

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

Daniel Montoya,<sup>1\*</sup> Miguel A. Zavala,<sup>1,2</sup> Miguel A. Rodríguez,<sup>1</sup> Drew W. Purves<sup>3</sup>

<sup>1</sup>Departamento de Ecología, Universidad de Alcalá, 28871 Alcalá de Henares, Madrid, Spain. <sup>2</sup>Centro de Investigación Forestal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Carretera de la Coruña km 7,5 28040 Madrid, Spain.

<sup>3</sup>Microsoft Research Cambridge, 7 J. J. Thomson Avenue, Cambridge CB3 0FB, UK.

\*To whom correspondence should be addressed. E-mail: daniel.montoya@alu.uah.es

**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  $\Omega_j$ , 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  $\Omega_j$  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  $\Omega_j$ . 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  $\Omega_j$  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  $\Omega_j$ . For species with statistically significant negative  $\Omega_j$  (those with confidence intervals not including zero),  $\Omega_j$  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 dispersal). 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  $\Omega_j$ : 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  $\Omega_j$  that can be attributed to phylogenetic relationships is low ( $R^2 = 0.11$ ). Moreover, an analysis of covariance (ANCOVA) including  $\Omega_j$  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 phylogenetic structure in the data) as covariables still found significant differences in  $\Omega_j$  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 multicollinearity 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  $\Omega_j$  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  $\Omega_j$  (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 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

1. R. V. Solé, J. Bascompte, *Self Organization in Complex Ecosystems* (Princeton Univ. Press, Princeton, NJ, 2007).
2. L. Fahrig, *Biol. Conserv.* **100**, 65 (2001).
3. I. Hanski, *Metapopulation Ecology* (Oxford Univ. Press, Oxford, 1999).
4. M. Rees, R. Condit, M. Crawley, S. Pacala, S. Tilman, *Science* **293**, 650 (2001).
5. E. I. Damschen, N. M. Haddad, J. L. Orrock, J. J. Tewksbury, D. J. Levey, *Science* **313**, 1284 (2006).
6. B. C.-L. Chetkiewicz, C. C. St. Clair, M. S. Boyce, *Annu. Rev. Ecol. Syst.* **37**, 317 (2006).
7. L. Conrath, T. J. Roper, C. D. Thomas, *Oikos* **95**, 416 (2001).
8. G. Ferraz *et al.*, *Science* **315**, 238 (2007).
9. I. Hanski, M. Kuussaari, M. Nieminen, *Ecology* **75**, 747 (1994).
10. *Segundo Inventario Forestal Nacional* (Ministerio de Agricultura, Pesca y Alimentación, Madrid, Spain, 1995).
11. Information on materials and methods is available as supporting material on *Science Online*.

12. F. González Manzanque, *Bosques Ibéricos: Una Interpretación Geobotánica* (Planeta, Barcelona, Spain, 2005).
13. J. Bascompte, M. A. Rodríguez, *Ecol. Lett.* **4**, 417 (2001).
14. L. Fahrig, *Annu. Rev. Ecol. Syst.* **34**, 487 (2003).
15. D. W. Purves, J. Dushoff, *J. Ecol.* **93**, 658 (2005).
16. I. Hanski, *Nature* **396**, 41 (1998).
17. D. W. Purves, M. A. Zavala, K. Ogle, F. Prieto, J. M. Rey-Benayas, *Ecol. Monogr.* **77**, 77 (2007).
18. K. Johst, R. Brandl, S. Eber, *Oikos* **98**, 263 (2002).
19. J. M. Gómez, *Ecography* **26**, 573 (2003).
20. B. McEuen, L. M. Curran, *Ecology* **85**, 507 (2004).
21. C. C. Smith, S. D. Fretwell, *Am. Nat.* **108**, 499 (1974).
22. D. Sánchez-Gomez, F. Valladares, M. A. Zavala, *New Phytol.* **170**, 795 (2006).
23. A. Purvis, P.-M. Agapow, J. L. Gittleman, G. M. Mace, *Science* **288**, 328 (2000).
24. O. Spiegel, R. Nathan, *Ecol. Lett.* **10**, 718 (2007).
25. P. Jordano, C. García, J. A. Godoy, J. L. García-Castaño, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 3278 (2007).
26. S. I. Higgins, R. Nathan, M. L. Cain, *Ecology* **84**, 1945 (2003).
27. C. Restrepo, N. Gómez, S. Heredia, *Ecology* **80**, 668 (1999).
28. J. M. Montoya, S. L. Pimm, R. V. Solé, *Nature* **442**, 259 (2006).
29. J. Bascompte, P. Jordano, *Annu. Rev. Ecol. Syst.* **38**, 567 (2007).
30. We thank the Ministerio de Medio Ambiente, Spain; R. Vallejo and J. A. Villanueva for help with IFN2 data; S. Pacala for hospitality during data preparation; J. A. F. Diniz-Filho, L. M. Bini, and M. A. Olalla-Tárraga for help with phylogenetic analyses; and B. A. Hawkins, J. M. Montoya, D. Coomes, and J.-C. Svenning for comments on manuscripts. D.M. was supported by the Spanish Ministry for Education and Science (fellowship AP2004-0075). M.A.R. and M.A.Z. were supported by the Spanish Ministry for Education and Science (grants CGL2006-03000/BOS and CGL2005-05830-C03-01/BOS, respectively).

## Supporting Online Material

[www.sciencemag.org/cgi/content/full/1158404/DC1](http://www.sciencemag.org/cgi/content/full/1158404/DC1)

Materials and Methods

Tables S1 to S4

Figs. S1 to S3

References

28 March 2008; accepted 15 May 2008

Published online 5 June 2008; 10.1126/science.1158404

Include this information when citing this paper.

**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.

**Fig. 2. (A)** Sensitivity of 34 Spanish tree species to reduction in local forest cover ( $\Omega_j$ ), 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.  $\Omega_j$  is defined as the natural logarithm of the ratio of occurrence probabilities at 0 and 75% cover. Negative  $\Omega_j$  implies a negative response to habitat loss. Species are ranked by  $\Omega_j$ . Error bars are 95% confidence intervals on  $\Omega_j$ , calculated conservatively (16). **(B)** Average  $\Omega_j$  of wind-dispersed species ( $n = 12$ ) and animal-dispersed species ( $n = 22$ ). Error bars are 95% confidence intervals on the mean  $\Omega_j$  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.





