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Transferability of vegetation recovery models based on remote sensing across different fire regimes

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Abstract

Aim: To evaluate the transferability between fire recurrence scenarios of post-fire vegetation cover models calibrated with satellite imagery data at different spatial resolutions within two Mediterranean pine forest sites affected by large wildfires in 2012.

Location: The northwest and east of the Iberian Peninsula.

Methods: In each study site, we defined three fire recurrence scenarios for a reference period of 35 years. We used image texture derived from the surface reflectance channels of WorldView-2 and Sentinel-2 (at a spatial resolution of 2 m × 2 m and 20 m × 20 m, respectively) as predictors of post-fire vegetation cover in Random Forest regression analysies. Percentage vegetation cover was sampled in two sets of field plots with a size roughly equivalent to the spatial resolution of the imagery. The plots were distributed following a stratified design according to fire recurrence scenarios. Model transferability was assessed within each study site by applying the vegetation cover model developed for a given fire recurrence scenario to predict vegetation cover in other scenarios, iteratively.

Results: For both wildfires, the highest model transferability between fire recurrence scenarios was achieved for those holding the most similar vegetation community composition regarding the balance of species abundance according to their plant-regenerative traits (root mean square error [RMSE] around or lower than 15%). Model transferability performance was highly improved by fine-grained remote-sensing data.

Conclusions: Fire recurrence is a major driver of community structure and composition so the framework proposed in this study would allow land managers to reduce efforts in the context of post-fire decision-making to assess vegetation recovery within large burned landscapes with fire regime variability.

KEYWORDS
image texture, megafire, model transferability, random forest regression, satellite imagery, Sentinel-2, vegetation cover, WorldView-2

1 | INTRODUCTION

Wildfires are one of the main disturbances in forest ecosystems around the world (Collins *et al.*, 2018), having a significant effect on their biological productivity and composition (Calvo *et al.*, 2008), as well as on their dynamics (Lozano *et al.*, 2008). Particularly in the Mediterranean Basin, large forest fires are becoming more recurrent, mainly due to global climate change (Quintano *et al.*, 2015), which implies more adverse ecological effects (Pausas *et al.*, 2008). These large and more recurrent fires may lead to severe post-fire environmental conditions (e.g., increased incident solar radiation), partial or total removal of vegetation cover and shifts in plant community structure and composition (Pausas *et al.*, 2008; Taboada *et al.*, 2017), due to induced variation in plant species fitness (Keeley *et al.*, 2011).

In this sense, plant-regenerative traits are key in plant species fitness and, therefore, in community resilience against disturbances (Lloret *et al.*, 2005; Keeley *et al.*, 2011). In the western Mediterranean Basin, post-fire vegetation recovery relies on two plant-regenerative traits: (a) resprouting from above-ground or below-ground surviving tissues (Pausas & Keeley, 2014; Moreira *et al.*, 2012); and (b) seedling recruitment from canopy or soil banks (Pausas & Keeley, 2014). Additionally, some species present both types of regeneration mechanisms and are referred to as facultative seeders (Pausas & Keeley, 2014; Lloret *et al.*, 2005). In general, the species assemblage of a single community presents both regeneration mechanisms (Pausas, 2001; Calvo *et al.*, 2008), although the proportion of obligate resprouters, obligate seeders and facultative seeders is affected by fire regime (Lloret *et al.*, 2005). For instance, it has been proposed that, under recurrent wildfires, obligate seeders could be hindered before they have accumulated a canopy or soil bank viable for persistence, obligate resprouter species being promoted (Pausas, 2001; Pausas & Keeley, 2014; Lloret *et al.*, 2005; Knox & Morrison, 2005; Taboada *et al.*, 2017; Taboada *et al.*, 2018).

Due to the influence of fire recurrence on the balance between resprouter and seeder abundance and, therefore, on the community structure and composition, it should be possible to achieve vegetation recovery models transferable between different fire recurrence scenarios of a burned landscape. The development of transferable models is very important as they may reduce the cost of gathering data within mega-fires (burned area >10,000 ha; Stephens *et al.*, 2014), in the context of post-fire decision-making (Latif *et al.*, 2016), and also support management decisions when large data deficiencies exist in some portions of the area being surveyed (Clark *et al.*, 2001). Model transferability can be assessed by determining whether a model calibrated under a given set of conditions (reference system) can successfully provide accurate predictions under different conditions (target system; Sequeira *et al.*, 2018). Nevertheless, model transferability may be hindered by different constraints such as study design, species traits, model type and/or input data (Yates *et al.*, 2018; Werkowska *et al.*, 2017; Jiménez-Alfaro *et al.*, 2018; Sequeira *et al.*, 2018). Particularly relevant are: (a) sampling bias in the reference system (Barnes *et al.*, 2014; Tsalyuk *et al.*, 2017); (b) non-appropriate model algorithm and model overfitting (Wenger *et al.*, 2011; Sequeira *et al.*, 2018); (c) non-stationarity of the ecological relationships (Osborne, Foody, & Suárez-Seoane, 2007; Whittingham *et al.*, 2007; Suárez-Seoane *et al.*, 2014; Fernández-Guisuraga *et al.*, 2019a); or (d) non-analogous conditions in the target system (Thuiller *et al.*, 2004). The evaluation of model transferability must deal with these constraints in order to improve analysis performance and provide a reliable tool to support resource management (Yates *et al.*, 2018; Sequeira *et al.*, 2018).

Recent developments in geospatial technologies have promoted the use of remote-sensing-derived products (Poursanidis *et al.*, 2017), which represent a great opportunity, together with field data gathering, to evaluate vegetation recovery in large burned landscapes (Fernández-Manso *et al.*, 2016; Fernández-Guisuraga *et al.*, 2019b). The use of high or very high spatial resolution imagery provided by space-borne sensors, such as Sentinel-2 (spatial resolution of 10–20–60 m) or WorldView-2 (spatial resolution of 2 m), represents a great advance in vegetation recovery monitoring in areas of high spatial heterogeneity (Meng *et al.*, 2017). In this sense, image texture analysis applied to remote-sensing data (Pu & Cheng, 2015) has been proven to be a useful proxy of vegetation structure parameters in heterogeneous burned landscapes, such as species richness (Viedma *et al.*, 2012) or vegetation biomass (Kelsey & Neff, 2014), height (Fernández-Guisuraga *et al.*, 2019b) and cover (Fernández-Guisuraga *et al.*, 2019a). Since the horizontal and vertical structure of vegetation influences canopy reflectance (Thenkabail *et al.*, 2011; Buchhorn *et al.*, 2013), the performance of post-fire recovery models is expected to vary across burned areas where different fire recurrence scenarios coexist and, therefore, where community composition may differ according to species regenerative traits.

Although the transferability of ecological models is a subject of particular research interest in fire ecology (Yates *et al.*, 2018; Werkowska *et al.*, 2017), only a few studies have addressed the transferability of either burn severity models (Fernández-García *et al.*, 2018) or post-fire vegetation recovery models (Fernández-Guisuraga *et al.*, 2019a) based on remote-sensing products. The transferability of post-fire vegetation cover models between fire recurrence scenarios in burned ecosystems can fill knowledge gaps, providing reliable insights to support post-fire decision-making in the most efficient way (Yates *et al.*, 2018; Sequeira *et al.*, 2018).

In this study, we aim to evaluate the transferability of remote-sensing-based recovery models between fire recurrence scenarios at different spatial resolutions within two fire-prone pine ecosystems of the western Mediterranean Basin with different environmental characteristics. In particular, we aim to answer the following questions: (a) could model transferability be influenced by fire regime and, therefore, by community species composition within two burned landscapes with different environmental characteristics; and (b) does the spatial resolution of the remote-sensing products used to feed the models constrain model transferability between fire recurrence scenarios? We expect that fire recurrence would modify the community composition given the species' adaptive traits to fire regime (Pausas & Keeley, 2014; Lloret *et al.*, 2005; Taboada *et al.*, 2018). Therefore, model transferability would perform better between fire recurrence scenarios with more similar community composition (Thomas & Vesk, 2017). Furthermore, we hypothesize that fine-grained remote-sensing products would offer a better performance than coarser products under heterogeneous recovery patterns of fire-prone ecosystems (Schoennagel *et al*., 2008). In these ecosystems, we expect that high-resolution products would capture at best ground local variations and complex ecological processes (Heinänen *et al*., 2012), improving model transferability (Sequeira *et al*., 2018).

2 | METHODS

2.1 | Study area

The study sites are located within the perimeter of two full stand-replacing mega-fires which occurred in summer 2012 in Spain (Figure 1).

The first site (Sierra del Teleno wildfire; Figure 1, A) is located in NW Spain within a burned area of 11,602 ha predominantly covered by a *Pinus pinaster* forest stand. The pine canopy was almost consumed by fire and the burned stands were salvage-logged (Taboada *et al*., 2018). The study site is located at an average altitude of 1,063 m a.s.l. The relief is dominated by quartzite crests, large valleys with moderate slopes and sedimentary plains. It is an Atlantic–Mediterranean transition climatic zone with an average annual rainfall of around 650 mm and an average annual temperature of 10°C, with a moderate summer drought (<2 months). Soils are predominantly acidic with a sandy texture. Vegetation cover in post-fire conditions is mainly constituted by *Pinus pinaster* Aiton seedlings, obligate seeder shrub species, such as *Halimium lasianthum* subsp. *alyssoides* (Lam.) Greuter, *Erica umbellata* L. and *Calluna vulgaris* (L.) Hull, as well as resprouter shrubs, such as *Pterospartum tridentatum* (L.) Willk. and *Erica australis* L. In the study area, these evergreen species reach the peak of their above-ground biomass in June and July.

The second site (Cortes de Pallás wildfire; Figure 1, B) is located in eastern Spain, within a megafire of 29,752 ha that completely consumed a *Pinus halepensis* Mill. and a *Pinus pinaster* stand. The altitude in the study site ranges between 114 and 995 m a.s.l. with steep slopes being present. Soils are predominantly basic with a sedimentary origin. The conditions in the region are typically Mediterranean, with an average annual rainfall of around 280 mm, an average annual temperature of 16°C and three months of summer drought. Post-fire vegetation cover is constituted by *Pinus pinaster* and *Pinus halepensis* regeneration stands in a seedling growth stage, obligate seeder shrubs, such as *Ulex parviflorus* Pourr. and *Rosmarinus officinalis* L., as well as resprouter shrubs, such as *Quercus coccifera* L. The peak of the growing season of these evergreen species is reached in May and June in the study area.

In both study sites, fire recurrence (number of wildfires) was estimated using a temporal series of Landsat imagery for the period 1978–2012. Recurrence values ranged between one and three (R1, R2 an R3; Fernández-García *et al*., 2019; Figure 1).

See Appendix S1 for a detailed list of tree and shrub species of each study site, including their growth form, regenerative traits and cover by fire recurrence scenario.

2.2 | Field data sampling

Four years after the wildfires, in spring–summer 2016, we defined a framework of 3,000 ha in each study site, where we established two independent sets of field plots of 2 m × 2 m (60 in Sierra del Teleno and 33 in Cortes de Pallás) and 30 m × 30 m (56 in Sierra del Teleno and 30 in Cortes de Pallás). This framework was used to focus

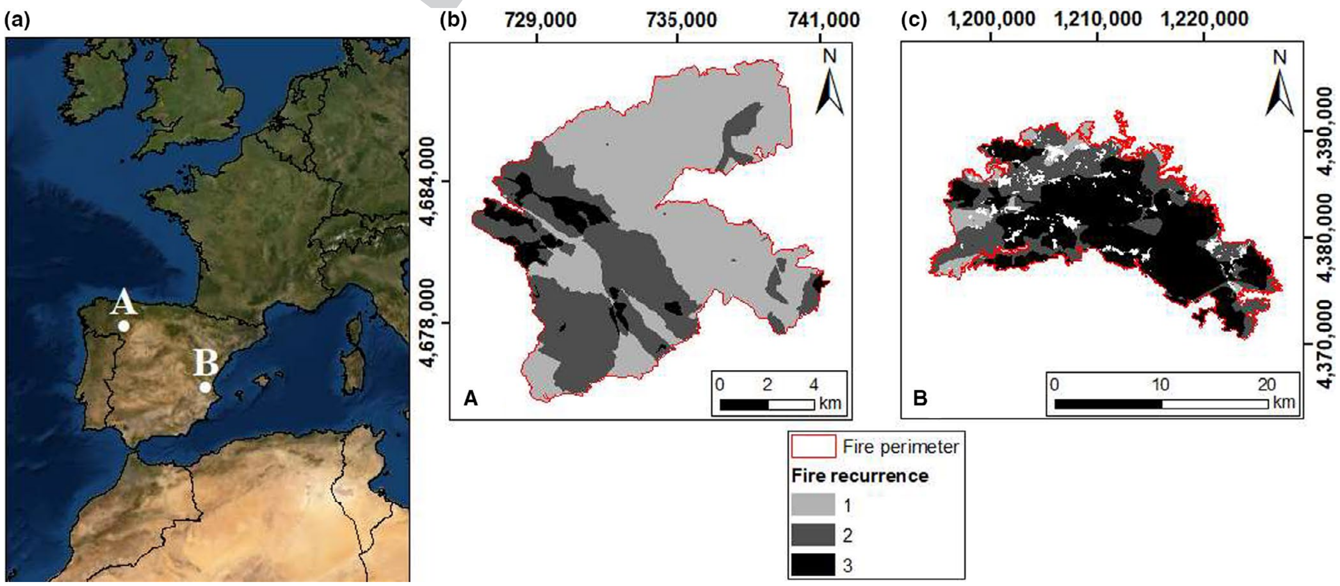

FIGURE 1 Location (ESRI, 2019) (a) and fire recurrence (b and c) for the period 1978–2012 of Sierra del Teleno (A) and Cortes de Pallás (B) wildfires. Fire recurrence maps were computed through visual interpretation of Landsat imagery covering the study period

the field sampling in areas dominated by pine ecosystems within the study areas (Fernández-García *et al.*, 2019). Plots were distributed following a stratified design using the fire recurrence scenarios as strata. Thus, the number of plots for each recurrence scenario was proportional to the relative area affected by each class of fire recurrence in each study framework. In each plot we assessed, at different spatial scales, the vegetation cover during the peak above-ground biomass as one of the parameters of the community structure. In particular, we used a visual estimation method (Calvo *et al.*, 2008) to quantify: (a) total vegetation cover percentage; (b) cover percentage of pine seedlings; (c) cover percentage by shrub species to obtain the cover of vegetation regenerative traits (obligate resprouters, obligate seeders and facultative seeders); and (d) woody debris cover percentage. Each field plot was georeferenced with a GPS receiver with X, Y accuracy higher than 0.50 m in post-processing mode.

2.3 | WorldView-2 and Sentinel-2 imagery and spectral products

WorldView-2 scenes were acquired for the Sierra del Teleno wildfire on 23 June 2016 at 11:38:02 UTC and for Cortes de Pallás on 15 June 2016 at 11:12:48 UTC. Cloud cover was lower than 0.3% in both scenes. The spatial resolution of the WorldView-2 multispectral sensor at nadir is 1.84 m, but the image was resampled to 2 m by the image provider. This sensor captures data along eight bands in the visible and near infrared (NIR) region: B1, coastal blue (400–450 nm); B2, blue (450–510 nm); B3, green (510–580 nm); B4, yellow (585–625 nm); B5, red (630–690 nm); B6, red edge (705–745 nm); B7, NIR1 (770–895 nm) and B8, NIR2 (860–1,040 nm; Appendix S2). WorldView-2 scenes were orthorectified with rational polynomial coefficients delivered with the image metadata, as well as with a Digital Elevation Model (DEM) with a spatial resolution of 5 m and an accuracy higher than 20 cm in Z, provided by the Spanish National Center of Geographic Information (http://www.cnig.es/). The scenes were atmospherically corrected to surface reflectance with the Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes algorithm (FLAASH; Matthew *et al.*, 2003) implemented in ENVI 5.3 software (https://www.harrisgeospatial.com/).

Sentinel-2 MSI Level 1C imagery was acquired for Sierra del Teleno wildfire from the Copernicus Open Access Hub (https://scihub.copernicus.eu/) on 5 August 2016 at 11:12:45 UTC and for Cortes de Pallás on 30 July 2016 at 10:53:38 UTC, both scenes being cloud cover-free. Sentinel-2 has thirteen bands at different spatial resolution over the visible, NIR and short wave IR (SWIR) regions: 10-m spatial resolution bands (B2 blue, 458–523 nm; B3 green, 543–578 nm; B4 red, 650–680 nm and B8 NIR, 785–899 nm); 20-m spatial resolution bands (B5 red edge 1, 698–713 nm; B6 red edge 2, 733–748 nm; B7 red edge 3, 773–793 nm; B8a narrow NIR, 855–875 nm; B11 SWIR1, 1,565–1,655 nm and B12 SWIR2, 2,100–2,280 nm); and 60-m spatial resolution bands (B1 coastal blue, 432–453 nm; B9 water vapor, 935–955 nm, B10 cirrus, 1,358–1,389 nm; Appendix S2). Sentinel-2 bands were resampled to 20 m using a nearest neighbor rule. Sentinel-2 MSI Level 1C imagery was already orthorectified by the supplier and the scenes were then only atmospherically corrected to surface reflectance with the FLAASH algorithm.

We computed two second-order texture features (mean and variance; Appendix S3) for each surface reflectance band of the processed WorldView-2 and Sentinel-2 imagery using a moving window of 3 × 3 pixels and the Gray Level Co-Occurrence Matrix (GLCM; Haralick *et al.*, 1973). The texture features and window size were chosen based on previous research carried out in burned landscapes of high spatial heterogeneity (Fernández-Guisuraga *et al.*, 2019a). Each texture was averaged for the four spatial directions to gather directionally invariant texture measures (Zhang & Xie, 2012). Texture values were extracted for each field plot location to be used as predictors of vegetation cover.

2.4 | Data analysis

A permutational multivariate analysis of variance (PERMANOVA) and a principal components analysis (PCA) were used to explore, within each study site, the multivariate associations between vegetation community composition (cover of vegetation regenerative traits, pine seedlings and woody debris) and fire recurrence. Then, the effects of fire recurrence on each specific community variable were analyzed through an analysis of variance (ANOVA) followed by a pairwise multiple comparison of means (Scheffe test). These analyses were performed using R (R Core Team, 2017) and the 'vegan' package (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

For its part, a correlation analysis was conducted in order to discard potential multicollinearity problems among the spectral predictors (second-order texture features, mean and variance) of vegetation cover. Bivariate Pearson correlations allowed for identifying groups of strongly correlated predictors ($r_{\text{Pearson}} > |0.7|$). The predictor with the highest biophysical meaning within each group was preserved for further analyses (Fernández-Guisuraga *et al.*, 2019b).

Vegetation cover model transferability between fire recurrence scenarios was assessed by means of Random Forest (RF) regression models (Breiman, 2001) based on WorldView-2 and Sentinel-2 spectral predictors. RF is a machine-learning algorithm based on classification and regression trees (CART; Oliveira *et al.*, 2012). It is insensitive to noisy datasets and makes no assumptions about the distribution of the response variable (Iqbal *et al.*, 2018). For each site, fire recurrence scenario and spatial resolution, we built a model of total vegetation cover. RF fits an ensemble of random binary trees to the data, each tree being generated by bootstrap samples (Breiman, 2001; Hong *et al.*, 2018; Iqbal *et al.*, 2018). Each split of the tree is defined using a random subset of the predictors at each node or sample (Oliveira *et al.*, 2012). The final output is the average of the results of every tree (Breiman, 2001). The value of the model parameter *mtry* (number of variables for each tree split) was set using the function tuneRF (Liaw & Wiener, 2002). This function searches below and above the default value of *mtry* (number of predictors/3) to find the value with the minimum error estimate (Liaw & Wiener, 2002; Oliveira *et al.*, 2012). The value of the model parameter ntree (number of trees) was set to 1,000 to obtain stable predictions (Oshiro *et al.*, 2012; Probst & Boulesteix, 2018). Predictor importance in the model was evaluated by means of the percentage increase in mean square error (%IncMSE), which represents the decrease in model accuracy if a variable is dropped from the model. The final model was obtained by averaging one hundred replicate RF models in order to produce stable model outputs (García-Llamas *et al.*, 2019). A parsimonious subset of predictors for each fire recurrence scenario, spatial resolution and site was selected through a forward model selection technique (see Kane *et al.*, 2015 and García-Llamas *et al.*, 2019 for more details). The variance explained by the models (pseudo-R^2) was calculated using the internal out-of-bag error rate (Liaw & Wiener, 2002).

Vegetation cover models calibrated in a particular fire recurrence scenario (reference system) were validated in the other scenarios (target systems) within each study site, iteratively. For instance, the spatial output of a model calibrated in scenario R1 was validated using data from scenarios R2 and R3 across the same wildfire. Model transferability performance was assessed using the root mean square error (RMSE; Equation 1) in percent cover.

$$\text{RMSE}\,(\%\text{cover}) = \sqrt{\frac{\sum_{i=1}^{n}\left(P_i - O_i\right)^2}{n}} \tag{1}$$

where O_i are observed vegetation cover values in the target system, P_i are the predicted vegetation cover values obtained by applying the RF model of the reference system to the target system, and n corresponds to the number of field plots in the target system.

Random Forest (RF) regression was applied using R (R Core Team, 2017) and the 'RandomForest' package (Liaw & Wiener, 2002).

3 | RESULTS

The community species composition showed a non-stationary response regarding the species' regenerative traits between fire recurrence scenarios in the Sierra del Teleno (PERMANOVA F = 95.94; p < 0.01) and Cortes de Pallás (F = 32.02; p < 0.01) wildfires. The first (Dim1) and second (Dim2) PCA axes explained 64.3% and 17.6% respectively of the variance in the Sierra del Teleno wildfire and 42.7% and 23.2% respectively in Cortes de Pallás. In the Sierra del Teleno wildfire, resprouter shrub species dominated over obligate seeder shrubs under high fire recurrence (R2 and R3). The opposite pattern was observed for the lowest recurrence scenario (R1), characterized by a higher cover of obligate seeders (shrubs and pine seedlings) and woody debris. Meanwhile, in the Cortes de Pallás wildfire, R1 and R2 fire recurrence scenarios were associated with a high cover of obligate seeders, the resprouters being the dominant shrub species in fire recurrence scenario R3 (Figure 2). In both study sites, resprouter cover tended to increase significantly (p < 0.01) with fire recurrence (R2 and R3 in the Sierra del Teleno wildfire and R3 in Cortes de Pallás), the seeder shrubs exhibiting the inverse pattern. For its part, there was a significant reduction (p < 0.01) in pine seedling regeneration within high fire recurrence scenarios (R2 and R3) in both study sites. Furthermore, the accumulation of woody debris was significantly higher (p < 0.01) under the low fire recurrence scenario (R1) in both wildfires (Figure 3).

The highest variance of total vegetation cover was explained by RF models under high fire recurrence scenarios (R2 and R3) for both study sites and sensors (Table 1). Model performance was better in the Sierra del Teleno wildfire than in Cortes de Pallás. The explained variance of the total vegetation cover was higher using WorldView-2 than Sentinel-2 textures as predictors (Table 1). For their part, the most parsimonious models were calibrated with four or less predictors. Mean texture features, especially those computed from the red-edge region of the spectrum (B6 for WorldView-2 and B5, B6 and B7 for Sentinel-2), were selected in almost all models (Table 1).

Model transferability error ranged between 5% and 35% in the Sierra del Teleno wildfire and between 13% and 32% in the Cortes de Pallás wildfire. Models calibrated with fine-grained satellite image texture exhibited the lowest transferability error. The best model transferability in the Sierra del Teleno wildfire was achieved between the areas affected by two and three fires (RMSE around 5%, using WorldView-2 textures as predictors). By contrast, in the Cortes de Pallás wildfire, the areas affected by one and two fires featured the lowest error in the transferability approach (RMSE around 15% for both remote sensing data; Figure 4).

4 | DISCUSSION

Predictive models have become essential tools in fire ecology (Pausas & Lloret, 2007; Canelles *et al.*, 2019) due to increasing social

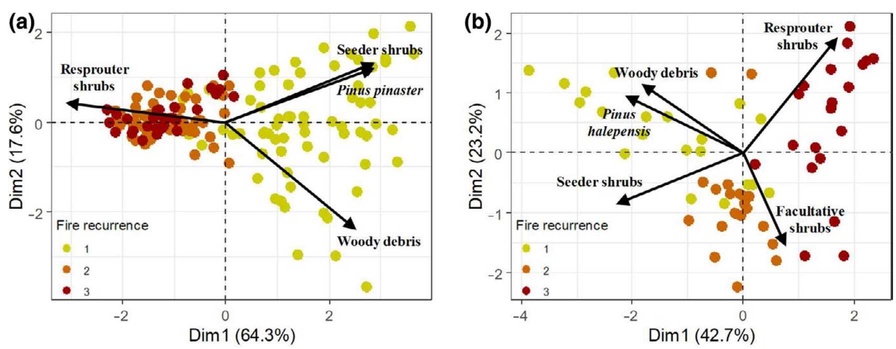

FIGURE 2 Principal components analysis (PCA) biplots of vegetation community composition, showing the distribution of the field plots under different fire recurrence scenarios (one, two and three fires) for Sierra del Teleno (a) and Cortes de Pallás (b) wildfires

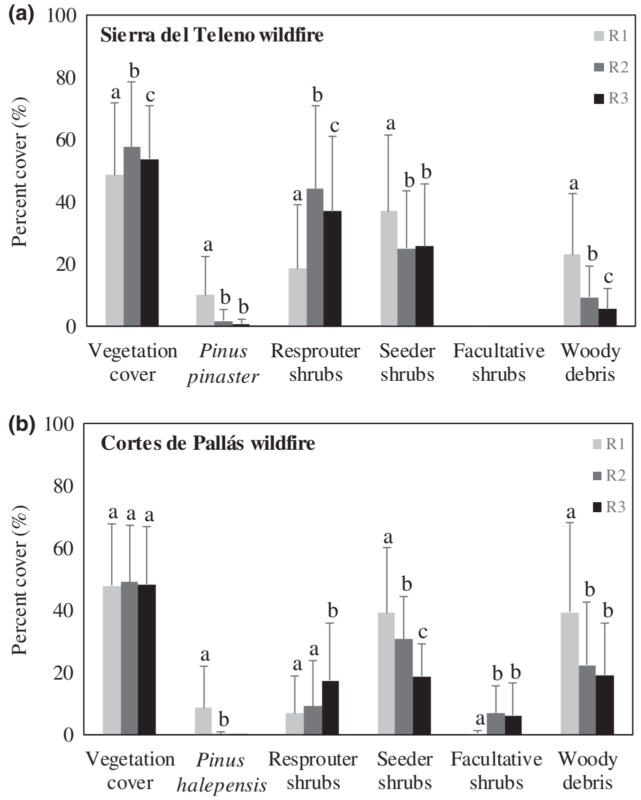

FIGURE 3 Mean cover and standard deviation of the community assemblage under one (R1), two (R2) and three (R3) number of fires in Sierra del Teleno (A) and Cortes de Pallás (B) wildfires. The letters located above the standard deviation bars (a, b and c) denote statistically significant differences between means ($p < 0.05$). Data were collected in 2 m × 2 m field plots

and scientific awareness about the consequences of global change regarding fire regime parameters (Fernández-García *et al.*, 2019). There is a growing interest in the attainment of transferable ecological models to support anticipatory predictions instead of explanatory models (Yates *et al.*, 2018) to enhance the efficiency of post-fire management actions, which are broadly context-dependent (Taboada *et al.*, 2017; Fernández-Guisuraga *et al.*, 2019a). The main novelty of this study lies in the evaluation of the remote-sensing potential at different spatial scales together with field measurements using a machine-learning approach to obtain transferable vegetation recovery models between areas affected by different fire recurrence for the case of two large burned areas with different climatic conditions. Our results highlighted the relevance of choosing the appropriate spatial resolution of remote-sensing products to be used as predictors in the proposed scheme. Models were transferable between fire recurrence scenarios in both study sites (RMSE lower than 35%), although the best results were obtained between scenarios with more similar community composition (RMSE of around 15% or lower) owing to the species' regenerative traits in responce to the disturbance regime and therefore have a stronger spectral similarity. 7

4.1 | Fire recurrence influence on community structure and composition

The relative abundance of woody understorey species, grouped according to their regenerative traits, and pine seedlings, varied with fire recurrence both in the Sierra del Teleno and Cortes de Pallás wildfires. We found that resprouter abundance tended to increase under high fire recurrence scenarios in both study sites. This could be attributable to the maximization of resprouter fitness by the resource allocation to above-ground or below-ground fire-resistant structures (Pausas & Vallejo, 1999; Knox & Morrison, 2005). In addition, the relative abundance of obligate seeder shrubs decreased under high fire recurrence scenarios, since they may not have become reproductively mature to produce a viable canopy or soil seed bank in the fire-free period (Pausas & Keeley, 2014; Lloret *et al.*, 2005). For its part, the dominance of obligate seeder shrubs in the Mediterranean site, especially in areas of low recurrence, could be attributed to their seed germination stimulated by fire (Pausas & Vallejo, 1999; Pausas & Keeley, 2014; Taboada *et al.*, 2018) and more tolerance to water deficit than resprouter shrubs during summer droughts (Pausas *et al.*, 2004).

TABLE 1 Mean explained variance of the one hundred Random Forest (RF) iterations for the most parsimonious models of vegetation cover for Sierra del Teleno and Cortes de Pallás wildfires using WorldView-2 (WV-2) and Sentinel-2 (S-2) mean and variance (var) textures as spectral predictors for areas burned one (R1), two (R2) and three (R3) times

	WV-2		S-2	
	Predictors	Variance (%)	Predictors	Variance (%)
Sierra del Teleno wildfire				
R1	Mean(B1,B3,B6), var(B6)	45.04	Mean(B1,B8A), var(B5)	25.32
R2	Mean(B6), var(B6)	51.18	Mean(B5), var(B3,B5,B8A)	39.12
R3	Mean(B3), var(B3,B6)	56.79	Mean(B12), var(B1,B5)	35.23
Cortes de Pallás wildfire				
R1	Mean(B3), var(B6)	37.74	Mean(B12), var(B8A)	22.60
R2	Mean(B1,B3)	50.32	Mean(B8A,B12)	34.76
R3	Mean(B3,B6)	41.44	Mean(B5,B12)	30.57

The standard deviation of the explained variance of the RF iterations for each model was <1%. WV-2 bands B1, B3 and B6 correspond to coastal blue, green and red edge spectral regions, respectively. Accordingly, S-2 bands B1, B3, B5, B8A and B12 correspond to coastal blue, green, red edge, NIR and SWIR spectral regions.

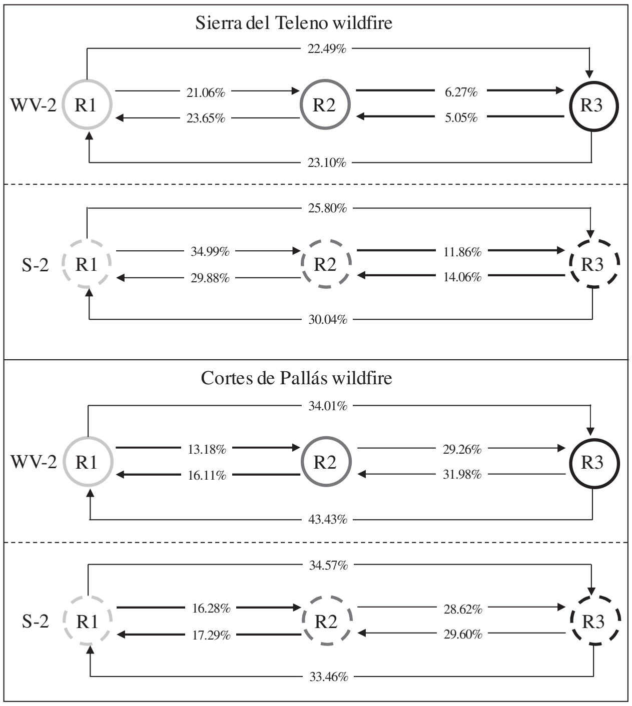

FIGURE 4 Mean model transferability performance (root mean square error [RMSE]) of the one hundred Random Forest (RF) iterations between one (R1), two (R2) and three (R3) fire recurrence scenarios in the Sierra del Teleno and Cortes de Pallás wildfires using WorldView-2 (WV-2) and Sentinel-2 (S-2) as spectral predictors. The thickest arrows correspond to model transferability errors of around 15% or lower. The standard deviation of the RMSE of the RF iterations for each model was less than 1%

4.2 | Predictive performance of remote-sensing data

It has been demonstrated that woody debris accumulation decreased with increasing fire recurrence (Taboada *et al.*, 2018; Fernández-García *et al.*, 2019). The highest model performance under high fire recurrence scenarios could be explained, in both wildfires, by the lower background influence of non-photosynthetic vegetation, such as woody debris, on the spectral signature of healthy vegetation (Montandon & Small, 2008; Schile *et al.*, 2013) in comparison to areas burned once. Fernández-Guisuraga *et al.* (2019b) also found the same pattern using a different modeling approach in a fire-prone ecosystem. Despite both study sites presenting heterogeneous post-fire recovery patterns of the vegetation, the narrower environmental variation and, therefore, the more homogeneous landscape of Sierra del Teleno, in comparison with Cortes de Pallás (Fernández-Guisuraga *et al.*, 2019a), may have led to improved model performance in the former site. In this regard, the high spatial variation of ground cover in both study sites requires the use of remote-sensing data at very high spatial resolution, such as those captured by WorldView-2, to obtain the best modeling results (Meng *et al.*, 2017). The ground heterogeneity of fire-prone ecosystems cannot be captured properly by coarse spatial resolution satellite imagery (Wood *et al.*, 2012) containing single pixel spectra from different ground features (Stefanov & Netzband, 2005; Xiao & Moody, 2005), which is known as the land cover aggregation effect (Munyati & Mboweni, 2013). For their part, texture features have been proven to be adequate remote-sensing products to model post-fire vegetation structure in fire-prone landscapes, as observed in several studies (Viedma *et al.*, 2012; Gu *et al.*, 2013; Fernández-Guisuraga *et al.*, 2019b). In areas of high spatial heterogeneity, texture analysis optimizes the spatial information characterization, since it accounts for both the pixel reflectance values and the spatial variation of these values between adjacent pixels (Fernández-Guisuraga *et al.*, 2019a, 2019b). Accordingly, image texture is highly sensitive in these areas to variations in vegetation structural parameters, such as leaf area index, canopy cover, height and density or vertical and horizontal heterogeneity (Sarker & Nichol, 2011; Wood *et al.*, 2012) than other satellite products, such as raw reflectance data or spectral indices (Sarker & Nichol, 2011; Eckert, 2012; Fernández-Guisuraga *et al.*, 2019b). Therefore, vegetation cover could be characterized by texture metrics in each fire recurrence scenario, with explained the variances around or higher than 40% using WorldView-2 texture predictors. The contribution of textures from the red-edge region of the electromagnetic spectrum to the vegetation cover modeling in both wildfires is worth mentioning. In areas with heterogeneous ground cover, high red-edge sensitivity to shifts in vegetation biophysical parameters, such as chlorophyll content or biomass density (Xie *et al.*, 2018), have led to a better model performance within each study site. Additionally, the red-edge region is quite efficient to discriminate the vegetation spectral signal from background features (Schumacher *et al.*, 2016).

4.3 | Transferability

Despite the potential of remote-sensing data to predict vegetation structure parameters at individual sites (Foody *et al.*, 2003; Cutler *et al.*, 2012; Fernández-Guisuraga *et al.*, 2019b), the attainment of transferable models as a cost-effective tool for land management decision-making remains challenging (Tsalyuk *et al.*, 2017; Sequeira *et al.*, 2018). The spatial variability of vegetation responses, along with field data collection and uncertainties related to satellite imagery pre-processing, may hinder the transferability of remote-sensing-based vegetation models between different areas (Tsalyuk *et al.*, 2017; Regos *et al.*, 2019).

Our results supported the hypothesis that species' regenerative traits had a significant impact on model transferability performance because these traits reflect the species' response to the disturbance regime and, therefore, their distribution and abundance (Syphard & Franklin, 2010; Street *et al.*, 2015; Regos *et al.*, 2019). A specific species assemblage as a result of plants' regenerative traits features a characteristic spectral profile arising from the phenology and physiological characteristics of the species (Ustin & Gamon, 2010), as well as from the structural layering and multiple scattering between different species (Verrelst *et al.*, 2009). Hence, vegetation cover models for both wildfires exhibited the highest transferability between burned areas with a more similar vegetation community composition (regarding the relative abundance of seeder and resprouter species) and spectral response. These scenarios corresponded to areas burned two and three times in the Sierra del Teleno wildfire and areas burned once and twice in Cortes de Pallás during the considered time period. Under these scenarios, the stationary vegetation responses enabled the modeled relationships between plant community composition and remote-sensing data to be kept relatively constant (Fernández-Guisuraga *et al.*, 2019a), therefore obtaining a good performance (RMSE of around 15% or lower, and even as low as 5%) of the model transferability approach (Maguire *et al.*, 2016; Osborne & Suárez-Seoane, 2002; Sequeira *et al.*, 2018). In less favorable transferability schemes, the performance was still acceptable (RMSE lower than 35%), probably because the spectral response dissimilarity between the reference and target systems (non-analogous conditions) arising from vegetation non-stationary responses was not high enough to produce truncation in the model calibration (Yates *et al.*, 2018; Regos *et al.*, 2019; Fernández-Guisuraga *et al.*, 2019a).

The spatial resolution of remote-sensing data had a significant impact on model transferability performance in both study sites. As expected, vegetation cover models calibrated with WorldView-2's fine-grained satellite texture exhibited the lowest transferability error. In landscapes with great spatial heterogeneity, the use of remote-sensing data at very high spatial resolution is advisable because it captures better the variability of the ground cover pattern, allowing better transferability of the modeled relationships between sites (Fernández-Guisuraga *et al.*, 2019b). Another probable explanation for the satisfactory results in the transferability approach could be related to the use of parsimonious models calibrated from few predictors (Wenger & Olden, 2012), since complex models could lead to model overfitting and, therefore, predictions cannot be adequately transferred to the target area (Yates *et al.*, 2018; Bell & Schlaepfer, 2016). Likewise, modeled relationships must be transferred to the target area using remote-sensing data acquired during the same phenological stage of the vegetation in which the relationships were calibrated in the reference area. In both study sites, the field-sampling campaign and, consequently, the model calibration in the reference areas were conducted during the peak of green biomass in spring/summer to minimize the effect of non-photosynthetic vegetation to the modeled relationships (Wehlage *et al.*, 2016; Jansen *et al.*, 2018). Although only the RF regression modeling approach was tested in our study, it has been reported to provide a good performance in ecological modeling transferability (Cutler *et al.*, 2007). However, the inability of RF regression to predict beyond the data range used for model calibration (Iqbal *et al.*, 2018; Sequeira *et al.*, 2018) may require the collection of field data covering a wider variability range to avoid non-analogous conditions.

5 | CONCLUSIONS

1. Fire recurrence is a major driver of both community structure and composition in fire-prone ecosystems of the Mediterranean Basin with different environmental characteristics.
2. Species responses to the disturbance regime have a large impact on the performance of vegetation cover model transferability analysis. The best transferability results are achieved between fire recurrence scenarios driving to similar vegetation community composition regarding the balance of plants' regenerative traits. Under these scenarios, the relationship between community composition and remote-sensing data is consistent because of the stationarity of the species responses.
3. The ground spatial heterogeneity of fire-prone ecosystems severely affects vegetation cover modeling based on remote-sensing data. In these ecosystems, the vegetation spectra may be highly influenced by background signal, requiring the use of very high spatial resolution instead of coarse satellite imagery to properly characterize the vegetation cover. Also, the performance of model transferability analysis is highly influenced by the spatial resolution of remote-sensing data used as predictors of vegetation cover.
4. The framework proposed in this research paper would presumably allow land managers to reduce efforts in data collection in the context of post-fire decision-making to assess vegetation recovery within large burned ecosystems with fire regime variability.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

SSS and LC conceived the research idea and designed the study; JMFG, SSS and LC collected data; JMFG performed statistical analyses and wrote the first draft of the manuscript with contributions from SSS and LC; SSS and LC revised the draft, improved the text and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data for this publication are stored in the internal database of the Applied Ecology and Remote Sensing research group in the University of León. The raw data used in this manuscript will be available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species list of each study site

Appendix S2. Vegetation spectral reflectance in the electromagnetic spectrum

Appendix S3. Second-order texture measures calculation using the Gray Level Co-Occurrence Matrix (GLCM)

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Graphical Abstract

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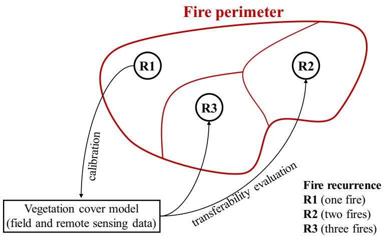

We evaluate transferability between fire recurrence scenarios of post-fire vegetation cover models calibrated with satellite imagery data. The best transferability results were obtained between areas with more homogeneous community composition arising from the species regenerative traits. The use of fine-grained satellite imagery for model calibration exhibited the lowest transferability error.