Animal Versus Wind Dispersal and the Robustness of Tree Species to Deforestation

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Studies suggest that populations of different species do not decline equally after habitat loss. However, empirical tests have been confined to fine spatiotemporal scales and have rarely included plants. Using data from 89,365 forest survey plots covering peninsular Spain, we explored, for each of 34 common tree species, the relationship between probability of occurrence and the local cover of remaining forest. Twenty-four species showed a significant negative response to forest loss, so that decreased forest cover had a negative effect on tree diversity, but the responses of individual species were highly variable. Animal-dispersed species were less vulnerable to forest loss, with six showing positive responses to decreased forest cover. The results imply that plant-animal interactions help prevent the collapse of forest communities that suffer habitat destruction.

Habitat destruction is often cited as the single greatest cause of global biodiversity loss (1). These anthropogenic changes trigger biological responses that sometimes end in a biotic collapse, a problem that has led ecologists to face the question of how much habitat is enough for species to persist (2). The dominant theoretical framework for understanding the effects of habitat loss is metapopulation theory, which focuses on the dynamic balance of local extinctions and colonizations that characterize fragmented populations at regional scales (3). According to this theory, regional habitat loss not only removes biodiversity held in the lost habitat but also reduces the occurrence of species within the remaining habitat (4). This idea has become a central tenet of conservation practice, causing a shift in focus from the local to the landscape scale. For example, it is the source of the current emphasis on the maintenance and creation of habitat corridors to foster dispersal among patches (5, 6). However, empirical tests of this prediction have been restricted to short-lived animal species [especially butterflies and birds (7, 8)], short spatial scales (9), and short time scales, over which observations are likely to be dominated by short-term responses that may or may not be indicative of the long-term impacts of habitat loss.

We analyzed the relationship between local forest cover and the occurrence of 34 canopy-dominant tree species [28 native to the study region and 6 exotic (table S1)] in 89,365 survey sites distributed across peninsular Spain (10) (Fig. 1). The data set was extracted from the Spanish Second National Forest Inventory (IFN2), which placed a 25-m-radius circular sample plot in each 1 × 1 km grid cell that it classified as being

forested [occupied by woody vegetation (11)]. For each plot q, we calculated a local forest cover H_q, defined as the fraction of the nearest eight grid cells to q that were also classified as forested in IFN2 (using a larger neighborhood degraded the statistical significance of some effects documented here but had no qualitative effect on conclusions). Because the Iberian Peninsula has chronically suffered from forest destruction and conversion into agricultural and degraded states (12), H_q is a measure of net forest loss from prehistory to the present. Thus, we interpret the species responses to H_q observed in the IFN2 survey as responses to forest loss.

We used logistic regression to quantify, for each species j, the probability of occurrence of j in plot q as a function of H_q. For comparison among species we used the fitted logistic curves to calculate, for each species j, a scalar Ω_j, defined as the natural log of the ratio of the probability of occurrence at 0% local forest cover to the probability of occurrence at 75% cover. Negative Ω_j implies that species j shows a negative response to decreased forest cover and vice versa.

We used error propagation to calculate a conservative (upper) estimate of the confidence interval for Ω_j. The results presented below are robust considering either native and exotic species combined or native species only [supporting online material (SOM)].

Of the 34 species, 24 showed a statistically significant negative response to decreased forest cover [negative Ω_j value with confidence intervals not including zero (Fig. 2A)]. This is consistent with the decrease in average tree species richness with decreased forest cover observed in the IFN2 data (Fig. 3) and in previous studies (13). The observed relationship between species richness in this case was approximately linear over most of the range in H_q, which was captured well by the logistic regressions (Fig. 3). However, richness was lower than expected for $H_q \geq 80\%$ and $H_q = 0$. Such abrupt changes could reflect the effects of spatial configuration (that is, fragmentation) when habitat cover goes from nearly continuous to fragmented (with the first appearance of edges) and falls to very low levels (14), although threshold responses can also result from some forms of animal-mediated dispersal (15).

Among species there was large and statistically significant variation in Ω_j. For species with statistically significant negative Ω_j (those with confidence intervals not including zero), Ω_j ranged from –0.03 to –1.53, which corresponds to a proportional reduction in probability of occurrence, for the 75 to 0% scenario, of 3 to 78%. Moreover, there were six species with statistically significant positive responses to reductions in forest cover (Fig. 2A). These species were more likely to be found in plots surrounded by nonforested land.

If this magnitude of interspecific variation in response to forest loss proves to be typical, it will be critical to identify measurable species traits that predict it. Although we did not attempt an exhaustive search of such traits, we did examine the importance of two traits related to dispersal (seed size and animal- versus wind-mediated seed dis-
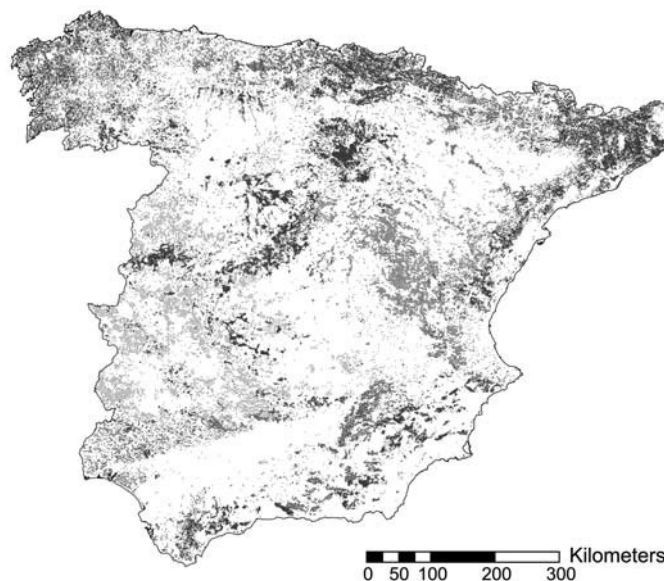
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Fig. 1. Distribution of survey sites in peninsular Spain. IFN2 consisted of 89,365 circular sampling sites (radius = 25 m) distributed across peninsular Spain (average density approximately one per square kilometer). Survey sites were placed in continuous forest locations, so their distribution matches that of the remaining forest.

persal). Metapopulation theory has identified dispersal as crucial in determining species responses to habitat loss (16), and recent modifications of the Levins metapopulation model predict that animal-mediated seed dispersal will confer increased species robustness to habitat loss (17). This is because, unlike wind, animals actively deliver seeds toward suitable patches (directed dispersal), and because some forms of animal dispersal increase the average dispersal distance (18). Both of these behaviors help keep physically isolated habitat patches demographically connected. Directed dispersal and long dispersal distances have been observed in our study region (19). Seed size affects dispersal distance (20) and is correlated with fecundity (21) and establishment probability (22), which are also highlighted as important by metapopulation theory.

We found that animal-dispersed species are, on average, less vulnerable to decreased forest cover than are wind-dispersed species (Fig. 2). The six species showing positive responses to deforestation were all animal-dispersed, and the two species with the largest negative response were wind-dispersed. To assess the possibility that the observed difference between the two groups (animal- and wind-dispersed) could have arisen by chance, we conducted a permutation test on the difference in the position of the groups in the list of species ranked by Ω_j: The probability of finding the observed difference was less than 0.005 (SOM).

The contrasted phylogenetic composition of wind- versus animal-dispersed species raises the possibility that phylogenetically conserved traits other than dispersal mode that are shared by closely related species caused the difference in response between animal- and wind-dispersed species (23). To examine this possibility, we used phylogenetic eigenvector regression [PVR (11)]. The proportion of variation of Ω_j that can be attributed to phylo-

genetic relationships is low ($R^2 = 0.11$). Moreover, an analysis of covariance (ANCOVA) including Ω_j as the response variable, dispersal mode as the explanatory variable, and the three main phylogenetic eigenvectors generated by PVR (which describe 92.5% of the phylogenentic structure in the data) as covariables still found significant differences in Ω_j between wind- and animal-dispersed species ($F = 7.75890$, $P < 0.05$).

In addition to the effects of forest cover, each tree species is likely to be affected by the pronounced gradients in climate, soil, and fire frequency observed in this region, and the interactions between all of these will need to be understood before any future species responses to changes in forest cover or climate can be predicted accurately. However, PCA showed no multicolinearity between forest cover and a set of 18 environmental variables that might be critical to plant growth, reproduction, and survival in Mediterranean and Atlantic systems (table S4). This shows that at the scale of peninsular Spain, local forest cover varies independently of climate, topography, soil, and major perturbation events, so that the simple logistic regression employed here would be expected to extract the correct average response to forest loss for each species. We also estimated Ω_j controlled for these environmental factors, using multiple logistic regression. The results support the conclusions of an overall negative, yet highly variable response to decreased forest cover among tree species, with some positive responses; and greater robustness of animal-dispersed species (fig. S3, $P < 0.005$).

Significant unexplained variation remains in the response of species within each dispersal group, but this is not surprising given the biological variation among species in either group. Just in terms of dispersal itself, both groups contain a large variation in seed size [although within either group we found no effect of seed weight on Ω_j (fig. S1)]; different

animal-dispersed species are dispersed by different combinations of birds and mammals [foraging behavior and body size differences among frugivores may affect seed dispersal distances (24, 25)]; and many of the species are likely to benefit from occasional long-distance dispersal events by agents other than the dominant disperser (26). These species are also likely to differ in the other traits that metapopulation theory has predicted to be crucial in determining response to habitat loss (such as fecundity and local extinction rates). Nonetheless, our analysis suggests that the differences in species responses to local forest cover are to a large extent driven by the dispersal vector used by trees. This is consistent with predictions from metapopulation theory about the effects of animal-mediated directed dispersal. However, additional detailed field observations would be needed to rule out alternative explanations based on the interaction between dispersal and habitat loss. For example, lower amounts of habitat cover may be correlated with increased edge habitat, which has been observed in some cases to be preferred by seed-dispersing animals (27).

Whatever the mechanisms involved, the finding that animal-dispersed tree species are more robust to the effects of deforestation has an obvious implication for conservation policy: In the absence of detailed data (such as was available here), it might be expected that deforestation in other regions is more likely to threaten a given wind-dispersed, than a given animal-dispersed, plant species. However, the weight attached to this prediction should reflect the substantial within-group variation in response documented here (Fig. 2) and the degree of extrapolation outside

Fig. 2. (A) Sensitivity of 34 Spanish tree species to reduction in local forest cover (Ω_j), estimated using the maximum likelihood estimate of the parameters of a logistic regression relating the probability of occurrence of species j to local forest cover. Gray arrows indicate non-native species. Ω_j is defined as the natural logarithm of the ratio of occurrence probabilities at 0 and 75% cover. Negative Ω_j implies a negative response to habitat loss. Species are ranked by Ω_j. Error bars are 95% confidence intervals on Ω_j, calculated conservatively (16). **(B)** Average Ω_j of wind-dispersed species ($n = 12$) and animal-dispersed species ($n = 22$). Error bars are 95% confidence intervals on the mean Ω_j for each group.
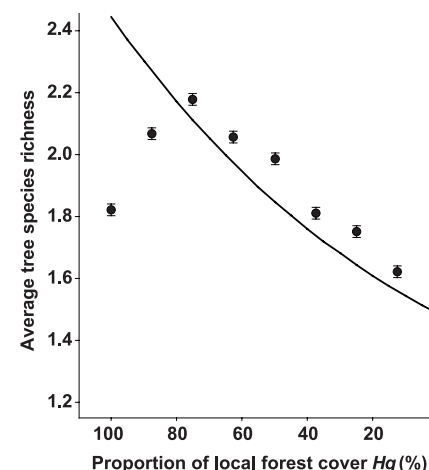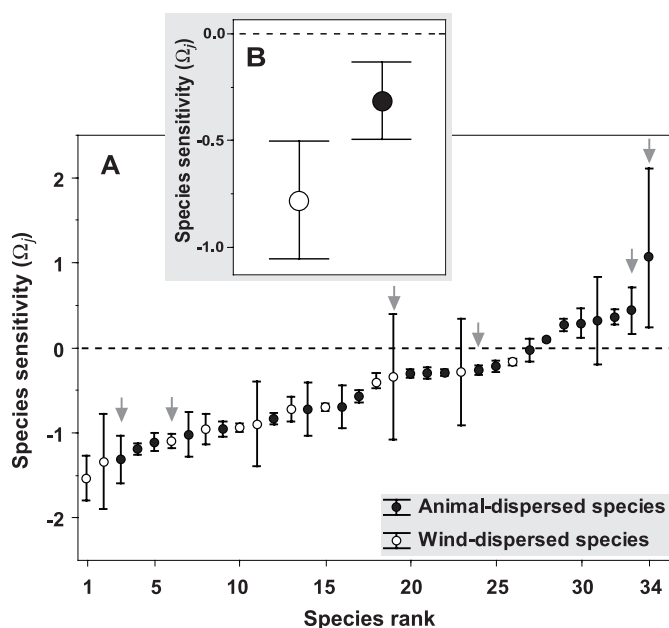
Fig. 3. Tree species richness (average number of species occurring in a 25-m-radius circular plot) versus local forest cover H_q: observed (points) and from the logistic regression (line, calculated by summing the predicted probability of occurrence over the 34 species). Error bars are standard errors on the observed average for each level of H_q. The observed richness is positively correlated with H_q; that is, negatively correlated with forest loss (Spearman rank test, $\rho_s = 0.73$, $P = 0.038$). Species richness was calculated by referring to data for the 34 study species only.

European temperate forests (such as to tropical forests or to plant species other than trees). Moreover, if seed-dispersing animals are as crucial to the persistence of plants as this and other studies suggest (*28*, *29*), then the combination of habitat loss with direct and indirect removal of animals, to which many of the world's most diverse forests are subject, is likely to have more drastic effects than either perturbation alone. In these circumstances, animal-dispersed species might be more, not less, sensitive to habitat loss. This points to the maintenance of the network of plant-animal interactions as a cornerstone of conservation policy and to the need for more studies of species responses to habitat loss.

References and Notes

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Supporting Online Material for

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SUPPORTING ONLINE MATERIAL

Material and Methods

Region and dataset

The Iberian Peninsula spans from 36ºN to 43.5ºN and 9ºW to 3ºE, housing a large altitudinal gradient (sea level – 3500 meters); it comprises a mosaic of different climates (from semiarid to Mediterranean and humid Atlantic climates), and a number of quite different landscapes such as natural and managed forests, savannas, shrublands, grasslands, agriculture fields and urban areas. This region is located in a known biodiversity hot-spot (Mediterranean basin; *S1*). The Second Spanish Forest Inventory (IFN2, 1986-1996; ICONA 1995) is an extensive dataset consisting of 91,200 circular sample plots distributed across the currently-wooded surface of peninsular Spain, with an approximate density of one site per 1 Km^2. Each sampling site was located in the field using pre-generated UTM coordinates, and was sampled for many attributes, including presence/absence of several species of trees; stem diameter and height for trees of some species; altitude and slope. The IFN2 assigns a code for each tree species or group of species. Because codes related to multiple species do not distinguish individual species, only species with specific codes (codes referring to single species) were considered here. For the purpose of this study, we extracted the presence/absence data for 34 canopy-dominant tree species commonly found in Mediterranean and Atlantic forests of the study region (where presence or absence means presence or absence of a living tree of the species within a circular survey plot with 25 m radius). These species comprise a wide range of niches and biological traits (Table *S1*). Tree species with a main distinctive dispersal mode (wind / animal) were studied (*S2- 4*); species with mixed dispersal (wind + animal) were excluded from the analyses (i.e. *Pinus pinea*). Sampling sites with georreferencing mismatches and errors in the climate variable estimations were excluded. This left 89,365 sites and 34 species in the analysis.

The IFN2 includes 6 exotic species that naturally invaded forest systems in the study region. These species were considered in our analyses provided they had a clear distinctive dispersal mode. In addition, part of the distribution area of some exotic species surveyed in the IFN2 consists of plantations. But importantly, considering only native species, or both native and exotic species, had no material impact on conclusions (Figure S2).

Since the survey sites were only placed in 1x1 km grid-cells currently occupied by forest (defined as dominated by woody plants), an estimate of the proportion of forest habitat cover could be estimated as *FS/NoFS*, where *FS* (Forest Sites) is the number of surveyed sites (those where trees are present) in a given neighbourhood around a focal site, and *NoFS* (Non-Forest Sites) is the number of sites within that neighbourhood that were not surveyed (those not dominated by woody plants). Thus, we generated a continuous 1 Km resolution grid covering peninsular Spain to which the survey network was superimposed. Points in this grid that matched the survey sites were defined as forest sites; conversely, non-matching points were defined as non-forest sites. 'Forest cover' measures the continuity of forest by looking at neighbour sites (corresponding to areas of 8Km^2 around each site), giving an estimation of habitat cover surface ranging from 0% to 100%.

Model

51   To avoid linearity assumptions in the relationship between species' occurrence
52   probability (which is bounded 0-1) and the proportion of forest cover, we fitted logistic
53   regression models to estimate the probability of occurrence of each species in each site.

54

55
$$P(j, H_q) = \frac{e^{-K(j,H_q)}}{1 + e^{-K(j,H_q)}} \qquad\qquad \text{(eq S1)}$$

56

57
$$K(j, H_q) = M_j + C_j(1 - H_q) \qquad\qquad \text{(eq S2)}$$

58

59   Where $P(j, H_q)$ is the probability of finding species j in site q with local habitat cover
60   H_q, and M_j and C_j are species-specific parameters. The logistic regression returned
61   maximum likelihood estimates (MLE) for M_j and C_j, together with 95% intervals on
62   each parameter. For each species, the regression was performed using 89,365 H_q, $O_{j,q}$
63   pairs, where $O_{j,q}$ is the observed occupancy of species j in plot q (1 present, 0 absent).
64   The regression treated these data as independent, and so did not include the potential
65   effects of spatial autocorrelation, i.e. a tendency for plots close to each other to have
66   similar H_q, and / or $O_{j,q}$, values. In reality this autocorrelation reduces the effective
67   sample size of the regression, compared to that carried out here, by a fraction that is
68   currently unknown; although the effects of this are unlikely to be substantial here
69   because the (uncorrected) sample size is so large (89,365 for each species) compared to
70   the number of parameters to be estimated (2 for each species), and because the standard
71   deviation on parameter estimates shows only a square-root relationship to sample size.
72   Moreover, we used a highly conservative method to estimate the confidence intervals on
73   Ω_j (see below): this method is likely to have increased the confidence intervals by a
74   larger fraction than would the inclusion of the effects of autocorrelation.

75

76   For each species j, the parameter estimates corresponded to a continuous
77   function relating habitat cover and occurrence, and the uncertainty in parameters
78   corresponded to uncertainty in this function. To facilitate comparison among species,
79   we needed, from these continuous functions, to generate a scalar metric measuring
80   sensitivity to forest loss. We chose to use the proportional reduction in occurrence
81   caused by a reduction in forest cover from a high value (0.75) to zero:

82

83
$$\Omega_j = \ln\{P(j, H_q = 0) / P(j, H_q = 0.75)\} \qquad\qquad \text{(eq S3)}$$

84

85   Where $P(j, H_q)$ is calculated using the MLE estimates for the parameters M_j and C_j.

86   Note that a negative Ω_j implies a negative response of occurrence to reduced local
87   forest cover. Also, the logarithmic scale makes the relationship between Ω_j and the
88   proportional reduction in occurrence non-linear: for example, $\Omega_j = -2$ implies an 86%
89   reduction in occurrence, -1 implies 63% reduction, -0.5 implies 40% reduction, and +1
90   implies a 170% increase in occurrence.
91   To produce confidence intervals on Ω_j for each species, we used the following
92   simple error propagation approach: (1) extract, for M_j and C_j, the lower and upper 95%
93   confidence interval; (2) generate the four combinations of M_j and C_j that can be given
94   by combining these lower and upper estimates; (3) apply eq. S3 using $P(j, H_q)$

95   calculated from each of the four combinations; (4) report the highest and lowest Ω_j
96   values from the four calculated values. This method allows for independent variation in

97   M_j and C_j , and allows for both parameters to be simultaneously at the edge of their 5%
98   confidence interval. It is therefore a conservative method compared to a formal error
99   propagation: i.e., the reported intervals are larger than those that would have been
100   produced from formal error propagation.
101
102   *Permutation Test*
103   We ranked species Ω_j (species 1, species2,…, species 34), so the average position of an
104   animal- and wind-dispersed species in that list could be obtained. The difference
105   between the average position numbers was used as a test statistic to evaluate the
106   probability of obtaining, by chance, the observed difference in average rank between
107   wind- and animal-dispersed species. 10,000 sets of random species ranks were
108   produced, where each species was assigned a rank (1-34) at random. For each of these
109   10,000 sets, the difference between the average rank for animal vs wind-dispersed
110   species was calculated. This yielded a frequency distribution of the difference between
111   the groups, corresponding to a null hypothesis of no true difference in Ω_j between the
112   groups. We then noted where the observed value of the difference between the groups
113   lay in the frequency distribution, which corresponded to the probability of obtaining the
114   observed difference without a true difference between the groups.
115
116   *Phylogenetic analyses*
117   The amount of phylogenetic signal in Ω_j was quantified with Phylogenetic eigenVector
118   Regression (PVR; *S5*). This method tests whether species traits (in this case, Ω_j) are
119   significantly associated with phylogeny, partitioning the phenotypic variation in a
120   certain trait into phylogenetic (among lineages, **P**) and nonphylogenetic or specific
121   (within species, **S**) components, based on multivariate analysis ($\Omega_j = \mathbf{P} + \mathbf{S}$). The idea is
122   that phylogeny can be expressed as a set of orthogonal vectors obtained by an
123   eigenanalysis of a phylogenetic distance matrix. These vectors can then be used as
124   predictors of Ω_j in any form of linear or non-linear modelling.
125
126   The starting point is the construction of the phylogenetic distance matrix **D**, for
127   which we used the phylogeny for existing seed-plant families hosted in the Webpage of
128   the Missouri Botanical Garden, and that has been compiled and is being continuously
129   updated by P.F. Stevens using different sources (the phylogeny and details about its
130   construction are available at: www.mobot.org/MOBOT/research/APweb/) (accessed,
131   December 2007). For each possible pair of species in **D**, we considered that their
132   phylogenetic distance was the minimum number of nodes connecting them in the
133   phylogeny. Then, we used principal coordinates analysis (PCoA) to extract eigenvalues
134   and eigenvectors from this matrix after performing a double-center transformation (the
135   row and column means were substracted from each element and the grand mean was
136   added, after transforming original distances into $-0.5D_{ij}^2$). We used the coefficients of
137   the eigenvectors of **D** as the coordinates of the species in the reduced multivariate space
138   expressing variation among them in the hyperspace defined by phylogenetic relatedness
139   (numerical details about PVR calculations are provided in *S5*).
140
141   The first three eigenvectors from the PVR explained most of the phylogenetic
142   structure existing in **D** (Table S2), and were identified as capturing meaningful
143   phylogenetic relationships by a scree-plot + 1 procedure, a conservative method of
144   eigenvector selection (*S6*). Accordingly, to test whether there were differences between
145   wind- and animal-dispersed species in terms of Ω_j that are independent of phylogenetic

146   inertia, we included these eigenvectors as covariables in an analysis of covariance
147   (ANCOVA) in which the response and explanatory variables were Ω_j and dispersal
148   mode, respectively. The two groups (animal dispersed, wind dispersed) showed
149   significantly different mean Ω_j values, either when considering all 34 species, or when
150   analyzing only the 28 species that are native to the study region (Table S3a, b).
151   Therefore, we concluded that the difference in average Ω_j between wind-dispersed and
152   animal-dispersed species was not caused by phylogenetic autocorrelation.
153
154   *Multicollinearity*
155   In addition to the effects of habitat cover, each tree species is likely to be affected by the
156   gradients in climate, soil and fire frequency occurring in the study region, raising the
157   possibility that apparent responses to habitat cover (and any apparent differences in
158   response among species) are driven by environmental factors correlated with habitat
159   cover (multicollinearity). This problem occurs in any study of species occurrence vs.
160   habitat cover, except in the rare cases where the habitat gradient has been exposed
161   experimentally. To assess the sensitivity of our conclusions to this problem, we first
162   extracted, for each survey site, a set of 18 climatic, topographic and soil variables (listed
163   in Table S4) which might be critical to plant physiological function and survival in the
164   Mediterranean and Atlantic systems. Principal component analysis showed no
165   multicollinearity between forest cover and these variables (Table S4). This showed that,
166   at the scale of peninsular Spain, forest cover varies almost independently of climate,
167   topography, soil, and major perturbation events (Figure S3), making mutlicollineariy an
168   unlikely explanation of the results.
169   As a additional check, we performed combined species-specific logistic regression that
170   included included environmental variables (the axis scores from the PCA described
171   above) and forest cover, in order to extract estimates for Ω_j controlled for
172   environmental factors (Fig. S3). The pattern of interspecific variation in Ω_j was not
173   qualitatively altered by including environmental variables (compare Fig S3 with Fig. 2),
174   and the difference in Ω_j between animal- and wind-dispersed species remained
175   statistically significant (permutation test: $p < 0.005$).

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189

190   Table S1.

191

Species	Dispersal mode	M_j	C_j	Ω_j
Populus tremula	Wind	4.572	2.054	-1.53
Picea abies	Wind	6.202	1.78	-1.33
Quercus borealis	Animal	4.83	1.763	-1.32
Fagus sylvatica	Animal	1.821	1.728	-1.22
Phyllirea latifolia	Animal	2.977	1.523	-1.12
Pinus radiata	Wind	2.434	1.542	-1.18
Quercus canariensis	Animal	4.873	1.363	-1.02
Pinus sylvestris	Wind	1.099	1.498	-0.99
Quercus petraea	Animal	2.696	1.325	-0.96
Abies alba	Wind	4.108	1.288	-0.96
Populus alba	Wind	7.455	1.198	-0.90
Ilex aquifolium	Animal	2.202	1.192	-0.85
Pinus pinaster	Wind	0.918	1.175	-0.74
Pinus uncinata	Wind	3.866	0.981	-0.73
Taxus baccata	Animal	5.458	0.967	-0.72
Malus sylvestris	Animal	5.019	0.929	-0.69
Corylus avellana	Animal	2.578	0.804	-0.58
Pinus nigra	Wind	1.806	0.643	-0.43
Ailanthus altissima	Wind	7.41	0.456	-0.34
Quercus robur	Animal	1.827	0.456	-0.31
Quercus faginea	Animal	1.448	0.471	-0.30
Quercus suber	Animal	2.581	0.419	-0.30
Abies pinsapo	Wind	7.129	0.376	-0.28
Castanea sativa	Animal	2.337	0.383	-0.27
Rhamnus alaternus	Animal	2.766	0.307	-0.22
Pinus halepensis	Wind	1.516	0.274	-0.17
Frangula alnus	Animal	4.251	0.037	-0.03
Quercus ilex	Animal	0.51	-0.202	0.09
Olea europaea	Animal	3.293	-0.375	0.27
Ceratonia siliqua	Animal	4.954	-0.39	0.29
Celtis australis	Animal	7.141	-0.423	0.32
Juniperus thurifera	Animal	3.603	-0.501	0.36
Juglans regia	Animal	5.947	-0.587	0.44
Rhus coriaria	Animal	9.959	-1.722	1.29

192

193

194   List of tree species included in the analysis. Dispersal mode is indicated. Parameter
195   estimates of the logistic regression models (M_j, C_j) are provided for each species,
196   together with Ω_j calculated at the MLE estimates for M_j and C_j. Species are given in
197   rank order of Ω_j (a negative Ω_j implies a negative response to forest loss). Exotic
198   species are highlighted in bold.

199 Table S2.
200
201

Eigenvector i	Eigenvalue	R^2	Cumulative R^2
1	5993.082637	79.3794	79.3794
2	678.8968592	8.9921	88.3715
3	310.1979661	4.1086	92.4801
4	210.6672177	2.7903	95.2705
5	94.52496831	1.252	96.5225
6	79.52899032	1.0534	97.5758
7	72.2764274	0.9573	98.5332
8	55.34903771	0.7331	99.2663
9	49.02118729	0.6493	99.9156
10	40.93208026	0.5422	100
11	30.89333637	0.4092	100
12	18	0.2384	100
13	1.69103547	0.0224	100
14	0.5	0.0066	100
15	0.5	0.0066	100
16	0.5	0.0066	100
17	0.5	0.0066	100
18	0.5	0.0066	100
19	0.5	0.0066	100
20	0.5	0.0066	100
21	0.5	0.0066	100
22	0.5	0.0066	100
23	0.5	0.0066	100
24	0.5	0.0066	100
25	0.5	0.0066	100
26	0.5	0.0066	100
27	0.5	0.0066	100
28	0.5	0.0066	100
29	0.5	0.0066	100
30	0.0	0.0	100
31	-3.48786972	-0.0462	100
32	-4.87072252	-0.0645	100
33	-25.88538769	-0.3429	100
34	-60.89671049	-0.8066	100

202
203
204 Eigenvectors generated by the eigenanalysis of the phylogenetic distance matrix D
205 among tree species. The first three eigenvectors explained 92.5% of the phylogenetic
206 signal and are emphasized in grey. These eigenvectors were identified by the scree-plot
207 + 1 method as the most meaningful ones (6) and used as covariables in ANCOVA
208 analysis.

209 Table S3.
210
211 **A**

N = 34	SS	df	MS	F	p
Intercept	17.39162	1	17.39162	31.21513	0.000005
Eigenvector 1	0.50904	1	0.50904	0.91365	0.347048
Eigenvector 2	0.00987	1	0.00987	0.01771	0.895042
Eigenvector 3	3.18965	1	3.18965	5.72490	0.023425
Dispersal	4.32290	1	4.32290	**7.75890**	**0.009321**
Error	16.15745	29	0.55715		

212
213
214 **B**

N = 28	SS	df	MS	F	p
Intercept	16.59317	1	16.59317	38.70054	0.000002
Eigenvector 1	0.86676	1	0.86676	2.02157	0.168498
Eigenvector 2	0.02190	1	0.02190	0.05107	0.823208
Eigenvector 3	0.81040	1	0.81040	1.89012	0.182435
Dispersal	3.15059	1	3.15059	**7.34817**	**0.012471**
Error	9.86144	23	0.42876		

215
216
217 Phylogenetically-controlled analysis of covariance (ANCOVA) on Ω_j. The first 3
218 eigenvectors generated by the eigenanalysis of the phylogenetic distance matrix were
219 used as covariates. (**A**) Results for native and exotic species (N = 34). (**B**) Results for
220 native species only (N = 28). (SS = Sum of squares; df = Degrees of freedom; MS =
221 Mean of squares).

222   Table S4.
223
224

Variables	Factor 1	Factor 2	Factor 3	Factor 4
Annual Precipitation	**0.746779**	-0.552574	0.116271	0.052051
Spring Precipitation	**0.797281**	-0.470433	0.117155	0.049064
Summer Precipitation	**0.844888**	-0.027751	0.022345	0.007831
Potential Evapotranspiration (Thornwaite's formula)	**-0.661225**	-0.327717	-0.049185	0.075896
Annual Hydric Index	-0.285126	-0.421425	0.113343	0.375789
Drougth Length	**-0.681720**	0.238016	-0.064637	-0.520283
Drougth Intensity	-0.541502	0.159017	-0.038245	**-0.647180**
Mean Annual Temperature	**-0.826864**	-0.502501	-0.139506	0.055236
Potential Evapotranspiration (Jensen & Haise formula)	**-0.934179**	-0.231905	-0.150795	0.109854
Annual Radiation	**-0.819787**	0.301444	-0.143696	0.176955
Mean Temperature Warmest Month	**-0.927510**	-0.084287	-0.170067	0.194822
Mean Temperature Coldest Month	-0.573380	**-0.756809**	-0.099752	-0.073076
Termal Oscillation	-0.535972	**0.650842**	-0.103618	0.304678
Altitude	0.362111	**0.805512**	0.018220	0.072400
Aspect	-0.100998	0.008870	-0.106684	0.163563
Slope	0.405246	0.160215	-0.131351	0.095624
Soil	0.049918	-0.182366	0.177293	-0.434954
Annual Fire Rate	0.158481	-0.553708	0.115610	-0.112220
Forest Cover (H_q)	-0.301332	0.028006	**0.848316**	0.081156

225
226
227   List of environmental variables included in the principal component analysis (PCA).
228   The list includes climatic, topographic, soil and disturbance variables that the authors
229   considered might be important to tree physiological function and survival in
230   Mediterranean and Atlantic ecosystems. Each variable was estimated for each survey
231   plot. The PCA shows that local forest habitat cover (H_q) is an independent factor not
232   related to climate, topography, soil or fire disturbance (factor 3).

233   Figure S1. Sensitivity of tree species to reductions in forest cover (Ω_j) as a function of
234   seed size. Species are ranked by Ω_j. Bubble size is proportional to seed weight. White
235   symbols are animal-dispersed species; gray symbols are wind-dispersed species. Only
236   23 species are shown, because seed weights were not available for the other species.
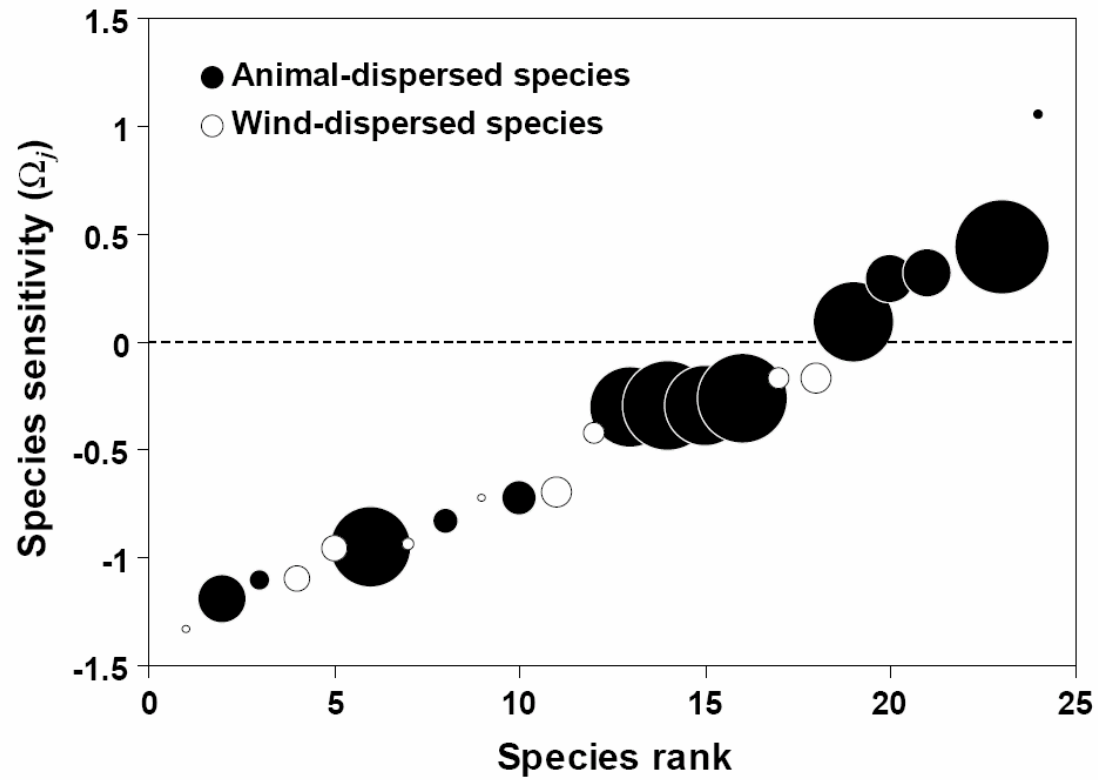237
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Figure S2. (**A**) Sensitivity of tree species to forest habitat loss Ω_j (at 1 Km) for native species only (N=28). Results from permutation test for average difference between animal- and wind-dispersed species: p<0.05. (**B**) Average Ω_j for native wind-dispersed species (n=10) and native animal-dispersed species (n=18). Error bars are 95% confidence intervals on the mean Ω_j for each group.
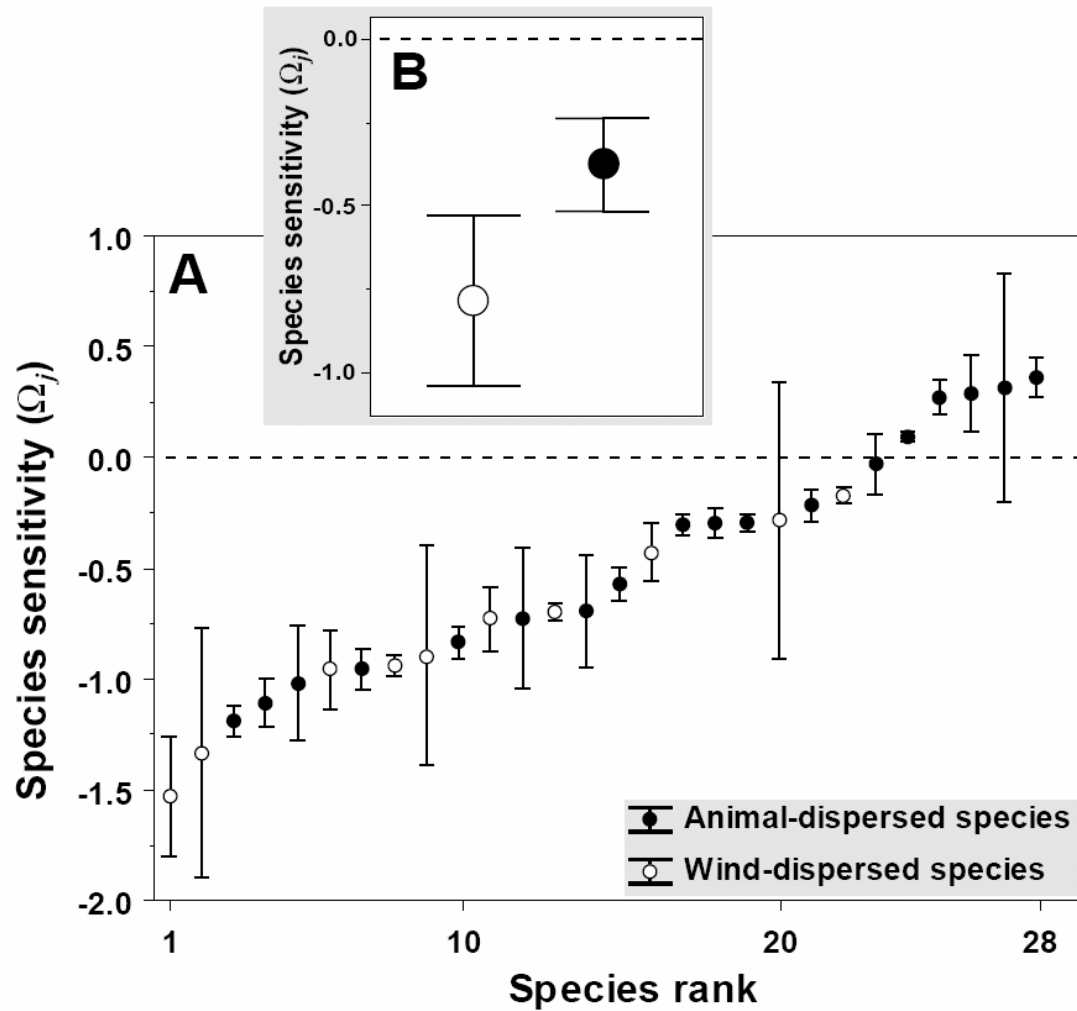
Figure S3. (**A**) Sensitivity of tree species to reductions in forest cover Ω_j after controlling for environmental factors. Results from permutation test for average difference between animal- and wind-dispersed species: $p<0.05$. (**B**) Average Ω_j of wind-dispersed species (n=12) and animal-dispersed species (n=22) after controlling for environmental factors. Error bars are 95% confidence intervals on the mean Ω_j for each group. Gray arrows indicate non-native species.