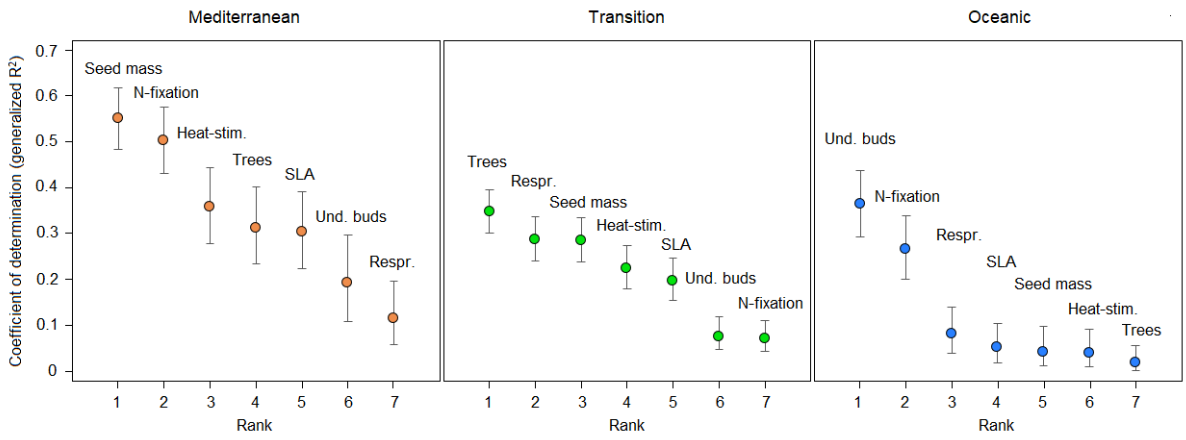

Figure 38. Rank of functional traits of the woody community in the three study sites (Mediterranean, Transition and Oceanic) according to the standardized generalized variance (mean generalized R^2) explained by the GLMMs performed with fire recurrence (number of fires) and burn severity (dNBR) as fixed-effects factors. Error bars indicate the 95% confidence intervals of the generalized R^2.

The RC of trees decreased from the Mediterranean to the Oceanic climate (Fig. 39a). Common trends were found in the three study sites, with the RC of trees decreasing from the less disturbed (i.e. one fire and the lowest severity) to the most disturbed scenario (i.e. three fires and the highest severity) (see arrows in Fig. 39a). The negative effects of fire recurrence on the RC of trees were significant only in the Mediterranean and Transition sites, whereas the negative effect of burn severity was significant only in the Mediterranean site.

Eco-physiological trait results showed that SLA increased from the Mediterranean to the Oceanic climate (Fig. 39b). The RC of species with high SLA increased from the less to the most disturbed scenario in the Mediterranean and Transition sites (see arrows in Fig. 39b), with significant effects of fire recurrence in both sites, and the effects of burn severity being significant only in the Mediterranean site. The RC of vegetation with N_2-fixing capacity did not show a clear pattern along the climatic gradient (Fig. 39c). The RC of N_2-fixing vegetation increased from the least to the most disturbed scenario in the three study sites (see arrows in Fig. 39c), with significant effects of fire recurrence in the Transition site, the effects of burn severity in the Mediterranean site, and the interaction between both in the Oceanic site.

There was a clear increase in the RC of species with resprouting ability from the Mediterranean to the Oceanic site (Fig. 39d). The RC of resprouters increased from the least disturbed to the most disturbed scenario in the Mediterranean and Transition sites (see arrows in Fig. 39d), with significant effects of fire recurrence in both sites, and the effects of burn severity in the Transition site.

Among the species able to resprout (resprouters and facultatives), those with underground buds dominated the Mediterranean site (Fig. 39e). Analyzing the change from the least to the most disturbed scenario, there was not a consistent pattern along the climatic gradient (see arrows in Fig. 39e). Fire recurrence and burn severity decreased the RC of resprouters with underground buds in the Mediterranean site, whereas burn severity caused an increase in the Transition site. In the Oceanic site there was a significant interaction between fire recurrence and burn severity.

Among the species that regenerate by seeds (obligate seeders and facultatives), those with high seed mass dominated the extremes of the climatic gradient (Fig. 39f). We found a common trend in the three sites, decreasing the RC of vegetation with high seed mass from the least to the most disturbed scenario (see arrows in Fig. 39f). The decreases caused by fire recurrence were significant in the Mediterranean and Transition sites. Positive relationships between burn severity and seed mass were found in the Mediterranean site, particularly after two and three wildfires. Conversely, the RC of vegetation with heat-stimulated germination increased from the least to the most disturbed scenario in the three study sites (see arrows in Fig. 39g). Both fire recurrence and burn severity tended to increase the RC of vegetation with heat-stimulated germination along the climatic gradient, with significant effects of burn severity in the Mediterranean site and the interaction in the Transition.

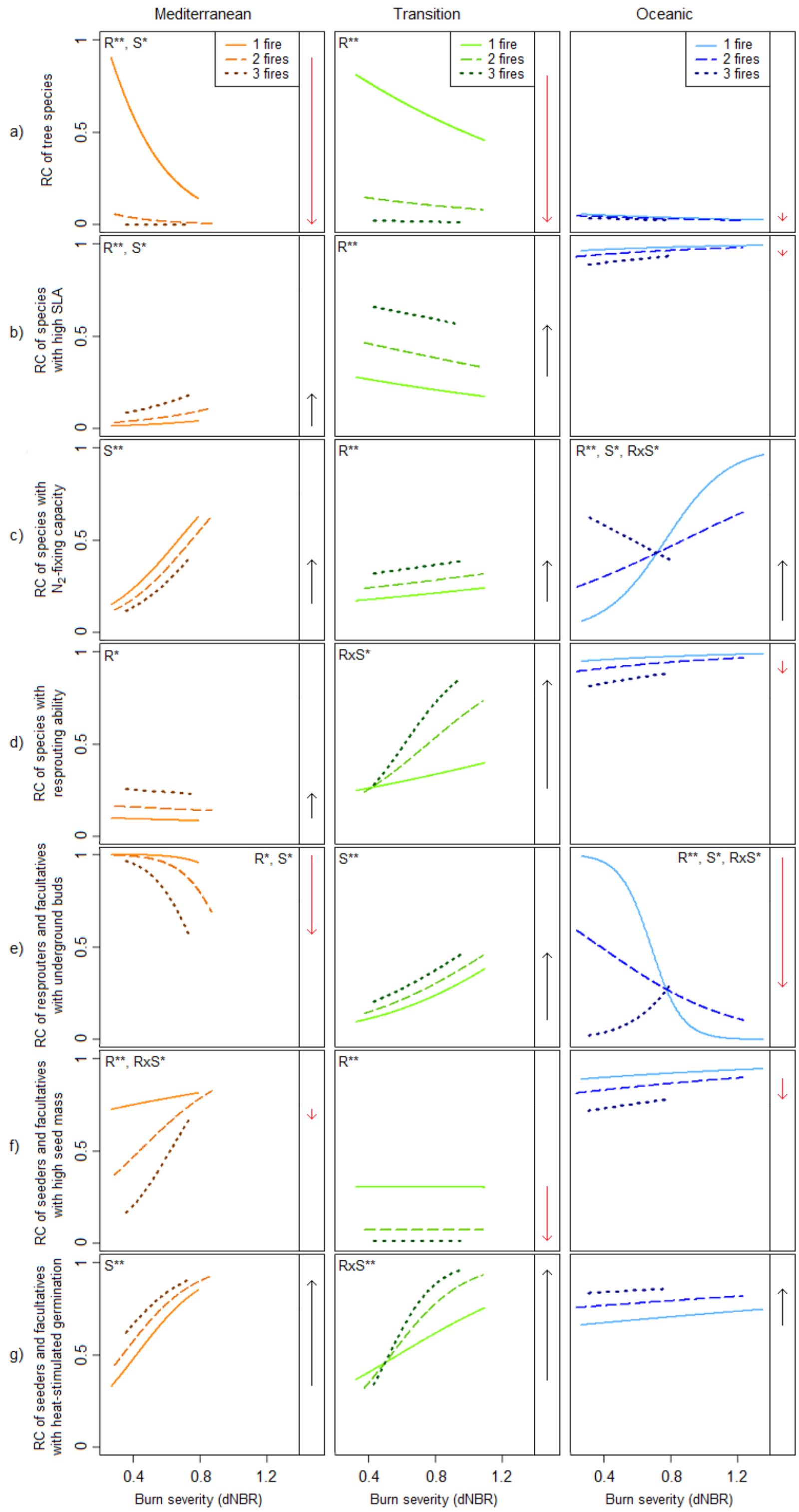

Figure 39. Mean predicted relative cover (RC) of (a) trees, (b) species with high specific leaf area (SLA), (c) species with N_2-fixing capacity, (d) species with resprouting ability, (e) resprouters and facultatives with underground buds, (f) seeders and resprouters with high seed mass, and (g) seeders and resprouters with heat-stimulated germination of the woody community, in relation to fire recurrence (number of fires) and burn severity (dNBR). Arrows on the right of the panels indicate the magnitude of change (positive in black, negative in red) in the mean predicted response variable from the least (one fire and the lowest severity) to the most (three fires and the highest severity) disturbed scenario. The significance of model predictors (recurrence: R, severity: S, and their interaction: R x S) is represented as * (*P* <0.05) and ** (*P* <0.01).

DISCUSSION

There is a growing awareness in the scientific community about global change impacts in plant communities (Pausas *et al.*, 2015; Guiot & Cramer, 2016; Hart *et al.*, 2019), including impacts caused by expected shifts in fire regimes (Mouillot *et al.*, 2002; Stephens *et al.*, 2013; Vázquez *et al.*, 2015; Enright *et al.*, 2015; Fréjaville & Curt, 2015; Parks *et al.*, 2016). The present study investigated the influence of fire recurrence and severity on the structure and traits of plant communities under different environmental conditions. Particularly, we focused in the Iberian Peninsula, which is the European region with the largest climate warming and drying projected for the fire season (Giorgi & Lionello, 2008). These projections, coupled with the increase in fuel loads during last decades (Pausas *et al*., 2008), point out this region as one in which fire regimes may change to a greater extent.

Effects of fire recurrence and burn severity on plant community structure

We found that modifications in fire regimes led to significant changes in woody community structure, particularly in Mediterranean and Transition climates. Alpha diversity (Shannon index) increased in the situations of high recurrence combined with high severity. Analyzing separately the effects of fire recurrence and burn severity on the components of the diversity (alpha species richness and evenness), we inferred that increases in Shannon diversity index were closely related with increases in species richness after recurrent fires, whereas increases in burn severity tended to counteract this shift. Although results in the literature are variable (e.g. Peterson & Reich, 2008; Pekin *et al.*, 2011), many previous studies agreed with our results, reporting increases in species diversity with fire recurrence (Beckage & Stout, 2000; Tessler *et al.*, 2016; Meyer *et al.*, 2019), because fire may prevent competitive exclusion (Schwilk *et al.*, 1997; Beckage & Stout, 2000). Accordingly, decreases in tree cover with fire recurrence can contribute to increase diversity of the understory community (Peterson & Reich, 2008; Tessler *et al.*, 2016; Meyer *et al.*, 2019), but when tree canopy cover is completely depleted further increases are not expected (Beckage & Stout, 2000). On the other hand, we found a decreasing trend in Shannon diversity index from low to high severities. This pattern can be related with the pre-fire canopy structure, as the highest severities usually occur in areas with high abundance of trees (Safford *et al.*, 2009; Shive *et al.*, 2013; García-Llamas *et al.*, 2019), which have, in general, a less diverse understory (Beckage & Stout, 2000; Peterson & Reich, 2008; Tessler *et al.*, 2016). We also found increases in total vegetation cover in the three study sites from the least (one fire and low severity) to the most disturbed scenario (three fires and high severity). This shift can be attributed to the faster recovery of shrubs, expected to dominate the most disturbed areas, than trees (Taboada *et al.*, 2017; Fernández-García *et al.*, 2018a). Thus, differences in structural parameters with fire recurrence and severity may be at expense of the transition from forest to shrub-dominated ecosystems.

Effects of fire recurrence and burn severity on plant traits

The influence of fire recurrence and burn severity on life forms support the assumptions expressed above, since we found significant decreases in the relative cover (RC) of tree vegetation. Previous studies in different ecosystems have found similar trends in relation to fire recurrence (Blair *et al.*, 2016; Tessler *et al.*, 2016; Kowaljow *et al.*, 2018) and burn severity (Crotteau *et al.*, 2013; Fernández-García *et al.*, 2018a). This result was expected because many shrub species in the study sites (e.g. Ericaceae and Cistaceae) find their optimal growth at short fire return intervals (5-10 years) (Fernández-García *et al.*, 2018a). In contrast, pines, which are the dominant trees in the three study sites, need longer periods to reach maturity and produce viable seed banks to ensure natural regeneration (Santana *et al.*, 2010), particularly under Mediterranean climates (Calvo *et al.*, 2013). Additionally, shrubs could be better colonizers than trees of gaps created by high severities (Crotteau *et al.*, 2013).

In relation to eco-physiological traits, we found that the RC of species with high SLA increased towards the humid side of the climatic gradient as well as in the areas of high recurrence and severity, mainly due to the effect of fire recurrence. Anacker *et al.* (2011)

found similar patterns three years after fire in chaparral ecosystems, with the SLA increasing in the most humid and frequently burned sites. Regardless of climate and soil, these authors attributed this result to the positive relationship between SLA and resprouting ability at the species level. However, in our study sites we did not find such a correlation, so results may be consequence of the different resource-use strategies between low and high SLA species (Dwyer *et al.*, 2014). Thus, high SLA could be advantageous under high recurrence and severity regimes, because these species are characterized by low investment per leaf area, short life-leaf spans, and rapid growth, rapidly reaching maturity (Dwyer *et al.*, 2014; Dirks *et al.*, 2017; Greenwood *et al.*, 2017). Likewise, we found that species with N_2-fixing capacity were favored in the most disturbed situation compared to the least-disturbed one. Increases in the abundance of N_2-fixing vegetation after fire have been detected previously (Cleveland *et al.*, 1999; Reich *et al.*, 2001), and can be related to soil nitrogen limitations for plant growth (Certini, 2005; Lajeunesse *et al.*, 2006) and to raised nitrogen demands for rapid regrowth under frequent disturbance regimes (Sheffer *et al.*, 2015). However, we found that N_2-fixing capacity was correlated with seed mass (Mediterranean site) and with heat-stimulated germination (Oceanic site), the behavior of each trait being dependent on the others, so further studies would be useful to clarify these relationships.

The dominant regenerative strategy varied along the climatic gradient from obligate seeders in the Mediterranean to vegetation able to resprout (resprouters and facultatives) in the Oceanic. We suggest that this difference could be attributed to the highest tolerance of obligate seeders to tissue dehydration, making them generally more resistant to droughts than resprouters (Pausas *et al.*, 2004; Pausas *et al.*, 2015), as well as to the limitation of available gaps for post-fire seedling recruitment in highly competitive environments (moist and fertile) such as the Oceanic (Clarke *et al.*, 2013; Pausas & Keeley, 2014). In the sites where both strategies coexist to a greater extent (Mediterranean and Transition sites), we confirm resprouting ability as a favourable trait to deal with high fire recurrences. This can be attributed to the capacity of resprouters to rapidly recover after fire, taking advantage of their surviving biomass (Calvo *et al.*, 1998; Pausas & Keeley, 2014) and because their regeneration does not depend upon seed production, which requires time to reach maturity (Pausas & Vallejo, 1999; Calvo *et al.*, 2003).

The location of vegetative buds in resprouters was the most relevant trait in relation to fire in the Oceanic site. In this site, having underground buds seems not benefitial under recurrent and severe fire regimes. However, Clarke *et al.* (2013) indicated that the number of buds as well as the available resources must be taken into consideration along with bud location to understand the behavior of resprouting. This assumption may support the positive effect of burn severity on species with underground buds in the Transition site, represented only by *Erica australis* (Table 25), as this species has a high number of buds as well as a lignotuber where it stores carbohydrates and mineral nutrients for resprouting (Calvo *et al.*, 1998; Tavsanoglu & Pausas, 2018).

Germination-related traits were among the most relevant in the Mediterranean side of the gradient. Nevertheless, light seeds and heat-stimulated germination were advantageous traits for seeders and facultatives along the entire gradient under combined increases in fire recurrence and severity, seed mass being more related to fire recurrence and heat-stimulated germination being more related to burn severity. Light seeds seem to be useful to colonize burned areas because they have a high dispersion capacity (Delgado *et al.*, 2008), and they show better fitness than heavy seeds in luminous conditions typical after fire (Dirks *et al.*, 2017). Furthermore, the correlation between species´ seed mass and time to reach maturity (Moles & Westoby, 2006) definitely suggests an advantage of light-seeded species in recurrent crown fire regimes. The positive effect of burn severity on the RC of species with heat-stimulated germination can be attributed to the massive germination caused by the thermal shock at temperatures between 60 ºC and 100 ºC (Baskin & Baskin, 2014).

Influence of environmental conditions on the effects of fire recurrence and burn severity

The three study sites have different environmental conditions (soil type, elevation, fire history and climate) that may affect vegetation structure and traits in different ways, potentially interacting with fire recurrence and severity. Nevertheless, we found that the strength of the effects of fire recurrence and burn severity on the structure and traits of woody vegetation varied with climate, increasing from the Oceanic to the Mediterranean site. We suggest that this pattern may not be casual, as it could be explained by (i) a fast post-fire recovery in humid climates, which rapidly attenuates the less persistent fire impacts (Pausas & Bradstock, 2007; Fernández-García *et al.*, 2018b). (ii) The high productivity in humid climates, which could counteract the effects of fire recurrence on traits linked to growth speed and time to reach maturity (e.g. SLA, resprouting ability, seed mass) (Enright *et al.*, 2015). (iii) Soil moisture content, which contribute to attenuate the temperatures reached during fire (Certini, 2005), potentially declining the stimulation of germination at low severities in humid climates. Furthermore, moisture facilitates the thermal transmissibility (Certini, 2005), likely increasing seed mortality at deep layers when the burn severity is high. (iv) Differences in competition, which is more relevant in highly productive environments, such as Oceanic sites, than in drier environments (Clarke *et al.*, 2013; Pausas & Keeley, 2014), potentially masking the effects of fire recurrence and severity on vegetation. (v) Several vegetation traits typical from fire-prone ecosystems (e.g. low SLA, resprouting ability, heat-stimulated germination) are considered advantageous to face both droughts and fires (Pausas *et al.*, 2004; Keeley *et al.*, 2011). In this sense, these traits could be doubly relevant in the Mediterranean side of the gradient, because water deficits can be aggravated after fire (Certini, 2005). As a result, our findings suggest that the relationship between fire-regime and plant traits requires a simultaneous consideration of climatic conditions (Pausas & Bradstock, 2007), although we recommend further evaluations to confirm this first evidence.

Concluding remarks

Given the evidence that changes in climate and land-use will modify fire regimes across the globe (Mouillot *et al.*, 2002; Stephens *et al.*, 2013; Enright *et al.*, 2015; Fréjaville & Curt, 2015; Vázquez *et al.*, 2015; Parks *et al.*, 2016), this study provides valuable information to predict future shifts in woody vegetation diversity and traits. Our results also indicate that these shifts could be more intense under warm climates with summer drought such as the Mediterranean and Transition climates than under Oceanic climates.

Among the effects of fire regimes on the woody community structure, we detected increases in alpha diversity of woody species with fire recurrence, partially counteracted at high severities. Focusing on plant traits, our findings indicate that high fire recurrence and severity contribute to the loss of forests, facilitating the transition from tree- to shrub-dominated ecosystems. Our results also revealed that woody vegetation with non-arboreal life form, high SLA, N_2-fixing capacity, resprouting ability, low seed mass and heat-stimulated germination is favored under regimes of high fire recurrence and severity.

We provide valuable information to implement new management strategies necessary to preserve forest ecosystems in a changing world, incorporating plant-trait responses to changes in fire regimes (Stephens *et al.*, 2013; Pausas *et al.*, 2015). According to our results, we highlight the importance of maintaining the plant trait diversity at the community level to maintain ecosystem resilience in the face of shifts in fire recurrence and severity.

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APPENDIX

Table 24. List of woody species sampled in the Mediterranean study site, mean cover and classification according to their functional traits. The presence of underground buds (in resprouters and facultatives) and the presence of high seed mass and heat-stimulated germination (in obligate seeders and facultatives) are indicated as sub-index in the strategy column. Aboveground = resprouters and facultatives without underground buds; underground = resprouters and facultatives with underground buds; light = obligate seeders and facultatives with light seeds, heavy = obligate seeders and facultatives with heavy seeds; stimulated = obligate seeders and facultatives with heat-stimulated germination; no-stimulated = obligate seeders and facultatives without heat-stimulated germination. SLA = Specific leaf area.

Taxon	Cover (%)	Tree	SLA	N_2-fixing capacity	Resprouting ability	Reproductive strategy
Argyrolobium zanonii	0.136	No	High	Yes	No	$S_{\text{heavy, stimulated}}$
Asparagus acutifolius	0.092	No	Low	No	Yes	$R_{\text{underground}}$
Bupleurum fruticescens	0.061	No	Low	No	Yes	F_{heavy}
Cistus albidus	3.194	No	Low	No	No	$S_{\text{light, stimulated}}$
Cistus clusii	0.342	No	Low	No	No	$S_{\text{light, stimulated}}$
Cistus ladanifer	0.125	No	Low	No	No	$S_{\text{light, stimulated}}$
Cistus monspeliensis	1.217	No	Low	No	No	$S_{\text{light, stimulated}}$
Cistus salviifolius	1.119	No	Low	No	No	$S_{\text{light, stimulated}}$
Coris monspeliensis	0.056	No	High	No	No	$S_{\text{light, no-stimulated}}$
Coronilla minima	0.025	No	High	Yes	Yes	$F_{\text{aboveground, light, stimulated}}$
Daphne gnidium	0.414	No	High	No	Yes	$R_{\text{underground}}$
Dorycnium pentaphyllum	2.394	No	High	Yes	Yes	$F_{\text{aboveground, heavy}}$
Erica multiflora	1.350	No	Low	No	Yes	$R_{\text{underground}}$
Erica terminalis	0.042	No	Low	No	Yes	$R_{\text{aboveground}}$
Fumana ericoides	1.186	No	Low	No	No	$S_{\text{heavy, no-stimulated}}$
Fumana laevipes	0.006	No	Low	No	No	$S_{\text{light, no-stimulated}}$
Fumana thymifolia	1.142	No	Low	No	No	$S_{\text{light, stimulated}}$
Genista scorpius	0.614	No	Low	Yes	Yes	$F_{\text{heavy, no-stimulated}}$
Globularia alypum	0.006	No	Low	No	Yes	$F_{\text{aboveground, light}}$
Helianthemum appeninum	0.247	No	High	No	No	$S_{\text{light, stimulated}}$

Helianthemum cinereum	0.728	No	Low	No	No	S
Helianthemum syriacum	1.750	No	Low	No	No	S light, no-stimulated
Helicrysum stoechas	0.092	No	High	No	-	-
Juniperus oxycedrus	0.342	No	Low	No	Yes	R underground
Linum suffruticosum	0.222	No	High	No	Yes	R underground
Lithodora fruticosa	0.100	No	Low	No	Yes	F underground, heavy
Olea europaea	0.033	Yes	Low	No	Yes	R underground
Onobrychis conferta	0.017	No		Yes	-	-
Ononis fruticosa	0.253	No	High	Yes	Yes	F heavy
Ononis minutissima	0.094	No	High	Yes	No	S light, stimulated
Phagnalon saxatile	0.078	No	High	No	No	S light
Pinus halepensis	3.408	Yes	Low	No	No	S heavy, no-stimulated
Pistacia lentiscus	0.772	No	Low	No	Yes	R underground
Polygala rupestris	0.092	No	High	No	No	S heavy
Quercus coccifera	7.436	No	Low	No	Yes	R underground
Quercus ilex	0.669	Yes	Low	No	Yes	R underground
Retama sphaerocarpa	0.097	No		Yes	Yes	F heavy
Rhamnus alaternus	0.128	No	High	No	Yes	R aboveground
Rhamnus lycioides	0.131	No	High	No	Yes	R
Rosmarinus officinalis	3.064	No	Low	No	No	S light, no-stimulated
Rubus ulmifolius	0.072	No	High	No	Yes	R underground
Satureja montana	0.011	No	High	No	No	S
Sideritis angustifolia	0.267	No	High	No	Yes	F light, no-stimulated
Staehelina dubia	0.014	No	High	No	Yes	F aboveground , heavy, no-stimulated
Teucrium capitatum	0.047	No	High	No	-	-
Teucrium chamaedrys	0.003	No	High	No	Yes	R
Thymus piperella	0.169	No	High	No	Yes	F light, stimulated
Thymus vulgaris	0.328	No	Low	No	Yes	F light, no-stimulated
Ulex parviflorus	14.794	No	Low	Yes	No	S heavy, stimulated

Table 25. List of woody species sampled in the Transition study site, mean cover and classification according to their functional traits. The presence of underground buds (in resprouters and facultatives) and the presence of high seed mass and heat-stimulated germination (in obligate seeders and facultatives) are indicated as sub-index in the strategy column. Aboveground = resprouters and facultatives without underground buds; underground = resprouters and facultatives with underground buds; light = obligate seeders and facultatives with light seeds, heavy = obligate seeders and facultatives with heavy seeds; stimulated = obligate seeders and facultatives with heat-stimulated germination; no-stimulated = obligate seeders and facultatives without heat-stimulated germination. SLA = Specific leaf area.

Taxon	Cover (%)	Tree	SLA	N_2-fixing capacity	Resprouting ability	Reproductive strategy
Calluna vulgaris	0.337	No	Low	No	No	$S_{\text{light, no-stimulated}}$
Cistus salviifolius	0.156	No	Low	No	No	$S_{\text{light, stimulated}}$
Erica arborea	0.285	No	High	No	Yes	$R_{\text{aboveground}}$
Erica australis	14.970	No	High	No	Yes	$R_{\text{underground}}$
Erica umbellata	6.830	No	High	No	No	$S_{\text{light, no-stimulated}}$
Genista florida	0.003	No	-	Yes	Yes	F
Halimium lasianthum	23.518	No	-	No	No	$S_{\text{light, stimulated}}$
Halimium umbellatum	0.543	No	Low	No	No	$S_{\text{stimulated}}$
Pinus pinaster	6.051	Yes	Low	No	No	$S_{\text{heavy, no-stimulated}}$
Polygala microphylla	0.033	No	-	No	-	-
Pterospartum tridentatum	22.489	No	Low	Yes	Yes	$R_{\text{aboveground}}$

Table 26. List of woody species sampled in the Oceanic study site, mean cover and classification according to their functional traits. The presence of underground buds (in resprouters and facultatives) and the presence of high seed mass and heat-stimulated germination (in obligate seeders and facultatives) are indicated as sub-index in the strategy column. Aboveground = resprouters and facultatives without underground buds; underground = resprouters and facultatives with underground buds; light = obligate seeders and facultatives with light seeds, heavy = obligate seeders and facultatives with heavy seeds; stimulated = obligate seeders and facultatives with heat-stimulated germination; no-stimulated = obligate seeders and facultatives without heat-stimulated germination. SLA = Specific leaf area.

Taxon	Cover (%)	Tree	SLA	N_2-fixing capacity	Resprouting ability	Reproductive strategy
Calluna vulgaris	1.052	No	Low	No	No	$S_{\text{light, no-stimulated}}$
Cytisus scoparius	5.879	No	High	Yes	Yes	$F_{\text{heavy, stimulated}}$
Cytisus striatus	0.035	No	-	Yes	Yes	$F_{\text{stimulated}}$
Daboecia cantabrica	0.006	No	-	No	Yes	$F_{\text{light, no-stimulated}}$
Daphne gnidium	0.498	No	High	No	Yes	$R_{\text{underground}}$
Erica ciliaris	1.283	No	-	No	No	$S_{\text{light, stimulated}}$
Erica cinerea	2.979	No	Low	No	Yes	$F_{\text{light, no-stimulated}}$
Erica tetralix	0.231	No	-	No	-	-
Erica umbellata	5.585	No	High	No	No	$S_{\text{light, no-stimulated}}$
Eucalyptus globulus	1.267	Yes	Low	No	Yes	$R_{\text{aboveground}}$
Frangula alnus	1.071	No	High	No	Yes	R
Genista berberidea	1.958	No	-	Yes	Yes	$F_{\text{stimulated}}$
Glandora prostrata	1.246	No	-	No	Yes	$F_{\text{underground, heavy}}$
Halimium lasianthum	3.960	No	-	No	No	$S_{\text{light, stimulated}}$
Hedera helix	0.006	No	High	No	Yes	$R_{\text{underground}}$
Lonicera periclymenum	0.108	No	High	No	-	-
Osyris alba	0.446	No	Low	No	Yes	$R_{\text{aboveground}}$
Pinus pinaster	3.248	Yes	Low	No	No	$S_{\text{heavy, no-stimulated}}$
Prunus spinosa	0.431	No	High	No	Yes	$R_{\text{underground}}$
Pterospartum tridentatum	1.929	No	Low	Yes	Yes	$R_{\text{aboveground}}$
Pyrus cordata	0.165	Yes	-	No	Yes	R
Quercus lusitanica	0.335	No	Low	No	Yes	$R_{\text{underground}}$
Quercus pyrenaica	0.219	Yes	High	No	Yes	$R_{\text{underground}}$
Quercus robur	0.610	Yes	High	No	Yes	$R_{\text{underground}}$

Rubus sp.	22.023	No	High	No	Yes	R underground
Salix atrocinerea	1.450	Yes	High	No	Yes	R
Ulex europaeus	20.988	No	High	Yes	Yes	F heavy, stimulated
Ulex galli	2.613	No	High	Yes	Yes	F heavy, stimulated

Table 27. Results of the fixed effects of the Generalized Linear Mixed Models (GLMMs) ['summary()' outputs] in the three study sites (Mediterranean, Transition and Oceanic), indicating the effects of the variables fire recurrence (number of fires) and burn severity (dNBR ranging from -2 to 2) on the woody community structure: alpha species richness, total cover, alpha evenness and alpha diversity calculated with the Shannon diversity index. Significant interactions were not detected. SE = standard error. Significant P-values (P <0.05) are in bold face.

Response variable	Predictor variable	Mediterranean			Transition			Oceanic		
		Estimat.	SE	*P*	Estimat.	SE	*P*	Estimat.	SE	*P*
Species richness (S)	Intercept	1.15	0.22	**<0.01**	1.17	0.09	<**0.01**	0.80	0.18	<**0.01**
	Recurrence	0.22	0.06	**<0.01**	0.06	0.03	**0.02**	0.13	0.08	0.13
	Severity	-0.06	0.26	0.83	-0.19	0.10	0.06	-0.05	0.21	0.83
Species cover (%)	Intercept	3.58	0.26	<**0.01**	4.06	0.10	<**0.01**	3.96	0.23	<**0.01**
	Recurrence	-0.04	0.07	0.58	0.10	0.03	<**0.01**	0.19	0.11	0.08
	Severity	0.57	0.32	0.08	0.08	0.10	0.44	-0.13	0.28	0.63
Species evenness (J)	Intercept	1.01	0.27	**<0.01**	1.37	0.19	**<0.01**	-1.51	0.27	<**0.01**
	Recurrence	0.13	0.08	0.09	0.07	0.05	0.17	0.06	0.13	0.61
	Severity	-0.13	0.33	0.70	-0.08	0.20	0.69	-0.36	0.32	0.27
Species diversity (H)	Intercept	1.19	0.28	<**0.01**	1.29	0.13	<**0.01**	0.81	0.20	<**0.01**
	Recurrence	0.28	0.08	<**0.01**	0.10	0.04	<**0.01**	0.16	0.09	0.08
	Severity	-0.13	0.34	0.71	-0.25	0.14	0.08	-0.28	0.24	0.25

Table 28. Results of the fixed effects of the Generalized Linear Mixed Models (GLMMs) ['summary()' outputs] in the three study sites (Mediterranean, Transition and Oceanic), indicating the effects of the variables fire recurrence (number of fires) and burn severity (dNBR ranging from -2 to 2) on the woody community traits expressed in relative cover (RC): RC of trees, RC of species with high specific leaf area (SLA), RC of species with N_2-fixing capacity, RC of species with resprouting ability, RC of resprouters and facultatives with underground buds, RC of seeders and facultatives with high seed mass, RC of seeders and facultatives with heat-stimulated germination. Interactions (R x S) were retained only when were significant. SE = standard error. Significant P-values (P <0.05) are in bold face.

Response variable	Predictor variable	Mediterranean			Transition			Oceanic		
		Estimat.	SE	*P*	Estimat.	SE	*P*	Estimat.	SE	*P*
RC of tree species	Intercept	2.80	1.46	0.06	0.77	0.67	0.25	-3.87	1.07	**<0.01**
	Recurrence	-2.94	0.50	**<0.01**	-1.85	0.20	**<0.01**	-0.20	0.51	0.70
	Severity	-4.00	1.80	**0.03**	-0.89	0.71	0.22	-0.75	1.27	0.55
RC of species with high SLA	Intercept	-5.92	0.84	**<0.01**	-1.56	0.52	**<0.01**	3.44	0.94	**<0.01**
	Recurrence	0.90	0.22	**<0.01**	0.85	0.14	**<0.01**	-0.59	0.43	0.18
	Severity	2.32	0.99	**0.03**	-0.79	0.56	0.16	1.21	1.07	0.27
RC of species with N_2-fixing capacity	Intercept	-2.58	0.74	**<0.01**	-2.16	0.46	**<0.01**	-6.84	2.10	**<0.01**
	Recurrence	-0.34	0.20	0.11	0.38	0.12	**<0.01**	2.65	0.96	**<0.01**
	Severity	4.33	0.91	**<0.01**	0.56	0.49	0.26	9.12	3.94	**0.03**
	R x S	-	-	-	-	-	-	-3.68	1.67	**0.03**
RC of species with resprouting ability	Intercept	-2.76	0.97	**<0.01**	-0.53	1.02	0.61	3.46	0.94	**<0.01**
	Recurrence	0.60	0.26	**0.03**	-0.90	0.63	0.15	-0.74	0.43	0.09
	Severity	-0.33	1.18	0.78	-1.24	1.30	0.34	0.96	1.07	0.37
	R x S	-	-	-	2.15	0.81	**0.01**	-	-	-
RC of resprouters and facultatives with underground buds	Intercept	11.10	3.13	**<0.01**	-3.32	0.74	**0.01**	13.62	4.69	**<0.01**
	Recurrence	-1.63	0.73	**0.03**	0.32	0.19	0.10	-6.52	2.17	**<0.01**
	Severity	-8.09	3.30	**0.02**	2.30	0.78	**<0.01**	-18.54	8.77	**0.04**
	R x S	-	-	-	-	-	-	8.27	3.71	**0.03**
RC of seeders and facultatives with high seed mass	Intercept	2.97	1.43	**0.04**	0.91	0.69	0.18	2.44	1.08	**0.02**
	Recurrence	-2.27	0.67	**<0.01**	-1.72	0.20	**<0.01**	-0.58	0.49	0.25
	Severity	-1.64	2.35	0.49	-0.02	0.74	0.97	0.69	1.13	0.54
	R x S	2.61	1.15	**0.03**	-	-	-	-	-	-
RC of seeders and facultatives with high heat-stimulated germination	Intercept	-2.39	1.05	**0.02**	0.01	1.18	0.99	0.08	1.07	0.94
	Recurrence	0.39	0.29	0.19	-1.28	0.74	0.09	0.46	0.49	0.36
	Severity	4.71	1.29	**<0.01**	-0.38	1.52	0.80	0.37	1.14	0.75
	R x S	-	-	-	2.54	0.97	**<0.01**	-	-	-

6. DISCUSSION

Fire regime characterization using remote sensing methods

Satellite imagery is essential for fire regime characterization in vast areas, and has the advantage of being applicable worldwide (Chuvieco, 2010). Specifically, we have found that the visual analysis of Landsat time series (MSS, TM, ETM + and OLI-TIRS sensors) using false-color composites allows to identify burned areas since the first Landsat satellites were launched in the 1970s (NASA, 2019). The use of false color composites takes advantage of the spectral resolution of Landsat scenes to identify fire scars (Röder *et al.*, 2008; Chuvieco, 2010; Bastarrika *et al.*, 2014). However, it is always advisable to validate the results with field-based information (Chuvieco, 1999) since, according to Bowman *et al.* (2003), the reliability of this method varies depending on the environmental conditions and ecosystem productivity. Once the fire scars have been identified, it is possible to calculate fire regime attributes such as fire size, fire recurrence and fire return interval, which are highly relevant to understand the ecological effects of fire, and can be useful variables to improve forest management (Eugenio *et al.*, 2006; Taboada *et al.*, 2017).

Burn severity is another fire regime attribute with ecological interest (Fernandes & Rigolot, 2007; Pausas & Keeley, 2014) that can be estimated using Landsat imagery (TM, ETM + and OLI sensors). Our results showed that the reflective spectral indices based on dNBR, such as dNBR itself (Key & Benson, 2006), RdNBR (Miller & Thode, 2007) or RBR (Parks *et al.*, 2014) are more suitable to determine burn severity than thermal or mixed indices. The dNBR-type indices are based on the near-infrared and short-wave infrared regions of the electromagnetic spectrum, which are related to the structure of the leaves and the moisture content of the ecosystem respectively (Chuvieco, 2010), that gradually change with burn severity (Key & Benson, 2006). However, the performance of these indices shows a high variability depending on the environmental conditions (Parks *et al.*, 2014), and raises several difficulties in determining the soil burn severity (Robichaud *et al.*, 2007). In order to solve these shortcomings, we have proposed a new index, the dNBR-EVI, which showed better performance than the other spectral indices in terms of accuracy and transferability along a climate gradient. The proper performance of dNBR-EVI compared to the other dNBR-type indices can be attributed to the inclusion of the red band, which is highly sensitive to leaf pigmentation; and the inclusion of the blue band, which can compensate for differences in atmospheric aerosols (Gao *et al.*, 2000; Chuvieco, 2010). In any case, our results showed that Landsat spectral indices have higher capacity to quantify site burn severity and vegetation burn severity than soil burn severity. This might be the consequence of the shielding effect of vegetation or its remains (Soverel *et al.*, 2011; Tanase *et al.*, 2011), but also the result of the influence of soil types on the spectral response to burn severity (Smith *et al.*, 2010). In this sense, characterizing soil burn severity with an accuracy comparable to that obtained when characterizing vegetation burn severity, remains a challenge, which may require the use of (i) high spatial resolution imagery, which would allow the partial elimination of the vegetation shadow (McKenna *et al.*, 2017); or (ii) hyperspectral sensors, which allow to discriminate very specific features of soil surface (Robichaud *et al.*, 2007).

Effects of fire recurrence and severity

Fire effects on soil and vegetation are heterogeneous, as they depend on multiple factors such as fire recurrence and burn severity (Bodí *et al.*, 2012). Our results showed that burn severity determines the soil status both immediately after fire and over the medium term (3 years) after fire. In relation to soil physical properties, we found that the size of soil aggregates decreases at high severities, which can be attributed to changes in the main binding agents (organic matter and clay minerals) at very high temperatures (Santín & Doerr, 2016). This result emphasizes the importance of limiting high severity fires if we aim to preserve the soil, as the destruction of soil aggregates leads to the loss of soil structure (Cerdà & Jordán, 2010) and increases the erosion rates (Vieira *et al.*, 2015). Moreover, we identified changes in soil chemical properties at moderate and high severities, such as increases in pH and available phosphorus concentration and decreases in organic carbon. Changes in these chemical properties are mainly a consequence of the organic matter mineralization and the deposition of ashes from vegetation combustion (Certini, 2005;

Marcos *et al.*, 2007; Caon *et al.*, 2014). Over the medium term after fire, the concentration of available phosphorus is still positively correlated with burn severity in siliceous soils. This pattern could be due to sorption-desorption processes (Serrasoles *et al.*, 2008), as phosphorus sorption hinders subsequent phosphorus losses by percolation or runoff, allowing its release in available form over the medium term (Serrasoles *et al.*, 2008; Otero *et al.*, 2015). However, in calcareous soils, part of the available phosphorus forms apatite after the fire, keeping phosphorus unavailable for biota over the medium term (Caon *et al.*, 2014; Otero *et al.*, 2015). However, although fire can increase the concentration of available phosphorus in soils, it is important to highlight that severe fires always produce phosphorus losses at the ecosystem level, by convection of ashes during the fire or by wind and water erosion (Boerner, 1982). Additionally, we demonstrated that biological soil properties (enzymatic activities and microbial biomass carbon) are the most sensitive to fire, decreasing drastically from low severity levels. This is consequence of protein inactivation and denaturation, and microorganism's mortality at relatively low temperatures (50-70 °C) (Tabatabai, 1994; Vega *et al.*, 2013; Santín & Doerr, 2016). Burn severity effects on biological properties persist over the medium term after fire, as fire modifies for several years soil micro-climatic conditions, litter and vegetation proportionally to burn severity (Keeley, 2009; Dooley & Treseder, 2012). According to our results, we can state that several soil properties (pH, available phosphorus, enzymatic activities β-glucosidase, urease and acid phosphatase, and microbial biomass carbon) can be used to monitor short-term fire impacts on soils, and to analyze the burn severity legacy over the medium term after fire in pine ecosystems, which is necessary to assess soil recovery (Hedo *et al.*, 2015; Muñoz-Rojas *et al.*, 2016).

The different sensitivity of soil properties to fire causes soil quotients (i.e. ratios between soil properties) to be modified with severity. Thus, in the present PhD Thesis we have proposed the study of soil quotients for a better understanding of burn severity impact on soil status and processes (Lagomarsino *et al.*, 2009; Paz-Ferreiro & Fu, 2016). Immediately after the fire, we found (i) a decrease in C:N ratio (organic carbon: total nitrogen) with the increase in burn severity, because the total nitrogen is more stable than the organic carbon at high severities (Vega et al., 2013); (ii) a decrease in the microbial quotient (microbial biomass carbon:organic carbon) in moderate and high severities, which can be attributed to microbial mortality and to the lack of labile carbon sources (Díaz-Raviña *et al*., 2012); and (iii) a severe decrease in the specific activity of the enzyme β-glucosidase (β-glucosidase activity per unit of microbial biomass carbon) from low burn severity levels, suggesting a decrease in the physiological capacity of the microbial community (Lagomarsino *et al.*, 2009). Soil quotient values are, in general, more uniform among soil types than the values of individual properties. Thus, we point out that soil quotients could be highly useful and generalizable to compare burn severity effects among different study sites. However, it is advisable to study the evolution of soil quotients in relation to burn severity several years after the fire, as the persistence of fire impact is different for each soil property (Certini, 2005; Alcañiz *et al.*, 2016; Muñoz-Rojas *et al.*, 2016).

Nowadays, it is helpful the use of satellite-derived products to identify the effects of wildfires on ecosystems. In the present PhD Thesis, we conducted a study of fire recurrence and severity effects on post-fire regeneration using a remote sensing approach. Results indicated that both fire regime attributes were significantly related to the vegetation greenness recovery 2 and 5 years after fire. In general, the post-fire greenness was closer to the pre-fire situation in the high recurrence (3 or more fires in 40 years) and low severity (CBI <2.25) situations. The rapid recovery in the high recurrence areas may be due to the high regenerative speed of herbaceous and shrub species, which dominate the frequently burned areas (Calvo *et al.*, 2008; Tessler *et al.*, 2016). Likewise, in low severity scenarios the initial change in the forest canopy and plant mortality is lower than in high severity areas (Key & Benson, 2006), which favors the recovery of the pre-fire greenness. Our results indicated that the combination of both fire recurrence and burn severity increased the predictive capacity on post-fire greenness recovery. Nevertheless, it is necessary to study the regeneration of the dominant pine species and the recovery of the rest of the plant community in the field to better understand the underlying mechanisms of post-fire greenness recovery (Taboada *et al.*, 2017; Yang *et al.*, 2017).

The field study of the dominant pine species (*P. pinaster* and *P. halepensis*) regeneration showed that combined increases in fire recurrence and burn severity decreased the post-fire density and development of pine seedlings to values that may hinder forest recovery (0.01 seedlings per square meter) (Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016). These negative effects were particularly significant in sites with a prolonged summer drought, such as the Mediterranean areas. Previous studies have indicated that high fire frequencies difficult the regeneration of the pine population due to an insufficient seed production (Eugenio *et al.*, 2006; Santana *et al.*, 2010) and to the deterioration of soil conditions for seedling establishment and development, including a low soil protection for seeds, unfavorable micro-climatic conditions and a poor nutrient concentrations (Pausas *et al.*, 2004; Taboada *et al.*, 2018). Likewise, severe fires cause mortality in the seed bank and high tree mortality rates, largely reducing the seed supplying capacity (Habrouk *et al.*, 1999; Fernandes & Rigolot, 2007), which contributes to a lower post-fire seedling density. These findings constitute a benchmark to encourage forest management aimed at reducing fire recurrence and burn severity in Mediterranean fire-prone ecosystems if the pine forest is to be maintained.

At the woody community level, we found that relatively high recurrences increased the species richness and diversity (Tessler *et al.*, 2016; Meyer *et al.*, 2019). This effect is associated with the removal of tree canopy after frequent fires, reducing the risk of competitive exclusion (Beckage & Stout, 2000). Moreover, high burn severities tend to decrease species richness and diversity, possibly because the highest severities occur in the areas with high abundance of trees (Shive *et al.*, 2013; García-Llamas *et al.*, 2019), which are a priori those with a less diverse understory (Beckage & Stout, 2000; Tessler *et al.*, 2016). We have also found that fire recurrence and severity modify plant functional traits at the community level. Specifically, species with a non-arboreal life form, high specific leaf area, N_2-fixing capacity, resprouting ability, low seed mass and heat-stimulated germination showed the hoguest resilience to high fire recurrences and severities, increasing their relative cover. These different behaviors can be related to key ecological features such as the ability to profusely colonize burned areas (Calvo *et al.*, 2013; Crotteau *et al.*, 2013), the ability to obtain resources and grow rapidly after fires (Dwyer *et al.*, 2014; Dirks *et al.*, 2017; Sheffer *et al.*, 2015), or reproductive precocity (Pausas, 1999; Santana *et al.*, 2010). As it occurred with *P. pinaster* and *P. halepensis*, the effects of fire recurrence and burn severity on the woody community were less significant in humid climates, probably because of the faster post-fire recovery and, therefore, the shorter time to reach maturity (Pausas & Bradstock, 2007; Enright *et al.*, 2015), and because of the relevance of competitive effects in highly productive environments (Clarke *et al.*, 2013; Pausas & Keeley, 2014), which might mask the impacts of fire recurrence and severity. Our results at the plant community level encourage to consider plant functional traits when designing management strategies to face changes in fire regimes that are expected in the current context of global change (Enright et al ., 2015; Vázquez *et al.*, 2015).

Scientific basis to optimize forest management

Over the past few decades, the post-fire management of *P. pinaster* and *P. halepensis* forests has focused on salvage logging and seedling or plantation with the dominant pine species in areas with poor natural regeneration (de las Heras *et al.*, 2012). Currently, advances in scientific knowledge aim to optimize forestry practices to achieve several key objectives such as improving soil protection, contributing to water cycle regulation, promoting diversity, maturity and productivity of pine ecosystems and increasing forest resistance and resilience to disturbances (Fernandes and Rigolot, 2007; Valdecantos *et al.*, 2009; de las Heras *et al.*, 2012). In this sense, results obtained in the present PhD Thesis indicate that fire recurrence and burn severity are two key factors that should be considered in forest management before and after the fire.

After a wildfire, emergency interventions are the first actions to be carried out. These actions should focus on reducing the risks to human life, personal properties and critical natural resources such as soil (de las Heras, 2012). High severities cause the breakage and collapse of soil aggregates, the loss of soil structure (Cerdà & Jordán, 2010), the depletion of litter and decreases in vegetation cover (Key & Benson, 2006), which persists several years after the fire, facilitating surface runoff and soil erosion losses (Vieira *et al.*, 2015). Therefore, forest management aimed at reducing erosion should focus on:

- Limiting burn severity of potential forest fires. The main drivers of burn severity in Mediterranean pine forests are the amount of pre-fire vegetation and fuel continuity (García-Llamas *et al.*, 2019). Therefore, actions aimed at reducing burn severity must be carried out in the pre-fire situation and should focus on reducing the amount of fuel, and its vertical and horizontal continuity with actions such as pruning, mechanical thinning or prescribed fires (Fernandes & Rigolot, 2007).
- Identifying the high severity areas after the fire. This should be done through fieldwork, and can be complemented with the use of spectral indexes obtained from moderate resolution satellite imagery.
- Focusing emergency actions aimed at soil protection in areas with high severity. However, it is also necessary to consider other factors such as climate, topography, soil type or surface hydrology (Renard *et al.*, 1997; Robichaud, 2009). It has been shown that several post-fire actions such as the application of mulch, the establishment of barriers to erosion or the protection of the post-fire regeneration by avoiding intensive grazing are useful in preventing post-fire erosion in fire-prone forests (Robichaud, 2009; de las Heras *et al.*, 2012).
- Avoiding soil tillage in high soil burn severity patches before evaluating the natural regeneration of vegetation over the medium term (1-3 years) after fire, as this action can aggravate soil erosion (Moreira *et al.*, 2012), while the natural regeneration might be sufficient.

After implementing the emergency actions and salvage logging if appropriate (which also affect natural regeneration; Taboada *et al.*, 2018), over the medium term after fire it is convenient to identify the scenarios in which natural regeneration is deficient and those where the density of pine seedlings is excessive (de las Heras *et al.*, 2012). High recurrence scenarios (3 fires in 34 years), as well as moderate recurrences combined with high severity (2 fires in 34 years) result in a low post-fire density and cover of pine seedlings, insufficient to guarantee forest recovery. (Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016). On the other hand, the abundant pine regeneration in low fire recurrence and low severity scenarios should also be managed (Fernandes & Rigolot, 2007; de las Heras *et al.*, 2012). In this regard, we recommend:

- Reducing the probability of recurrent and severe fires. Fire suppression can be facilitated through the establishment and maintenance of firebreaks (Fernandes & Rigolot, 2007), or a landscape mosaic structure, with different vegetation types and tree densities (de las Heras *et al.*, 2012). In this sense, previous studies stated that densities of 100-300 pines/ha prevent the occurrence of crown fires (Fernandes & Rigolot, 2007). Additionally, performing selective silvicultural treatments aimed at reducing the amount of highly flammable vegetation and the amount of fuel can be useful to limit fire frequency and severity (Baeza & Vallejo, 2008).
- Characterizing fire recurrence and burn severity in order to define target areas for the post-fire management of the dominant pine species. To achieve this, remote sensing techniques based on Landsat imagery are highly suitability for fire recurrence and vegetation burn severity characterization.
- Implementing forest management considering the abundance of pines in each fire recurrence and severity scenario. In order to maintain the pine forest we recommend planting or sowing pines only in the scenarios that show a very low seedling density the first years after fire (<0.20 pines/m^2; Rodríguez-García *et al.*, 2011; Torres *et al.*, 2016), and limiting grazing by sheep and goats (de las Heras *et*

al., 2012). In areas with a very high density of pine seedlings, we recommend thinning to enhance forest productivity and to facilitate early reproductive maturity (de las Heras *et al.*, 2012).

Another goal of forest management is to increase the species diversity and forest resilience to disturbances (Valdecantos *et al.*, 2009). In this sense, high fire recurrences increase the diversity of woody species, but at the expense of the elimination of the tree canopy, which is undesirable (Fernandes & Rigolot, 2007). Besides, maintaining plant communities with diverse functional traits enhances community resilience to changing fire regimes. Therefore, we encourage:

- To preserve the diversity of functional traits of the vegetation, with special consideration of those enhancing vegetation resilience under potential scenarios of high recurrence and severity. These biological traits include non-arboreal life forms, high specific leaf area, N_2-fixing capacity, resprouting ability, low seed mass and heat-stimulated germination.

We have highlighted the relevance of monitoring fire effects on soil and vegetation to identify target areas for each forest management action, however, it is also equally relevant to monitor and evaluate the effectiveness of management actions. This process is useful to confirm the effectiveness or to redirect the management actions and contributes optimize future forest management (Moreira *et al.*, 2012).

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7. CONCLUSIONS

Characterization of fire recurrence and severity

Visual analysis of Landsat time series is a suitable method to characterize fire recurrence in pine ecosystems. Even so, it is advisable to validate the remote sensing products from Landsat with field information.

The use of Landsat spectral indices, calculated from both mono- and bi-temporal approaches, is appropriate to assess site and vegetation burn severity in pine ecosystems, but its capacity to determine soil burn severity should be improved.

Landsat spectral indices based on the optical region of the spectrum outperformed indices calculated with the thermal region of the spectrum (thermal metrics and mixed indices) in determining burn severity.

The proposed index, dNBR-EVI, which combines information from the blue, red, near-infrared and short-wave infrared regions of the spectrum, is the spectral index with higher capacity to determine burn severity in pine ecosystems, as well as the best transferability among different climatic regions.

Effects of burn severity on soil properties

Burn severity significantly affects physical, chemical and biological properties of siliceous soils immediately after fire. Soil biological properties are more sensitive to burn severity than physical and chemical properties. Particularly, the β-glucosidase and acid phosphatase activities showed the highest sensivity, decreasing from low severity scenarios to almost disappearing in the highest severity situations.

The soil quotients affected by burn severity are the organic carbon:total nitrogen ratio, microbial quotient and the β-glucosidase: microbial biomass carbon ratio. The use of soil quotients might be more generalizable than individual properties when comparing fire effects among different sites.

The effects of burn severity can persist overt the medium term after fire (three years) on chemical (available phosphorus) and biological (β-glucosidase, urease, acid phosphatase and microbial biomass carbon) properties of soils in pine ecosystems. β-glucosidase activity, urease activity and microbial biomass carbon showed common patterns in relation to burn severity in *P. pinaster* (siliceous soils) and *P. halepensis* (calcareous soils) ecosystems.

Soil pH, the relationship organic carbon:total nitrogen, enzymatic activities (β-glucosidase, urease and acid phosphatase) and microbial biomass carbon might be potential indicators to monitor burn severity effects on soils.

Effects of fire recurrence and severity on the post-fire regeneration of vegetation

Both fire recurrence and burn severity significantly affect the post-fire recovery of vegetation greenness estimated by remote sensing techniques.

The combined consideration of fire recurrence and burn severity is more effective than the individual use of them to discriminate the different post-fire greenness recovery situations according to the NDVI index. The high recurrence with low severity scenario show the highest greenness recovery.

Fire recurrence and burn severity significantly affect the post-fire regeneration of serotinous pine species. Combined increases in fire recurrence and burn severity decrease the density and cover of pine seedlings, which are also shorter after recurrent wildires.

The interspecific competition between pine seedlings and other woody species is remarkable in the most favorable fire recurrence and severity scenarios for the establishment and development of pine seedlings, particularly in low recurrence situations.

Increases in fire recurrence lead to increases in woody species richness and diversity in pine ecosystems, which are partially counteracted if burn severity also increases. These changes in the plant community structure are due to the loss of tree canopy and the increase in the dominance of shrub species after recurrent fires.

Fire recurrence and burn severity effects on woody vegetation depend on plant functional traits. In this sense, species with high specific leaf area, N_2-fixing capacity, resprouting ability, low seed mass or heat-stimulated germination might be more resilient to combined increases in recurrence and severity.

Fire recurrence and severity impacts on both, the regeneration of dominant pine species and the structure and functional composition of the plant community, are more significant under Mediterranean climatic conditions than in climates with less prolonged summer drought.

Scientific basis to optimize forest management

Fire impacts on soil properties include the breakage of soil aggregates at high severities, leading to a high erosion risk. Therefore, areas with high severity should be considered a priority to implement emergency actions aimed at soil conservation. The assessments to identify high soil burn severity areas must be done in the field, although they can be supported by multispectral Landsat imagery.

The low density and cover of pine seedlings in high recurrence scenarios (3 fires in 34 years), as well as in moderate recurrences combined with high severity (2 fires in 34 years), may be insufficient to ensure full recovery of tree canopy. In all other recurrence and severity scenarios, pine regeneration is abundant and thinning may be necessary over the medium term after fire. Landsat products are suitable for managers to classify these fire recurrence and severity situations.

Vegetation responses to fire recurrence and severity are determined by plant functional traits, and therefore they should be considered in the design of forest management strategies. Maintaining a high diversity of functional traits enhances the resilience of the plant community to changes in fire regimes.

The largest impacts of fire on soil and vegetation occur with high fire recurrences and/or high severities, so pre-fire forest management should focus on reducing the risk of frequent and severe fires.