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**History matters: previous land use changes determine post-fire vegetation  
recovery in forested Mediterranean landscapes**

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## 24    **Abstract**

25    Land use changes and shifts in disturbance regimes (e.g. wildfires) are recognized  
26    worldwide as two of the major drivers of the current global change in terrestrial  
27    ecosystems. We expect that, in areas with large-scale land use changes, legacies  
28    from previous land uses persist and affect current ecosystem responses to climate-  
29    associated disturbances like fire. This study analyses whether post-fire vegetation  
30    dynamics may differ according to specific historical land use histories in a  
31    Mediterranean forest landscape of about 60,000 ha that was burnt by extensive fires.  
32    For that, we assessed land use history of the whole area through the second half of  
33    the XXth century, and evaluated the post-fire regeneration success in terms of: i)  
34    forest cover and ii) tree species composition (biotic-dispersed, resprouter species,  
35    *Quercus* spp. vs. wind-dispersed species with or without fire-resistant seed bank,  
36    *Pinus* spp.). Results showed that stable forest areas exhibited a higher post-fire  
37    recovery than younger forests. Furthermore, the longer since crop abandonment  
38    translates into a faster post-fire recovery. Results highlight that to anticipate the  
39    impacts of disturbances on ecosystems, historical land trajectories should be taken  
40    into account.

41    *Keywords:* Global change, Mediterranean forest, *Quercus*, *Pinus*, passive  
42    restoration,

## 43    **1. Introduction**

44    Understanding the interactions between different drivers of global change is one of the key  
45    present challenges among politicians, economists, ecologists, and society in general (IPCC,  
46    2007; FAO et al., 2008). Land use changes and shifts in disturbance regimes (e.g. wildfires) are  
47    recognized worldwide as two of the major drivers of the current global change in terrestrial  
48    ecosystems (Vitusek, 1992; Rudel et al., 2005; Fraterrigo et al., 2006, Hermy and Verheyen,  
49    2007). Surprisingly, the interaction between past land uses and fire impacts has received little  
50    attention. However, their tight coexistence can make us hypothesise that fire may have different  
51    effects in areas undergoing different land use trajectories in the past (Duguy et al., 2007; Walck  
52    et al., 2011). The Mediterranean rim may act as an ideal scenario to analyse the interaction  
53    between disturbances, such as fire, and land use changes (in particular crop abandonment)  
54    because both components of global change are largely present in many areas since the last  
55    decades (Blondel and Aronson, 1999; Palahí et al., 2008). In the northern rim of the  
56    Mediterranean Basin, the general trend to the abandonment of less fertile agricultural areas  
57    during the second half of the XXth century has resulted in an increasing expansion and  
58    connectivity of woodlands, particularly by either natural colonization and densification of the  
59    existing forests or, to a lesser extent, by active afforestation (Debussche et al., 1996; Lloret et al.,  
60    2002; Mouillot et al., 2005; Améztegui et al., 2010). Vegetation recovery has been argued in turn  
61    to be a major factor behind recent changes in fire regime together with changing climate  
62    conditions leading to an increase number of fire prone days per year (Piñol et al., 1998; Rudel et  
63    al., 2005). Indeed, the increase in fire recurrence and surface burned in the recent decades in  
64    Mediterranean-type forests and shrublands has been attributed to extensive forest recovery  
65    (Pausas, 2004).

66

67 Plant responses to fire and cropland abandonment are likely to be determined by  
68 species-specific functional traits (Pausas, 1999; Mouillot et al., 2005). In the present  
69 global change context, advancing in the understanding of these mechanisms is  
70 critical since they may play a determinant role for the maintenance (e.g. reduce soil  
71 erosion) and functioning (e.g. carbon sequestration) of forest ecosystems (Rudel et  
72 al., 2005; Thompson et al., 2009; FAO et al., 2008). Land use changes are known to  
73 impact different ecological processes and influence soil properties (Fraterrigo et al.,  
74 2006; Hermy and Verheyen, 2007) leading to the general hypothesis that areas  
75 undergoing different land use trajectories are likely to differently respond to fire thus  
76 leading to differences in post-fire regeneration patterns (Duguy et al., 2007; Walck et  
77 al., 2011; Foster, 1992).

78 Specific land use changes over time are likely to leave a strong signal on the capacity  
79 of the system to respond to fire. Land use changes might modulate the relative  
80 presence of species having distinct functional traits (Foster, 1992; Hermy and  
81 Verheyen, 2007) which can be related to post-fire responses (Pausas et al., 1999;  
82 Rodrigo et al., 2004). For example, small-seeded, wind-dispersed woody species  
83 (e.g. *Pinus* sp) are generally early pioneers that successfully quickly colonize  
84 abandoned croplands (Richardson and Rejmanek, 2004; Picon-Cochard et al., 2006).  
85 Since these species do not resprout after fire, post-fire regeneration will be totally  
86 dependent on seed dispersal from nearby unburnt adults or a viable seed bank after  
87 fire (Rodrigo et al., 2004). On the other hand, large-seed and biotic-dispersed species  
88 (e.g. *Quercus* sp) will be short-distance passively dispersed and will require some  
89 degree of previous perches and vegetation shelter to ensure effective biotic dispersal  
90 and further establishment (Gómez et al., 2008; Gómez-Aparicio et al., 2009; García

91 et al., 2010; Zamora et al., 2010), which implies a slower colonization rate in open  
92 areas (such as crops recently abandoned). However, once established, these species  
93 will be highly resilient to fire occurrence, as post-fire natural regeneration is usually  
94 guaranteed by resprouting from protected buds, thus maintaining the same  
95 individuals' density in the burnt area (López-Soria and Castell, 1992; Espelta et al.,  
96 2003; Bonfil et al., 2004).

97

98 The main objective of this study is to analyze whether post-fire vegetation  
99 regeneration differ according to specific historical land use trajectories. We  
100 hypothesised that time since land abandonment will determine pre-fire vegetation  
101 (abundance of resprouters in the case of *Quercus* sp. and *Pinus* sp. with or without  
102 fire-resistant canopy seed bank based on serotinous cones, hereafter resprouters and  
103 serotinous/non serotinous species) and thus be a critical factor determining post-fire  
104 regeneration. This hypothesis was tested in an area burnt by two extensive wildfires  
105 (c.a. 60,000 ha). We analyzed the relationship between land use history (years 1956,  
106 1978 and 1993) and the post-fire regeneration success in terms of land cover and  
107 species composition (biotic-dispersed and resprouter species, *Quercus* spp. vs. wind-  
108 dispersed serotinous or non serotinous species, *Pinus* spp.). According to the  
109 functional traits of these species, we expected that: i) changes in forest cover after  
110 fire will depend on land use trajectory of the site, i.e. long standing forest areas will  
111 exhibit a higher and faster recovery than those that recently became forested, ii)  
112 species composition will depend on previous land uses and fire history: presence of  
113 *Quercus* sp. (resprouters) in the site will be influenced by time since cropland  
114 abandonment and not by fire occurrence while the presence of *Pinus* sp (seeders) will

115 be less conditioned by time since cropland abandonment and more determined by  
116 fire and iii) whatever the influence of land use history in post-fire recovery, this  
117 process will vary along the landscape, being faster in northern aspect sites (i.e. cooler  
118 and more humid) than in southern sites, due to the general and critical water deficit  
119 that characterizes the Mediterranean climate.

120

## 121 **2. Material and methods**

### 122 *2.1. Species and study area*

123 The study area comprises 63.190 ha distributed in Catalonia (NE Spain, 41°45′-42°6′N;  
124 1°38′-2°1′E, Fig 1). The area presents a gentle relief with low hills ranging in elevation 320-  
125 1500 m.a.s.l. and a dry-subhumid to sub-humid Mediterranean climate (according to the  
126 Thornwaite index), with mean annual temperature 10-13 °C and annual precipitation  
127 ranging 600-900 mm. According to the data provided by the Forest Ecological Inventory of  
128 Catalonia (IEFC; Gracia et al., 2002) and the Spanish Second National Forest Inventory  
129 (NFI2; ICONA, 1993-2000), in 1990 the area was extensively covered by a mosaic  
130 landscape of forests (71%), cereal croplands (27%) and scarce shrublands and pastures  
131 (2%). The dominant forest tree species in the area were: *Pinus nigra* Arnold (63% of the  
132 forested area), *Pinus halepensis* Mill. (18%), *Pinus sylvestris* L. (14%) and mixed *Quercus*  
133 *ilex* L. and *Quercus cerrioides* Wk. et Costa forests (5%). While none of the *Pinus* species  
134 can resprout and all have small wind-dispersed seeds, only *P. halepensis* possesses a fire-  
135 resistant canopy seed bank which can release their seeds after fire (Habrouk et al., 1999;  
136 Tapias et al., 2004). On the contrary, *Quercus* species can resprout and have bigger seeds  
137 biotically dispersed mainly by jays and rodents (Gómez, 2003; Gómez et al., 2008).  
138 In 1994 and 1998, two extensive summer wildfires burnt 61% of the surface included in the

study area (c.a 24.300 ha in 1994 and 14.300 ha in 1998). These extremely intense crown fires, resulted in the lost of almost all above-ground living biomass of trees inside the perimeter of the burnt surface (Retana et al., 2002). Before these fire events, the area had not burned for at least 70 years (Espelta et al., 2002).

143

## 2.2. Land use histories and estimation of forest responses to fire

We used two complimentary data sources to gather information on spatial heterogeneity in post-fire vegetation responses: 1) forest inventory data, based on permanents plots to gather species-specific information and 2) remote sensing imagery, based on a wider area to obtain estimates of forest densification.

First, we used 565 plots (25 m radius) covering the study area using a 1x1 km systematic sampling carried out in 1993 (before the fire events) during the Spanish Second National Forest Inventory (NFI2; ICONA, 1993-2000) and re-sampled again in 2001 during the Spanish Third National Forest Inventory (NFI3; DGCN, 2005). NFI plots were selected because had only natural regeneration and no thinning management applied to the stands.

Comparison of the data provided by the NFI2 and the NFI3 allowed us to identify whether a given plot had burnt during the 1994 and 1998 wildfires (249 plots burned out of 565, 44 %). Presence and density (stems/ha) of the five tree forest species dominant in the area (*Q. ilex* and *Q. cerrioides* (resprouters with biotic-dispersed seeds); *P. nigra*, *P. sylvestris* (non-serotinous and wind-dispersed seed) and *P. halepensis* (serotinous and wind-dispersed seeds) was assessed in the 565 plots through the NFI3 forest inventory dataset carried out in 2001. The density of each species includes stems >2.5 cm of basal diameter. To account for the presence of each species, apart of stems >2.5 cm, we also considered the presence (or absence) of individuals <2.5 cm diameter.



164

165

166 Since 1993 all plots were considered to be within a forested land use category as they  
167 had been included in both the second and third national forest inventories (NFI2,  
168 NFI3). Previous land use in the inventoried plots (forests ,F, or croplands, C) was  
169 assessed from (1) direct photointerpretation of aerial photographs (year 1956) and (2)  
170 the existing Land Use Map of the Spanish Ministerio de Agricultura, Pesca y  
171 Alimentación (Mapa de Cultivos y Aprovechamientos) (year 1978). This allowed us  
172 to assign to each plot of the NFI a historical land use trajectory: CCF (cropland in  
173 1956 and 1978, forest in 1993), CFF (cropland in 1956, forest in 1978 and 1993) and  
174 FFF (forest in 1956, 1978 and 1993) (See Fig. 1). Plots in the category FCF (forest in  
175 1956, cropland in 1978, and forest in 1993) were excluded because of their low  
176 number (7). These different historical land use trajectories were considered as an  
177 estimator of the time since cropland abandonment.

178

179 Finally, we evaluated forest cover in 1956 and 1993 in a subsample of the area (the  
180 1998 burnt area, Fig. 1) using direct photointerpretation from aerial photographs. The  
181 analysed area was then classified according to (1) the trajectory of land use between  
182 1956 and 1993 (i.e.  $C \rightarrow F$  or  $F \rightarrow F$ ) (Fig 1f, called Land use hereafter) and (2) the  
183 variation of forest cover between periods (only for the F areas, Forest density  
184 hereafter) using three different classes: high density (>70% of tree cover), medium  
185 density (40-70 %), low density (20-40%).

186 Post-fire vegetation regeneration was then estimated using NFI3 data remote sensing  
187 vegetation indices (NDVI) as surrogates of vegetation vigour and cover (Lopez-

188 Zozaya et al., 2011). NDVI values were taken in a date when all the deciduous trees  
189 had full-formed leaves (May 19<sup>th</sup>, 2002). Forest cover was estimated in both North  
190 and South aspects because in a Mediterranean-type climate they are the two extreme  
191 situations in terms of the main abiotic factors (temperature, soil and air moisture,  
192 irradiance, etc.) affecting plant distribution (Blondel and Aronson, 1999; Pausas et  
193 al., 1999). NDVI values were extracted from randomly selected points that combined  
194 each category of (1) historic land-use trajectory (CF, FF), (2) pre-fire cover dynamics  
195 (decrease, stable, increase) and (3) aspect (North/South), at a density of 1 point/ha  
196 per category\*aspect combination.

197

### 198 2.3. Data analysis

199 We used log-linear models to analyse the effect of the historical land use trajectory  
200 (CCF, CFF, or FFF) and wildfire (burned, unburned) on the presence/absence of each  
201 of the tree species considered (*Q. ilex*, *Q. cerrioides*, *P. nigra*, *P. sylvestris* and *P.*  
202 *halepensis*). This log-linear analysis fitted a saturated model to the dataset,  
203 considering all interactions, indicated by 123 (1=fire, 2=land uses, 3=presence of the  
204 considered species). Here the null hypothesis is that presence of the tree species is  
205 independent of fire occurrence and land uses. The effects of fire and land uses on  
206 presence of each five tree species can be tested by comparing different fitted models  
207 with this one using likelihood ratio tests. We used automatic selection (one, two and  
208 three way interactions models are tested successively) to select the best-fitting  
209 model. Then, no significant interactions were eliminated to keep the model that  
210 includes the least number of interactions necessary to fit the observed dataset  
211 (Ordoñez et al., 2006). After choosing the best-fitting model, to test the effect of fire

occurrence or land use separately, different chi-square tests were carried out to compare the number of plots with presence or absence of each of the species. Differences in the density of *P. nigra*, *P. sylvestris*, *P. halepensis*, *Q. ilex* and *Q. cerrioides* (in those plots where they were present) due to the effect of time since abandonment of croplands were analyzed using one-way ANOVAs. The predictor variable was the land use category in 1956 (cropland or forest). We did not consider the trajectory of land uses from 1956 to 1978 because of the scarce number of samples in some of the categories. Data of density were log-transformed before the analyses to meet the criteria of normality. Statistical differences among land use trajectories in forest cover after fire (estimated from NDVI values) were calculated by resampling subsets of 200 points per combination of Land Use\*aspect and Forest density\*aspect by using 1000 bootstrap runnings. Then, we calculated the mean and 95% confidence intervals for each category and aspect. When confidence intervals did not overlap we considered significant differences among land-use trajectories.

### 3. Results

Overall, during the second half of the XX century, the rates of crop abandonment in benefit of the forest have increased in the study area, with a faster rate between 1956 and 1978 than between 1978 and 2001 (Fig. 1). From the 565 plots included in the NFI3 forest inventory carried out in 2001, 75 % were yet occupied by forests in 1956, this increased to 94.3% in 1978, to finally reach the 100 % in 1993, before fire occurred (Fig. 1).

235 Concerning the post-fire presence of the five species, in 2001: *Q. ilex* and *Q. humilis*  
236 were present in 95% of the plots, while *P. nigra*, *P. sylvestris* and *P. halepensis* in  
237 75.5% of the plots. Pure forests of *Quercus* and *Pinus* species accounted respectively  
238 for 24% and 5.4 % of the plots, while the rest (70.6 % of the plots) were mixed oak-  
239 pine forests.

240 The presence of non-serotinous pines (*P. nigra* and *P. sylvestris*) was negatively  
241 associated with fire occurrence, and was independent of time since cropland  
242 abandonment (Table 1, Table 2, Fig. 2a). *Pinus nigra* was present in 55.4 % of  
243 unburnt plots whereas it decreased to 32.7% on burnt ones (Fig. 2a). *Pinus sylvestris*  
244 followed a similar trend but more pronounced, namely it was present in 49.7 % of  
245 unburnt plots and only in 9.2 % of the burned ones (Fig. 2). Conversely, the presence  
246 of *Q. cerrioides* was associated with time since cropland abandonment but was  
247 independent from fire occurrence (Table 1, Table 2, Fig. 2). Presence of *Q.*  
248 *cerrioides* was higher in FFF plots (88.1 %) than in the other two categories (80.9 %  
249 in CCF and 77.5% in CFF) (Fig. 2). The presence of *P. halepensis* and *Q. ilex* was  
250 independent of fire occurrence and time since cropland abandonment (Table 1,  
251 Fig.2).

252 Time since cropland abandonment had a different effect on the density of *Q. ilex*,  
253 having higher densities in FFF plots (423 stems/ha, n= 82) than in new forests arisen  
254 after 1956 (242 stems/ha, n= 34) ( $F=7.63$ ,  $p=0.08$ ). Conversely, the density of *Q.*  
255 *cerrioides* and the three *Pinus* species was not affected by time since abandonment,  
256 reaching similar densities in croplands abandoned after 1956 than in those abandoned  
257 before 1956 or never cultivated (*Q. cerrioides*:  $255.8 \pm 16$ , *P. nigra*:  $546.3 \pm 35$ , *P.*  
258 *sylvestris*:  $514.0 \pm 40$ , *P. halepensis*:  $443.2 \pm 43$  stems/ha).

Overall, northern slopes showed higher post-fire recovering than southern slopes (Fig. 3). In the northern slopes, stable forest areas showed higher post-fire vegetation regeneration (thus higher NDVI values), than those that were crops in 1956 and later became forested areas (Fig 3a). The opposite pattern appear in the southern slopes, with higher NDVI values in areas that were crops in 1956 and then forest in 1993 than those that remained a forest through all this period (Fig. 3a). Interestingly, within the northern slopes forest recovering after fire (estimated from NDVI values) was equivalent whether forest cover had increased or remained similar from 1956 to 1993, but substantially higher than those recorded in areas where forest cover had decreased (Fig 3b). Southern slopes that have increased, decreased, or remained the same in terms of forest cover density, showed no significant differences of post-fire forest recovering (Fig. 3b).

#### 4. Discussion

We found an important role of historic land use changes and fire disturbance (and, more important, the interaction between them) on post-fire forest recovering in terms of forest cover, species composition and densities. Long-standing forest areas exhibited a higher post-fire recovery and less change in species composition than those previously used in agriculture (i.e. younger forests).

As hypothesized, and first reported by Foster (1992), in our study post-fire species composition - and the associated functional traits - depended on previous land uses.

Overall, the abundance of *Quercus* sp. was more heavily influenced by time since cropland abandonment than by fire occurrence while the presence of *Pinus* sp. was less conditioned by time since cropland abandonment and more determined by fire.

In contrast, oaks seem to colonize new areas at a slower speed, owing to the need of secondary dispersers such as Eurasian jay (*Garrulus glandarius*) or several species of mice (mainly *Apodemus sylvaticus* and *Mus spretus*). The same pattern is likely to appear in other biotic plant-frugivorous interactions requiring some degree of forest structure and/or shelter to attain effective seed dispersal (Castro et al., 2010; Gómez-Aparicio et al., 2009; Rost et al., 2009; Lehouck et al., 2009; Uriarte et al., 2011). Indeed, dispersal limitation has been proposed as more critical than recruitment limitation for the colonization of old-forest-specialized plant species after agriculture abandonment (reviewed in Hermy and Verheyen, 2007). Furthermore, animal-dispersed species have often the most habitat-restricted requirements thus it is reasonable if they need more time to disperse seeds into abandoned fields (Uriarte et al., 2011; Lehouck et al., 2009). Conversely, wind-dispersed *Pinus* species can successfully colonize recently abandoned areas (Ordoñez et al., 2006), and this faster establishment capacity - at a shorter period than the years between consecutive aerial photographs used for this study - is supported by the fact that *Pinus* sp. densities did not vary along land use trajectories. Although whether this situation is general for other wind-dispersed species as well is still uncertain (Foster, 1992; Soon and Heil, 2002).

Forest recovering after fire substantially varied according to pre-fire plant composition and cover dynamics. Species with resprouting ability (i.e. *Quercus* sp) dominated post-fire ground surface, while the establishment of post-fire non-resprouter species (*Pinus* sp) depended on the presence of seed sources nearby the burnt area or in their capacity to maintain a canopy seed bank resistant to fire. This

species turnover and losses in biodiversity compared to old-grown forests have been reported in many other studies (Trabaud and Lepart, 1981; Pausas et al., 1999; Retana et al., 2002; Rodrigo et al., 2004; Duguy and Vallejo, 2008; among others). The lack of influence of fire occurrence on the presence of *Q. ilex* and *Q. humilis* may be explained by the high resilience they exhibit to burning, through vigorous resprouting from the root collar (Espelta et al., 2003). Indeed, both oak species are able to survive and resprout even after repeated burning (e.g. three consecutive wildfires in less than ten years in Bonfil et al., 2004). Differences in recovery between pines associated to specific traits appeared very clearly, with the presence of those species without a canopy seed bank resistant to fire (*P. nigra* and *P. sylvestris*) being negatively associated with fire occurrence. On the contrary, the presence of *P. halepensis*, that have a fire resistant canopy seed bank (i.e. including serotinous cones), was independent of fire occurrence and time since cropland abandonment, as found in previous studies (Pausas et al., 1999; Rodrigo et al., 2004). It is important to note that the two fires studied in this work were large and massive-crown fires that hindered the arrival of seeds from not burned areas (Ordoñez et al., 2006; Rodrigo et al., 2004). Furthermore, it also seems that, in areas that were cultivated in the past and that recently became *Pinus* spp forests, the post-fire regeneration and forest cover were reduced compared to the long-term forested areas. Overall, while land cover was mainly occupied by *P. nigra* and *P. sylvestris* forests before fire events; after the disturbance, *Quercus* species dominated the landscape (Rodrigo et al., 2004, Arnán et al., 2007). Hence, fire acted as a drastic mechanism of turnover between one group of species and the other as found in former studies (Foster, 1992; Pausas et al., 1999; Puerta-Piñero et al., 2011; Rudel et al., 2005).

331  
332 Our results suggest that the longer the time since crop abandonment, the more  
333 heterogeneity in species and diversity of functional responses to potential  
334 perturbations are present, as previously reported (Rudel et al., 2005, Fraterrigo et al.,  
335 2006; Hermy and Verheyen, 2007), which thus increases the probability of rapid  
336 post-fire forest regeneration. Apart from the presence of nearby seed sources, the  
337 regeneration of a burnt area seems to depend either in the presence of fire-resistant  
338 soil and canopy seed banks or in the presence of species with resprouting ability  
339 (Rodrigo et al., 2004). All these crucial traits that assure the potential resilience of  
340 forests to fire are widespread among Mediterranean species (Paula et al., 2009).  
341 Within this framework, long standing forests with higher number of species and thus,  
342 more diverse in functional traits ensuring forest recovery after fire will have a higher  
343 resilience after this intense disturbance (Thompson et al., 2009; Puerta-Piñero et al.,  
344 2011; FAO et al., 2008; Walck et al., 2011).  
345  
346 In this study, we found the recovery of burnt sites to be significantly worse in the  
347 southern slopes compared to the northern ones. Therefore, we should also consider  
348 that some of the patterns that we found could be constrained by other environmental  
349 factors (Arnan et al., 2007; Pausas et al., 1999). In the Mediterranean basin, for  
350 example, marked differences exist between the type of vegetation growing in  
351 northern and southern slopes, the latter mainly dominated by drought-tolerant species  
352 which are able to survive under high rates of evaporative demand (Zavala et al.,  
353 2000; Pausas et al., 1999; Kutiel, 1997). Abiotic factors the years following the fire,  
354 such as temperature or water availability, could substantially vary among different  
355 parts of the landscape. Furthermore, topographic factors such as elevation, slope or



356 aspect could also play a major role, particularly in areas characterized by harsh  
357 climates (Pausas et al., 1999; Kutiel, 1997; Broncano et al., 2005).

358

359 On the whole, our findings highlight that predictions on how extensive disturbances  
360 such as fire affect the regeneration and further distribution of plants, should take into  
361 account also historical land trajectories. In the light of global change a key challenge  
362 will be to anticipate the impacts of disturbances on ecosystems. We could point out  
363 the need of increasing the diversification of the forests and promoting the presence of  
364 woody resprouters (e.g. in conifer monocultures) to help the system to progressively  
365 acquire a self-capacity to respond to natural or human-induced disturbances.

366

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## 373   **References**

- 374   Améztegui, A., Brotons, L., Coll, L., 2010. Land-use changes as major drivers of  
375       mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology*  
376       and *Biogeography* 19, 632-641.
- 377   Arnan, X., Rodrigo, A., Retana, J., 2007 Post-fire regeneration of Mediterranean plant  
378       communities at a regional scale is dependent on vegetation type and dryness.  
379       *Journal of Vegetation Science* 18, 111-122.
- 380   Blondel, J., Aronson, J., 1999. *Biology and wildlife of the Mediterranean region*.  
381       Oxford University Press, USA.
- 382   Bonfil, C., Cortés, P., Espelta, J.M., Retana, J. 2004. The role of disturbance in the co-  
383       existence of the evergreen *Quercus ilex* and the deciduous *Quercus cerrioides*.”  
384       *Journal of vegetation science* 15, 423–430.
- 385   Broncano, M.J., Retana, J., Rodrigo, A., 2005. Predicting the recovery of *Pinus*  
386       *halepensis* and *Quercus ilex* forests after a large wildfire in northeastern Spain.  
387       *Plant Ecology* 180, 47-56
- 388   Castro, J., Moreno-Rueda, G., Hódar, J. 2010. Experimental Test of Postfire  
389       Management in Pine Forests: Impact of Salvage Logging versus Partial Cutting  
390       and Nonintervention on Bird–Species Assemblages. *Conservation Biology* 24,  
391       810-819.
- 392   Debussche, M., Escarré, J., Lepart, J., Houssard, C., Lavorel S., 1996. Changes in  
393       Mediterranean plant succession: old-fields revisited. *Journal of Vegetation*  
394       *Science* 7, 519–526.
- 395   DGCN, 2005. Tercer Inventario Forestal Nacional (1997-2007): Cataluña. Ministerio  
396       de Medio Ambiente, Madrid.
- 397   Duguy, B., Rovira, P., Vallejo, R., 2007. Land-use history and fire effects on soil  
398       fertility in eastern Spain. *European journal of soil science* 58, 83–91.
- 399   Duguy, B., Vallejo, V.R.. 2008. Land-use and fire history effects on post-fire  
400       vegetation dynamics in eastern Spain. *Journal of Vegetation Science* 19, 97–108.
- 401   Espelta, J.M., Retana, J., Habrouk, A. 2003. An economic and ecological multi-criteria  
402       evaluation of reforestation methods to recover burned *Pinus nigra* forests in NE  
403       Spain. *Forest Ecology and Management* 180,185-198

404 FAO, UNDP, UNEP, 2008. UN Collaborative Programme on Reducing Emissions  
 405 from Deforestation and Forest Degradation in Developing Countries (UN-REDD).  
 406 New York: United Nations (pp. 1-27).  
 407 Foster D.R., 1992. Land-use history (1730-1990) and vegetation dynamics in central  
 408 New England, USA. *Journal of Ecology* 80, 753–772.  
 409 Fraterrigo J.M., Turner M.G., Pearson S.M., 2006. Previous land use alters plant  
 410 allocation and growth in forest herbs. *Journal of Ecology* 94, 548-557.  
 411 doi:10.1111/j.1365-2745.2005.01081.x  
 412 García, D., Zamora, R., Amico, G.C., 2010. Birds as Suppliers of Seed Dispersal in  
 413 Temperate Ecosystems: Conservation Guidelines from Real-World Landscapes.  
 414 *Conservation Biology* 24, 1070-1079  
 415 Gómez, J.M., 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns  
 416 by jays in a heterogeneous landscape. *Ecography* 26, 573–584.  
 417 Gómez, J.M., Puerta-Piñero, C., Schupp, E.W., 2008. Effectiveness of rodents as local  
 418 seed dispersers of Holm oaks. *Oecologia* 155, 529–537.  
 419 Gómez-Aparicio, L., Zavala, M.A., Bonet, F., Zamora, R., 2009. Are pine plantations  
 420 valid tools for restoring Mediterranean forests? An assessment along abiotic and  
 421 biotic gradients. *Ecological Applications* 19, 2124-2141.  
 422 Gracia, M., Retana, J., Roig, P. 2002. Mid-term successional patterns after fire of  
 423 mixed pine-oak forests in NE Spain. *Acta Oecologica* 23, 405-411  
 424 Habrouk, A., Retana, J., Espelta, J.M., 1999. Role of heat tolerance and cone  
 425 protection of seeds in the response of three pine species to wildfires. *Plant*  
 426 *Ecology* 145, 91-99  
 427 Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest  
 428 biodiversity : a review of past land-use effects on forest plant species composition  
 429 and diversity. *Ecological Research* 22, 361-371. doi:10.1007/s11284-007-0354-3  
 430 ICONA, 1993-2000. Segundo Inventario Forestal Nacional 1986-1995. Cataluña:  
 431 Lleida and Barcelona. ICONA, MAPA, Madrid  
 432 IPCC (Intergovernmental Panel on Climate Change), 2007. Climate change 2007: the  
 433 physical science basis. Contribution of Working Group I to the Fourth Assessment  
 434 Report of the IPCC

435 Kutiel, P., 1997. Spatial and temporal heterogeneity of species diversity in a  
 436 Mediterranean ecosystem following fire. *International Journal of Wildland Fire* 7,  
 437 307–315.

438 Lehouck, V., Spanhove, T., Vangeste, I. C., Cordeiro, N. J., Lens, L.. 2009. Does  
 439 landscape structure affect resource tracking by avian frugivores in a fragmented  
 440 Afrotropical forest? *Ecography* 32, 789–799.

441 Levey, D.J., Silva, W.R., Galetti, M., 2005. Seed dispersal and frugivory: ecology,  
 442 evolution, and conservation. CABI.

443 Lloret, F., Calvo, E., Pons, X., Díaz-Delgado, R., 2002. Wildfires and landscape  
 444 patterns in the Eastern Iberian Peninsula. *Landscape Ecology* 17, 745-759.

445 López-Soria, L., Castell, C., 1992. Comparative genet survival after fire in woody  
 446 Mediterranean species. *Oecologia* 91, 493-499.

447 Mouillot, F., Ratte, J.P., Joffre, R., Mouillot, D., Rambal, S., 2005. Long-term forest  
 448 dynamic after land abandonment in a fire prone Mediterranean landscape (central  
 449 Corsica, France) *Landscape ecology* 20, 101–112.

450 Ordóñez, J.L., Molowny-Horas, R., Retana, J., 2006. A model of the recruitment of  
 451 *Pinus nigra* from unburned edges after large wildfires. *Ecological modeling* 197,  
 452 405–417.

453 Palahí, M., Mavsar, R., Gracia, C., Birot, Y. 2008. Mediterranean Forests under focus.  
 454 *International Forestry Review* 10, 676-688.

455 Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., Ojeda,  
 456 F., Luna, B., Moreno, J.M., Rodrigo, A., Espelta, J.M., Palacio, S., Fernández-  
 457 Santos, B., Fernandes, P.M., Pausas, J.G., 2009. Fire-related traits for plant  
 458 species of the Mediterranean Basin. *Ecology* 90, 1420-1420.

459 Pausas, J.G., 1999. Response of plant functional types to changes in the fire regime in  
 460 Mediterranean ecosystems. A simulation approach. *Journal of Vegetation Science*  
 461 10, 717-722.

462 Pausas, J.G., 2004 Changes in fire and climate in the eastern Iberian Peninsula  
 463 (Mediterranean basin). *Climatic Change* 63, 337-350

464 Pausas, J.G., Carbó, E., Caturla, R.N., Gil, J.M., Vallejo, R., 1999. Post-fire  
 465 regeneration patterns in the Eastern Iberian Peninsula. *Acta Oecologica* 20, 499-  
 466 508.

467 Picon-Cochard, C., Coll, L., Balandier, P., 2006. The role of below-ground  
 468 competition during early stages of secondary succession: the case of 3-years-old  
 469 Scots pine (*Pinus sylvestris* L.) seedlings in an abandoned grassland. *Oecologia*  
 470 148, 373-383.

471 Piñol, J., Terradas, J., Lloret, F., 1998. Climate warming, wildfire hazard and wildfire  
 472 occurrence in coastal Eastern Spain. *Climatic Change* 38, 345-357

473 Puerta Piñero, C., Brotons, L., Coll, L., González-Olabarría, J.R., 2011. Valuing acorn  
 474 dispersal and resprouting capacity ecological functions to ensure Mediterranean  
 475 forest resilience after fire. *European Journal of Forest Research*. In press.

476 Retana, J., Espelta, J.M., Habrouk, A., Ordoñez, J.L., de Sola-Morales, F., 2002.  
 477 Regeneration patterns of three Mediterranean pines and forest changes after a  
 478 large wildfire in northeastern Spain. *Ecoscience* 9, 89-97.

479 Richardson, D.M., Rejmánek, M., 2004. Conifers as invasive aliens: a global survey  
 480 and predictive framework *Diversity and Distributions* 10, 321-331.

481 Rodrigo, A., Retana, J., Picó, X., 2004. Direct regeneration is not the only response of  
 482 Mediterranean forests to large fires. *Ecology* 85, 716-729

483 Rost, J., Pons, P., Bas, J.M. 2009. Can salvage logging affect seed dispersal by birds  
 484 into burned forests? *Acta Oecologica* 35, 763-768.

485 Rudel, T.K., Coomes, O.T., Moran, E., Achard, F., Angelsen, A., Xu, J., Lambin, E.,  
 486 2005. Forest transitions : towards a global understanding of land use change.  
 487 *Global Environmental Change* 15, 23-31. doi:10.1016/j.gloenvcha.2004.11.001

488 Soons, M.B., Hei,l G.W. 2002. Reduced colonization capacity in fragmented  
 489 populations of wind-dispersed grassland forbs. *Journal of Ecology* 90, 1033-1043.

490 Tapias, R., Climent, J., Pardos, J.A Gil, J., 2004. Life histories in Mediterranean pines.  
 491 *Plant Ecology*. 171, 53-68.

492 Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience,  
 493 Biodiversity, and Climate Change: A synthesis of the  
 494 biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the  
 495 Convention on Biological Diversity, Montreal.

496 Trabaud, L., Lepart, J., 1981. Changes in the floristic composition of a *Quercus*  
 497 *coccifera* L. garrigue in relation to different fire regimes. *Plant Ecology* 46, 105-  
 498 116.

499 Uriarte, M., Anciaes, M., da Silva, M. T. B., Rubim, P, Johnson, E., Bruna, E. M.  
 500 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds  
 501 in an experimentally fragmented landscape. *Ecology* 92, 924–937.  
 502 Vitousek, P.M., 1992. Global environmental change: an introduction. *Annual Review*  
 503 *of Ecology and Systematics* 23, 1–14.  
 504 Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K., Poschlod, P., 2011. Climate  
 505 change and plant regeneration from seed. *Global Change Biology* 17, 2145–2161.  
 506 Zamora, R., Hódar, J.A., Matías, L., Mendoza, I., 2010. Positive adjacency effects  
 507 mediated by seed disperser birds in pine plantations. *Ecological Applications* 20,  
 508 1053-1060.  
 509 Zavala, M.A., Espelta, J.M., Retana, J. 2000. Constraints and trade-offs in  
 510 Mediterranean plant communities: the case of holm oak-Aleppo pine forests. *The*  
 511 *Botanical Review* 66, 119-149.  
 512 Zozaya, E.L., Brotons, L., Vallecillo, S. 2011. Bird community responses to  
 513 vegetation heterogeneity following non-direct regeneration of Mediterranean  
 514 forests after fire. *Ardea* 99, 73–84.  
 515



Table 1. Main parameters of the best-fitting log-linear models relating (1) land use trajectories (CCF: crop in 1956-crop in 1978-forest in 1993, CFF: crop(56)-forest(78)-forest(93), or FFF: forest(56)-forest(78)-forest(93) and (2) wildfire (burned, unburned) with the presence/absence after fire of each one of the five tree species considered (*Q. ilex*, *Q. cerrioides*, *P. nigra*, *P. sylvestris* and *P. halepensis*). Variables included in the model are: 1 = wildfire occurrence, 2 = time since cropland abandonment, 3 = presence of the species. Independence of two variables is indicated separating them with a coma while interaction between them is indicated by the absence of coma.

Species	Best-fitting model	Person Chi square	df	p ‡
<i>P. nigra</i>	13, 2	5.45	6	0.49
<i>P. sylvestris</i>	13, 2	5.54	6	0.48
<i>P. halepensis</i>	1, 2, 3	5.12	7	0.64
<i>Q. ilex</i>	1, 2, 3	8.53	7	0.29
<i>Q. cerrioides</i>	1, 23	6.50	5	0.26

‡ Note that non-significant p-values indicate a good fit between observed frequencies and expected frequencies generated by the model.



529 Table 2. Species presence in relation to fire occurrence and time since crop  
 530 abandonment. Values of the Pearson chi squared test for the comparison of fire  
 531 occurrence (burnt, unburnt) and time since cropland abandonment (CCF:crop-crop-  
 532 forest, CFF:crop-forest-forest, or FFF:forest-forest-forest) on the presence/absence of *Q.*  
 533 *ilex*, *Q. cerrioides*, *P. nigra*, *P. sylvestris* and *P. halepensis* are shown. Significant  
 534 differences at  $p = 0.05$  are indicated in bold.

Species	Fire occurrence			Time since cropland abandonment		
	df	$\chi^2$	p	df	$\chi^2$	p
<i>P. nigra</i>	1	<b>29.12</b>	<b>&lt;0.001</b>	2	2.97	0.226
<i>P. sylvestris</i>	1	<b>105.81</b>	<b>&lt;0.001</b>	2	1.78	0.411
<i>P. halepensis</i>	1	0.47	0.829	2	1.75	0.417
<i>Q. ilex</i>	1	0.84	0.361	2	3.21	0.201
<i>Q. cerrioides</i>	1	0.30	0.581	2	<b>16.25</b>	<b>&lt;0.001</b>

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**Figure 1.** Historical land use changes and forest cover from 1956 to 1993 in the 1998-fire study area (note that the remaining 1994-fire area is absent in this figure). a: Land uses in 1956; b: Land uses in 1978; c: Land uses in 1993; d, land use changes over time Legend: FFF (never cultivated or cropland abandoned before 1956), CFF (Cropland abandoned between 1956 and 1978) and CCF (cropland abandoned between 1978 and 1993); e-f: sub-sampled area considered for estimation of post-fire forest cover (NDVI computations); e: Land-use changes between 1956-1993, categories CF (crop in 56, forest in 93) and FF (forest in 56, forest in 93); f: Forest density changes between 1956 and 1993, categories: decreased, equal, or increase forest cover density. Points indicate the locations of the NFI plots, orange for FC (forest in 1993, and cropland or non-forested area in 2001) green for FF (forest in 1993 and 2001) transitions.

**Figure 2.** Presence of *P. nigra*, *P. sylvestris*, *P. halepensis*, *Q. ilex* and *Q. cerrioides* attending to fire occurrence (a) and time since abandonment (b). Different letters indicate significantly different values at  $p = 0.05$  according to the Pearson chi-square test; ns indicates no significant differences. N = 565

**Figure 3.** Forest cover after fire (estimated by NDVI) in relation to land use change (A), changes in forest density (B) and aspect (North vs. South). Whiskers and dashed lines identify confidence intervals at 5% after 1000 bootstrap re-sampling over 200 NDVI focal points at each category \*aspect combination (see methods).



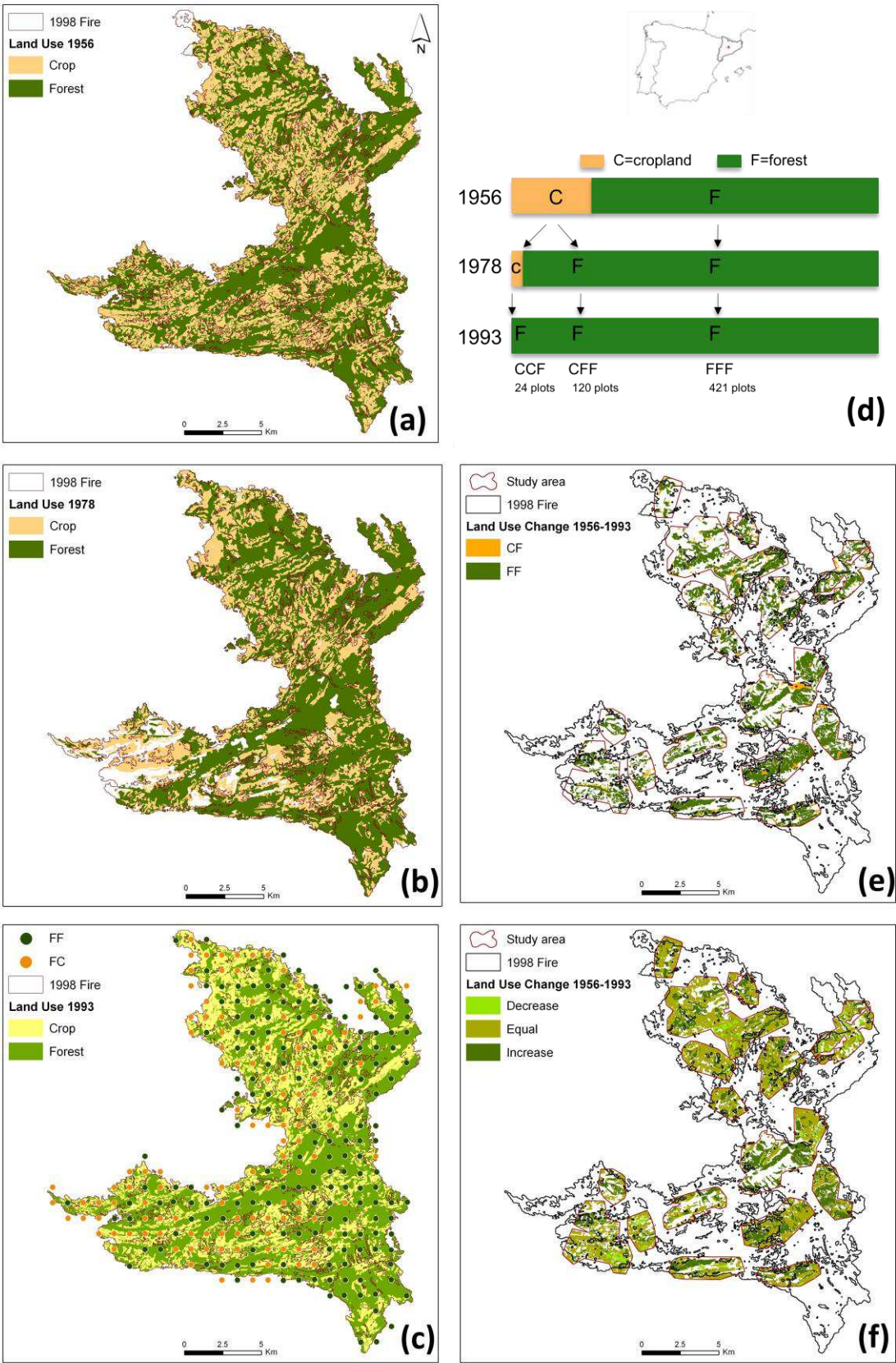
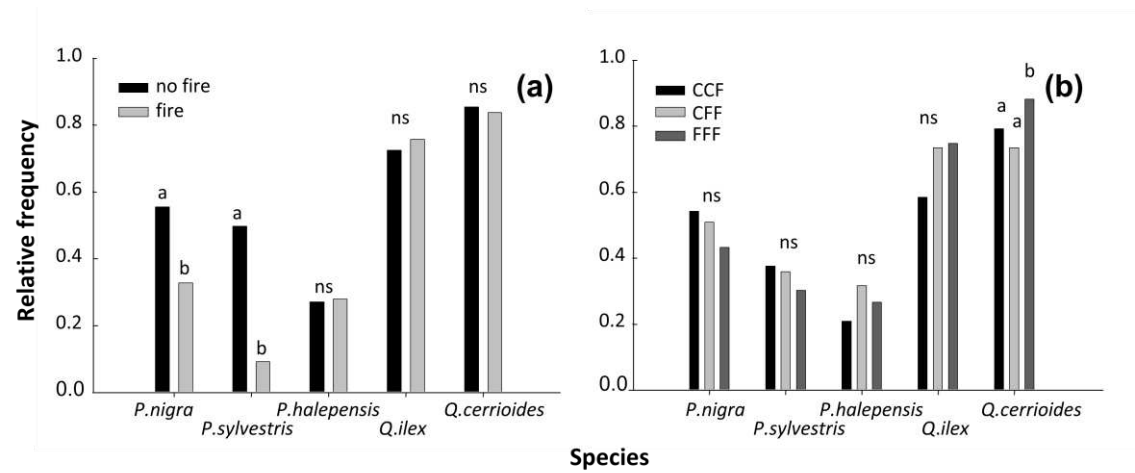
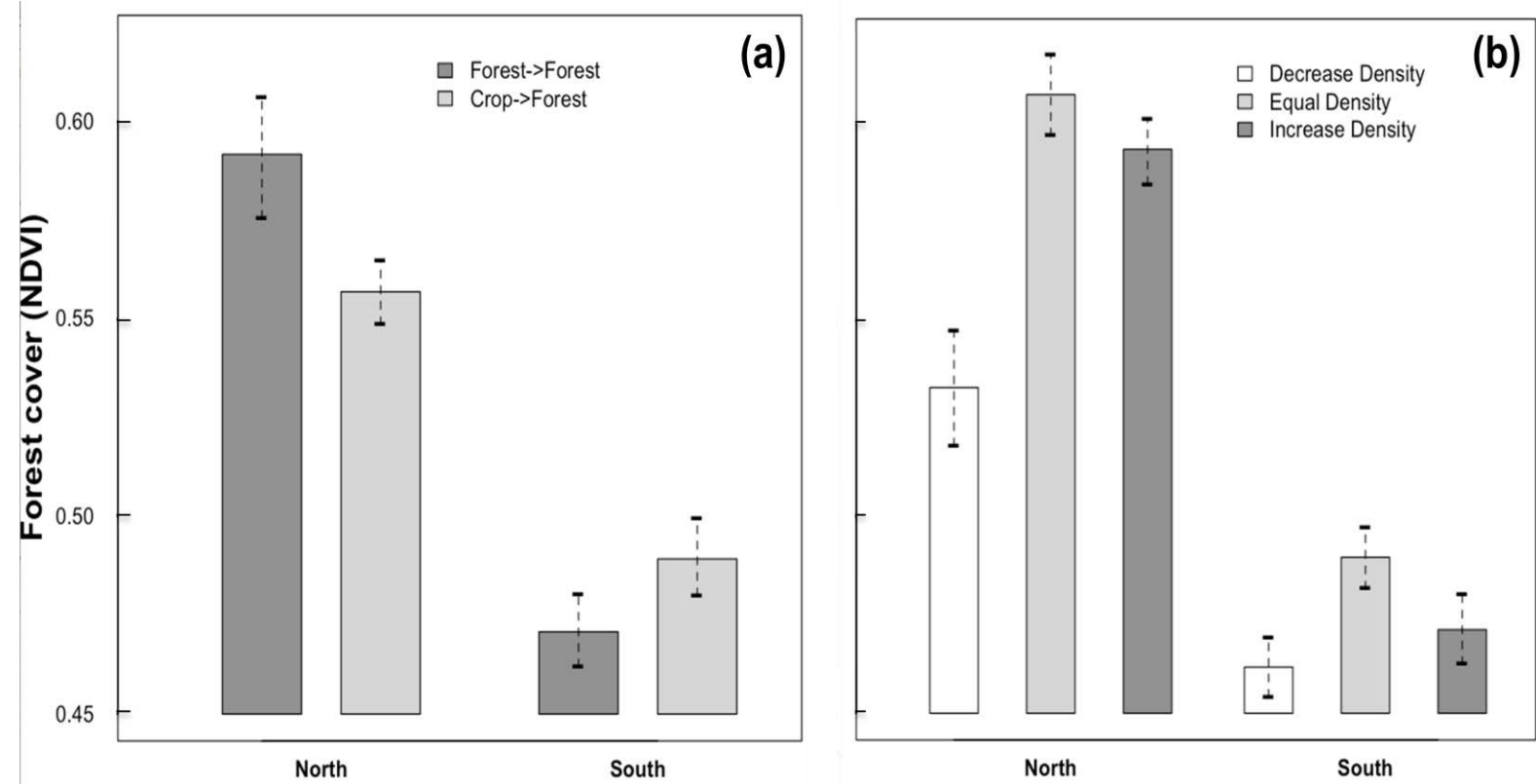


Figure 2



571 **Figure 3**



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