UNIVERSIDAD DE ALCALÁ
Departamento de Ecología

Programa de Doctorado Cambio Global y Desarrollo Sostenible

Space and Species: On the Relationships between Spatial Processes and Diversity Patterns of Trees

Memoria presentada para optar al grado de
Doctor por la Universidad de Alcalá

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Alcalá de Henares, Noviembre 2009

Universidad de Alcalá
DEPARTAMENTO DE ECOLOGÍA

Miguel Ángel Rodríguez Fernández, Profesor Titular de Ecología de la Universidad de Alcalá, y como co-director de la Tesis Doctoral,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado **"Space and Species: On the Relationships between Spatial Processes and Diversity Patterns of Trees"**, ha sido realizado bajo su dirección por D. Daniel Montoya Terán dentro del Programa de Doctorado 'Cambio Global y Desarrollo sostenible', adscrito al Departamento de Ecología de la Universidad de Alcalá. Esta tesis reúne los requisitos propios de este tipo de trabajo: rigor científico, aportaciones novedosas y aplicación de una metodología adecuada. Por lo tanto, doy mi Visto Bueno a la presentación de dicha Tesis Doctoral.

Alcalá de Henares, a 23 de Septiembre de dos mil nueve,

Dr. Miguel Ángel Rodríguez Fernández

Universidad de Alcalá

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Julio Camargo Benjumeda, Profesor Titular de Ecología de la Universidad de Alcalá y Director del Departamento de Ecología,

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Alcalá de Henares, a 23 de Septiembre de dos mil nueve,

Dr. Julio Camargo Benjumeda

A mis padres

Agradecimientos

Estoy caminando…Llevo tanto tiempo haciéndolo que casi no recuerdo cómo he comenzado. Ya es tarde para dar la vuelta y retroceder. Además, me parece ver un oasis al fondo, no muy lejos…¿Será el final de este viaje? ¿O solamente un pequeño descanso en una ruta más larga? Son las peores horas del día para caminar, así que decido sentarme a reflexionar. No puedo evitar pensar en cómo empezó todo ésto…

Recuerdo haber terminado la carrera y comenzar un periodo lleno de incertidumbre en el que tuve la sensación de que todo lo aprendido habita en el olvido. Durante un año estuve dándole vueltas a la cabeza, dedicando el tiempo a cosas lo más alejadas posibles de mi formación, hasta que al final llegué a una intersección de caminos. Hay que tomar una decisión…La pregunta es: ¿qué quiero hacer, con quien y dónde quiero hacerlo? Este último detalle, dónde hacer la tesis, es lo más importante para mi. En Madrid no hay costa y quería irme a un lugar junto al mar…Hoy estoy en Alcalá de Henares. Fracaso absoluto. ¿Cómo ocurrió todo esto?

¡Ya lo sé! En la intersección había un hombre misterioso que respondía al nombre de Miguel Ángel Rodríguez (MAR). Él tiene la culpa de que no pueda contemplar el mar cada mañana. Me reuní con él una mañana de septiembre. Entré en su despacho con toda mi inocencia y mis ideas sobre fragmentación. "Interesante, pero la mayoría las preguntas que planteas han sido ya respondidas". Segundo fracaso. Aquella mañana hablamos durante una hora y media. No sé explicar qué ocurrió, pero a pesar de mi decepción, MAR reanimó el gusanillo de la ciencia en mí (después de agitarlo y aplastarlo). Unos días y varias conversaciones después (algunas sobre la genética familiar), MAR me hace una oferta que no podré rechazar. "Si quieres más información sigue el sendero de la izquierda. Un poco más adelante encontrarás a otro hombre que te dará más pistas. Obedece al nombre de Zavala, Miguel Ángel Zavala". Así comenzó todo…

Sentado al borde del camino pienso que, desde aquel momento hasta ahora, MAR ha sido un apoyo muy fuerte y continuo en los últimos cinco años. He aprendido mucho con él, desde aspectos científicos hasta aspectos prácticos de la investigación. A pesar de no haber coincidido en California (estoy convencido de que lo pasaríamos en grande), ha sido genial participar de tu intuición para generar ideas y de tu capacidad para dar una vuelta de tuerca más a cada una de ellas. Ojala me sigas contagiando tu entusiasmo por la investigación; que se repitan los almuerzos en el Grill y las discusiones científicas aliñadas con zumo de cebada en compañía de Jordi, Brad o Alexandre en el irlandés de Alcalá.

Pero he de ser sincero: hay otro Miguel Ángel en mi vida. Entro en su despacho de Alcalá por primera vez y le digo que el hombre de la intersección me ha dicho que será uno de mis jefes. Ahora sonrío recordando lo inocente que fui…Ese señor, Miguel Ángel Zavala (MAZ), me da una charla sobre lo que supone una tesis, la importancia de plantearse una pregunta, y el compromiso que requiere. Confieso que me asusto un poco. No dejaré de sospechar durante los primeros meses que MAZ se esconde tras los árboles que rodean el camino y que me pone a prueba para evaluar mi capacidad para desarrollar una tesis. Durante este tiempo no hago otra cosa que encerrarme a leer artículos y tratar de buscar respuestas a sus preguntas. A pesar de esta ligera tensión, cada día con MAZ aprendo una cosa nueva sobre la ciencia. Gracias por inculcarme la idea de buscar el equilibrio entre la teoría y lo experimental. Ojala se repitan esas charlas junto al fuego, las salidas de campo, las conversaciones filosóficas para comer (a veces junto a Nico) y las charlas telefónicas surrealistas.

La mayor parte del recorrido me he sentido arropado por el departamento de Ecología de la Universidad de Alcalá. Ha sido una zona de avituallamiento constante (y no lo digo por Ruzafa). Estoy muy agradecido a cada un@ de sus integrantes, en especial a Ana (mi salvadora en muchos momentos), Nico y el PEHE. Alberto, Lucía, Mariano, Luises (Cayuela y Merino), Edu, Itzi, Óscar, Mycky, Marta, Fabio, Maria José, Quique, Virginia, Bárbara, Carlota, Jorge, Nacho y toda la comunidad latina…compañer@s y amig@s, gracias por crear un ambiente tan relajado y sano de trabajo. Me he sentido como en casa y he aprendido mucho de vosotr@s. Gracias a Edu, Micky, Fabio, Marta, Itzi y Nacho por compartir ideas y charlas científicas. Aunque no me he dejado ver mucho por el departamento en los últimos tiempos (sabéis que la tesis es una amante muy celosa), os adoro y os deseo lo mejor a tod@s.

Estos años han servido para construir una red de colaboraciones muy estimulante. Arriba en la colina, Brad, *the cowboy*, representa el equilibrio perfecto entre entusiasmo y es-

cepticismo tan esencial para la ciencia; gracias por las discusiones en California, por los viajes en porche descapotable de Tijuana a Beverly Hills y por tus increíblemente inspiradoras ideas. Drew está sentado en esa curva, con una capacidad sobrehumana para hacer que el ejercicio de modelización parezca sencillo; gracias por sacar tiempo de donde no lo hay; a ti te debo muchos de mis conocimientos en modelos de simulación; gracias por tu inspiración y generosidad en Princeton y Cambridge.

Por el camino he ido encontrando muchas personas y recogiendo un poco de cada una de ellas. La gente del Queen Mary College de Londres (Guy, Gabriel, Julia, etc) y de la universidad de Princeton (¡¡Fede!!, Stephen Pacala, Jeremy Lichstein, Robert Holt, Simon Levin) me han tratado muy bien y me han inculcado la buenísima costumbre de crear grupos de discusión en la universidad. También agradezco mucho los consejos y la simpatía de Alexandre, Luis Mauricio y Paulo. Ricard Solé y Sergi Valverde también han sido tremendamente inspiradores; gracias por mostrar tanto entusiasmo y compromiso conmigo, por vuestra cuerda locura, por aquella comida en la playa (yo pagué la última vez). Asimismo quiero agradecer el trato recibido por el INIA-CIFOR en el último año y medio y a la gente de los cursos de doctorado (Laura, Itziar, ¿por dónde andáis? ¡Apenas nos vemos desde la primera intersección!). Y, cómo no, a los becarios del Museo Nacional de Ciencias Naturales (María, Raúl, Pilar, Mariana, Sara,…) por el estímulo tan grande que he recibido y el grupo de discusión que hemos creado este año. Por último, agradecer la ayuda económica del Ministerio de Educación y Ciencia a través de la beca FPU AP 2004-0075.

Mi familia y amig@s 'no investigadores' han sido un apoyo constante e imprescindible. Mi familia, aumentada hace poco, siempre me ha ayudado y ha comprendido mis locuras, desde el momento en que comenzó todo, cuando no tenía un duro en el bolsillo, ni beca y me fui a vivir a Alcalá. Os debo mucho más de lo que imagináis. *Yous*, a ti te agradezco especialmente el apoyo y los consejos durante la tesis; ojala sigan repitiéndose los paseos por Lozoya discutiendo de Ecología y generando nuevas ideas para hacer juntos; mis viajes a Barcelona; las gambas y sardinas a la plancha en la terraza de casa; las 'buceadas'…¡Muchas gracias, brother!

Mis queridos amig@s del 'Bout', Peter…Habéis sido un elemento clave para ayudarme a desconectar y relajarme. Sois los masajistas y fisioterapeutas en cada etapa. Aunque a veces me he sentido perdido, me habéis ayudado mucho a sanear mi cabeza y poner los pies en la tierra. Lucas *el chino*, Silvia, Dani,…Me encanta charlar con vosotr@s de lo divino y lo humano, ¡a ver si nos reunimos de nuevo en aquel garaje! Tanja, gracias por ser tan optimista y risueña; Ricky, gracias por tu sonrisa y tu insistencia en aquél motel

de mala muerte de Nueva York; Maja y Gema, gracias por haberme querido tanto y por haber hecho sentirme especial. Amig@s del planeta Suecia: Maddeleine, Daniel, Charlie, Diana, Juan Pablo, Karin, Pär,….espero continuar nuestras charlas mixtas y seguir atiborrándonos de *kanelbullar* por muchos años. Y, más que a nadie, quiero dar las gracias a Vanessa por haber aparecido en mi vida y por haber compartido los momentos más bonitos de estos años; aunque eres una cabecita loca y me has hecho pasar noches muy malas, *jag har alltid dig i min hjärta*.

La tesis ha sido un periodo de amores no correspondidos, de noches en vela y de fiestas intempestivas; un tiempo compartido entre Madrid, Alcalá, California, Nueva York, Londres, Barcelona y Gotemburgo. Todas estas ciudades han sido el escenario donde he vivido, he aprendido y he amado; escenario de muchos paseos con la cabeza llena de pájaros, de miles de cafés y de cientos (de miles) cervezas; de acordes que ya no suenan tan bien…El sendero me ha llevado a perderme en todas ellas, a sentirme a veces solo y a veces acompañado. Tengo la sensación encontrada de haber pasado los mejores y los peores momentos de mi vida en estos años…Una sonrisa de melancolía se dibuja en mi cara. Quizá sea la silueta de una incipiente nostalgia por una época que termina...

Ya ha bajado el sol. Creo que es un buen momento para continuar caminando. Tengo las piernas cansadas, pero sé que falta poco. Me incorporo de un salto. Este último tramo lo recorro solo, pero…

¡Gracias a tod@s!

Índice

Resumen

A pesar de que el mundo es inevitablemente espacial, y que cada organismo es una entidad discreta que existe e interacciona con su entorno más inmediato, estas realidades han sido tradicionalmente ignoradas durante mucho tiempo por la mayoría de los ecólogos debido a que pueden complicar bastante tanto el trabajo de campo como el ejercicio de modelización. Sin embargo, varias líneas de investigación han destacado en las últimas dos décadas el papel potencialmente crítico del espacio a la hora de entender una gran diversidad de patrones biológicos, desarrollando un interés creciente por la Ecología Espacial.

En esta tesis nos centramos en el estudio de procesos que poseen una estructura espacial determinada y que afectan directamente a diversos patrones de diversidad observados en la naturaleza. En un primer capítulo, hemos estudiado un proceso espacial que ha tenido lugar a lo largo de un periodo de tiempo y que, por tanto, presenta una dinámica concreta en el tiempo (i.e. retirada de los glaciares en el post-Pleistoceno). De modo similar, la pérdida y fragmentación de hábitat influye de forma directa en los patrones de presencia/ausencia, riqueza, abundancia y extinción de especies, y ha sido uno de los ejes principales de esta tesis cuya exposición ocupa dos capítulos. Por último, hemos aplicado técnicas de análisis espacial para explorar el grado de validez de los denominados Modelos de Distribución de Especies a la hora de explicar la estructura espacial de las especies dentro de sus rangos de distribución, información que hemos empleado para deducir procesos espaciales determinantes de estos patrones.

El estudio de los procesos espaciales ha sido realizado para especies de árboles. Esta decisión se basa en dos motivos: (1) mantener la coherencia entre los diferentes capítulos de la tesis respecto al grupo biológico objeto de estudio, y (2) la mayor disponibilidad de datos y la mejor calidad de los mismos referentes a patrones de presencia/ausencia y riqueza de especies para árboles. Para el desarrollo de la tesis

hemos empleado datos empíricos de diferentes bases de datos y a diferentes escalas geográficas, sistemas de información geográfica, modelos matemáticos y de simulación, y técnicas de análisis espacial ampliamente utilizadas en Ecología Espacial.

A modo de resumen, la investigación contenida en esta tesis puede resumirse en tres grandes bloques:

1. Influencia de procesos espacio-temporales en patrones de riqueza a gran escala

Uno de los primeros y mejor documentados patrones en Ecología es la variación geográfica en la riqueza de especies a escalas espaciales amplias. En esta línea, el clima contemporáneo es ampliamente aceptado como el principal factor explicativo de los patrones de distribución de la riqueza de las especies a escalas espaciales desde lo regional hasta lo continental. Para especies vegetales, los modelos climáticos basados en dinámicas de agua - energía explican sustancialmente dichos patrones.

No obstante, las condiciones climáticas de hoy son estacionales, en el sentido que representan un patrón determinado en un periodo de tiempo concreto, y varían respecto a patrones climáticos anteriores. A este respecto, una cuestión fundamental es: ¿Hasta qué punto la evolución histórica del clima determina los patrones de diversidad observados en los ecosistemas forestales? Para resolver esta pregunta, digitalizamos una base de datos de árboles de Europa y Norte América (que representan la mayor parte de la superficie afectada por la última glaciación) a la que hemos asociado un conjunto amplio de variables climáticas contemporáneas y una variable que refleja la estructura espacial y temporal de la retirada glaciar.

Los resultados obtenidos muestran una huella global de la evolución climática reciente sobre la riqueza de las especies de árboles en Europa y Norte América (Hawkins et al. 2007, Montoya et al. 2007). Los resultados reflejan cómo un proceso espacial y definido en el tiempo influido directamente por un cambio climático (retirada glaciar post-Pleistocénica) afecta a la riqueza forestal actual. Por lo tanto, la inclusión de procesos espaciales (contemporáneos e históricos) es crítica para comprender los patrones de diversidad biológica actuales.

2. Pérdida y fragmentación de hábitat y riesgos de extinción de especies

La pérdida de hábitat y la fragmentación del paisaje, junto con el cambio climático, constituyen la primera causa de pérdida de biodiversidad del planeta. La riqueza de especies de un determinado ecosistema (i.e la suma total de las especies que coexisten en el ecosistema) disminuye con la pérdida de hábitat. Sin embargo, estudios previos afirman que, a pesar de que esta tendencia parece ser global, las especies individuales no manifiestan patrones de respuesta similares, sino más bien existe una variación inter-específica en la sensibilidad de las especies y su riesgo de extinción frente a la pérdida de hábitat. Esto ha llevado a numerosos ecólogos a plantearse la cuestión acerca de cuáles son los mecanismos que hay detrás de los patrones de respuesta de las especies a la pérdida de hábitat. En otras palabras, ¿por qué unas especies son más sensibles que otras a la pérdida de hábitat?

Por otro lado, estudios teóricos y empíricos sugieren que la relación entre el tamaño demográfico de una especie y la cantidad de hábitat disponible no es proporcional, y predicen un umbral de cantidad de hábitat por debajo del cual la población se extingue (i.e. umbral de extinción). Aunque el umbral de extinción es una consecuencia directa de la pérdida de hábitat *per se* (i.e. pérdida cuantitativa de hábitat), la teoría ecológica sugiere que la fragmentación del hábitat (i.e. configuración espacial del hábitat que permanece intacto) puede alterar la localización de este umbral reduciendo su aparición hacia niveles más bajos de pérdida de hábitat. En otras palabras, se espera que la extinción de especies pueda ocurrir antes en el gradiente de cobertura de hábitat cuando la fragmentación actúa. Sin embargo, poco se conoce acerca de esta predicción teórica y su validez requiere de un test empírico.

Utilizando una base de datos muy extensa sobre especies de árboles de la Península Ibérica intentamos resolver las dos cuestiones planteadas anteriormente. Nuestros resultados ponen de manifiesto respuestas no lineales de las especies de árboless a la falta de hábitat, en sintonía con otros estudios previos. Sin embargo, las especies responden de formas diferentes a la pérdida de hábitat forestal. A pesar de que los impactos sobre las especies son generalmente negativos (aunque se observan respuestas positivas en algunas especies), lo que se manifiesta en la correlación positiva detectada entre cantidad de hábitat y riqueza forestal, las especies individuales muestran intensidades de respuesta muy dispares. En general, se observa una mayor vulnerabilidad en las especies de dispersión anemócora frente a las especies de dispersión animal (Montoya et

al. 2008). No obstante, esta observación es cierta siempre y cuando los dispersores animales no hayan desaparecido del ecosistema forestal. En caso de extinción de los dispersores, las especies de dispersión animal serían más vulnerables a la pérdida de hábitat.

Nuestros resultados ponen de manifiesto que las interacciones de dispersión planta-animal aumentan la resistencia de las especies a la pérdida de hábitat. Estos resultados tienen implicaciones directas para la conservación, ya que es una primera aproximación que proporciona información sobre las especies cuya protección es más crítica. Estos resultados pueden ayudar a orientar las políticas de conservación no solamente hacia especies vulnerables concretas, sino hacia interacciones entre especies.

En segundo lugar, los resultados sobre los patrones de respuesta específicos a la pérdida y fragmentación de hábitat indican que la fragmentación puede distorsionar el umbral de extinción de las especies, aunque no siempre de la forma predicha por la teoría ecológica (Montoya et al. *En Revisión*). La fragmentación no tiene ningún efecto o tiene efectos positivos sobre la probabilidad de ocurrencia de las especies. Solamente las especies estrictamente forestales y con capacidades dispersivas limitadas se ven afectadas negativamente por la fragmentación del hábitat y parecen confirmar la hipótesis del umbral de extinción. Estos resultados ayudan a comprender algunos de los patrones de riqueza y presencia/ausencia de especies en paisajes fragmentados.

3. Modelos de Distribución de Especies y estructura espacial de la distribución de especies

La mayoría de las aproximaciones en torno a la predicción de los rangos contemporáneos de distribución de las especies y de los posibles cambios de distribución como respuesta al cambio global se basan en el esquema de modelización desarrollado por los Modelos de Distribución de Especies (MDEs). Este campo ha experimentado un desarrollo extraordinario en la última década en Ecología, y su idea clave es establecer las relaciones actuales clima-diversidad de especies y emplear tales relaciones para predecir futuros rangos de distribución. Sin embargo, esta familia de modelos ha sido criticada por no incluir procesos no climáticos tales como interacciones biológicas, dispersión, y destrucción de hábitat, entre otros.

Nuestro punto de partida consiste en construir MDEs y llevar a cabo análisis de la estructura espacial de los rangos de varias especies de árboles cuya distribución está

extensamente documentada, y comparar los patrones espaciales observados con los patrones espaciales de los MDEs para cada especie. Posibles inconsistencias entre la estructura espacial observada en la naturaleza y la explicada por los modelos indicaría que existen factores no climáticos que son relevantes para explicar la estructura espacial de las especies y que están ausentes en los modelos. En función del tipo de inconsistencia observada entre el modelo y las observaciones, pueden establecerse hipótesis sobre otros mecanismos subyacentes de relevancia para entender los patrones observados.

Los resultados muestran que, a pesar de que los MDEs predicen con mucho rigor algunos aspectos de la estructura espacial de las especies de árboles dentro de sus rangos de distribución, existen inconsistencias en el grado de agregación espacial de las especies forestales ibéricas: las especies están generalmente más agregadas en el espacio que lo predicho por los modelos (Montoya et al. 2009. *En prensa*). Estos resultados muestran que existen procesos muy importantes para explicar la diversidad de las especies estudiadas que tienden a agregar a las mismas en el espacio. Este resultado es consistente con trabajos científicos previos y pone de manifiesto procesos como la dispersión de especies y la pérdida y fragmentación del hábitat. Asimismo, este resultado respalda la importancia de estudiar la influencia de la destrucción del hábitat en la diversidad de las especies forestales.

Los resultados obtenidos en esta tesis son relevantes en el campo de la Ecología de comunidades, y ponen de manifiesto que la inclusión de procesos que poseen una determinada estructura espacial alejada del azar es clave para entender diversos patrones de diversidad a varias escalas. Por otro lado, algunos de los resultados obtenidos tienen implicaciones directas para la conservación, ya que proporcionan información sobre las especies cuya protección debería ser más crítica en paisajes donde la pérdida de hábitat es importante. Confiamos que esos resultados ayuden a orientar las políticas de conservación no solamente hacia especies vulnerables, sino hacia interacciones entre especies.

Summary

Although the world is unavoidably spatial, and each organism is a discrete entity that exists and interacts only within its inmediate neighborhood, these realities long have been ignored by most ecologists because they can greatly complicate field research and modeling. However, several lines of inquiry have highlighted the potentially critical roles of space and led to growing interest in Spatial Ecology.

In the present thesis we focus on the study of processes characterized by a certain spatial structure that may directly affect the diversity patterns observed in nature. In the first chapter, we have explored a spatial process which showed a temporal structure as well (i.e. historical pattern of glacial retreat in response to post-Pleistocene global warming). Similarly, habitat loss and fragmentation influences the observed patterns of presence/absence, richness, abundance and extinction of species, and thus this process has been a main milestone of this thesis. Last, we have applied spatial analysis techniques to investigate the validity of the so-called Species Distribution Models (SDMs) to explain the spatial structure of species within their distribution ranges; this information has been used to deduce spatial processes underlying such patterns.

The study of these spatial processes has been conducted for tree species. This decision has been made following two criteria: (1) to maintain coherence among the different chapters of this thesis with respect to the biological group subject of analysis, and (2) because of the higher data availability and quality on presence/absence and richness patterns for tree species. To conduct this thesis we have used empirical data from different datasets, and used different methods and techniques that range from Geographic Information Systems to mathematical and simulation models and spatial structure analyses widely used in Spatial Ecology.

To summarize, the research of this thesis can be divided into three big blocks:

1. Influence of spatio-temporal processes on species richness patterns at large scales

One of the first and well documented patterns in Ecology is the geographical variation in species richness at large spatial scales. In this sense, contemporary climate is widely accepted as the main explanatory factor of the current distribution patterns of species from regional to continental scales. For plants, climate models based on water - energy dynamics explain substantially such patterns.

However, the current climatic conditions are stationary and are significantly different from previous climatic patterns. A fundamental question is: To what extent the evolutionary history of climate determines the observed diversity of forest ecosystems? To solve this question we digitalized a dataset of European and North American trees (these regions represent most of the surface affected by the last glaciation) to which a large set of contemporary climate variables was associated together with a variable reflecting the spatio - temporal structure of the glacial retreat in response to post - Pleistocene global warming.

Our results show a global fingerprint of the recent evolution of climate on the species richness of trees in Europe and North America (Hawkins et al. 2007, Montoya et al. 2007). The results reflect how a spatio - temporal process directly influenced by global warming affects the contemporary tree richness. Therefore, including spatial process (both contemporary and historical ones) is critical to understand the diversity patterns observed today.

2. Habitat loss and fragmentation and the risk of species extinction

Habitat loss and landscape fragmentation are, together with climate change, the main causes of the current biodiversity crisis. Species richness in an ecosystem (i.e. the sum of species that coexist in that ecosystem) decreases with habitat loss. However, previous studies suggest that, even though this trend seems to be universal, individual species do not show similar response patterns to habitat loss: there is an interspecific variation in the vulnerability and risk of extinction to habitat loss. This has lead many ecologists to explore which ecological mechanisms underlie the species' response patterns to this perturbation. In other words, why some species are more vulnerable to habitat loss than

others?

On the other hand, both theoretical and empirical studies suggest that the relationship between the population size of single species and the amount of suitable habitat is not proportional, predicting a threshold habitat level below which the population becomes extinct (extinction threshold). Although the extinction threshold is a direct consequence of habitat loss *per se*, ecological theory suggests that habitat fragmentation may affect the location of the extinction threshold by reducing its predicted occurrence to lower levels of habitat loss. That is, species extinction is expected to occur sooner in the habitat cover gradient when fragmentation operates. However, there have been very few verifications of the so-called extinction threshold hypothesis and the validity of its predictions begs for empirical test.

By using a large dataset on tree species in the Iberian Peninsula we aim to investigate the two questions menctioned above. Our results show non-linear responses of biological species to decreasing habitat amount, which agrees with previous studies on this topic. However, responses to habitat loss differ among tree species. Although the overall effects of habitat loss on the probability of occurrence of tree species are negative (with some species showing even positive responses to this perturbation), which is indicated by a positive correlation between habitat amount and species richness, individual species show diverse response patterns. In general, wind-dispersed species are more vulnerable to habitat loss than animal-dispersed species (Montoya et al. 2008). However, this trend is true provided seed dispersers have not disappeared from the forest ecosystem. If this is not the case (species higher in the trophic chain are usually more vulnerable to habitat loss), animal-dispersed species might be more, not less, vulnerable to habitat destruction.

Our results highlight that plant-animal interactions (dispersal, in this case) increase species resistance to habitat destruction. These results have implications for conservation ecology because they represent a first approximation that provides information about what species are more prone to extinction. We believe that these results will help to guide policies not only towards the conservation of single species but for conservation of ecological interactions.

On the second hand, results on the relationships between individual species responses to habitat loss and habitat fragmentation indicate that habitat fragmentation can alter the extinction threshold of species, although not always in the way predicted by theory (Montoya et al. *In review*). Fragmentation has either null or positive effects on the

probability of occurrence of tree species. Only forest-specialist species and species with limited dispersal ability are negatively affected by habitat fragmentation and confirm the extinction threshold hypothesis. These results and have implications for conservation and help to understand some of the presence/absence and richness patterns of species in fragmented landscapes.

3. Species Distribution Models and spatial structure of species distribution ranges

Most of the approaches to explain the current distribution patterns of species and to predict future ranges under global change are based on the modeling framework of Species Distribution Models (SDMs). This field of Ecology has experienced an extraordinary development in the last decade. The fundamental idea behind these modelling approach is to associate species patterns to contemporary climate conditions, and then use these relationships to predict future species ranges under global change. However, SDMs have been recently criticized because they do not include processes other than climate such as ecological interactions among species, dispersal, and habitat destruction, among others.

The starting point of our work consists on building SDMs and performing analyses on the spatial structure of species ranges for several tree species whose geographical distributions are well documented. Superimposing spatial correlograms generated from the predictions of the SDMs over those generated from the raw data allows a model-observation comparison of the spatial structure of tree species within the species ranges. The rationale is as follows: possible inconsistencies in the spatial structure between models and observations may indicate the existence of other complementary factors not included in SDMs that are relevant to explain the spatial structure of species distributions. Moreover, depending on the kind of inconsistence reported in the analyses, hypotheses may be established about the underlying mechanisms that are behind the observed patterns.

We found that, even though SDMs predict accurately some elements of the spatial structure of tree species within their distribution ranges, inconsistencies in the level of aggregation of species in space are common: trees are generally more aggregated in space than that predicted by models (Montoya et al. *In press*). These results point to the existence of other non-climatic processes that are very important to explain species diversity, and that tend to aggregate species. This is consistent with previous scientific

works and indicates that processes such as dispersal and habitat loss and fragmentation should be taken into account within the SDMs framework. Further, these results highlight the importance of studying the influence of habitat destruction on the diversity of forest species.

The results obtained in this thesis are relevant in Community Ecology and highlight that processes with a certain spatial structure (and thus not spatially stochastic) are key to understand a diverse set of diversity patterns observed in nature. Some of the results have direct implications for conservation due to they provide relevant information on species whose protection should be critical in landscapes where habitat loss is important. We believe that these results will help to guide policies to the conservation of not only single species but also ecological interactions.

List of papers

Hawkins, B. A., Montoya, D., Rodríguez, M. A., Olalla-Tárraga, M. A. & Zavala, M. A. (2007). Global models for predicting woody plant richness from climate: comment. Ecology 88(1), 255-259.

Montoya, D., Rodríguez, M. A., Zavala, M. A. & Hawkins, B. A. (2007). Contemporary richness of Holarctic trees and the historical pattern of glacial retreat. Ecography 30, 173-182.

Montoya, D., Zavala, M. A., Rodríguez, M. A. & Purves, D. W. (2008). Animal versus wind dispersal and the robustness of tree species to deforestation. Science 320, 1502-1504.

Montoya, D. Alburquerque, F.S., Rueda, M. & Rodríguez, M.A. Species response patterns to habitat fragmentation: do trees support the extinction threshold hypothesis? *In review*

Montoya, D., Purves, D.W., Urbieta, I.R. & Zavala, M.A. (2009). Do Species Distribution Models explain spatial structure within tree species ranges? Global Ecology & Biogeography. *In press*

Capítulo 1

Introducción general. Ecología espacial y modelos espaciales

Scientists are divided in two groups: those looking for rules and those looking for exceptions

H. Haeckel (1960)

Se estima que existen entre 5 y 15 millones de especies diferentes (1.6 millones conocidas, Hammond 1995, May 1999). Cada una de estas especies posee una idiosincrasia biológica propia manifestada, entre otros, a través de su ciclo de vida, su uso de los recursos y su interacción con otras especies de su entorno. Esta enorme complejidad biológica que observamos puede impedir *a priori* el enunciado de principios generales, restringir la capacidad predictiva como ciencia y, en definitiva, limitar la Ecología a una ciencia puramente descriptiva. No obstante, existen elementos que se repiten con independencia del sistema de estudio y que permiten plantear y responder cuestiones más generales. Uno de estos elementos universales es el espacio.

Cada especie desarrolla un ciclo de vida característico, modifica su entorno de forma particular, se dispersa a través de vectores específicos e interacciona con otras especies de una forma única. Sin embargo, a pesar de esta complejidad, todos los procesos y mecanismos biológicos tienen lugar en un espacio de tres dimensiones. El espacio no es simplemente el escenario donde coexisten e interaccionan las especies, sino que desempeña un papel activo para la coexistencia de las mismas. Vivimos por lo tanto en un mundo eminentemente espacial donde cada organismo constituye una entidad discreta que vive e interactúa con su entorno más inmediato y vecino. El elemento espacial ha sido ignorado durante mucho tiempo por lo ecólogos, principalmente porque complica mucho el trabajo de investigación y, concretamente, porque supone un ejercicio de modelización muchas veces complejo. Sin embargo, desde los trabajos pioneros de Gause (1935) y Huffaker (1958) con dinámicas depredador-presa, los ecólogos han reconocido la importancia que los procesos espaciales tienen en la generación y predicción de patrones de diversidad biológica, lo que ha activado el interés por la Ecología espacial.

Proceso espacial *Vs*. Proceso no espacial

¿Cuál es la diferencia entre un proceso espacial y un proceso no espacial en el ámbito de la Ecología? La diferencia básica es una cuestión de restricción o limitación en el rango geográfico o espacial en el cual el proceso tiene lugar: mientras que un proceso no espacial carece de rango geográfico, un proceso espacial posee una estructura y dinámica determinadas, lo que limita su campo de influencia. Por ejemplo, los modelos bioclimáticos que se utilizan habitualmente para predecir las distribuciones futuras de especies cuyos rangos de distribución actual están amenazados por el cambio climático, asumen una dispersión global de los organismos (Thuiller et al. 2008). De esta forma, un individuo de una especie determinada sería capaz de ocupar todo su futuro rango de distribución potencial. Esta asunción no es realista ya que las especies se dispersan localmente y tienen distancias de dispersión diferentes que vienen determinadas, a su vez, por las interacciones con otras especies y por la distribución del hábitat no destruido disponible para la colonización. La dispersión, por lo tanto, es un proceso que posee una estructura espacial determinada que limita la capacidad de una especie para ocupar todo su rango potencial de distribución. Asimismo, la pérdida del hábitat disponible es otro proceso con una determinada estructura espacial que juega otro papel importante en este ámbito.

Otra diferencia, aunque no indispensable y necesaria, entre procesos espaciales y no espaciales es el grado de aleatoriedad espacial. Por ejemplo, la pérdida de hábitat o la dispersión de organismos no suelen ser procesos aleatorios en el espacio. Al contrario, estos procesos tienen una estructura y dinámica que se alejan del azar. Sin embargo, podrían existir procesos cuya estructura espacial es aleatoria. De hecho, muchos modelos espacialmente explícitos no distinguen esta diferencia (autómatas celulares sencillos, por ejemplo), por lo que esta característica no es condición *sine qua non* de los procesos espaciales.

Orígenes de la Ecología Espacial

Uno de los primeros grandes cuerpos de conocimiento que sitúa el espacio en primer plano para entender los patrones biológicos observados es la teoría de la biogeografía de islas de McArthur y Wilson (1967). Esta teoría, que supuso una revolución en la Ecología de los años sesenta y posteriores, despertó el interés de los biólogos conservacionistas por los procesos espaciales. La idea básica de la teoría de McArthur y Wilson consiste en que los patrones biológicos de riqueza y abundancia de especies en islas son

el resultado del equilibrio dinámico que se establece entre las tasas de colonización y extinción de las especies. Estos procesos son eminentemente espaciales y dependen tanto del área de la islas como de la distancia a la fuente o *pool* de especies de donde proceden las especies colonizadoras. De esta forma, el número de especies de un determinado grupo taxonómico en una región dada es una función exponencial del área de dicha región, lo que se conoce como relación especies-área. Aunque simple en su formulación y conceptualmente neutral (todas las especies son consideradas iguales), la teoría de biogeografía de islas supuso una primera aproximación para destacar que determinados procesos o características espaciales influyen en los patrones de diversidad observados.

La Ecología Espacial ha proporcionado soluciones a aspectos conceptuales clásicos de la Ecología. Uno de estos aspectos fue formulado por Hutchinson en su trabajo clásico '*Homage to Santa Rosalia, or why are there so many kinds of animals?*' (1959). Hutchinson se planteaba la siguiente pregunta: si el principio de exclusión competitiva rige en la naturaleza (aquél por el cual la competencia local entre especies hace que dos especies que compiten por un mismo recurso no puedan coexistir en el espacio), ¿por qué observamos tantas especies coexistiendo en un mismo territorio? Esta cuestión, conocida como la 'paradoja de la biodiversidad' (Hutchinson 1961) y de gran relevancia especialmente en regiones tropicales donde la diversidad es muy elevada, no fue resuelta hasta la aparición de los modelos espaciales. La razón fundamental es que los modelos clásicos de competencia no incluían coordenadas espaciales para describir la localización de los organismos potencialmente competitivos. Hutchinson ya avanzó que evitar esta asunción ayudaría a resolver la paradoja, y Tilman (1994), partiendo del modelo metapoblacional clásico de Levins (1969), generó un modelo donde demostró que la coexistencia de especies potencialmente competitivas requiere un balance interespecífico ('*interspecific trade-off*') entre la habilidad competitiva y la capacidad dispersiva de las especies. De esta forma, para que la coexistencia sea posible las especies deberían estar jerarquizadas en un gradiente de capacidad competitiva (malas competidoras-buenas colonizadoras *vs*. buenas competidoras-malas colonizadoras), balance que se observa comúnmente en la naturaleza. Aunque otros modelos han surgido en la literatura para explicar la paradoja de la biodiversidad (Hubbell 2001, Clark et al. 2005), el elemento común a todos ellos es la consideración de procesos que tienen una clara estructura espacial para explicar patrones biológicos.

Asimismo, los modelos espaciales se han utilizado ampliamente en otros campos de la Ecología, como en estudios de dinámicas de huésped-parasitoide (Hassell & Wilson 1997), o en genética de poblaciones (Antonovics et al. 1997). La estructura espacial que subyace a muchos procesos ecológicos es además la base de uno de los conceptos más estimulantes de las dos últimas décadas en Ecología: la teoría de metapoblaciones (Hanski 1999).

Modelos espacialmente implícitos *Vs*. Modelos espacialmente explícitos

Los modelos espaciales pueden dividirse en dos grandes grupos: modelos espacialmente implícitos y modelos espacialmente explícitos. Los primeros consideran el espacio de forma implícita, es decir, sin otorgar coordenadas espaciales específicas a las especies y/o procesos ecológicos objeto de estudio. De esta forma, aunque tienen en consideración procesos espaciales, éstos no son incorporados de forma detallada dentro del modelo. Por el contrario, los modelos espacialmente explícitos sí incorporan reglas detalladas en el modelo espacial de tal forma que cada especie y/o proceso ecológico posee coordenadas o restricciones espaciales determinadas.

El modelo de Levins (1969) para la dinámica de una metapoblacional ofrece un ejemplo clásico de modelo espacialmente implícito. El modelo de Levins es un modelo simple, analítico, y fácilmente manejable, que proporciona una descripción simple de la dinámica de una especie en un determinado hábitat en función del territorio ocupado y disponible. De esta forma, el modelo de Levins hace dos asunciones: (1) el territorio disponible para la colonización es homogéneo, y (2) la dispersión de los individuos es aleatoria y global. Existen extensiones del modelo de Levins que incorporan mayor complejidad. Una de estas extensiones introduce la pérdida de hábitat en el esquema analítico del modelo, de forma que el territorio potencialmente disponible es aquel que está libre y no destruido (habitualmente como resultado de actividades humanas). La dinámica metapoblacional de una especie depende ahora no sólo de que un individuo encuentre un territorio libre de otros individuos, sino que ese territorio no se haya perdido físicamente. Otra extensión ya comentada del modelo de Levins es la realizada por Tilman (1994) para explicar la paradoja de la biodiversidad. Tanto el modelo original de Levins y sus extensiones (ver también las funciones de incidencia de Hanski, Hanski 1994, 1997) como otros modelos espacialmente implícitos (ej. Lande 1987) constituyen un avance respecto a los modelos anteriores: aunque el espacio no se trata de forma explícita, estos modelos muestran que existen ciertos efectos del espacio en la diversidad e interacciones entre especies. En concreto, una de las predicciones más interesantes de estos modelos es que ninguna especie puede ocupar todo el hábitat potencialmente disponible, lo que tiene implicaciones importantes para la biodiversidad.

Un paso más adelante en términos de realismo biológico es el que llevan a cabo los modelos espacialmente explícitos. Este tipo de modelos contienen mucho más detalle y proporcionan mucha más información que los anteriores modelos de campo medio

donde el espacio es considerado de forma implícita, simplemente porque en sistemas espacialmente explícitos tenemos tantas variables como territorio disponible o fragmentos (resultado de la discretización del espacio en celdas o cuadrículas). Dado que los individuos llevan asociadas ciertas coordenadas espaciales dentro del modelo, las asunciones de dispersión aleatoria y global no son realizadas. Al contrario, en modelos espacialmente explícitos como los *coupled map lattices* (CML) y los autómatas celulares, la dispersión de los individuos es local. Esta característica genera patrones espaciales concretos (ej. distribuciones agregadas de individuos en el espacio) y fenómenos naturales que no se observan en los modelos espacialmente implícitos (ej. umbrales de percolación, Solé & Bascompte 2007). La capacidad teórica de estos modelos para admitir grados de realismo elevados es una de sus principales virtudes. Dada su mayor complejidad derivada de su mayor realismo biológico, estos modelos normalmente se ejecutan a través de simulaciones computacionales.

Por último, un tipo alternativo de modelos espacialmente explícitos son los modelos de reacción-difusión (Tilman et al. 1997). En ellos, a diferencia de los modelos espacialmente explícitos que discretizan el espacio en celdas o cuadrículas, el espacio es considerado como una variable continua y la dispersión de los individuos se aproxima mediante un proceso de difusión. Este tipo de modelos son analíticos y fácilmente manejables, y proporcionan un buen esquema de modelización para explorar numéricamente las implicaciones de determinadas asunciones sobre la naturaleza de las interacciones entre especies, la dispersión y el hábitat disponible.

En resumen, las aproximaciones de modelización espacial han supuesto un avance muy importante en la comprensión de los patrones de diversidad. Por un lado, nos muestran que todo el territorio potencialmente disponible para una especie no es o no será ocupado por la misma en condiciones naturales. Por otro lado, resaltan la importancia de procesos como la dispersión o la destrucción del hábitat, que poseen una estructura espacial determinada, para explicar que ciertas especies estén presentes o ausentes en una determinada región, así como en la distribución geográfica de las mismas. Los modelos espaciales, además, son capaces de generar predicciones teóricas, como los umbrales de extinción de especies, que no pueden derivarse a partir de modelos no espaciales y que describen de manera realista fenómenos observados en la naturaleza. La principal conclusión de los modelos espaciales es, por tanto, que procesos con una determinada estructura y dinámica espacial (normalmente alejada del azar) influyen en los patrones de diversidad biológica de las especies.

Objetivo general de la Tesis Doctoral

El objetivo general de esta tesis doctoral consiste en estudiar determinados patrones de diversidad y su relación con procesos que tienen una clara estructura espacial. Para ello, los organismos de estudio serán los árboles, donde *a priori* los procesos espaciales imponen mayores limitaciones ya que los árboles son organismos sésiles terrestres (poseen menor capacidad dispersiva, entre otras características).

Los procesos espaciales estudiados no son el centro de gravedad de esta tesis doctoral, sino la relación entre éstos y los patrones observados en especies de árboles. Por lo tanto, los procesos espaciales estudiados son diferentes a lo largo de los capítulos. Por otro lado, un elemento importante a la hora de analizar procesos espaciales es la escala. Existen procesos espaciales que se desarrollan a diferentes escalas, de modo que la escala de referencia determinará el proceso espacial subyacente a considerar. Por ejemplo, en estudios de presencia/ausencia de especies a nivel local, procesos como la dispersión y la disponibilidad de hábitat son más relevantes que procesos a gran escala como la paleoclimatología (ej. la última glaciación que afectó a Europa y Norte América). Dado que los procesos espaciales pueden desarrollarse a diferentes escalas, a lo largo de los capítulos podrá observarse un cambio en las escalas de análisis en función del proceso espacial subyacente, desde la escala continental a la escala más local o regional.

Nota: Durante el desarrollo de esta tesis el autor ha participado en el desarrollo de otras investigaciones, algunas de ellas relacionadas con los objetivos de la tesis. Estos trabajos han arrojado resultados en forma de publicaciones:

Montoya, D., Valverde, S., Solé, R.V. & Montoya, J.M. Trophic response patterns and indirect effects of ecological communties under habitat loss. *In Preparation*

Alburqueque, F.S., Olalla-Tárraga, M.A., Montoya, D., Hawkins, B.A. & Rodríguez, M.A. Scale effects and environ mental determinants of plant species richness patterns in Great Britain. *In review*

Montoya, D. (2009). Resistencia a la deforestación. Los beneficios de la dispersión de semillas por animales. Revista Investigación y Ciencia 390, 12-13.

Bini, L. M. et al. (2009). Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spa tial regression. Ecography 32, 1-12.

Montoya, D. Habitat loss, dispersal, and the probability of extinction of tree species. (2008). Communicative & Integrative Biology 1:2, 1-2.

Hawkins et al. (2007). A global evaluation of Metabolic Theory as an explanation for terrestrial species richness gra dients. Ecology 88(8), 1877-1888

Estructura y objetivos específicos de la Tesis Doctoral

Esta Tesis Doctoral está estructurada en 6 capítulos en formato de artículos científicos. Tras este capítulo introductorio, se presentan cuatro capítulos en inglés con sus correspondientes secciones de introducción, material y métodos, resultados y discusión, todos ellos precedidos de un resumen en castellano e inglés. Estos capítulos reproducen los contenidos de artículos ya publicados (capítulos 2, 3 y 5) o en revisión (capítulo 4). Por último, el capítulo 6 expone las conclusiones generales de esta Tesis Doctoral. Cada capítulo tiene su propia sección de referencias bibliográficas. A continuación se expone el contexto científico y se describen los contenidos y los objetivos específicos de cada capítulo. La metodología concreta empleada se desarrolla con detalle en los capítulos correspondientes.

	Proceso espacial analizado	**Patrón de diversidad estudiado**	**Zona de estudio**	**Especies de estudio**	**Resultados**
Capítulo 2	Retirada glacial del post-Pleistoceno	Riqueza de especies	Europa y Norte América	Árboles	Montoya et al. (2007)
Capítulo 3	Pérdida de hábitat	Probabilidad de ocurrencia de especies	Península Ibérica	Árboles	Montoya et al. (2008)
Capítulo 4	Pérdida y fragmentación del hábitat	Umbral de extinción de especies	Península Ibérica	Árboles	Montoya et al. (Oikos, *En Revisión*)
Capítulo 5	Diversos*	Estructura espacial de especies dentro de su rango de distribución	Península Ibérica	Árboles	Montoya et al. (Geb 2009, *En Prensa*)

* El proceso espacial analizado en este capítulo no es único. Este trabajo deduce, apoyándose en la literatura y la teoría ecológica, procesos espaciales que pueden explicar el patrón de diversidad estudiado.

Capítulo 2. Modelos globales para predecir la riqueza de árboles a partir del clima: comentario (Hawkins et al., Ecology 2007)

Riqueza actual de árboles del Holártico y el patrón de la retirada glacial (Montoya et al., Ecography 2007)

Uno de los primeros y mejor documentados patrones en Ecología es la variación geográfica en la riqueza de especies a escalas espaciales amplias (Hawkins 2001). En esta línea, el clima contemporáneo es ampliamente aceptado como el principal factor explicativo de los patrones de distribución de la riqueza de las especies tanto a escala continental (Hawkins et al 2003, Svenning & Skov 2004) como regional (Rouget et al. 2001, Thuiller et al. 2003). Para especies vegetales, existe evidencia empírica muy fuerte de que el agua y la energía explican los patrones de diversidad y riqueza observados (Stephenson 1990; O'Brien 1993, 1998; Francis & Currie 2003; Field et al. 2005), y los modelos climáticos basados en dinámicas de agua - energía explican sustanciamente dichos patrones.

Actualmente existen dos modelos climáticos de relevancia para predecir la riqueza de plantas. El primero de ellos, desarrollado desde la década de los 90 hasta fechas recientes (O'Brien 1993, 1998, Field et al. 2005), es el denominado '*Interim General Model*' (IGM), del cual existen dos versiones (IGM1, IGM2). Estos modelos, cuya variable predictora fundamental es el volumen de precipitación de agua líquida (lluvia o "*rainfall*"), fueron desarrollados a partir de datos de riqueza vegetal de África, y su capacidad explicativa ha podido comprobarse mediante la comparación entre la riqueza simulada a través del modelo y la observada en la actualidad. El segundo de los modelos climáticos importantes, desarrollado también recientemente (Francis & Currie 2003), ha sido construido para explicar y predecir la riqueza de familias de plantas angiospermas a escala global.

Aunque ambos modelos han sido erigidos por sus autores como globalmente válidos, los modelos generados conjuntamente por O'Brien, Field y Whittaker (O'Brien 1993, 1998, Field et al. 2005) han demostrado mayor eficacia y realismo funcional (Field et al. 2005). Sin embargo, no existe evidencia empírica sobre la validez de los IGMs a otras latitudes que nos sean tropicales o subtropicales. Por lo tanto, el primer objetivo de este capítulo es comprobar el grado de extrapolación de los IGMs para explicar la diversidad de plantas en continentes templados como Europa y Norte América.

Los modelos climáticos no proporcionan una explicación completa de la varia-

ción que existe en los patrones de riqueza de especies de árboles en todo el mundo. Este hecho se observa especialmente en regiones de latitudes templadas con superficie y condiciones climáticas similares y que, no obstante, muestran diferencias significativas en la diversidad regional de árboles, sugiriendo que debe haber otros factores que contribuyen a originar tales diferencias (Latham & Ricklefs 1993; Qian & Ricklefs 1999). Asimismo, los modelos de riqueza de especies vegetales no alcanzan a explicar en ningún caso más del 75% de la variación en la riqueza forestal, dejando sin explicar un porcentaje demasiado elevado para ser asociado a procesos puramente estocásticos.

Procesos independientes del clima actual, por lo tanto, podrían jugar un papel relevante para determinar los gradientes globales de riqueza actuales. Estos procesos incluyen, entre otros, tasas diferenciales de especiación y extinción entre regiones históricamente distintas, factores edáficos limitantes, interacciones entre especies, regímenes de perturbación (ej. incendios, huracanes, tormentas) y climatología histórica (ej. el efecto derivado de la inercia de los procesos glaciales del Cuaternario).

Existen indicios de que este último factor histórico podría ser algo más que una mera hipótesis (Mönkkönen 1994; McGlone 1996), dado que estudios filogeográficos (Avise 2000) y otras investigaciones recientes han descubierto que el patrón global de endemismos de plantas y otros organismos está estrechamente asociado al cambio climático acontecido en el Cuaternario (Jansson 2003). Asimismo, Hawkins & Porter (2003) han demostrado la existencia de evidencia residual de la retirada del hielo en la última glaciación sobre los patrones de diversidad de aves y mamíferos en Norte América. El mecanismo que subyace bajo esta hipótesis es que la retirada del hielo ha seguido un patrón espacio-temporal concreto que ha establecido tasas territoriales de recolonización post-glacial diferentes, de modo que áreas donde el hielo se ha retirado antes han sido susceptibles de ser colonizadas por árboles y otros organismos durante más tiempo y presentarían valores más altos de riqueza. La riqueza de árboles dependería en parte de las tasas de recolonización post-glacial, las cuales, a su vez, estarían ligadas directamente a la estructura espacial de la retirada de los glaciares del Pleistoceno.

No obstante, aún no existe evidencia empírica de que la riqueza de árboles en los continentes refleje, al menos en parte, la retirada del hielo. Más bien al contrario: los estudios existentes dirigidos directamente a testar la hipótesis de la recolonización post-glacial en árboles de regiones templadas de finales de los años 80 concluyeron que no existe evidencia empírica que ratifique la hipótesis (Currie & Paquin 1987, Adams & Woodward 1989. La discrepancia existente entre estos resultados y los obtenidos por Hawkins & Porter (2003) para aves y mamíferos de Norte América es sorprendente,

dado que las especies de vertebrados tienen en promedio mayor capacidad de dispersión que las plantas, por lo que parece poco probable que estos grupos de vertebrados hayan sido afectados por la última glaciación mientras que los árboles no se muestren afectados. El segundo y principal objetivo de este capítulo consiste en estudiar el patrón espacio-temporal de la retirada de los hielos glaciales en respuesta al calentamiento post-Pleistocénico y evaluar la validez de la hipótesis de recolonización post-glacial en el patrón de riqueza de árboles de Europa y Norte América.

Capítulo 3. Dispersión animal frente a dispersión anemócora y la vulnerabilidad de las especies de árboles a la deforestación (Montoya et al., Science 2008)

En este capítulo y en el siguiente el proceso espacial estudiado es la pérdida de hábitat forestal. La pérdida de hábitat y la fragmentación del paisaje, junto con el cambio climático, constituyen la primera causa de pérdida de biodiversidad del planeta (Leakey & Lewin 1997). Según la FAO, la deforestación produjo una pérdida neta de 180 millones de hectáreas entre 1980 y 1995, es decir, una pérdida media de 12 millones de hectáreas al año (aproximadamente 1/4 de la superficie de la España continental), con extensas pérdidas observadas en todos los continentes del planeta (FAO 1997). Esta perturbación física debida al hombre genera cambios en los patrones de diversidad de árboles que en ocasiones desembocan en la extinción de especies y en el colapso biológico de los ecosistemas.

Los modelos espaciales dominantes que se han utilizado para estudiar las relaciones entre la pérdida de hábitat y los patrones de diversidad biológica se enmarcan dentro de la teoría de metapoblaciones, que estudia el balance dinámico que se establece entre la colonización y la extinción locales características de las poblaciones que viven en territorios fragmentados (Hanski 1999). Según esta teoría, la pérdida de hábitat no solamente elimina las especies en las regiones afectadas directamente por la pérdida, sino que altera los patrones de diversidad de especies en los territorios que permanecen sin destruir. Esta idea es la base de conceptos ampliamente utilizados en Ecología de conservación como los corredores ecológicos para conectar áreas no destruidas (Damschen et al. 2006, B. C.-L. Chetkiewicz 2006).

Los estudios sobre el impacto de la pérdida de hábitat en poblaciones biológicas revelan, sin embargo, que todas las especies no responden de igual forma frente a esta perturbación (Tilman et al. 1994, Cardillo & Bronham 2001, Henle et al. 2004, Solé &

Montoya 2005). Las extensiones del modelo clásico de Levins ponen además de manifiesto que la capacidad de dispersión de una especie es determinante a la hora de comprender su respuesta a la destrucción del hábitat (Purves & Dushoff 2005, Purves et al. 2007). Sin embargo, la mayoría de los estudios existentes dirigidos a comprobar estas predicciones han sido restringidos a especies animales de corto ciclo de vida (especialmente mariposas y aves [Conradt et al. 2001, Ferraz et al. 2007]), y escalas espaciales reducidas (Hanski et al. 1994), donde es difícil determinar el impacto a largo plazo de la pérdida de hábitat forestal sobre las comunidades de árboles.

El objetivo de este capítulo consiste en estudiar cómo el proceso de pérdida de hábitat forestal a escala local afecta a los patrones de presencia/ausencia de las especies de árboles de la península Ibérica. Para ello, generamos una extensa base de datos de árboles a partir del 2º Inventario Forestal Nacional (IFN2). Queremos además testar empíricamente la hipótesis planteada por trabajos recientes sobre el modelo de Levins y la teoría de metapoblaciones acerca de que el tipo de dispersión de las especies es un factor importante para entender la respuesta de las especies forestales a la pérdida de hábitat.

Capítulo 4. Patrones de respuesta de las especies a la fragmentación de hábitat: ¿confirman los árboles la hipótesis del umbral de extinción? (Oikos, in review)

Este capítulo está asociado al anterior debido a que el proceso espacial estudiado es la pérdida y fragmentación del hábitat. Sin embargo, en este capítulo queremos poner de manifiesto la diferencia entre los conceptos 'pérdida' y 'fragmentación' de hábitat. El primero refleja la eliminación cuantitativa de hábitat disponible. El segundo está relacionado con los cambios en la configuración espacial del hábitat que no se ha destruido y aún está disponible. Estos cambios están habitualmente asociados a un aumento en el número de fragmentos de hábitat, disminución en el tamaño de los fragmentos, aumento en el aislamiento de los fragmentos y reducción en la conectividad física entre fragmentos (McGarigal et al. 2002). La existencia de ambos procesos en la naturaleza constituye una de las diferencias entre los modelos espacialmente implícitos y los modelos espacialmente explícitos: los modelos espacialmente explícitos son capaces de abordar estudios de fragmentación que no pueden ser investigados a través de modelos espacialmente implícitos.

La distinción de ambos conceptos es importante para comprender cómo las espe-

cies de árboles responden al proceso de pérdida de hábitat. Estudios teóricos sugieren que la relación entre el tamaño demográfico de una especie y la cantidad de hábitat disponible no es lineal, sino que existe un umbral de cantidad de hábitat por debajo del cual la población se extingue (Bascompte & Solé 1996, Boswell et al. 1998, Hill & Caswell 1999, Solé & Bascompte 2007). Aunque este umbral de extinción es consecuencia de la pérdida cuantitativa de hábitat, la teoría ecológica sugiere que la fragmentación puede afectar a la localización de este umbral haciendo que su aparición se produzca antes en el gradiente de pérdida de hábitat (Fahrig 2003). Es decir, la fragmentación podría agravar la respuesta de una especie a la pérdida de hábitat reduciendo su probabilidad de ocurrencia. Sin embargo, aún no se ha verificado esta hipótesis, de modo que sus predicciones requieren un test empírico.

El objetivo de este capítulo es comprobar la validez de la hipótesis del umbral de extinción en escenarios donde la fragmentación del hábitat es diferente. Es decir, mediante la caracterización de los umbrales de extinción, abordamos cómo el proceso espacial de la fragmentación del hábitat puede influir sobre el patrón de extinción de especies en árboles. Para ello utilizamos especies de árboles nativos comunes en la península Ibérica que han mostrado en el capítulo anterior respuestas negativas a la pérdida forestal local. Observamos la probabilidad de presencia de cada una de las especies en función de la pérdida de hábitat para escenarios donde la fragmentación es importante y donde no lo es, y discutimos algunas de las carácterísticas específicas que pueden explicar los patrones observados frente a dicha perturbación.

Capítulo 5. ¿Explican los Modelos de Distribución de las Especies (MDEs) la estructura espacial de las comunidades forestales dentro de los rangos de distribución de las especies? (Montoya et al., In press Global Ecology & Biogeography)

Uno de los efectos más destacados a consecuencia del cambio global que empieza a observarse en la naturaleza lo constituye los cambios en los rangos de distribución de las especies (Thuiller et al. 2008). Las predicciones de los rangos de distribución de las especies se basan fundamentalmente en los llamados genéricamente modelos bioclimáticos o Modelos de Distribución de Especies (MDEs). Este tipo de modelos establece relaciones estadísticas entre la distribución espacial de una especie y las condiciones ambientales asociadas a dicha distribución. Estas relaciones pueden extrapolarse en el futuro mediante el uso de las predicciones que los institutos meteorológicos llevan a

cabo acerca de los cambios en la distribución de valores de las variables ambientales como resultado del cambio global.

Los modelos bioclimáticos son una herramienta muy útil y adecuada para describir las relaciones entre el clima y la distribución de especies debido a que el clima es el factor más determinante para explicar la distribución geográfica de las especies (Hawkins et al. 2003) y a que la capacidad de estos modelos no depende de los niveles tróficos considerados (Huntley et al. 2004). Sin embargo, el hecho de que el clima describa adecuadamente la distribución de una especie no significa necesariamente que puede explicar la estructura espacial de dicha especie dentro de su rango de distribución. De hecho, son numerosos los estudios que sugieren que los factores demográficos son los verdaderos culpables de algunos de los patrones espaciales observados en la estructura espacial de las especies dentro de su distribución (Tilman & Kareiva 1997). Específicamente, el patrón de agregación de las especies dentro de sus rangos podría ser el resultado de procesos espaciales diferentes del clima, tales como la dispersión de semillas, la disponibilidad de hábitat, los regímenes de perturbación y las interacciones entre especies.

Todos los procesos citados anteriormente tienen una determinada estructura espacial y presentan una tendencia general a agregar las especies dentro de sus rangos de distribución. Por ejemplo, los MDEs empleados para predecir las distribuciones futuras de especies cuyos rangos de distribución actual están amenazados por el cambio climático, asumen una dispersión global de los organismos (Thuiller et al. 2008). De esta forma, un individuo de una especie determinada sería capaz de ocupar todo su futuro rango de distribución potencial. Esta asunción no es realista ya que las especies se dispersan localmente (a excepción de los fenómenos poco comunes de dispersión a largas distancias) y tienen distancias de dispersión diferentes que vienen determinadas, a su vez, por las interacciones con otras especies y por la distribución del hábitat disponible. La dispersión, en definitiva, limita la capacidad de una especie para ocupar o colonizar todo su rango potencial de distribución. Dentro de los rangos de distribución, la dispersión, caracterizada por ser un proceso espacial que se manifiesta a escalas locales, puede además agregar las especies dentro de dichos rangos. En definitiva, procesos demográficos como los citados, dada su estructura espacial, son capaces de generar patrones espaciales no uniformes (Pacala & Levin 1997).

El objetivo de este capítulo consiste en desarrollar MDEs para describir los rangos de distribución de especies de árboles de la península Ibérica e investigar hasta qué punto los modelos generados son capaces de explicar la estructura espacial de las espe-

cies analizadas dentro de sus rangos de distribución. Nuestra hipótesis fundamental es que el patrón espacial de agregación de las especies queda, en términos generales, fuera de la capacidad predictiva de los MDEs debido a la influencia de procesos espaciales de carácter demográfico.

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2. Glacial dynamics and tree species richness

2a. Bradford A. Hawkins, Daniel Montoya, Miguel A. Rodríguez, Miguel A. Olalla-Tárraga & Miguel A. Zavala

Comment published in *Ecology* **88**, 255-259 (2007)

2b. Daniel Montoya, Miguel A. Rodríguez, Miguel A. Zavala & Bradford A. Hawkins

Article published in *Ecography* **30**, 173-182 (2007)

Capítulo 2a

Modelos globales para la predicción de la riqueza de especies de plantas leñosas a partir del clima: comentario

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Hawkins, B. A., Montoya, D., Rodríguez, M. A., Migel A. Olalla-Tárraga & Zavala, M. A. (2007). Global models for predicting woody plant richness from climate: comment. Ecology 88, 255-259.

Resumen

Existe amplia evidencia empírica de que las condiciones climáticas contemporáneas determinan de forma importante los patrones geográficos de riqueza de especies. Sin embargo, hay pocos modelos generales para describir las relaciones clima-riqueza a escala global. Uno de estos modelos es el llamado 'Interim General Model' (IGM). Los creadores del IGM han argumentado que este tipo de modelo es una aproximación bastante precisa para determinar las relaciones clima-riqueza en todo el mundo. Sin embargo, su validez ha sido únicamente probada a latitudes tropicales (concretamente en África), donde las condiciones climáticas pueden diferir de las de otras regiones de la Tierra, especialmente de latitudes templadas y frías. Por lo tanto, el grado de validez del IGM a escala global no está confirmado. En este trabajo, utilizando datos de riqueza de árboles en Europa y Norte América (latitudes templadas y frías), reparametrizamos el IGM para investigar su grado de validez fuera de las regiones donde se ha empleado habitualmente. Nuestros resultados constituyen un ejercicio de modelización independiente y muestran que el IGM es una buena aproximación a las relaciones clima-riqueza de árboles a escala global.

Ecology, 88(1), 2007, pp. 255–259
Ecological Society of America

Global models for predicting woody plant richness from climate: comment

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There is abundant evidence that climate strongly influences current patterns of species richness (Wright et al. 1993, Hawkins et al. 2003a), but there have been few attempts to generate global-scale models of climate–richness relationships that can predict richness in areas for which empirical data are lacking or predict how richness will respond to global climate change. One such modeling approach for woody plants was proposed by O'Brien (1993), using gridded species richness and climate data, based on the premise that Thornthwaite's minimum monthly potential evapotranspiration (PET, a measure of winter energy inputs) and liquid rainfall (a measure of water availability) are the key climatic variables that set the environmental capacity for tree richness at the macro scale in southern Africa. O'Brien (1998) subsequently developed the first ''interim general model'' (IGM), derived from the initial southern African model, but with reference to the whole of Africa. O'Brien et al. (1998, 2000) then further modeled southern African woody plants at the genus and family levels (O'Brien et al. 1998) and included topographical relief in all three models (species, genus, and family) to capture orographic effects generating finer scale climatic gradients (O'Brien 2000 et al. 2000). Field et al. (2005) recently returned to the protocols developed by the series of papers by O'Brien and colleagues to produce five additional versions of the IGMs, with and without topography, and at three taxonomic levels (species, genus, and family). They also tested the ability of the IGMs to predict woody plant richness patterns in tropical Africa (Kenya) as well as to predict relative richness patterns for the entire continent. Finally, they compared and contrasted the IGMs with a soil water–energy model developed by Francis and Currie (2003) fitted to global angiosperm family richness, the merits of which have also been debated by Qian and Ricklefs (2004) and Currie and Francis (2004).

A key issue with any statistical model designed to explain an ecological gradient is its ability to predict a pattern in regions outside of the original study area. As suggested by their names, the IGMs are intended to predict the pattern and amplitude of tree (and shrub) richness globally. However, although the test of the IGMs using the newer Kenyan data represents an independent test of the models, it remains that they were parameterized and validated using data from

within Africa. Further, although IGM1 was previously used to generate maps of the predicted climatic potential for tree species richness in some nontropical regions (USA and China; O'Brien 1998), the predictions could not be validated with data at the same scale as her analysis. Perhaps most importantly, the temperate regions used to evaluate IGM1 do not extend north of 50ºN, leaving a significant proportion of the world's landmass beyond the scope of O'Brien's (1998) attempt to examine IGM predictions against existing data. If the IGMs are truly global, ideally they must be shown to provide reasonable predictions in the northern temperate and boreal zones, or at least it must be demonstrated that the underlying logic of the models applies in all climates.

O'Brien (1998) and Field et al. (2005) argued that in mid to high latitudes, where minimum monthly PET equals zero, IGMs can still be used to model tree richness patterns since rainfall, which describes the availability of liquid water, reflects conditions when there is sufficient energy for trees to be active. The idea that (liquid) rainfall can predict plant richness in the far north is in stark contrast to theories claiming that energy drives diversity gradients either via metabolic effects operating at the cellular level (Allen et al. 2002, Brown et al. 2004) or via a general intolerance of organisms to very cold winter temperatures at high latitudes (Currie 1991, Hawkins et al. 2003b). Given that all previous analyses of plant diversity encompassing high latitudes have included explicit measures of energy either independently of, or combined with, water variables (e.g., actual evapotranspiration [Currie and Paquin 1987], Chickugo's productivity model [Adams and Woodward 1989], a rescaled inverse of annual temperature [Allen et al. 2002], and annual PET or annual temperature [Francis and Currie 2003]), the prediction of Field et al. that tree diversity gradients in cold climates can be reasonably modeled by rainfall alone begs for empirical verification.

We generated a GIS database of tree species in North America and Europe (generally defined as woody plants reaching >4 m in height somewhere within their range). A total of 676 species are represented in North America north of Mexico and 187 species in Europe west of Russia. The latitudinal span of the database is from 25ºN to 70ºN. Range maps obtained or generated from a variety of sources were digitized in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, California, USA) and rasterized at 110 x 110 km grain size. The mapped area includes 1830 cells, 1444 in North America, and 386 in Europe. Details of the sources and maps illustrating the richness gradients will be presented elsewhere.

Following O'Brien (1998) and Field et al. (2005), we calculated the minimum monthly potential evapotranspiration (hereafter PET_{min}) using Thornthwaite's formula (Thornthwaite 1948, Bonan 2002), and rainfall was estimated as total precipitation for all months with a mean temperature above 0ºC. We also calculated ln(transformed) elevation (derived from GTOPO30 digital elevation model [DEM] data with a horizontal grid spacing of 30 arc-seconds (*available online*)[1], maximum monthly PET and annual PET (calculated as above), and annual temperature (*available online*)[2] as potential predictors of tree species richness. Finally, we estimated the potential growing season as the number of months when mean temperature was >0ºC.

Because the IGMs are parameterized for tree and shrub richness, whereas our database comprises only trees, we cannot directly compare observed *vs*. predicted richness values using our richness data. More importantly, our climatic data are gridded and interpolated, whereas Field et al. (2005) based their analysis on weather station data, and a precise test of the parameterized IGMs would require that our climatic predictors be measured with the methods used by Field et al. However, although we cannot generate predicted values for each IGM against which to compare observed richness, we can test the prediction that rainfall accounts

[1]http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htmli>

[2]http://www.grid.unep.ch/data/summary.php?dataid=GNV15>

for tree richness better than energy in temperate climates. As far as we know, the ‘‘water–energy dynamics’’ hypothesis underlying the IGMs is the only theory for diversity gradients that makes this prediction; thus, this represents a relatively strong test of the hypothesis. We test this using reparameterized equivalents of the IGMs that contain combinations of the variables predicted to explain diversity.

We first tested the independent contribution of the energy component of the IGMs (PET_{min}) to tree richness across both regions, which we expected to have limited explanatory power given that it has a value of zero in 77.1% of our cells (80.6% of the North American cells and 63.5% of the European cells). It explained 18.5% of the variance. We then tested a model equivalent to a ‘‘reduced’’ IGM1 containing rainfall alone and found that it accounted for 64.1% of the variance in tree richness. Further, the relationship is linear throughout the full range of the data (Fig. 1), indicating that rainfall statistically explains tree richness in Alaska as well as in Alabama, USA. There are noticeable outliers in both North America and Europe (Fig. 1), which in the former case are all Pacific Northwest coastal cells located between Oregon and southern Alaska (where trees may be unable to respond to the massive amounts of rain falling within a short growing season), but in Europe the outliers are scattered throughout the continent. Despite these outliers, the prediction that rainfall limits tree richness even in extremely cold climates is broadly supported. This is further confirmed by adding PET_{min} and ln(range in elevation) to the model (thus generating the equivalent to a reparameterized IGM2). This model explained 65.1% of the variance, only 1.0% more than the reduced IGM1.

The ability of liquid rainfall to explain statistically almost two-thirds of the variance in tree richness across two continents dominated by cool climates seems to confirm the logic underlying the IGMs as argued by

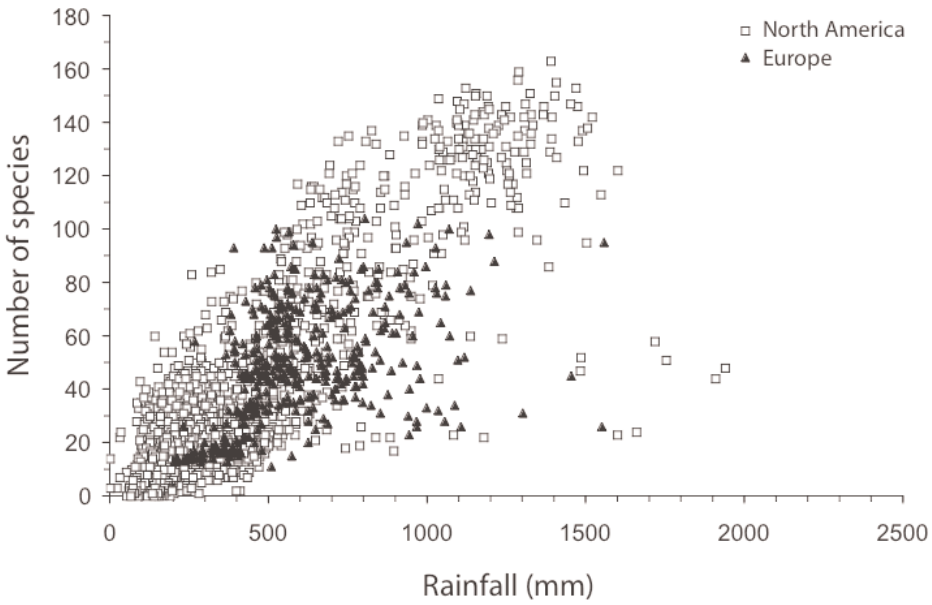

Figure 1. Relationship between annual rainfall (precipitation falling in months with an average temperature >0ºC) and tree species richness in 110 x 110 km cells in North America and Europe. Coastal cells with land areas <50% of inland cells have been excluded.

O'Brien (1993, 1998) and Field et al. (2005). But even if true, we note that the coefficients of determination of the IGMs vary between regions: the fitted IGM2 explains 78.8% of the variance in southern Africa and 79.1% of the variance in Kenya, whereas in the Holarctic the fitted equivalent of IGM2 explains 65.1% of the variance (almost all due to rainfall). The reduced fit in the Holarctic could be due to the use of an inappropriate measure of energy (PET_{min}) when climates are cold, or to the influences of factors found in the north that do not operate in Africa (a possibility also noted by O'Brien [1998]), especially in Europe. Although not discussed by Field et al. (2005), O'Brien (1998) recommended that when PET_{min} is <14 or >45 mm and rainfall <1000 mm, the maximum monthly PET (i.e., energy input in the summer) should be used rather than the minimum monthly PET. In the Holarctic 95.2% of the cells have PET_{min} of <14 or >45, and 90.5% have rainfall <1000 mm, so we used PET_{max} to generate a modified equivalent to IGM1, which increased the explanatory power of the model to 64.7%, only 0.6% more than the rainfall model. We also converted annual temperature using one of the linear transformations dictated by metabolic theory (1000/[T + 273]; Allen et al. 2002) and added it to the rainfall model to investigate its ability to improve the predictions. However, it explained only an additional 1.2% of the variance, so temperature provides no explanatory power beyond that provided by rainfall (it independently explained only 21.8% of the variance in richness). Finally, we examined annual PET (which by itself explained 44.7% of the variance in tree richness) and found that it improved the coefficient of determination of the rainfall model to 0.681, enough to suggest that energy input summed over the entire year has a measurable effect on tree richness independently of summer conditions. Even so, it appears that using a range of measures of energy does not greatly improve the fit of the models, so additional processes unrelated to contemporary climatic conditions may be operating in the temperate zone (e.g., Pleistocene glaciation cycles, edaphic effects, or human impacts). Future research can explore this issue.

Given the clear importance of rainfall to tree richness gradients over this span of latitudes, it is also necessary to ask if richness is most strongly associated with the total amount of rainfall falling over the growing season or, as alluded to above with respect to the Pacific coast, if the length of the growing season itself is what matters. Growing season varies substantially between Alaska and Florida (or Norway and Greece), and annual rainfall is greater towards the south partially as a consequence of the extra time over which water accumulates. Indeed, there was a strong correlation between length of growing season and annual rainfall (r = 0.800), indicating that the latter contains an implicit energy component. However, growing season length explained substantially less of the variance in tree richness than rainfall (47.7% vs. 64.1%, respectively), and adding growing season to the rainfall model increased the coefficient of determination by only 0.007. So, tree richness appears to be associated more with the total amount of rain than with the length of time over which the rain falls. It is important to note that this does not mean that energy does not influence tree richness, only that it is not critical to include an explicit energy variable in climatically based models.

In sum, the logic underlying the IGMs is able to explain the broad species richness patterns of trees reasonably well in regions strikingly different climatically from the regions used to generate the models, and the supposition of O'Brien (1998) and Field et al. (2005) that summer rainfall by itself represents a reasonable predictor of tree diversity in northern latitudes is confirmed. Thus, we have an independent validation of the explanation for woody plant species richness gradients developed by O'Brien (1993, 1998) and Field et al. (2005). Of course, contemporary climate cannot explain everything, since climate models, including the IGMs, lack the speciation – extinction dynamics that are needed to link the past with the present. Even so, if we want to understand how currently existing tree species distribute themselves geographically, ''water–energy dynamics'' seems to offer a useful conceptual and empirical framework.

Acknowledgements

This study was supported by the Spanish Ministry of Education and Science (Grant: REN2003-03989/GLO to M. A. Rodríguez). We thank Robert J. Whittaker, Richard Field, Eileen O'Brien, and an anonymous reviewer for their comments on the manuscript, and Irene L. López for help in the generation of the tree richness data.

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Capítulo 2b

Riqueza contemporánea de árboles holárticos y el patrón histórico de la retirada glaciar

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Montoya, D., Rodríguez, M. A., Zavala, M. A. & Hawkins, B. A. (2007). Contemporary richness of Holarctic trees and the historical pattern of glacial retreat. Ecography 30, 173-182.

Resumen

La cantidad de tiempo que un territorio ha sido apto para la recolonización por plantas y otros organismos podría dar una explicación parcial de los gradientes de riqueza de plantas observados actualmente. Según esta hipótesis, los territorios disponibles durante más tiempo llevan asociados mayores probabilidades de recolonización, lo que conlleva efectos positivos sobre la riqueza de árboles. Para comprobar ésto, generamos una base de datos de árboles del Holártico y evaluamos la influencia de la 'edad de la celda', variable que contempla el tiempo desde el cual un determinado territorio ha estado libre de hielo, en los gradientes de riqueza de árboles observados. Encontramos que la variable 'edad de la celda' está asociada con la riqueza en Europa y Norte América, después de controlar los patrones climáticos contemporáneos, lo que sugiere que el patrón histórico de la retirada glaciar debido al calentamiento global ocurrido en el Post-Pleistoceno ha dejado una señal que todavía puede detectarse después de 14000 años. Estos resultados fueron consistentes usando diferentes aproximaciones de modelización o considerando Europa y Norte América de forma conjunta o separada para el análisis. Concluimos que, aunque ejerciendo un papel secundario respecto al clima actual, la hipótesis de la recolonización post-glacial es ampliamente apoyada a latitudes templadas.

Ecography 30: 173182, 2007
doi: 10.1111/j.2006.0906-7590.04873.x

Subject Editor: Jens-Christian Svenning. Accepted 5 December 2006

Contemporary richness of holarctic trees and the historical pattern of glacial retreat

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Abstract

The length of time land has been available for colonization by plants and other organisms could provide a partial explanation of the contemporary richness gradients of trees. According to this hypothesis, increasing times of land availability entail higher chances of recolonization, which eventually have positive effects on tree richness. To test this, we generated a dataset of the Holarctic trees and evaluated the influence of cell age, a measure of the time since an area became free of ice, on the observed tree richness gradients. We found that cell age is associated with richness in both Europe and North America, after controlling for contemporary climate patterns, suggesting that the historical pattern of glacial retreat in response to post-Pleistocene global warming has left a signal still detectable after at least 14 000 yr. The results were consistent using a range of modelling approaches or whether Europe and North America were analyzed separately or in concert. We conclude that, although secondary to contemporary climate, the post-glacial recolonization hypothesis is broadly supported at temperate latitudes.

Introduction

The extent to which past events drive broad-scale gradients in species richness forms the basis of hypotheses focused on a range of historical factors (Qian and Ricklefs 1999, Ricklefs and Latham 1999, Svenning and Skov 2005). One such hypothesis argues that the length of time since an area has become suitable for species establishment, termed ‘‘environmental age’’ (Begon et al. 1996), ‘‘patch age’’ (Hastings 2003) or simply ‘‘age’’ (Hawkins and Porter 2003, Rodríguez et al. 2006), can be an important determinant of species richness. This is well established in the context of island biogeography (MacArthur and Wilson 1967), but has also been applied to areas that became habitable after the retreat of Pleistocene ice sheets (Currie 1991). The prediction in the latter case is that species richness in areas that remained uncovered by ice during the last glacial period (between 20000 and 10000 yr BP) will be greater than in areas covered by ice. Recent support for this post-glacial

recolonization hypothesis has been reported for northern North American mammals and birds, although the effects were secondary compared to those of current climate (Hawkins and Porter 2003). In contrast, earlier studies focused on trees found no evidence of effects of recent glacial history on the richness gradients of North America (Currie and Paquin 1987, Adams and Woodward 1989) and Eurasia (Adams and Woodward 1989). This discrepancy is intriguing, since animals, especially vertebrates, are on average probably much more dispersive than plants, and it seems unlikely that vertebrates have been affected by glaciation whereas trees have not.

A fundamental issue when testing hypotheses of richness gradients at broad scales is that experiments are impossible, so we have to rely on the strength of correlations of richness patterns with explanatory variables linked with the hypotheses of interest, many of which may be collinear. The rationale is that if a particular variable accounts for very little independent variance in richness, then the hypothesis to which the variable is related is probably not a good proximate explanation (Currie 1991, Hawkins et al. 2003). The choice of variables to include in analyses also becomes critical and can obviously influence conclusions, and this may be especially important when testing historical hypothesis. For example, Currie and Paquin (1987) estimated glacial effects by differentiating only between glaciated and non glaciated areas. This does not take into account the pace at which the ice sheets retreated nor the spatial pattern of retreat. Adams and Woodward (1989), on the other hand, concluded that recent glacial history had no effect on tree richness based entirely on indirect evidence; that is, by claiming that models including contemporary factors explained so much of the variance in tree richness that there was no need to invoke historical explanations. This overlooks the fact that strong associations between richness and current conditions do not exclude a possible secondary role of recent glacial history (Whittaker and Field 2000, Hawkins and Porter 2003).

Here we revisit the question of whether recent glacial history has influenced the tree richness gradient of the Holarctic using an age variable that reflects the spatiotemporal pattern of glacial retreat, measured by the time previously glaciated areas became free of ice coverage (Turner et al. 1988, Hawkins and Porter 2003, Rodríguez et al. 2006). Our rationale resembles that proposed by Whittaker and Field (2000) to asses the impact of historical legacies in determining gradients of tree richness (Hawkins and Porter 2003). However, whereas these authors suggested building climate models for richness in regions not impacted by a certain historical factor, and then examine residuals over regions expected to be impacted by that factor, we directly generate contemporary climate models for areas that are previously thought to be affected by cell age and determine if adding this factor to the models improves their explanatory power. We also evaluate the effects of glacial history by adding age to reparameterized versions of published models generated to explain global biogeographic patterns of woody plant species richness (O'Brien 1998, Field et al. 2005), or to explain global gradients of angiosperm family richness (Francis and Currie 2003). Our goals are to determine 1) whether a historical signal of the last glaciation exists in northern temperate regions, and 2) the relative role this signal plays in explaining the contemporary diversity patterns of temperate trees.

Material and methods

Tree richness

We constructed a GIS database containing all tree species (defined as any woody plant growing to >=4 m anywhere in its range) present in North America (676 species) and Europe (187 species). Complete range maps were found in the literature for all North American and most European (84.5%) tree species. For the remaining European species, partial distribution maps (5%) or no maps were available (11%). In such cases, maps were drawn based on written descriptions of the distribution of each species (see Appendix 1 for details and references to build the database). For both continents, maps were digitized in ArcGis 9.1 and rasterized at two grains

(27.5x27.5 km for mapping and 110x110 km for statistical analysis). The larger grain generated 1830 cells: 1444 cells for North America and 386 cells for Europe). All islands except Great Britain as well as all coastal cells covering <50% of inland cells were excluded from the analysis.

Environmental and historical predictors

Selection of environmental predictor variables was based on previous studies of broad-scale plant richness gradients (Currie and Paquin 1987, Adams and Woodward 1989, Currie 1991, Francis and Currie 2003, Hawkins et al. 2003, Field et al. 2005). To explore all previous approaches used to model richness, 11 non-historical environmental variables were generated. Mean annual temperature (MeanTemp), annual temperature range (TempRange, the difference between mean maximum and minimum monthly temperature) and mean January temperature (JanTemp, Currie and Paquin 1987, Adams and Woodward 1989) were obtained at <http://www.grid.unep.ch/data/summary.php?dataid/GNV15> and annual potential evapotranspiration (PET_{PT}, calculated using the Priestley- Taylor formula) and annual actual evapotranspiration (AET) at <http://www.grid.unep.ch/data/summary.php?dataid/GNV183>. Water deficit (WD) was estimated as the difference between PET and AET (Francis and Currie 2003). Annual precipitation (AnnPrecip) is available at <http://www.grid.unep.ch/ data/grid/gnv174.php>. Rainfall, a measure of the availability of liquid water, was estimated as the total monthly precipitation for all months with a mean temperature above 0ºC (O'Brien 1998, Field et al. 2005, Hawkins et al. in press). We also calculated minimum monthly potential evapotranspiration (hereafter $minPET_{Th}$) using Thornwaite's formula (Thornwaite 1948) for use when generating models based on O'Brien's (1998) water-energy dynamics framework. O'Brien (1998) recommended that when minPET <14 or >45 mm and rainfall <1000 mm, the maximum monthly PET ($maxPET_{Th}$) should be used rather than the minimum monthly PET. Since 95.2% of the cells in the Holarctic have minPET <14 or >45 mm, and 90.5% have rainfall <1000 mm, we also estimated $maxPET_{Th}$. Range in elevation (ER) was used as an estimate of mesoscale vertical climatic variation within cells, calculated as the difference between maximum and minimum elevation within a grid cell and lntransformed (O'Brien 1998, Field et al. 2005). DEM data are available at <http://www.ngdc.noaa.gov/seg/ cdroms/ged_iia/datasets/a13/fnoc.htm>. Insolation/ solar radiation data (Rad) (Currie and Paquin 1987, Adams and Woodward 1989), defined as the monthly averaged insolation incident on a horizontal surface for a given month, were obtained from <http://eosweb. larc.nasa.gov/cgi-bin/sse/global.cgi>, and estimated as the yearly total solar radiation incident on each cell. Growing season length/potential growing season (PGS) was calculated as the number of months with mean temperature >0ºC (O'Brien 1993, 1998). No productivity measure was included in the analysis for two reasons. First, climate strongly influences plant productivity at large extents, so including both climatic and productivity variables does not test alternative hypotheses, but only adds an intermediate link in the presumed causal chain leading from climate to tree richness. Second, when working with trees, climatic-richness relationships should focus on more direct estimators of climate rather than indirect or non-independent variables such as productivity, which depend on biological activity (Whittaker and Field 2000).

Finally, we calculated cell age to reflect the time a cell has been available for colonization by trees and other organisms as Pleistocene ice sheets retreated. Cell age was estimated for Europe using changes in ice cover at 1 Kyr intervals from Peltier (1993). For North America, we used the temporal series of maps developed by Dykes and Prest (1987). Cells not completely covered by ice during the last glacial maximum were assigned an age of 20000 yr (Rodríguez et al. 2006).

Analytical protocols

The relationships between predictor variables and tree richness were tested using standard regression and model selection techniques based on Information theory (Burnham and Anderson 2002, Johnson and Omland

2004). Candidate models were ranked based on the Akaike information criterion (AIC), which measures the information lost when approximating reality by a model, so the model with the lowest value was considered the best given the data. For each model, AIC was computed as AIC = $n\log(\varepsilon^2) + 2K$, where *n* represents the sample size, ε^2 is the variance of the residuals of each regression model, and *K* is the number of parameters in the model.

Regression models based on gridded richness data often contain small-scale spatial autocorrelation in the residuals, which leads to a violation of independence (Diniz-Filho et al. 2003) and, consequently, underestimation of variances in the residuals and inflated degrees of freedom. This can influence AIC since it is calculated using the model residuals. To resolve this potential problem, we corrected the residual variances of all models by recalculating geographically effective sample sizes (n*), as $n^* = n/[(1+p)/(1-p)]$, where *p* is the first-order autoregressive parameter of the residuals, approximated by the standardized Moran's *I* at the first distance class (Cressie 1993, Haining 2003), estimated for each model. The corrected AIC (AIC_c) thus allows models to be ranked and weighted after correcting for the presence of small-scale residual autocorrelation, thereby providing a quantitative measure of relative support for each competing model. Model's performance was addressed using ΔAIC_c, which is a measure of each model relative to the best model, and is given by the difference between AIC_c of each model and the minimum AIC_c found (the best model having $\Delta AIC_c=0$). The level of support to choose among competing models was fixed at $\Delta AIC_c<=2$ (Burnham and Anderson 2002). Thus, values of $\Delta AIC_c<=2$ (independent of AIC scale) suggest the models are equally likely, whereas $\Delta AIC_c>10$ indicates poor fit relative to the best model, and the model is very unlikely. All statistical analyses were performed using STATISTICA (StatSoft 2003) and Spatial Analyses in Macroecology [SAM] (Rangel et al. 2005).

We note that the analysis might be considered ''biased'' by the inclusion of many contemporary variables but only one historical variable. We took this conservative approach because historical effects are more controversial than modern climate. Also, we are not examining all possible historical effects, but a specific effect related to a single event (the most recent Ice Age). The selection of environmental variables was not random but was based on previous analyses connecting broad-scale richness patterns of these regions to contemporary climate (see above). The main goal of the analysis was not to test associations between contemporary climate and tree richness patterns, which are already well documented; rather, we focused on the statistical contribution of glacial history to richness patterns. Our initial approach was to identify the best regression models describing richness patterns of temperate trees of Europe and North America considered together based on contemporary climatic variables, and then adding cell age and test for improved model fit. Climatic models were based on modelling frameworks that have shown strong statistical explanatory power of broad-scale richness patterns of vegetation: two versions of O'Brien's water-energy models (hereafter regional water-energy models [RWEM]; O'Brien 1998, Field et al. 2005) and the water deficit model of Francis and Currie (2003) (hereafter F&C). The widely reported parabolic relationship between energy and richness may fail to be detected at temperate latitudes because studies restricted to this latitudinal range represent a portion of the theoretical energy-richness curve, and a positive, monotonic relationship between richness and climatic energy can be expected at high latitudes (Whittaker and Field 2000). Following this argument and because AIC penalizes for the addition of variables into the models, linear and non-linear versions of the RWEM and F&C models were also compared and tested with AIC_c. In addition, we also used an *ad hoc* approach to generate models different from the former ones and that potentially included all climatic variables which have been shown to correlate with tree richness. Multicollinearity was minimized both by using energy and water variables that were not strongly correlated with each other ($r <0.6$), and by restricting the *ad hoc* models to one energy variable and one water variable. Because effects of glacial retreat would be expected to be strongest where the land was covered by ice, we first analyzed only glaciated

cells. However, to test if the historical signal was detectable at the continental scale, we also generated models for the entire continents. We then generated multiple regression models for the glaciated parts of Europe and North America separately to determine if the results across both regions were consistent within each geographic region.

Finally, past and present climates are spatially correlated across Europe and North America, and therefore collinearity between cell age and climatic variables can complicate interpretation of the regression models, even if independent effects are detected in the multiple regressions. To explore this we used partial regression to partition the variance explained by contemporary (environmental effects) and historical (glaciation) effects into independent and covarying components (Legendre and Legendre 1998). The coefficients of determination for the current environmental variables and cell age were obtained separately from simple regression, while for climate and age combined were generated from multiple regressions. Once we obtained the three coefficients of determination (climate, age, climate+age), we proceeded to partition the independent effects of climate and age, as well as the combined effect of overlapping climate and age. Because of broad consistency in the results across Europe and North America, partial regressions were performed on the combined data only.

Results

Tree richness

The spatial distribution of tree species richness in Europe presents a clear latitudinal pattern, with more species in the southern mountainous areas and the Mediterranean regions (Mediterranean basin hotspot, Myers et al. 2000)

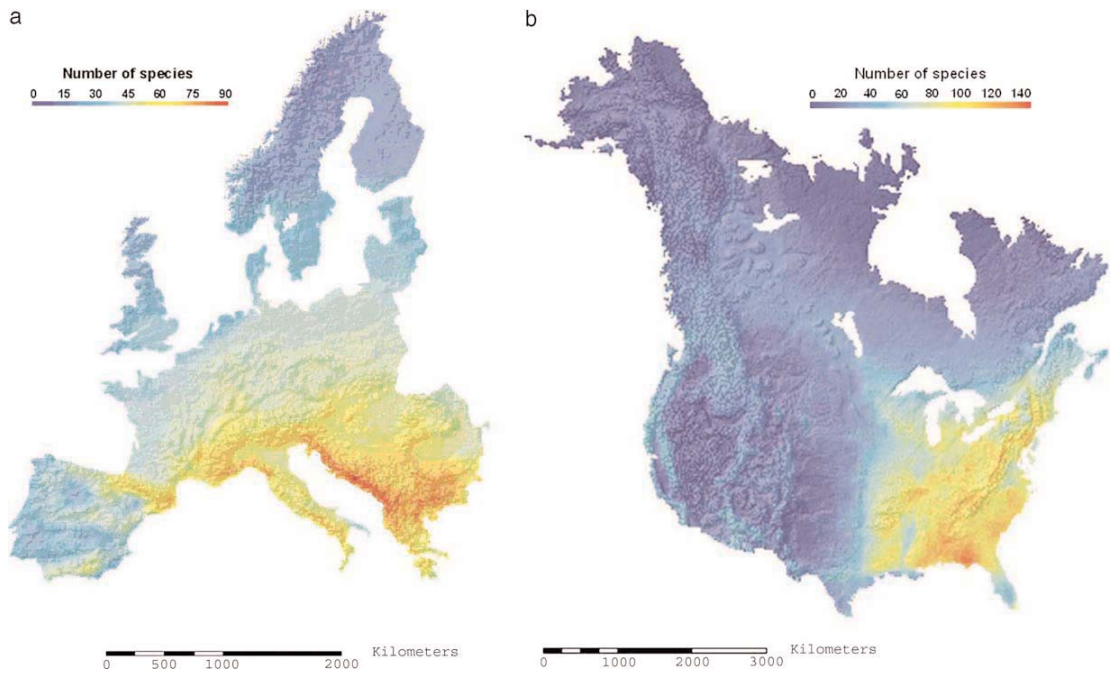


Figure 1. Tree richness distribution for Europe and North America at 27.5 km^2 grain.

(Fig. 1a). There is also a west-to-east gradient of increasing richness, which combined with the latitudinal gradient results in the highest richness in the Balkans and the eastern coast of the Adriatic Sea. Maximum richness in North America is in the coastal southeast (Fig. 1b), further to the south than reported in an earlier tree analysis (Currie and Paquin 1987). Western North America has lower richness than the east, but with relatively high diversity in the California floristic province (Myers et al. 2000). Similar patterns are found at both 27.5x25.7 km and 110x110 km grains (110x110 km maps are provided in Appendix 3).

Glaciated areas

If cell age influences the pattern of recolonization following glacial retreat, it should be most obvious in the region historically covered by ice (Rodríguez et al. 2006). Even so, in this part of the world, as expected, most of the variation in temperate tree richness can be accounted using variables describing present climatic conditions (Tables 1A, B and Appendix 2). On the other hand, the addition of cell age substantially increased the explanatory power of regression models using all four modelling approaches, as indicated by ΔAIC_c (Tables 1A, B). Clearly, the strongest models combine contemporary and historical climatic patterns irrespective of the combination of specific predictor variables in the models.

In terms of model fit, coefficients of determination of climate models are moderate to high (Table 1), and adding cell age to the models contributes substantial independent explanatory power, especially to models containing fewer predictor variables. The weakest contribution of history occurs in our best *ad hoc* model (Table 1A), a clear indication of collinearity among cell age and the additional climatic predictors in this more complex model. Indeed, partial regressions show that most of the

Table 1. Summary of regression models for tree richness using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age. For each region, the AIC_c compares the best model (ΔAIC_c=0) with the best models generated under each of the other three modelling frameworks. R^2 of each model is also given.

Model type	Predictors in model						AIC_c	ΔAIC_c	R^2
A) Glaciated regions									
RWEM1	Rainfall	$minPET_{Th}$	$minPET_{Th}^2$				2649.4		0.430
	Rainfall	$minPET_{Th}$	$minPET_{Th}^2$	Age			2479.0	332.4	0.592
RWEM2	Rainfall	$minPET_{Th}$	$minPET_{Th}^2$	Ln(ER)			2637.4		0.434
	Rainfall	$minPET_{Th}$	$minPET_{Th}^2$	Ln(ER)	Age		2477.6	331.0	0.593
F&C	WD	PET_{PT}	PET_{PT}^2				2300.3		0.730
	WD	PET_{PT}	PET_{PT}^2	Age			2146.6	0	0.792
ad hoc	Rainfall	PET_{PT}	PET_{PT}^2	Ln(ER)	PGS		2275.1		0.694
	Rainfall	PET_{PT}	PET_{PT}^2	Ln(ER)	PGS	Age	2241.8	95.2	0.727
B) Entire regions									
RWEM1	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$				5670.8		0.648
	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$	Age			5649.3	78.7	0.683
RWEM2	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$	Ln(ER)			5592.7	22.1	0.661
	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$	Ln(ER)	Age		5613.0		0.689
F&C	WD	PET_{PT}	PET_{PT}^2				6070.1		0.725
	WD	PET_{PT}	PET_{PT}^2	Age			6031.0	460.4	0.739
ad hoc	Rainfall	PET_{PT}	PET_{PT}^2				5570.6	0	0.738
	Rainfall	PET_{PT}	PET_{PT}^2	Age			5596.3		0.740

Predictors: rainfall=total precipitation in months when mean temperature >0ºC; $maxPET_{Th}$=maximum monthly potential evapotranspiration (Thornwaite's formula); $minPET_{Th}$=minimum monthly potential evapotranspiration (Thornwaite's formula); ER=elevation range (O'Brien 1993, 1998, Field et al. 2005); PET_{PT}=annual potential evapotranspiration (Presley-Taylor formula); WD=water deficit (Francis and Currie 2003); PGS=potential growing season (O'Brien 1993, 1998); TempRange=annual temperature range (Currie and Paquin 1987, Adams and Woodward 1989); Age=number of years cell exposed after glacial retreat; RWEM1=regional water-energy models (O'Brien 1998, Field et al. 2005); F&C=the water-energy model of Francis and Currie (2003).

Table 2. Summary of regression models for tree richness in the glaciated parts of Europe and North America, using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age. For each region, the AIC_c compares the best model (ΔAIC_c=0) with the best models generated under each of the other three modelling frameworks. R^2 of each model is also given.

Model type		Predictors in model						AIC_c	ΔAIC_c	R^2
A) Glaciated Europe										
RWEM1	Rainfall	$maxPET_{Th}$						325.1		0.522
	Rainfall	$maxPET_{Th}$	Age					250.7	21.6	0.713
RWEM2	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$	Ln(ER)				261.9		0.707
	Rainfall	$maxPET_{Th}$	$maxPET_{Th}^2$	Ln(ER)	Age			242.4	13.3	0.765
F&C	WD	PET_{PT}	PET_{PT}^2					266.8		0.691
	WD	PET_{PT}	PET_{PT}^2	Age				248.2	19.1	0.763
ad hoc	Rainfall	TempRange	PET_{PT}^2					233.8		0.755
	Rainfall	TempRange	PET_{PT}^2	Age				229.1	0	0.784
B) Glaciated North America										
RWEM1	Rainfall	$minPET_{Th}$						2272.6		0.466
	Rainfall	$minPET_{Th}$	Age					2033.1	184.5	0.667
RWEM2	Rainfall	$minPET_{Th}$	Ln(ER)					2266.6		0.469
	Rainfall	$minPET_{Th}$	Ln(ER)	Age				2025.3	176.7	0.672
F&C	WD	PET_{PT}	PET_{PT}^2					1982.2		0.766
	WD	PET_{PT}	PET_{PT}^2	Age				1884.8	36.1	0.806
ad hoc	Rainfall	PET_{PT}	PET_{PT}^2	WD	Ln(ER)	PGS		1924.8		0.784
	Rainfall	PET_{PT}	PET_{PT}^2	WD	Ln(ER)	PGS	Age	1848.6	0	0.815

Predictors: rainfall=total precipitation in months when mean temperature >0ºC; $maxPET_{Th}$=maximum monthly potential evapotranspiration (Thornwaite's formula); $minPET_{Th}$=minimum monthly potential evapotranspiration (Thornwaite's formula); ER=elevation range (O'Brien 1993, 1998, Field et al. 2005); PET_{PT}=annual potential evapotranspiration (Presley-Taylor formula); WD=water deficit (Francis and Currie 2003); PGS=potential growing season (O'Brien 1993, 1998); TempRange=annual temperature range (Currie and Paquin 1987, Adams and Woodward 1989); Age=number of years cell exposed after glacial retreat; RWEM1=regional water-energy models (O'Brien 1998, Field et al. 2005); F&C=the water-energy model of Francis and Currie (2003).

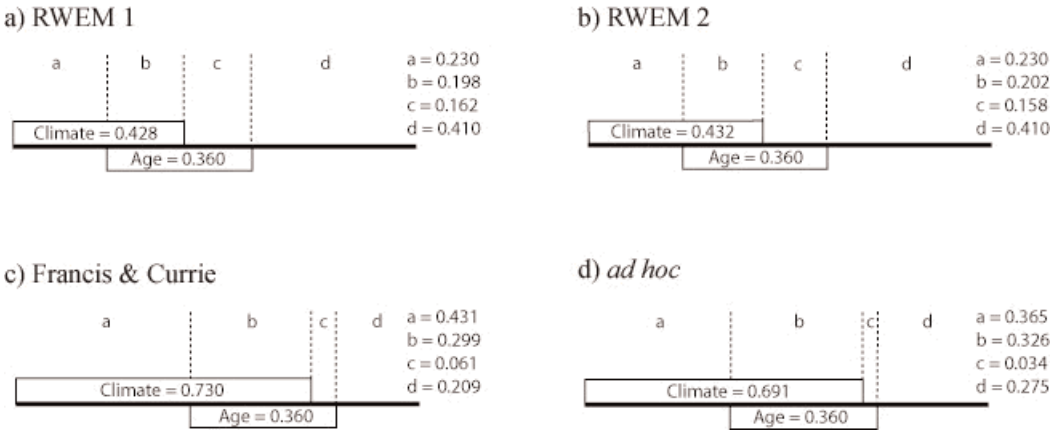
''effects'' of post-Pleistocene global warming are collinear with contemporary climate (Fig. 2). However, it remains that, after accounting for climate, cell age explained an additional 6.1 and 15.8% of the variance in tree richness with respect to the best published models (F&C and quadratic RWEM2, respectively), and 3.4% relative to the best model generated in our *ad hoc* approach. These results are consistent with a secondary influence of glacial history on the contemporary richness patterns of trees in the far north.

Regression models generated for Europe and North America separately sometimes differed from the biregional models in the particular predictor variables included, but the inclusion of cell age significantly reduced the AIC_c in all eight cases (Table 2A, B). Thus, any independent historical effects operating in the Nearctic and Palearctic do not alter the finding that cell age contributes explanatory power to environmental models across the Holarctic.

Entire regions

Even when including parts of North America and Europe that were not glaciated during the most recent glacial cycle, cell age generated better fitting models than when it was excluded in three of our four best models (Table 1B). Exceptionally in our best *ad hoc* model, including age did not increase the predictive power of the model. Also, even in the three other models, where age improves the predictions, increases in model R^2's were substantially lower (14%) than when modelling richness in the parts of the Holarctic that were covered by ice.

Figure 2. Partial regression analyses for the best models describing tree richness in the glaciated regions of North America and Europe combined, partitioning the independent contributions of climate (a) and cell age (c), and the covariance between climate and cell age (b). (d) represents the proportion of variation in richness not explained by either factor.



Discussion

We find that incorporating a variable that quantifies the spatial pattern of glacial retreat increases the statistical explanatory power of regression models of tree richness, irrespective of the particular model approach used or whether considering Europe and North America separately or in concert. These results are similar to those reported by Hawkins and Porter (2003) for northern North American birds and mammals and are consistent with the hypothesis that the length of time an area has been deglaciated has left a detectable legacy on the contemporary richness gradient of trees. Araújo and Pearson (2005), using bioclimatic envelope modeling of European plants, reptiles and amphibians, similarly concluded that current species distributions are not at equilibrium with the contemporary climate, due to lagged recolonization of northern latitudes following Holocene warming. In addition, Svenning and Skov (*in press*) have shown that the governing climatic conditions of the Last Glacial Maximum strongly control tree richness of species with restricted geographical ranges over the unglaciated European regions, which might be reflecting the historical glacial refugia of these trees.

Although Europe and North America have experienced different glacial histories (Elenga et al. 2000, Prentice et al. 2000, Tarasov et al. 2000, Williams et al. 2000), the effects derived from glacial retreat on contemporary tree richness display a global and consistent historical signal. Given that late-Pleistocene glaciers were restricted to the far northern latitudes and glaciation was not extensive in Asia and the Southern Hemisphere (Hewitt 2000), the historical signal we detect synthesizes the emergence of nearly all of the new colonisable territories after post-Pleistocene global warming and its effects on tree richness. This suggests that historical factors widely shape currently observed diversity patterns, and first approaches to explore their influence may follow a top-down analysis from general signals to more specific and regionally-dependent historical effects.

In all tests of historical *vs.* contemporary influences on diversity gradients, it is difficult to be certain what variables measure, as many elements of climate are collinear. Past and present climatic gradients are especially strongly correlated at large extents, making it difficult to partition their effects on richness patterns (Hawkins et al. 2006, and Fig. 2). Thus, it remains possible that cell age

covaries with some unknown element of contemporary climate, and this is what generates the observed relationships, or vice versa. We cannot exclude this possibility, but because we investigated a large number of climate variables, it reduces the probability that we have missed something. Second, we used a range of modelling approaches, and all lead to the same conclusion (although the strength of the historical signal is clearly influenced by the structure of the specific regression model). Finally, the collinearity problem exists for all environmental predictors, present or past, and it has even been argued that it is the correlations with current conditions that are artifactual and historical conditions actually drive tree diversity (McGlone 1996). We are unable to resolve this fundamental issue, but it remains that our historical variable contributes to statistical models of tree richness under almost all approaches, while at the same it is not the best predictor by itself. A reasonable conclusion is that both past and current climates drive the richness pattern, not one or the other in isolation.

It is not surprising that partial coefficients of determination for cell age are stronger in models restricted to glaciated areas of Europe and North America than in models for the entire continents. Glaciation effects would be expected to be weaker when non-glaciated areas are included, as trees were not excluded from southern Europe (Bennett et al. 1991) or even from the non-glaciated parts of extreme northwestern North America (Brubaker et al. 2005). Further, although we can date the exposure of land within glaciated areas using maps of ice coverage, we assigned a single arbitrary age on non-glaciated cells, irrespective of the presence of absence of forest during the glacial maximum. The lack of temporal resolution for cells in these areas is very likely to weaken any models using regression.

The quantitative contribution of cell age varies substantially depending on the climatic modelling approach we use. The strongest apparent relationship of richness and history is found when using O'Brien's water-energy models (RWEM1 and RWEM2) in the glaciated regions, whether regions are modelled combined or separately. In these models, the differences between predicted and residual richness are substantial. For North America, the observed richness for recently exposed cells (<7000 yr BP) averages 7.2 species, whereas the RWEM2 predicts 20.0, suggesting that less than half of the species that should exist in northeastern Canada are actually present. Even using the *ad hoc* climate model, in which the contribution of age is much less (Table 2B), predicted richness is still 11.2 species. Thus, both models suggest a substantial lag in recolonization in the far northeast. In contrast, observed richness in the youngest European cells (exposed <10000 yr BP) averages 16 species, whereas the RWEM2 predicts 17.2 species, and the *ad hoc* model predicts 15.6. That Europe should show weaker effects of glacial retreat than North America is expected (Hawkins and Porter 2003), since the area covered by ice was much smaller in Europe (advancing forest species had less distance to move), and the ice melted earlier (there has been more time for species to reach exposed areas). This is despite the fact that the overall response of trees to glacial history suggests stronger effects in European tree patterns, as previous phylogeographical and paleoecological studies have shown (Elenga et al. 2000, Prentice et al. 2000, Tarasov et al. 2000, Williams et al. 2000).

The analysis raises an obvious paradox. We found a clear effect of time since glaciation on species richness despite the evidence from the pollen record that boreal forests rapidly advanced behind the retreating ice sheets (Strong and Hills 2005), and that postglacial migration of trees northward was completed thousands of years ago (Kullman 2002). Although some of these studies are controversial, and other studies claim that migration lags after ice melting might be involved (Fang and Lechowicz [2006] for the distribution of *Fagus sylvatica* in northern Britain, and Svenning and Skov 2004), it has been suggested that the effects of glacial retreat are not due to delayed recolonization, but to an increased rate of global extinction following ineffective migration (Turner 2004). Provided the larger amplitude of climatic change at higher latitudes, it is likely that ice extension-contraction processes have selectively extirpated species and clades more strongly at higher latitudes, which would explain

the largely depressed tree richness observed in these regions.

It is important to bear in mind that our test of ''historical'' effects is focused on a relatively short time period, and somewhat crudely measures ''history'' in contrast to contemporary climate. Any patterns we observe have been derived from the most recent historical period of climatic change, and thus do not explicitly include long-term differential rates of diversification and speciation within the Holarctic during the glacial-interglacial cycles. Since colonization may occur relatively rapidly (average rates of spread of 100-1000 m yr^{-1} for trees that have successfully recolonized the far north; McLachlan et al. 2005), the historical signal estimated by cell age is primarily a consequence of the spatial rearrangement of species already existing in the Pleistocene. Other potential effects of history based on speciation and extinction cycles on current tree richness remain unquantified, and might well be hidden in the variance that was not explained by our models, or possibly embedded in the structure of the explained variance (Bennett et al. 1991, Qian and Ricklefs 1999), generating the complex signal we detect. For example, there is evidence that cold climates in northern and central regions and dry conditions in southern peninsulas have strongly shaped the tree species pool in Europe (Bennet et al. 1991, Willis 1996, Svenning 2003, Willis and van Andel 2004), and polar desert conditions near the ice-sheets and in recently deglaciated areas may have contributed to lagged recolonization by trees (migration lags) and delays in ecological communities establishment over newly available territories (Hewitt 1999, Svenning and Skov 2004, 2005). These conditions extended further south in Europe and North America (Hewitt 2000) and may have been crucial for diversity patterns of sessile organisms, likely generating non-linear responses of trees to global warming. Also, cell age implicitly makes the unlikely assumption that recolonizable land and non-glaciated regions (cell age = 20000 yr) are physically homogeneous, and ignores geographical barriers to migration and different dispersal capabilities of species. These potential effects cannot be directly evaluated with our data, which makes our analysis conservative with respect to modern climate. However, given that the older the effects are the more difficult they are to detect, and that cell age directly tracks the spatiotemporal pattern of ice retreat following the most recent glacial episode, it seems reasonable to consider cell age as an indicator that primarily describes the effects associated with glacial retreat, even though it might also include additional correlated effects. Consideration of different historical influences on diversity patterns of species represents an important line for future research.

In sum, following many authors we find that the main driver of the broad scale variation of tree richness in Europe and North America is the current climate, but unlike previous studies, we also find that the shrinking of ice sheets at the end of the Pleistocene has apparently left a detectable signal in the tree richness gradient, at least in the northern half of the Holarctic. Thus, a full understanding of contemporary species richness gradients requires an understanding of spatial patterns of climate change as well as static climatic patterns estimated at any point in time. Given the rapid rate as which climates are currently changing, this message seems particularly timely.

Appendix. Appendix 1 includes the source references to build tree richness maps for North America and Europa. Appendix 2 details the coefficients of the regression models used in the analysis. Appendix 3 includes a map of the tree richness distribution of Europe and North America at 110x110 Km^2 grain.

Acknowledgments

We thank M.A. Olalla-Tárraga and I.L. López for assistance with data preparation, and J.A.F. Diniz-Filho for assistance with the statistical analysis. We also thank J.-C. Svenning, R.J. Whittaker, and J.R.G. Turner for their comments and suggestions. This study was supported by the Spanish Ministry of Education and Science (grant REN2003-03989/GLO to M.A.R.). D.M. was supported by a FPU fellowship from the Spanish MEC (AP2004-0075).

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Appendix 1

SOURCE REFERENCES TO BUIL TREE RICHNESS MAPS FOR NORTH AMERI CA (1) AND EUROPE (2).

1. North America

The database comprises 676 North American tree species (defined as any woody plant growing to ?4 m anywhere in its range). Range maps were available for every spe cies and were taken primarily from Little (1971), supple mented with Elias (1980) and Hosie (1990).

North American refrences:

Elias, T. S. 1980. The Complete Trees of North America. Reinhold, New York.

Little, E. J. Jr. 1971. Atlas of United States Trees Vols 1-5. US Govt. Printing Office, Washington, DC.

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2. Europe

Plant families and their 187 tree species native to Western Europe were included. For each species, the "source type" code indicates whether its range map was establis hed by digitizing published maps ("m"), through written descriptions of its distribution ("d"), or by combining both methods ("m / d") when published maps only cove red its range partially (see references included in the last column and below the Table). Complete and partial range maps were used for 158 (84.5%), and 9 (5%) species, res pectively; and written descriptions of range distributions for 20 (11%) species. The latter were converted into maps following a three step process. First, we checked the digi tal version of Flora Europaea (ref. 28) to know the coun tries in which each species was present. Second, we sear ched national and regional floras, as well as the electro nic database EUNIS (ref. 8) for written descriptions of the presence of each species in specific areas and locali ties. And third, we reconstructed the range distribution map of the species by taking into account these informa tions. For one species (Arbutus andrachne) it was neces sary to take into account its habitats combined with the CORINE Land Cover database (ref. 9) to attain a finer picture of its distribution.

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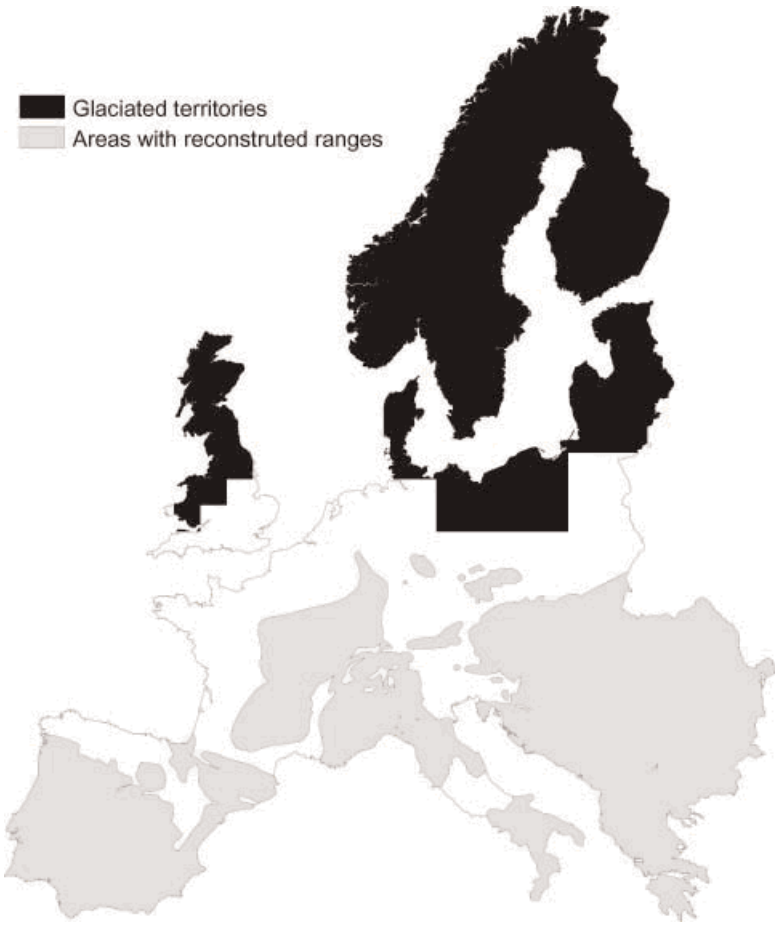
Family	Genus	Species	Source type	References
Aceraceae	*Acer*	*campestre*	m	10
Aceraceae	*Acer*	*granatense*	m	10
Aceraceae	*Acer*	*heldreichii*	m	11, 28
Aceraceae	*Acer*	*hyrcanum*	m	11, 28
Aceraceae	*Acer*	*lobelii*	m	10
Aceraceae	*Acer*	*monspessulanum*	m	10
Aceraceae	*Acer*	*obtusatum*	m	10
Aceraceae	*Acer*	*opalus*	m	10
Aceraceae	*Acer*	*platanoides*	m	10
Aceraceae	*Acer*	*pseudoplatanus*	m	10
Aceraceae	*Acer*	*tataricum*	m / d	11, 13, 28
Anacardiaceae	*Pistacia*	*atlantica*	m	11, 28
Anacardiaceae	*Pistacia*	*lentiscus*	m	10

Family	Genus	Species	Source type	References
Anacardiaceae	*Pistacia*	*terebinthus*	m	10
Anacardiaceae	*Rhus*	*coriaria*	m	10
Apocynaceae	*Nerium*	*oleander*	d	5, 21, 22, 23, 24, 26, 28
Aquifoliaceae	*Ilex*	*aquifolium*	m	10
Betulaceae	*Alnus*	*cordata*	m	10, 17
Betulaceae	*Alnus*	*glutinosa*	m	10, 17
Betulaceae	*Alnus*	*incana*	m	10, 17
Betulaceae	*Betula*	*pendula*	m	10, 17
Betulaceae	*Betula*	*pubescens*	m	10, 17
Buxaceae	*Buxus*	*balearica*	m	4, 28
Buxaceae	*Buxus*	*sempervirens*	m	10
Caprifoliaceae	*Sambucus*	*nigra*	m	10
Celastraceae	*Euonymus*	*europaeus*	m	10
Celastraceae	*Euonymus*	*latifolius*	m	10
Cornaceae	*Cornus*	*mas*	m	10
Corylaceae	*Carpinus*	*betulus*	m	10, 17
Corylaceae	*Carpinus*	*orientalis*	m	17
Corylaceae	*Corylus*	*colurna*	m	10, 17
Corylaceae	*Corylus*	*maxima*	m	10, 17
Corylaceae	*Ostrya*	*carpinifolia*	m	10, 17
Cupressaceae	*Cupressus*	*sempervirens*	m	10, 17
Cupressaceae	*Juniperus*	*communis*	m	10, 17
Cupressaceae	*Juniperus*	*drupacea*	m	18
Cupressaceae	*Juniperus*	*excelsa*	m	10, 17
Cupressaceae	*Juniperus*	*foetidissima*	m	10, 17
Cupressaceae	*Juniperus*	*navicularis*	d	6, 28
Cupressaceae	*Juniperus*	*oxycedrus*	m	10, 17
Cupressaceae	*Juniperus*	*phoenicea*	m	10, 17
Cupressaceae	*Juniperus*	*thurifera*	m	10, 17
Cupressaceae	*Tetraclinis*	*articulata*	m	10, 17
Elaeagnaceae	*Hippophae*	*rhamnoides*	m	10
Ericaceae	*Arbutus*	*andrachne*	d	8, 9, 12, 21, 28
Ericaceae	*Arbutus*	*unedo*	m	10
Ericaceae	*Erica*	*arborea*	m	10
Ericaceae	*Vaccinium*	*arctostaphylos*	d	8, 28
Fagaceae	*Castanea*	*sativa*	m	10, 17
Fagaceae	*Fagus*	*sylvatica* + subsp. *orientalis*	m	10, 17
Fagaceae	*Quercus*	*canariensis*	m	10, 17
Fagaceae	*Quercus*	*cerris*	m	10, 17
Fagaceae	*Quercus*	*coccifera*	m	10, 17
Fagaceae	*Quercus*	*congesta*	m	10, 17
Fagaceae	*Quercus*	*dalechampii*	m	10
Fagaceae	*Quercus*	*faginea*	m	10, 17
Fagaceae	*Quercus*	*frainetto*	m	10, 17
Fagaceae	*Quercus*	*hartwissiana*	m	17
Fagaceae	*Quercus*	*ilex*	m	10, 17
Fagaceae	*Quercus*	*macrolepis*	m	10, 17
Fagaceae	*Quercus*	*mas*	m	19
Fagaceae	*Quercus*	*pedunculiflora*	m	10, 17
Fagaceae	*Quercus*	*petraea*	m	10, 17
Fagaceae	*Quercus*	*polycarpa*	m	10
Fagaceae	*Quercus*	*pubescens*	m	10, 17
Fagaceae	*Quercus*	*pyrenaica*	m	10, 17
Fagaceae	*Quercus*	*robur*	m	10, 17
Fagaceae	*Quercus*	*suber*	m	10, 17
Fagaceae	*Quercus*	*trojana*	m	10, 17
Hippocastanaceae	*Aesculus*	*hippocastanum*	m	10
Juglandaceae	*Juglans*	*regia*	m	10, 17
Lauraceae	*Laurus*	*nobilis*	m	10, 17
Leguminosae	*Ceratonia*	*siliqua*	m	10
Leguminosae	*Cercis*	*siliquastrum*	m	10
Leguminosae	*Laburnum*	*alpinum*	m	10

Family	Genus	Species	Source type	References
Leguminosae	*Laburnum*	*anagyroides*	m	10
Moraceae	*Ficus*	*carica*	m	10, 17
Oleaceae	*Fraxinus*	*angustifolia*	m	10
Oleaceae	*Fraxinus*	*excelsior*	m	10
Oleaceae	*Fraxinus*	*ornus*	m	10
Oleaceae	*Fraxinus*	*pallisiae*	m	11, 28
Oleaceae	*Olea*	*europaea*	m	10
Oleaceae	*Phillyrea*	*latifolia*	m	10
Oleaceae	*Syringa*	*josikaea*	d	2, 28
Oleaceae	*Syringa*	*vulgaris*	m	10
Pinaceae	*Abies*	*alba*	m	10, 17
Pinaceae	*Abies*	*cephalonica*	m	10, 17
Pinaceae	*Abies*	*pinsapo*	m	10, 17
Pinaceae	*Abies*	*sibirica*	m	10, 17
Pinaceae	*Larix*	*decidua*	m	10, 17
Pinaceae	*Larix*	*sibirica*	m	10, 17
Pinaceae	*Picea*	*abies*	m	10, 17
Pinaceae	*Picea*	*omorika*	m	10, 17
Pinaceae	*Pinus*	*cembra*	m	10, 17
Pinaceae	*Pinus*	*halepensis*	m	10, 17
Pinaceae	*Pinus*	*heldreichii* + var. *leucodermis*	m	10, 17
Pinaceae	*Pinus*	*nigra*	m	10, 17
Pinaceae	*Pinus*	*peuce*	m	10, 17
Pinaceae	*Pinus*	*pinaster*	m	10, 17
Pinaceae	*Pinus*	*pinea*	m	10, 17
Pinaceae	*Pinus*	*sylvestris*	m	10, 17
Pinaceae	*Pinus*	*uncinata*	m	10, 17
Platanaceae	*Platanus*	*orientalis*	m	20
Rhamnaceae	*Frangula*	*alnus*	m	10
Rhamnaceae	*Rhamnus*	*catharticus*	m	10
Rosaceae	*Crataegus*	*calycina*	m	16, 28
Rosaceae	*Crataegus*	*laciniata*	d	1, 6, 8, 12, 27, 28
Rosaceae	*Crataegus*	*monogyna*	m	10
Rosaceae	*Crataegus*	*nigra*	d	1, 3, 7, 14, 25, 26, 28
Rosaceae	*Crataegus*	*pentagyna*	d	1, 2, 7, 14, 26, 28
Rosaceae	*Malus*	*dasyphylla*	d	1, 2, 7, 12, 25, 26, 27, 28
Rosaceae	*Malus*	*florentina*	m / d	13, 22, 28
Rosaceae	*Malus*	*sylvestris*	m	10
Rosaceae	*Mespilus*	*germanica*	m	10
Rosaceae	*Prunus*	*avium*	m	10
Rosaceae	*Prunus*	*brigantina*	m / d	5, 22, 28
Rosaceae	*Prunus*	*cerasifera*	m	10
Rosaceae	*Prunus*	*cocomilia*	m / d	8, 22, 28
Rosaceae	*Prunus*	*domestica*	m	11, 28
Rosaceae	*Prunus*	*laurocerasus*	m / d	11, 13, 28
Rosaceae	*Prunus*	*lusitanica*	m	10
Rosaceae	*Prunus*	*mahaleb*	m	10
Rosaceae	*Prunus*	*padus*	m	10
Rosaceae	*Prunus*	*webbii*	m	22, 28
Rosaceae	*Pyrus*	*amygdaliformis*	m	10
Rosaceae	*Pyrus*	*austriaca*	d	14, 15, 28
Rosaceae	*Pyrus*	*bourgaeana*	m / d	6, 11, 28
Rosaceae	*Pyrus*	*cordata*	m	10
Rosaceae	*Pyrus*	*elaeagrifolia*	m	11, 28
Rosaceae	*Pyrus*	*magyarica*	d	26, 28
Rosaceae	*Pyrus*	*nivalis*	m / d	1, 3, 13, 15, 22, 23, 25, 26, 28
Rosaceae	*Pyrus*	*pyraster*	m	13, 28
Rosaceae	*Sorbus*	*aria*	m	10
Rosaceae	*Sorbus*	*aucuparia*	m	10
Rosaceae	*Sorbus*	*austriaca*	d	13, 28
Rosaceae	*Sorbus*	*dacica*	d	2, 28

Family	Genus	Species	Source type	References
Rosaceae	*Sorbus*	*domestica*	m	10
Rosaceae	*Sorbus*	*graeca*	d	1, 2, 3, 12, 13, 15, 25, 27, 28
Rosaceae	*Sorbus*	*hybrida*	m	16, 28
Rosaceae	*Sorbus*	*intermedia*	m	10
Rosaceae	*Sorbus*	*latifolia*	d	1, 6, 13, 23, 28
Rosaceae	*Sorbus*	*meinichii*	m	16, 28
Rosaceae	*Sorbus*	*mougeotii*	m / d	11, 13, 28
Rosaceae	*Sorbus*	*torminalis*	m	10
Rosaceae	*Sorbus*	*umbellata*	m	11, 28
Salicaceae	*Populus*	*alba*	m	10, 17
Salicaceae	*Populus*	*canescens*	m	10, 17
Salicaceae	*Populus*	*nigra*	m	10, 17
Salicaceae	*Populus*	*tremula*	m	10, 17
Salicaceae	*Salix*	*acutifolia*	m	10, 17
Salicaceae	*Salix*	*aegyptiaca*	m	10, 17
Salicaceae	*Salix*	*alba*	m	10, 17
Salicaceae	*Salix*	*appendiculata*	m	10, 17
Salicaceae	*Salix*	*atrocinerea*	m	10, 17
Salicaceae	*Salix*	*borealis*	m	10
Salicaceae	*Salix*	*caprea*	m	10, 17
Salicaceae	*Salix*	*daphnoides*	m	10, 17
Salicaceae	*Salix*	*fragilis*	m	10, 17
Salicaceae	*Salix*	*pedicellata*	m	10, 17
Salicaceae	*Salix*	*pentandra*	m	10, 17
Salicaceae	*Salix*	*pyrolifolia*	m	10, 17
Salicaceae	*Salix*	*salviifolia*	m	10, 17
Salicaceae	*Salix*	*triandra*	m	10, 17
Salicaceae	*Salix*	*viminalis*	m	17
Salicaceae	*Salix*	*xerophila*	m	10, 17
Styracaceae	*Styrax*	*officinalis*	m	11, 28
Tamaricaceae	*Tamarix*	*africana*	m	10
Tamaricaceae	*Tamarix*	*boveana*	m	10
Tamaricaceae	*Tamarix*	*canariensis*	m	10
Tamaricaceae	*Tamarix*	*dalmatica*	m / d	8, 22, 28
Tamaricaceae	*Tamarix*	*gallica*	m	10
Tamaricaceae	*Tamarix*	*hampeana*	d	8, 12, 28
Tamaricaceae	*Tamarix*	*parviflora*	d	12, 28
Tamaricaceae	*Tamarix*	*smyrnensis*	d	2, 8, 12, 28
Tamaricaceae	*Tamarix*	*tetrandra*	d	8, 12, 28
Taxaceae	*Taxus*	*baccata*	m	10, 17
Tiliaceae	*Tilia*	*cordata*	m	10
Tiliaceae	*Tilia*	*platyphyllos*	m	10
Tiliaceae	*Tilia*	*rubra*	m	11, 28
Tiliaceae	*Tilia*	*tomentosa*	m	11, 28
Ulmaceae	*Celtis*	*australis*	m	10, 17
Ulmaceae	*Celtis*	*caucasica*	m	10, 17
Ulmaceae	*Celtis*	*tournefortii*	m	10, 17
Ulmaceae	*Ulmus*	*glabra*	m	10, 17
Ulmaceae	*Ulmus*	*laevis*	m	10, 17
Ulmaceae	*Ulmus*	*minor*	m	10, 17
		+ subsp. *canescens*		
		+ *procera*		

Figure 1. European territories covered by ice during the last Pleistocene glaciation and areas including tree species for which only partial range maps (*Acer tataricum, Malus florentina, Prunus brigantina, P. cocomilia, P. laurocerasus, Pyrus bourgaeana, P. nivalis, Sorbus mougeotii, Tamarix dalma tica*), or no maps were found (*Arbutus andrachne, Cotoneaster granatensis, Crataegus laciniata, C. nigra, C. pentagyna, Juniperus navicularis, Malus dasyphylla, Nerium oleander, Pyrus austriaca, P. magyarica, Sorbus austriaca, S. dacica, S. graeca, S. latifolia, Syringa josikaea, Tamarix hampeana, T. parviflora, T. smyrnensis, T. tetrandra, Vaccinium arctostaphylos*). The range maps of these species were drawn by taking into account published des criptions of their areas of distribution. This was not necessary for any of the tree species present in the glaciated territories, as for all of them a comple te range map was found in the literature.



Appendix 2

COEFFICIENTS OF REGRESSION MODELS.

Table 1. Summary of regression models for tree richness using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age.

Model type	Predictors in model					
A) Glaciated regions						
RWEM1	0.724*Rainfall	-0.740*minPET$_{Th}$	0.486*minPET$_{Th}^2$			
	0.548*Rainfall	-0.590*minPET$_{Th}$	0.295*minPET$_{Th}^2$	0.445*Age		
RWEM2	0.731*Rainfall	-0.740*minPET$_{Th}$	0.482*minPET$_{Th}^2$	0.064*Ln(ER)		
	0.551*Rainfall	-0.590*minPET$_{Th}$	0.295*minPET$_{Th}^2$	0.024*Ln(ER)	0.443*Age	
F&C	-0.530*WD	0.518*PET$_{PT}$	0.600*PET$_{PT}^2$			
	-0.480*WD	0.386*PET$_{PT}$	0.578*PET$_{PT}^2$	0.278*Age		
ad hoc	0.229*Rainfall	0.443*PET$_{PT}$	0.133*PET$_{PT}^2$	0.089*Ln(ER)	0.207*PGS	
	0.238*Rainfall	0.422*PET$_{PT}$	0.110*PET$_{PT}^2$	0.039*Ln(ER)	0.067*PGS	0.238*Age
B) Entire regions						
RWEM1	0.791*Rainfall	0.204*maxPET$_{Th}$	-0.130*maxPET$_{Th}^2$			
	0.710*Rainfall	0.234*maxPET$_{Th}$	-0.180*maxPET$_{Th}^2$	0.207*Age		
RWEM2	0.820*Rainfall	0.293*maxPET$_{Th}$	-0.210*maxPET$_{Th}^2$	0.122*Ln(ER)		
	0.736*Rainfall	0.289*maxPET$_{Th}$	-0.230*maxPET$_{Th}^2$	0.079*Ln(ER)	0.188*Age	
F&C	-0.730*WD	1.510*PET$_{PT}$	-0.350*PET$_{PT}^2$			
	-0.730*WD	1.340*PET$_{PT}$	-0.250*PET$_{PT}^2$	0.145*Age		
ad hoc	0.650*Rainfall	0.781*PET$_{PT}$	-0.450*PET$_{PT}^2$			
	0.612*Rainfall	0.715*PET$_{PT}$	-0.420*PET$_{PT}^2$	0.060*Age		

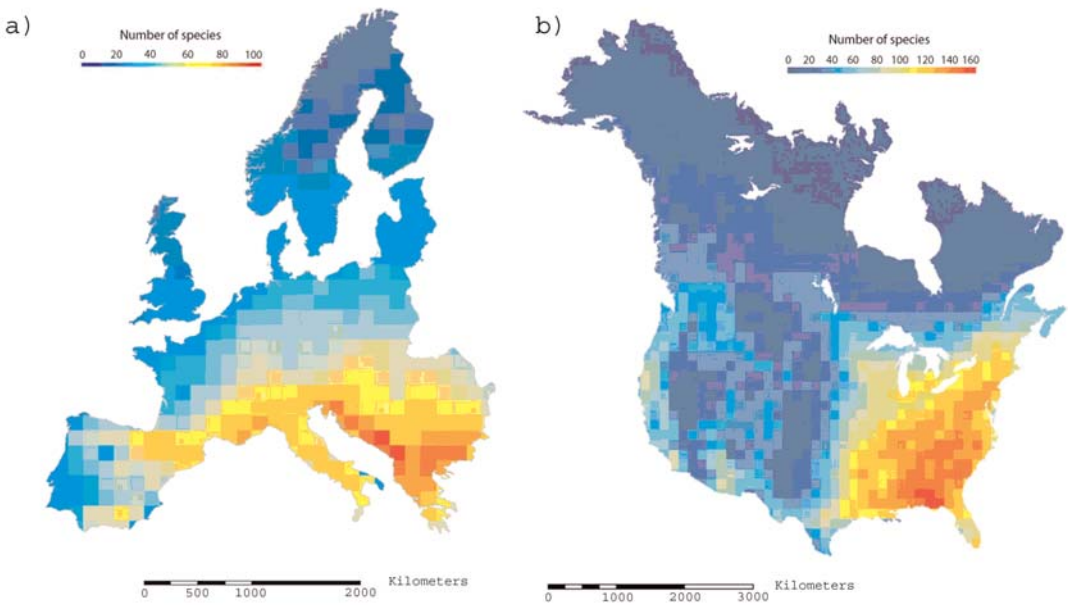
Predictors: rainfall=total precipitation in months when mean temperature >0ºC; maxPET$_{Th}$=maximum monthly potential evapotranspiration (Thornwaite's formula); minPET$_{Th}$=minimum monthly potential evapotranspiration (Thornwaite's formula); ER=elevation range (O'Brien 1993, 1998, Field et al. 2005); PET$_{PT}$=annual potential evapotranspiration (Presley-Taylor formula);WD=water deficit (Francis and Currie 2003); PGS=potential growing season (O'Brien 1993, 1998); TempRange=annual temperature range (Currie and Paquin 1987, Adams and Woodward 1989); Age=number of years cell exposed after glacial retreat; RWEM1=regio-

Essentially, the relationship between tree richness and water and energy is positive across Europe and North America (Table 1B), with higher energy-water inputs increasing richness levels: highest richness is found in hot and wet areas. Water deficit is negatively related to tree richness, indicating that water stress constraints the number of species. Elevation range, a measure of the mesoscale vertical climatic variation, is positively associated to richness, given that highly heterogeneous regions encompass more species. For glaciated regions together and glaciated North America (Tables 1A, 2B), these relationships hold except for minPET$_{Th}$, which has negative coefficients. We believe this is because minPET$_{Th}$ represents the energy of the coldest month and above a certain line of latitude its value drops to zero. This is the likely reason why RWEMs generally perform worst in our study areas. PGS reflects favourable conditions for trees to grow and reproduce and is positively associated to tree richness in the models. Glaciated Europe (Table 2A) shows some intri guing coefficients which differ from the general pattern. Rainfall is negatively associated with rich ness. That tree richness at higher latitudes is not restricted by water but energy is commonly argued, but North America indeed has positive rainfall coefficients. One possible explanation is that different climatic patterns between the continents result in trees growing in glaciated Europe more stressed by excessive water and flooded soils. This is supported by the WD coefficients: richness increases with WD, in contrast to glaciated North America. Also, historical factors might be driving richness in glaciated Europe more strongly than in glaciated North America, as paleoecological studies have shown. MaxPET$_{Th}$ also has negative coefficients. We believe maxPET$_{Th}$ is not a good energy measure (it measures energy in the warmest month); in fact, a positive relationship between energy and tree richness is shown in F&C model, which uses PET$_{PT}$ instead of maxPET$_{Th}$, and the F&C model globally performs better than RWEMs

in temperate regions. Elevation range is negatively associated with tree richness. In northern regions, high altitudes represent cold conditions unfavourable to tree's growth, and elevation range conse quently relates negatively to richness. Although ln(ER) has positive coefficients in glaciated North America (Table 2B) and across both glaciated regions (Table 1A), its coefficients are very low, even shifting to negative values (RWEM2 + Age, Table 2B). Range in elevation may have more influence on tree richness at more local scales. Age is positively associated with tree richness in every model and region analyzed (Tables 1, 2), indicating that longer times of land availability for trees (free of ice) are associated with higher richness.

Appendix 3

TREE RICHNESS DISTRIBUTION FOR EUROPE AND NORTH AMERICA AT 110 KM^2 GRAIN. SCALE IS PROVIDED.



3. Habitat loss, dispersal and species extinction

Daniel Montoya, Miguel A. Zavala, Miguel A. Rodríguez & Drew W. Purves

Article published in *Science* **320**, 1502-1504 (2008)

Capítulo 3

Dispersión animal frente a dispersión anemócora y la vulnerabilidad de las especies de árboles a la deforestación

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Montoya, D., Miguel A. Zavala, Miguel A. Rodríguez and Drew W. Purves (2008). Animal Versus Wind Dispersal and the Robustness of Tree Species to Deforestation. Science 320, 1502-1504.

Resumen

Estudios en ecología sugieren que las poblaciones de diferentes especies no declinan de la misma forma después de la pérdida de hábitat. Sin embargo, los tests empíricos para confirmar este patrón han sido restringidos a escalas espacio-temporales pequeñas y pocas veces han incluido plantas. Utilizando datos de 89365 puntos de muestreo que cubren la superficie forestal de la España continental, exploramos la relación entre la probabilidad de ocurrencia de 34 especies de árboles y la cobertura local de bosque. 24 especies mostraron respuestas negativas significativas a la pérdida de bosque, lo que indica que la pérdida de cobertura forestal tiene un efecto negativo sobre la diversidad de árboles, aunque las respuestas de las especies individuales fueron altamente variadas. Las especies de dispersión animal fueron menos vunerables a la pérdida de bosque, y seis de ellas mostraron respuestas positivas a dicha pérdida. Estos resultados implican que las interacciones planta-animal son imporatntes para prevenir el colapso de las comunidades forestales que sufren el impacto de la destrucción del hábitat.

Science 320, 1502- 1504 (2008)
doi: 10.1126/science.1158404

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

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Abstract

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.

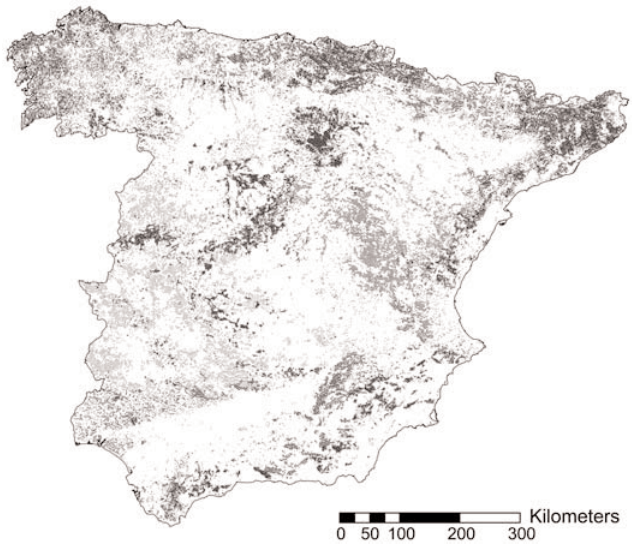

Figure 1. Distribution of survey sites in peninsular Spain. IFN2 consisted of 89,365 circular sampling sites (radius = 25 m) distributed across peninsular Spain (average density approximately one per square kilometer). Survey sites were placed in continuous forest locations, so their distribution matches that of the remaining forest.

We analyzed the relationship between local forest cover and the occurrence of 34 canopydominant 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 thethe 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 = 80% and H_q = 0. Such abrupt changes could reflect the effects of spatial configuration (that is, fragmentation) when habitat cover goes from nearly con

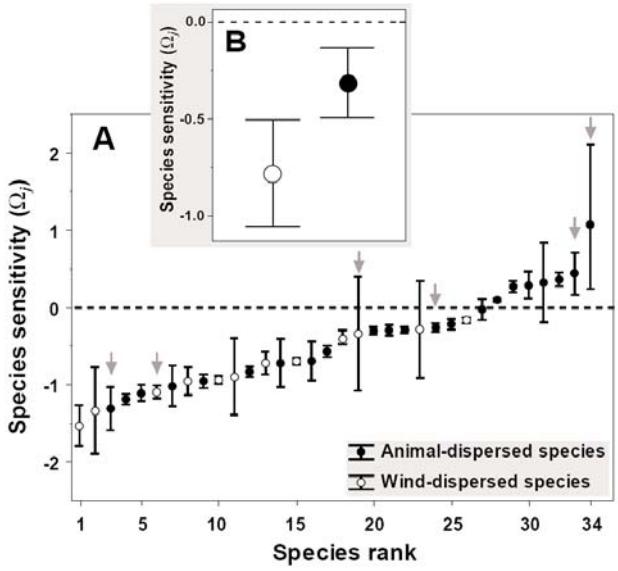

Figure 2. (**A**) Sensitivity of 34 Spanish tree species to reduction in local forest cover (Ω_j), estimated using the maximum likelihood estimate of the parameters of a logistic regression relating the probability of occurrence of species *j* to local forest cover. Gray arrows indicate non-native species. 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.

tinuous 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%.

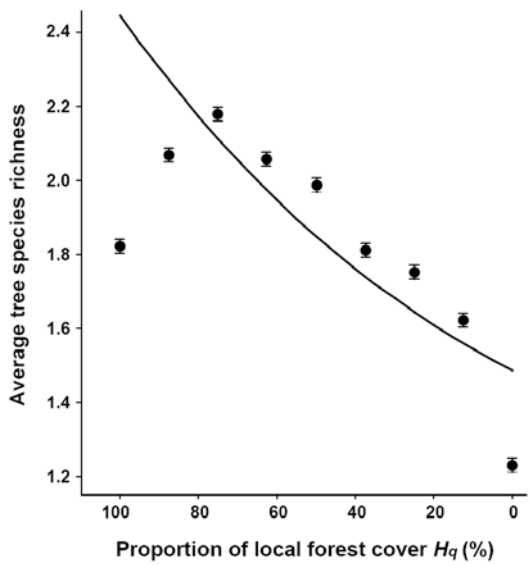

Figure 3. Tree species richness (average number of species occurring in a 25-m-radius circular plot) versus local forest cover H_q: observed (points) an from the logistic regression (line, calculated by summing the predicted probability of occurrence over the 34 species). Error bars are standard errors 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.

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 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 phylogenetic 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 describes 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 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.

Supporting Online Material. Material and methods. Figures S1 to S3. Tables S1 to S4. References.

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SUPPORTING ONLINE MATERIAL
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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 cli mates), 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 1 x 1 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

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

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

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

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

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

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

Where $P(j,H_q)$ is calculated using the MLE estimates for the parameters M_j and C_j. Note that a negative j implies a negative response of occurrence to reduced local forest cover. Also, the logarithmic scale makes the relationship between j and the proportional reduction in occurrence non-linear: for example, j = -2 implies an 86% reduction in occurrence, -1 implies 63% reduction, -0.5 implies 40% reduction, and +1 implies a 170% increase in occurrence.

To produce confidence intervals on j for each species, we used the following simple error propagation approach: (1) extract, for M_j and C_j, the lower and upper 95% confidence interval; (2) generate the four combinations of M_j and C_j that can be given by combining these lower and upper estimates; (3) apply eq. S3 using calculated from each of the four combinations; (4) report the highest and lowest j values from the four calculated values. This method allows for independent variation in M_j and C_j, and allows for both parameters to be simultaneously at the edge of their 5% confidence interval. It is therefore a conservative method compared to a formal error propagation: i.e., the reported intervals are larger than those that would have been produced from formal error propagation.

Permutation Test

We ranked species j (species 1, species2,…, species 34), so the average position of an animal- and wind-dispersed

species in that list could be obtained. The difference between the average position numbers was used as a test statistic to evaluate the probability of obtaining, by chance, the observed difference in average rank between wind- and animal-dispersed species. 10,000 sets of random species ranks were produced, where each species was assigned a rank (1-34) at random. For each of these 10,000 sets, the difference between the average rank for animal vs wind-dispersed species was calculated. This yielded a frequency distribution of the difference between the groups, corresponding to a null hypothesis of no true difference in *j* between the groups. We then noted where the observed value of the difference between the groups lay in the frequency distribution, which corresponded to the probability of obtaining the observed difference without a true difference between the groups.

Phylogenetic analyses

The amount of phylogenetic signal in $\boldsymbol{\Omega_j}$ was quantified with Phylogenetic eigenVector Regression (PVR; S5). This method tests whether species traits (in this case, $\boldsymbol{\Omega_j}$) are significantly associated with phylogeny, partitioning the phenotypic variation in a certain trait into phylogenetic (among lineages, **P**) and nonphylogenetic or specific (within species, **S**) components, based on multivariate analysis ($\boldsymbol{\Omega_j} = \mathbf{P} + \mathbf{S}$). The idea is that phylogeny can be expressed as a set of orthogonal vectors obtained by an eigenanalysis of a phylogenetic distance matrix. These vectors can then be used as predictors of $\boldsymbol{\Omega_j}$ in any form of linear or non-linear modelling.

The starting point is the construction of the phylogenetic distance matrix **D**, for which we used the phylogeny for existing seed-plant families hosted in the Webpage of the Missouri Botanical Garden, and that has been compiled and is being continuously updated by P. F. Stevens using different sources (the phylogeny and details about its construction are available at: www.mobot.org/MOBOT/research/APweb/) (accessed, December 2007). For each possible pair of species in **D**, we considered that their phylogenetic distance was the minimum number of nodes connecting them in the phylogeny. Then, we used principal coordinates analysis (PCoA) to extract eigenvalues and eigenvectors from this matrix after performing a double-center transformation (the row and column means were substracted from each element and the grand mean was added, after transforming original distances into $-0.5D_{ij}^2$). We used the coefficients of the eigenvectors of **D** as the coordinates of the species in the reduced multivariate space expressing variation among them in the hyperspace defined by phylogenetic relatedness (numerical details about PVR calculations are provided in *S5*).

The first three eigenvectors from the PVR explained most of the phylogenetic structure existing in **D** (Table *S2*), and were identified as capturing meaningful phylogenetic relationships by a scree-plot + 1 procedure, a conservative method of eigenvector selection (*S6*). Accordingly, to test whether there were differences between wind- and animal-dispersed species in terms of $\boldsymbol{\Omega_j}$ that are independent of phylogenetic inertia, we included these eigenvectors as covariables in an analysis of covariance (ANCOVA) in which the response and explanatory variables were $\boldsymbol{\Omega_j}$ and dispersal mode, respectively. The two groups (animal dispersed, wind dispersed) showed significantly different mean $\boldsymbol{\Omega_j}$ values, either when considering all 34 species, or when analyzing only the 28 species that are native to the study region (Table *S3a, b*). Therefore, we concluded that the difference in average $\boldsymbol{\Omega_j}$ between wind-dispersed and animal-dispersed species was not caused by phylogenetic autocorrelation.

Multicollinearity

In addition to the effects of habitat cover, each tree species is likely to be affected by the gradients in climate, soil and fire frequency occurring in the study region, raising the possibility that apparent responses to habitat cover (and any apparent differences in response among species) are driven by environmental factors correlated with habitat cover (multicollinearity). This problem occurs in any study of species occurrence *vs*. habitat

cover, except in the rare cases where the habitat gradient has been exposed experimentally. To assess the sensitivity of our conclusions to this problem, we first extracted, for each survey site, a set of 18 climatic, topographic and soil variables (listed in Table *S4*) which might be critical to plant physiological function and survival in the Mediterranean and Atlantic systems. Principal component analysis showed no multicollinearity between forest cover and these variables (Table *S4*). This showed that, at the scale of peninsular Spain, forest cover varies almost independently of climate, topography, soil, and major perturbation events (Figure *S3*), making mutlicollineariy an unlikely explanation of the results.

As an additional check, we performed combined species-specific logistic regression that included included environmental variables (the axis scores from the PCA described above) and forest cover, in order to extract estimates for Ω_j controlled for environmental factors (Fig. *S3*). The pattern of interspecific variation in Ω_j was not qualitatively altered by including environmental variables (compare Fig *S3* with Fig. 2), and the difference in Ω_j between animal- and wind-dispersed species remained statistically significant (permutation test: $p < 0.005$).

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Table S1. List of tree species included in the analysis. Dispersal mode is indicated. Parameter estimates of the logistic regression models (M_j, C_j) are provided for each species, together with Ω_j calculated at the MLE estimates for M_j and C_j. Species are given in rank order of Ω_j (a negative Ω_j implies a negative response to forest loss). Exotic species are highlighted in bold.

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

Table S2. Eigenvectors generated by the eigenanalysis of the phylogenetic distance matrix **D** among tree species. The first three eigenvectors explained 92.5% of the phylogenetic signal and are emphasized in grey. These eigenvectors were identified by the scree-plot + 1 method as the most meaningful ones (*6*) and used as covariables in ANCOVA analysis.

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

Table S3. Phylogenetically-controlled analysis of covariance (ANCOVA) on Ω_j. The first 3 eigenvectors generated by the eigenanalysis of the phylogenetic distance matrix were used as covariates. (**A**) Results for native and exotic species (N = 34). (**B**) Results for native species only (N = 28). (SS = Sum of squares; df = Degrees of freedom; MS = Mean of squares).

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		

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		

Table S4. List of environmental variables included in the principal component analysis (PCA). The list includes climatic, topographic, soil and disturbance variables that the authors considered might be important to tree physiological function and survival in Mediterranean and Atlantic ecosystems. Each variable was estimated for each survey plot. The PCA shows that local forest habitat cover (H_q) is an independent factor not related to climate, topography, soil or fire disturbance (factor 3).

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

Figure S1. Sensitivity of tree species to reductions in forest cover (Ω_j) as a function of seed size. Species are ranked by Ω_j. Bubble size is proportional to seed weight. White symbols are animal-dispersed species; gray symbols are wind-dispersed species. Only 23 species are shown, because seed weights were not available for the other species.

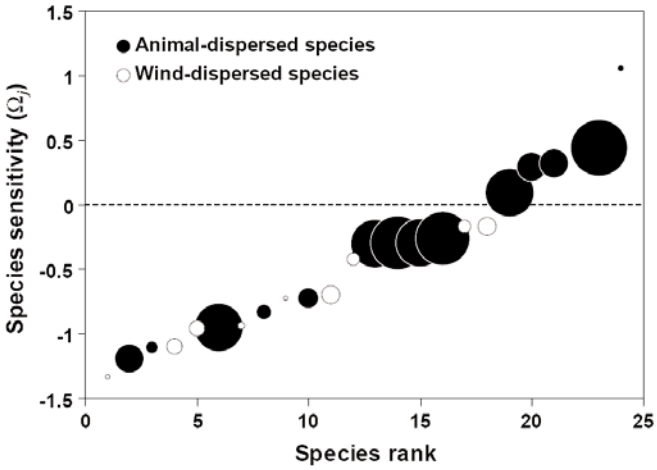
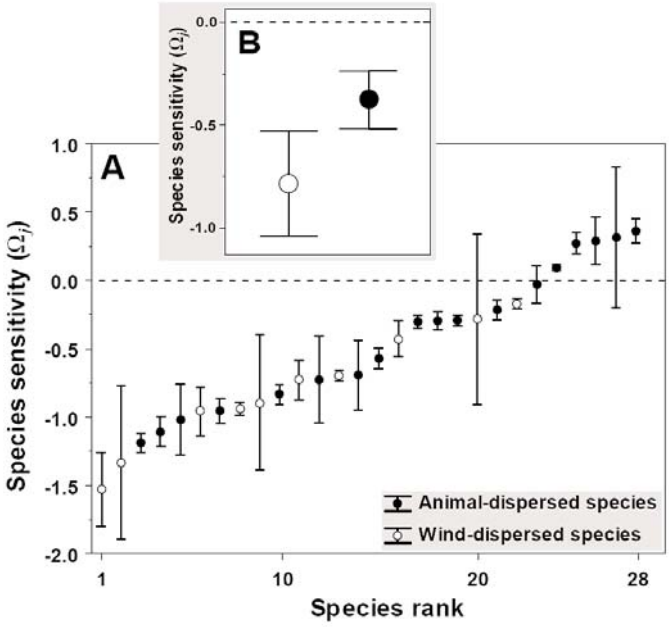


Figure S2. (**A**) Sensitivity of tree species to forest habitat loss Ω_j (at 1 Km) for native species only (N=28). Results from permutation test for average difference between animal- and wind-dispersed species: p<0.05. (**B**) Average Ω_j for native wind-dispersed species (n=10) and native animal-dispersed species (n=18). Error bars are 95% confidence intervals on the mean Ω_j for each group.



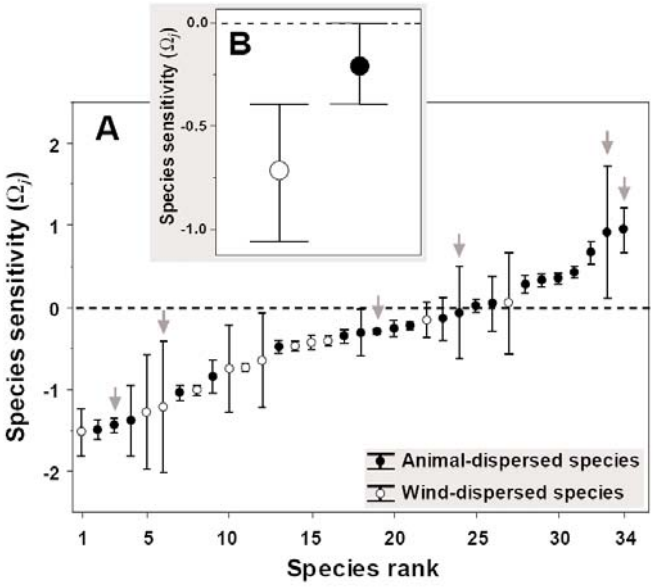


Figure S3. (**A**) Sensitivity of tree species to reductions in forest cover Ω_j after controlling for environmental factors. Results from permutation test for average difference between animal- and wind-dispersed species: p<0.05. (**B**) Average Ω_j of wind-dispersed species (n=12) and animal-dispersed 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.

4. Habitat fragmentation and the extinction threshold

Daniel Montoya, Fabio S. Alburquerque, Marta Rueda & Miguel A. Rodríguez

Article submitted to *Oikos (In review)*

Capítulo 4

Patrones de respuesta de las especies a la fragmentación del hábitat: ¿confirman los árboles la hipótesis del umbral de extinción?

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Montoya, D., Alburquerque, F. S., Rueda, M. & Rodríguez, M. A. Species' response patterns to habitat fragmentation: do trees support the extinction threshold hypothesis?. *In review in Oikos*.

Resumen

En paisajes fragmentados, la relación entre la probabilidad de ocurrencia de las especies y la cantidad de hábitat disponible habitualmente no es proporcional, existiendo un umbral de cantidad de hábitat por debajo del cual las poblaciones se extinguen. La teoría ecológica predice que, aunque el umbral de extinción es una consecuencia directa de la pérdida cuantitativa de hábitat, la fragmentación del hábitat - los cambios cualitativos en la configuración espacial del hábitat remanente - podría influir en la localización de este umbral reduciendo su aparición a niveles más bajos de cantidad de hábitat. Sin embargo, existe mucha incertidumbre acerca de la validez de la hipótesis del umbral de extinción. En este trabajo llevamos a cabo análisis sobre las relaciones entre la probabilidad de ocurrencia de ocho especies de árboles y la disponibilidad de hábitat forestal para dos escenarios empíricos diferentes de baja *y* moderada-alta fragmentación. Dividimos los efectos de pérdida de hábitat *vs*. fragmentación mediante el uso de dos variables: (i) porcentage de cubierta forestal, y (ii) proporción de este porcentaje que abarca la mancha de bosque más grande. Encontramos que, a pesar de que la pérdida de cubierta forestal tuvo efectos negativos en la ocurrencia de las especies arbóreas independiemtemente de los niveles de fragmentación, la fragmentación del bosque modificó significativamente el umbral de extinción en seis especies, aunque sólo una de ellas confirmó la hipótesis del umbral de extinción. Para la mayoría de las especies la fragmentación o bien no afectó significativamente o bien tuvo efectos positivos en la probabilidad de ocurrencia de las especies. Ésto indica que los efectos de la fragmentación del hábitat en las especies de árboles son débiles comparados con los efectos de la cantidad de hábitat disponible, que es el factor principal de la extinción de especies en paisajes fragmentados. Estos resultados también sugieren que las especies 'especialistas de bosque' - especies que están más intrínsicamente asociadas al hábitat forestal - y las especies con capacidades dispersivas limitadas se ven afectadas de forma severa por la fragmentación del bosque, y por lo tanto, la hipótesis del umbral de extinción tiene mayor probabilidad de verse confirmada en estas especies.

Species' response patterns to habitat fragmentation: do trees support the extinction threshold hypothesis?

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Abstract

In fragmented landscapes the relationship between the probability of occurrence of single species and the amount of suitable habitat is usually not proportional, with a threshold habitat level below which the population becomes extinct. Ecological theory predicts that, although the extinction threshold is a direct consequence of habitat loss - i.e. the quantitative removal of habitat -, habitat fragmentation - i.e. changes in the spatial configuration of the remaining suitable habitat - might affect the location of this threshold by reducing its predicted occurrence to lower levels of habitat amount. However, little is known about the validity of this extinction threshold hypothesis. Here, we performed analyses on the relationships between the probability of occurrence of eight tree species and the availability of forest habitat for two different empirical scenarios of low and moderate to high fragmentation. We partitioned the effects of habitat amount *vs*. fragmentation by using two metrics: (i) the percentage of forest cover, and (ii) the proportion of this percentage occurring in the largest forest patch. We find that, although decreasing forest cover had negative effects on the occurrence of tree species irrespective of fragmentation levels, forest fragmentation significantly modified the extinction threshold in six tree species, although only one species confirmed the extinction threshold hypothesis. For most species, fragmentation either had positive effects or did not affect significantly the species' probability of occurrence. This indicates that the effects of habitat fragmentation on tree species are weak relative to the effects of habitat amount, which is the main determinant of species extinction in fragmented landscapes. These results also suggest that forest-specialist tree species -i.e. species that are more closely linked to forest habitat - and species with low dispersal ability are severely affected by forest fragmentation, and thus, the extinction threshold hypothesis is more likely confirmed in these species.

Introduction

The current, massive anthropogenic alteration of natural habitats is one main threat to terrestrial biodiversity (Baille et al. 2004). Recent changes in habitat availability have been observed to affect species richness patterns (e.g. Bascompte and Rodríguez 2001, Montoya et al. 2008), population abundance and distributions (Lande 1987, Hanski et al. 1996, Venier and Fahrig 1996, Donovan and Flather 2002), species range sizes (Purvis et al. 2000), population growth rates (Bascompte et al. 2002), trophic chain lengths (Komonen et al. 2000), species interactions (Taylor and Merriam 1995, Fortuna and Bacompte 2006), animal body sizes (McKinney 1997, Cardillo and Bromham 2001), and genetic diversity (Gibbs 2001). These studies and many others (Fahrig 2003) demonstrate that the modification of habitat areas where species grow and interact may significantly alter the ecological structure and dynamics of ecosystems, as well as drive individual species to extinction.

Human-impacted habitats typically appear fragmented -i.e. broken into more or less isolated patches-, for which the expression habitat fragmentation has been commonly used as a general term encapsulating the variety of patterns and processes that accompany landscape change (Lindenmayer and Fischer 2006). However, as noted by Fahrig (2003), a clear distinction between the *per se* consequences of habitat loss and habitat fragmentation (i.e., of the rupture of habitat after controlling for habitat loss) is needed to understand how this whole phenomenon operates. From the comprehensive review of empirical studies made by this author (see Fahrig 2003), it seems that whereas habitat loss *per se* effects on biodiversity are strong and consistently negative, those of habitat fragmentation *per se* are much weaker and at least as likely to be positive as negative. This contradicts the findings of several theoretical studies indicating that fragmentation per se aggravates the effects of habitat loss (e.g. Bascompte and Solé 1996, Boswell et al. 1998, Hill and Caswell 1999, Solé and Bascompte 2007). The conclusions of these theoretical studies are summarized by the extinction threshold hypothesis (reviewed by Fahrig 2002), which predicts that fragmentation causes (1) an accelerated decrease of population sizes across the gradient of shrinking habitat, and (2) a sooner appearance in this gradient of the so called extinction threshold (i.e. the amount of habitat below which the population cannot sustain itself and goes extinct). However, there have been very few empirical investigations addressing this hypothesis (e.g. Jansson and Angelstam 1999) and the validity of these predictions begs for empirical tests (Fahrig 2002, 2003).

An important issue for any habitat-related study is its definition of habitat. According to Hall et al. (1997) and Lindenmayer and Fischer (2006), the precise meaning of this term refers to the resources and conditions present in an area that produce occupancy for a particular species. Because of the species-specific nature of this definition, habitat loss and fragmentation are also species-specific entities (see Lindenmayer and Fischer 2006) and should be treated as such by any strict analysis of species-habitat relationships. This habitat definition is the one implicitly assumed in theoretical studies (and, hence, in the extinction threshold hypothesis), as modeled species and habitats posses the attributes that the researcher has assigned to them. However, for empirical studies, particularly for those involving several species, using this precise definition is not possible in many instances, as it requires an in depth information of the key habitat needs of every species, which is unlikely to be available in advance in many instances. This explains why a common, operational practice is to focus not on habitats, but on vegetation types (e.g. forest) or land uses, and on species that are believed to be strongly linked to them (e.g. forest species) (see Lindenmayer and Fischer 2006). Investigating species reactions to changes in these habitat proxies has the inherent, practical interest that vegetation and land use types are common references for decision making in conservation. Further, although theory-derived predictions of species-habitat relationships cannot be expected to apply fully when using these habitat proxies, to what extent they do also merits evaluation. Indeed, for the particular case of the extinction threshold hypothesis, if it was observed that many species fitted its

predictions, then this would send a clear applied message: that fragmentation of the focal vegetation (or land use) type does generally limit species' persistence and, hence, should be taken into account in multispecies conservation plans.

In the present study we built on the findings of a previous broad-scale investigation that involved ~90,000 survey sites distributed across peninsular Spain, 34 tree species that are native (28) or introduced (6) to this region, and that used forest as habitat proxy for these species (Montoya et al. 2008). These authors analyzed how the occurrence of each tree species was determined by local forest amount, which they defined as the fraction of area covered by forest in the local neighbourhood (a square area of 3km x 3km centred on each survey site). They found that while some species exhibit null (4) or positive responses (6) to decreasing local forest cover, most species (24) have negative responses. These results support the use of forest as habitat proxy for most tree species (the latter ones) and, hence, that conservation plans aimed at protecting or increasing local forest cover are likely to have positive impacts on the persistence of these trees, at least in peninsular Spain. However, Montoya et al. (2008) did not quantify forest fragmentation, for which the question of whether forest spatial configuration is also important for tree species occurrence remains open.

Here, we address this issue for a subset of eight tree species (namely *Fagus sylvatica* L., *Ilex aquifolium* L., *Pinus nigra* J.F. Arnold, *Pinus sylvestris* L., *Quercus faginea* Lam., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., and *Quercus suber* L.), which we selected because they meet the following three characteristics: to be negatively associated with decreasing forest amount (as indicated by Montoya's et al. 2008 results), to be native for peninsular Spain (exotics were excluded because of their frequent use as plantations in the study area, which might underestimate the effects of habitat cover and fragmentation; see Costa et al. 2001), and to have a broad native range distribution within this region (i.e. >121,200 km^2, or >=25% of the study area), to facilitate building robust statistical models. In order to test the predictions of the extinction threshold hypothesis directly, we used an approach similar to that of theoretical studies. That is, we investigated the effects of forest amount and fragmentation at the landscape level (*sensu* McGarigal and Cushman 2002), with each landscape consisting on a 10km x 10km cell, and the set of studied cells covering the whole study area. This means that each of our analysis units (cells) consisted in a constellation of forest patches, not in an individual patch. Approaches using individual patches (instead of constellations of patches in predefined areas) as analysis units are more common in the literature, but as discussed by Fahrig (2003), they are less appropriate to investigate theoretical propositions such as the extinction threshold hypothesis.

There are at least 40 fragmentation measures (McGarigal et al. 2002), many of which have strong relationships with each other and with the amount of habitat (see Fahrig 2003 and references therein). This makes the question of how to differentiate between more and less fragmented sites a difficult issue. To solve this we adopted a strategy based on quantifying, for each cell, both its percentage of forest cover (hereafter PFC), and the proportion of this percentage occurring in the largest forest patch (hereafter, relative largest patch size [rLPS]). By combining these two metrics we were able to differentiate among empirical scenarios reflecting low and moderate to high fragmentation (see Fahrig 2002). Our rationale is as follows. For any given PFC value, scarcely fragmented cells are those having most of its forest cover concentrated into a single patch (i.e. with high rLPS), as it is obvious that the remaining forest will be too limited as to constitute many additional fragments. Conversely, for the same PFC value, cells with a reduced largest patch (i.e. with lower rLPS) should be more fragmented, as the rest of their patches will be even smaller, and often more numerous than in the former case since patch areas ought to sum up to give the same amount of PFC. This approach allowed us estimating species' occurrence probabilities along the forest cover gradient for different levels of fragmentation, as well as testing directly the extinction threshold hypothesis. We specifically addressed two questions: (1) How do probabilities of occurrence of indi-

vidual tree species change with forest cover reduction in situations with low and higher fragmentation? (2) To what extent the extinction threshold hypothesis can be generalized across tree species?

Material and Methods

Dataset

We analysed data from an extensive field survey carried out in peninsular Spain (492,173 km^2). This region spans from 36ºN to 43.5ºN and 9ºW to 3ºE, housing a large altitudinal gradient (sea level - 3,500 meters); it comprises a mosaic of different climates (from semiarid climates to Mediterranean and humid Atlantic climates), and a number of different landscapes. The Second Spanish Forest Inventory (Inventario Forestal Nacional 1986-1996, ICONA, 1995) surveyed this area according to a 1 km resolution grid, yielding ~90,000 circular survey sites of 25 meter radius each distributed across the woody surface of this region. Each site was sampled for many attributes, including presence/absence of several species of trees; stem diameter and height; altitude and slope.

For the purpose of this study, the original presence/absence data for the eight selected tree species (species' selection criteria were described in the Introduction) were re-scaled from their original resolution to a grid comprising 6,757 cells of 10km x 10km each, in which each single cell contained 0-100 original survey sites (0-100 presences of any given tree species). We focused on relationships occurring within the native range distribution of each species in Peninsular Spain, for which we crossed our grid with published species' range maps (Montoya et al. 2007) and excluded, for each species, all cells that lied outside of its native range. Exotic species were thus excluded because most of them have been traditionally used in our study region as plantations (Costa et al. 2001), which might underestimate the effects of habitat loss and fragmentation. This rendered different numbers of analysis cells for each species, being *Quercus robur* the one with a lower representation in our dataset (a total of 1,212 cells in which the species was present or absent; see Table S1 for the numbers of cells of the rest of the species). Note that the tree species selected to test the extinction threshold hypothesis were all widely distributed within the study region, and that their occurrences have been previously documented to be positively related with the amount of forest cover in the local neighbourhood, so that reductions in this cover result in reductions of the likelihood of finding the species in all cases (Montoya et al. 2008).

Forest cover and fragmentation were quantified by processing the CORINE Land Cover database 2000 (CLC2000), a satellite imagery-based land cover classification with a 100-m pixel resolution. CLC2000 provides consistent information on land cover across Europe and is divided into 44 classes (http://natlan.eea.europa.eu/dataservice/metadetails.asp?id=822). We focused on three of these classes describing the distribution of broadleaved, coniferous and mixed forests, and classified each pixel as forest habitat, depending on whether they were included or not in any of these three categories. Then, we used these data to compute the percentage of forest cover (i.e. PFC) and the proportion of this percentage occurring in the largest forest patch (i.e. rLPS) for each cell (see Introduction).

Analytical protocols

Given that our analysis cells contain 0-100 original survey sites, we used Poisson models to explore species responses to forest amount and fragmentation. The Poisson distribution describes the probability to find a certain number of events (observed number of presences of a given species [0-100]) in a given amount of time or space (i.e. the cells' PFC values, in our case).

$$P(\rho_j, PFC_q) = \frac{\lambda^{\rho_j} \cdot e^{-\lambda}}{\rho_j!} \quad (1)$$

$$\lambda(j, PFC_q) = M_j + (C_j \cdot PFC_q) \quad (2)$$

where ρ_j is the density of occupancy of species *j* in cell

q (0<= ρ_j <=100); PFC_q represents the proportion of forest cover in cell q; λ is the rate parameter of the Poisson distribution, which here represents the expected value of the density of occupancy of species j along the PFC gradient; e is the base of the natural logarithm; and M_j and C_j are species-specific parameters for species j and with respect to PFC_q.

Given the structure of this model, the probability of presence of species j is zero when

$$P(\rho_j = 0, PFC_q) = e^{-\lambda} \quad (3)$$

To explore how forest cover affects the probability of presence of species j, we can transform equation (3) as

$$P(\rho_j > 0, PFC_q) = 1 - e^{-\lambda} \quad (4)$$

Equation (4) thus gives the probability of finding a given species j along the PFC gradient (Hilborn and Mangel 1997) irrespective of the number of presences in cell q. This allowed us to explore the relationships between PFC and species probability of occurrence.

To investigate how forest fragmentation influences the probability of occurrence of tree species, we divided the cells corresponding to each species (i.e. those laying within its native range distribution in Peninsular Spain) into two separate groups according to the proportion of PFC represented by rLPS. As explained above (see Introduction), forest fragmentation levels increase as rLPS values decrease. Thus, we defined the two fragmentation groups as: (1) cells where rLPS >= 90% of PFC (very low fragmentation), and (2) cells where rLPS <= 50% of PFC (moderate to high fragmentation). In order to test if this selection criterion might affect the results, we also performed the analyses using a different break-point criteria (rLPS >= 90%, <90% of PFC). Note that using rLPS >= 90%, <90% of PFC is very conservative, since a break-point criterion of 90% implies that the cells below the break-point (rLPS < 90% of PFC) comprise a high variation in terms of rLPS, and are thus underestimating the effects of habitat fragmentation. The selection of different break-point criteria, however, did not change our main results (see appendix).

We used likelihood ratio tests (LRT) to evaluate the goodness of fit between null models (intercept model) and models with PFC_q as predictor of species' probability of occurrence. LRT is a statistical test to compare hierarchically nested models that approximately follows a chi-square distribution (Huelsenbeck and Crandall 1997, Huelsenbeck and Rannala 1997). LRT assigns likelihood scores to models and determines whether the difference in likelihood scores between two models is statistically significant by considering the degrees of freedom, which, in the LRT, are equal to the number of additional parameters in the more complex model. This information is then used to determine the critical value of the test statistic from standard statistical tables. Here, we compare models that differ in one parameter (PFC_q), so the expected difference between null models and PFC_q models at $p<0.05$ must be >=3.84 (or >=19.51 at $p<0.00001$). In all cases, likelihood ratio tests selected the more complex models containing PFC_q as a predictor of species' probability of occurrence (Table 1, S1).

The regression models treated the data as independent, and so did not include the potential effects of spatial autocorrelation, i.e. a tendency for plots close to each other to have similar PFC_q, and / or λ (j, PFC_q), values. This autocorrelation reduces the effective sample size of the regression (Diniz-Filho 2003), compared to that carried out here, by a fraction that is currently unknown; however, the effects of this are unlikely to be substantial here because the (uncorrected) sample size is so large (756-4150 for each species) compared to the number of parameters to be estimated (2 for each species). Moreover, we used different break-point criteria to estimate the effects of forest fragmentation on the probability of presence of tree species, one of them being highly conservative (see above): this method is likely to have increased the confidence intervals of C_j and M_j by a larger fraction that would the inclusion of the effects of spatial autocorrelation.

Results

Probabilities of occurrence significantly decreased along with the reduction of forest cover for all eight tree species, both in cells with low fragmentation (with rLPS >=90%), and in those with moderate-to-high fragmentation (rLPS<=50%) (Figure 1). However, there were clear differences in how species reacted to forest cover reduction in each fragmentation scenario. Superposition of species-forest cover relationships in different fragmentation scenarios showed that habitat fragmentation significantly modified species' probability of occurrence along the habitat cover gradient in six tree species (Figures 1, S1). The observed mismatches between species' probability of occurrence between these scenarios showed that most tree species were benefited by moderate to high levels of fragmentation.

The only species that matched the predictions of the extinction threshold hypothesis is *Fagus sylvatica* (Figures 1a, S1a). That is, while in the moderate-to-high fragmentation scenarios the occurrence probability of this species showed an accelerated decrease with forest cover reduction and a clear extinction threshold (i.e. there was a point in which its occurrence probability fell to 0), in the low fragmentation scenario the probability of occurrence declined more gently and no extinction point was found.

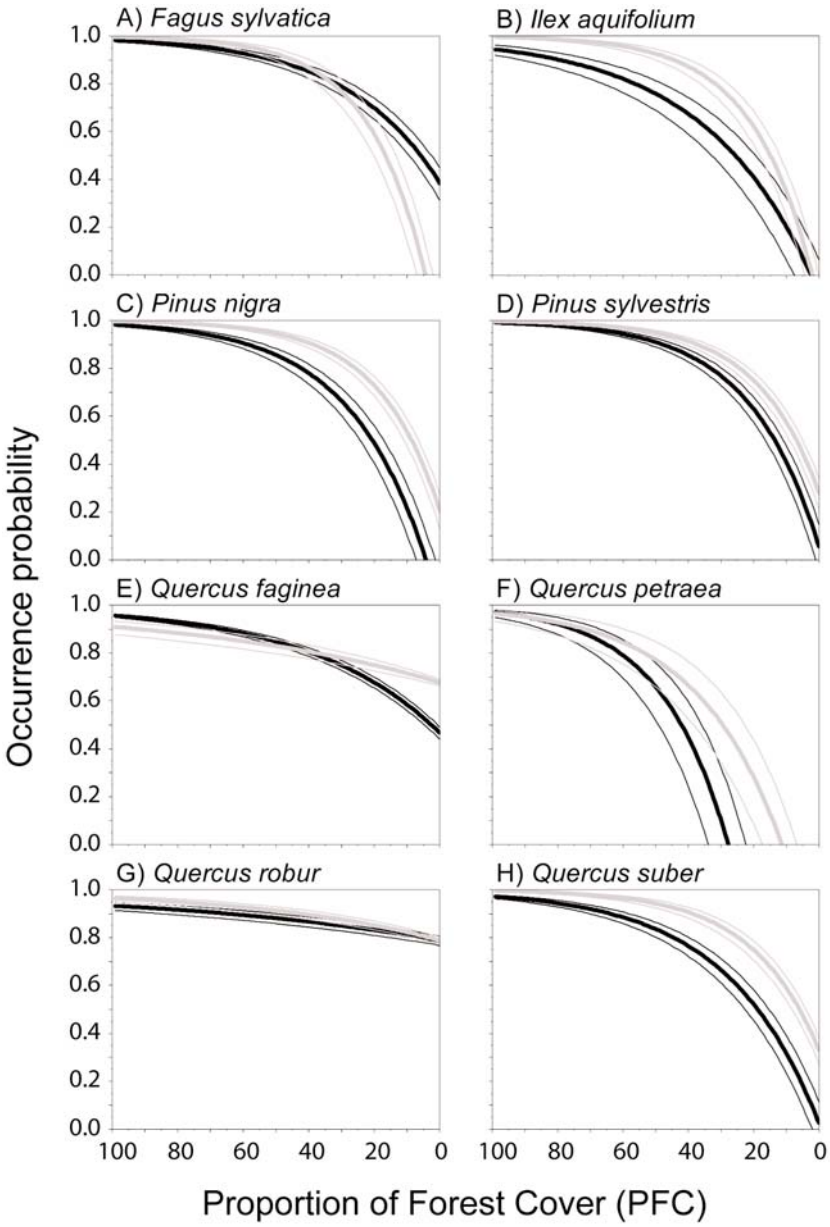
Ilex aquifolium and *Quercus robur* neither confirmed nor rejected the extinction threshold hypothesis (they showed similar occurrence probabilities in different fragmentation scenarios). For *Ilex aquifolium*, occurrence probabilities were higher for the case of moderate-to-high fragmentation when PFC was above ~20% (Figure 1b). This suggests that, as long as forest cover does not drop to very low levels, this species might in fact be benefited by fragmentation. Probability of occurrence of *Quercus robur*, on the other hand, did not significantly changed between fragmentation scenarios (Figure 1g).

Five out of eight species rejected the extinction threshold hypothesis (*Quercus faginea*, *Quercus petraea*, *Quercus suber*, *Pinus nigra*, *Pinus sylvestris*), irrespective of the break point criterion used to discriminate between different fragmentation scenarios (Figures 1, S1). These species showed higher probabilities of occurrence

Table 1. Parameter estimates (MLE) of the Poisson models (M_j, C_j) and their lower and upper 95% Confidence Intervals obtained for each tree species for cells with very low (rLPS >= 90% of PFC) and moderate-to-high (rLPS <50% of PFC) forest fragmentation. Species are listed in rank order of total number of analyzed cells (N). Likelihood ratio Chi^2 tests of model fit and their *p* values are also provided.

Fragmentation level & tree species	N	M_j (lower; upper)	C_j (lower; upper)	Model fit (L.Ratio Chi^2 test)	
				L.Ratio Chi^2	*p*
Low fragmentation (rLPS >= 90% PFC)					
Quercus faginea	1073	0.025 (0.024; 0.026)	0.628 (0.580; 0.676)	1646.56	< 0.001
Quercus petraea	393	0.049 (0.046; 0.051)	-1.348 (-1.542; -1.154)	1419.08	< 0.001
Quercus suber	442	0.036 (0.034; 0.037)	0.026 (-0.070; 0.122)	1453.76	< 0.001
Ilex aquifolium	331	0.030 (0.027; 0.032)	-0.070 (-0.208; 0.069)	710.96	< 0.001
Pinus nigra	381	0.042 (0.041; 0.044)	-0.178 (-0.293; -0.063)	2647.26	< 0.001
Pinus sylvestris	365	0.047 (0.045; 0.049)	0.058 (-0.046; 0.162)	3281.76	< 0.001
Fagus sylvatica	275	0.036 (0.034; 0.037)	0.486 (0.380; 0.60)	1904.25	< 0.001
Quercus robur	275	0.012 (0.010; 0.013)	1.549 (1.459; 1.639)	190.56	< 0.001
Moderate-to-high fragmentation (rLPS < 50% PFC)					
Quercus faginea	1358	0.013 (0.010; 0.015)	1.130 (1.089; 1.171)	85.22	< 0.001
Quercus petraea	592	0.038 (0.033; 0.044)	-0.432 (-0.568; -0.296)	183.54	< 0.001
Quercus suber	565	0.049 (0.045; 0.053)	0.401 (0.321; 0.482)	518.47	< 0.001
Ilex aquifolium	601	0.054 (0.050; 0.058)	-0.110 (-0.217; -0.003)	734.33	< 0.001
Pinus nigra	487	0.054 (0.051; 0.056)	0.232 (0.140; 0.323)	1326.24	< 0.001
Pinus sylvestris	480	0.053 (0.050; 0.055)	0.329 (0.242; 0.417)	1478.87	< 0.001
Fagus sylvatica	499	0.057 (0.053; 0.061)	-0.251 (-0.372; -0.129)	675.62	< 0.001
Quercus robur	481	0.018 (0.015; 0.020)	1.554 (1.488; 1.620)	152.78	< 0.001

Figure 1. Variation of tree species' occurrence probabilities across the gradient of decreasing forest cover (note that PFC decreases to the right) in scenarios with very low (black curves) and moderate-to-high (grey curves) forest fragmentation (i.e. with rLPS >= 90% of PFC, and rLPS <50% of PFC, respectively). Thin lines represent 95% Confidence Intervals for each curve.



in fragmented areas, and thus positive effects of fragmentation were the norm for these species.

Discussion

This is to our knowledge the first broad-scale study exploring the effects of forest amount and fragmentation on the presence probability of different tree species. Given that each point in the forest cover gradient was related to different levels of fragmentation, relationships of species' occurrence probabilities with forest cover could be compared between different fragmentation scenarios across the species' native ranges in our study region (Peninsular Spain), which in turn allowed investigating predictions of the extinction threshold hypothesis for each species (see Fahrig 2002). A first conclusion that can be derived from our results is that, irrespective of the level of forest fragmentation, the occurrence probability of all tree species tends to decrease along with diminishing forest cover. This was expected, as it is consistent with the responses of the same and additional tree species to forest cover variation found in the same region at a fined-grained scale (Montoya et al. 2008), and with the reactions generally reported in the literature for many other animals and plants in other areas (e.g. see Andrén 1994, Boutin and Hebert 2002, Fahrig 2002, 2003, and references therein).

Beyond this common trend, our data also show that only one species (*Fagus sylvatica*) supports the predictions of the extinction threshold hypothesis. That is, when forest fragmentation was moderate to high, the occurrence probability of this species declined more sharply with the reduction of forest cover, and an extinction threshold (the amount of forest cover at which the species' occurrence probability becomes zero) was reached, whereas no such threshold was found when fragmentation was low (see Figures 1a and S1a). Conversely, the other species showed a range of responses that included null and even positive reactions to increased fragmentation, and none showed a higher extinction threshold in the more fragmented scenarios. Taken together, these results can be interpreted in line with the general conclusions reached by Fahrig (2003); i.e., that the occurrences of most species are commonly more limited by habitat amount than by habitat fragmentation, which may even have positive effects on persistence (see also Andrén 1994, Boutin and Hebert 2002), and that the extinction threshold hypothesis is not generally supported by empirical data.

Why tree species behave differently under different forest fragmentation scenarios?

According to Kunstler et al. (2005), *F. sylvatica* is a late successional tree with a large tolerance to low light conditions (see also Pacala et al. 1994, Lin et al. 2002), and clearly specialized to live in dense forest plots, where it shows higher recruitment rates. This is consistent with Montoya's et al. (2008) observation that *F. sylvatica* is the most vulnerable tree of our species group to decreasing forest cover levels measured at fine-grained scale, and may, at least in part (see below), explain why this species supported the extinction threshold hypothesis. Conversely, even though the occurrence of the other species we studied was also positively related with forest cover (see Montoya et al. 2008), previous evidence suggests that they are not so closely associated with forest interior conditions as *F. sylvatica* does, which may explain their different responses to fragmentation (Fahrig 2002). For instance, Arrieta and Suarez (2005) investigated the seedling emergence and survival rates of *Ilex aquifolium* in landscapes of our study region, and found that both characteristics were higher in forest edges. This suggests that forest edges constitute a good habitat for this species. Similarly, a common characteristic among European oaks (*Quercus robur*) is that they require high solar irradiances, especially at the seedling stage (Barry-Langer and Nebout 1993). Moreover, *Quercus* species with sclerophyllous leaves show intermediate to high tolerance to solar radiation (e.g. *Q. suber*; Valladares 2005, Valladares and Niinemets 2008), which again indicates good survival opportunities for *Quercus* species at the edge of forest patches. Moreover, this might also be true for *Pinus* species given their reported tolerance to

high light conditions (Debain et al. 2003, Kunstler et al. 2006). The relative amount of forest edge is expected to be larger in fragmented forests compared with non-fragmented ones for the same level of forest cover, and this increased edge amount may in fact lead to more opportunities for establishment and survival of edge tolerant/loving species (Fahrig 2002). This in turn might explain both the positive or null reactions to forest fragmentation of *Ilex*, *Quercus*, and *Pinus* species, as well as their lack of support to the extinction threshold hypothesis.

In addition to this, complementary explanations for our findings can be provided by the different dispersal capabilities of the studied species. For instance, Kunstler et al. (2007) found that distance to the nearest adult population (a fragmentation variable) was the main explanatory variable of beech populations' recruitment rates and survival in fragmented landscapes, which these authors related with the limited dispersal abilities shown by this species. Thus, larger difficulties of *F. sylvatica* to colonizing remaining forest patches may have limited its persistence where fragmentation was higher, which constitutes an additional reason for the support given by this species to the extinction threshold hypothesis (see Fahrig 2002). Conversely, our observation that the occurrence probabilities of *P. nigra* and *P. sylvestris* were higher when fragmentation was moderate to high (see Figures 1 and S1), may be related with the good colonizing abilities that have been reported for *Pinus* species (Debain et al. 2003, Kunstler et al. 2006). Indeed, this characteristic is likely to have favoured the survival and recruitment rates of individuals of these species in cells with greater fragmentation. Likewise, in the case of *Quercus* species, observed positive (*Q. faginea*, *Q. petraea* and *Q. suber*) and null (*Q. robur*) effects of forest fragmentation on occurrence probabilities can be accounted for by the fact that these species are mainly dispersed by birds and mammals (e.g. the European jay [*Garrulus glandarius*], Gómez 2003). This interpretation is consistent with that, unlike wind, animals actively deliver seeds toward suitable habitat remnants (directed dispersal) and may increase average dispersal distances (Johst et al. 2002; see also Montoya et al. 2008), as well as with the prediction of recent theoretical models that animal-mediated seed dispersal confers increased species robustness to habitat loss (Purves et al. 2007). All in all, these evidences coupled with our results suggest that life-history traits and, especially, dispersal capabilities, play a key role in determining the response of each species to forest fragmentation, as well as its potential conformity with the extinction threshold hypothesis (see Fahrig 2002).

Another aspect to consider when interpreting our results is how we differentiated between more and less fragmented cells. Habitat fragmentation is a complex process that may alter habitat configuration in many ways, affecting, among other aspects, the number, size, shape and physical connectivity of the remaining patches, the inter-patch distances, and the ratio of edge-to-interior habitat in the landscape. The consequences of these changes for populations and communities are not mutually independent; they feed back on each other and with habitat amount in ways that can amplify their individual effects, and this complicates the selection of variables to differentiate between high and low fragmented areas to a large extent (e.g. McGarigal et al. 2002, Fahrig 2003). Here, we used the proportion of the cell's forest cover that is concentrated into the largest patch (rLPS) as an indicative variable of forest fragmentation. This is because, when most of the existing forest cover appears concentrated into one, relatively large patch of continuous forest (e.g. with rLPS >= 90% of PFC), we can be reasonably certain that the level of fragmentation is very low. Conversely, when this does not occur (e.g. with rLPS < 50% of PFC), this is an indication that all existing patches are relatively small (i.e. no large portions of continuous forest exist), and that fragmentation is higher (see Fahrig 2002). This is indeed a simple and crude way of characterizing fragmentation levels, as it is clear that cells showing similar forest cover and rLPS values may, to some unknown extent, differ in terms of the above-mentioned characteristics that define the spatial configuration of habitats. In this way, although our characterization of less and more fragmented cells could be viewed as conservative, as it did not capture all the spatial subtleties that might affect species' occurrences in fragmented habi-

tats, we believe that it was sufficient to uncover any strong signal left by forest fragmentation on the distribution of the studied species. Moreover, given that we found qualitatively similar results for different rLPS cut-off levels (i.e. Figure 1: >= 90% and < 50%; and Figure S1: >= 90% and < 90%), we see unlikely that a finer characterization of forest fragmentation levels could render radically different results.

We want to note that even though introduced species have been excluded from the current analysis, our subset of species has been also subject to human influences in some parts of Continental Spain (e.g. *Quercus suber*, *Pinus sylvestris*; Blondel and Aronson 1999). Although this may be affecting the observed response patterns of tree species, the effects of habitat amount and habitat fragmentation would be underestimated in plantations, and therefore, the observed relationships between species' probability of occurrence and habitat amount and fragmentation might be even more pronounced for these tree species.

To summarize, by using a large database that reflects the current distribution of eight tree species across Peninsular Spain, we have investigated how each species' occurrence probabilities vary with forest cover in different scenarios of forest fragmentation, and to what extent the observed patterns lend support to the extinction threshold hypothesis. Even though the probability of occurrence decreased with forest cover in all cases, only one species (*F. sylvatica*) agreed with the predictions of this hypothesis, which we attributed to a larger linkage with forest interior conditions and more limited dispersal abilities of beech populations. In opposition, larger tolerance to (or preference for) solar radiation (i.e. forest edge situations) and better dispersal capabilities can explain why this hypothesis was not sustained by the other species. So, although our study only lent support to the extinction threshold hypothesis for one out of the eight species analyzed, it also permitted us conjecturing which characteristics may lead a particular species to show conformity with this hypothesis. In particular, to posses a limited dispersal and a low tolerance to isolation typical of habitat edge environments. This is indeed a simple message, but still one worthy of further attention. Specially because, if it was confirmed by future studies, then biodiversity conservation in fragmented landscapes would benefit from having a simple rule to differentiate among species that may suffer or benefit from fragmentation.

Appendix. Table S1 provides the parameter estimates (MLE) of the Poisson models (M_j, C_j) and their lower and upper 95% Confidence Intervals obtained for each tree species for cells with very low (rLPS >= 90% of PFC) and moderate-to-high (rLPS <90% of PFC) forest fragmentation. Figure S1 gives the variation of tree species' occurrence probabilities across the gradient of decreasing forest cover in scenarios with very low and large forest fragmentation (i.e. with rLPS >= 90% of PFC, and rLPS <90% of PFC).

Acknowledgments

We thank the Ministerio de Medio Ambiente, Spain, and R. Vallejo and J. A. Villanueva for help with IFN2 data. This study was supported by the Spanish Ministry of Science and Innovation (grant CGL2006-03000/BOS to M.Á.R.). D.M. was supported by the Spanish Ministry for Education and Science (fellowship AP2004-0075). M.R. was supported by a postdoc grant from University of Alcalá. F.S.A. was supported by a Miguel de Cervantes grant awarded by the Banco de Santander and the Spanish AECID.

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SUPPLEMENTARY MATERIAL

Table S1

Table S1. Parameter estimates (MLE) of the Poisson models (M_j, C_j) and their lower and upper 95% Confidence Intervals obtained for each tree species for cells with very low (rLPS >= 90% of PFC) and moderate-to-high (rLPS <90% of PFC) forest fragmentation. Species are listed in rank order of total number of analyzed cells (N). Likelihood ratio Chi^2 tests of model fit and their *p* values are also provided.

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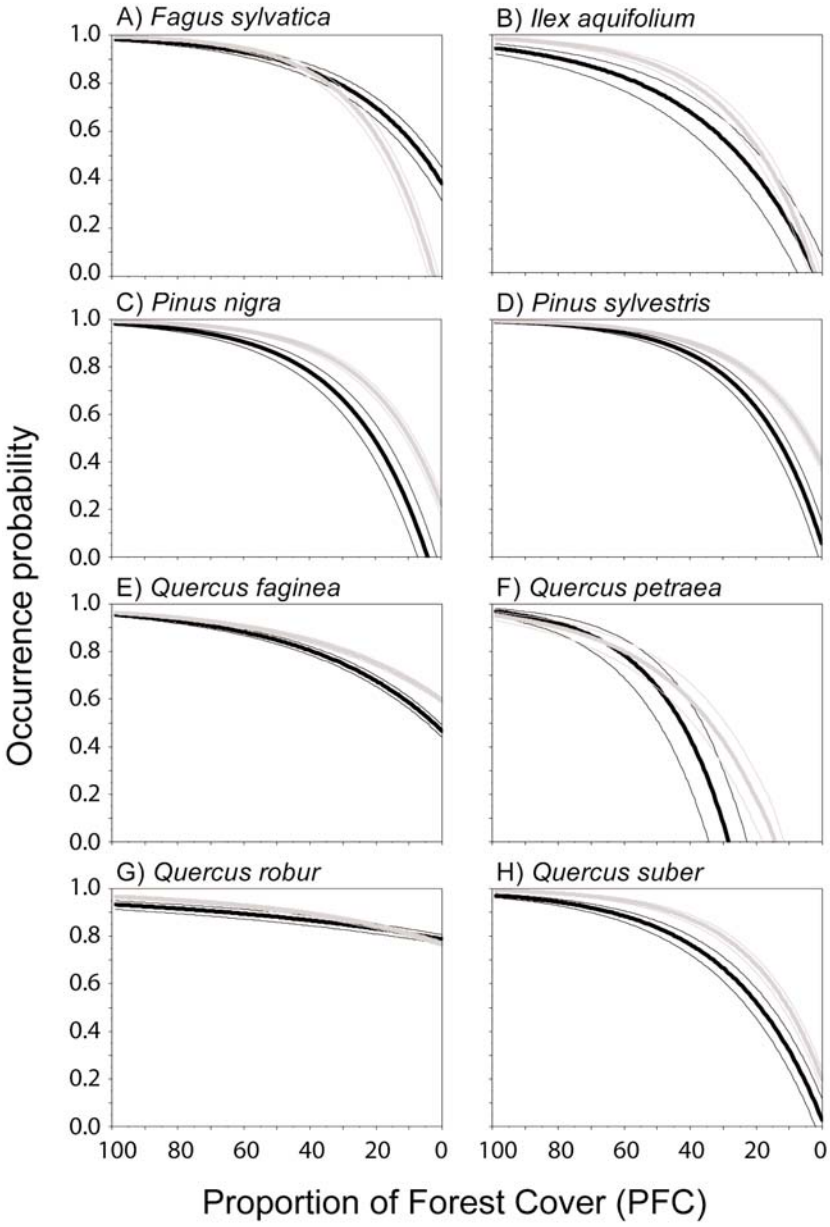
Higher fragmentation (rLPS < 90% PFC)					
Quercus faginea	3077	0.024 (0.023; 0.026)	0.90 (0.87; 0.93)	1212.95	< 0.001
Quercus petraea	1350	0.035 (0.033; 0.038)	-0.496 (-0.583; -0.409)	608.37	< 0.001
Quercus suber	1295	0.046 (0.044; 0.048)	0.219 (0.163; 0.274)	1376.43	< 0.001
Ilex aquifolium	1247	0.043 (0.040; 0.045)	-0.094 (-0.164; -0.023)	1505.42	< 0.001
Pinus nigra	1194	0.047 (0.045; 0.048)	0.247 (0.191; 0.304)	3891.21	< 0.001
Pinus sylvestris	1179	0.046 (0.045; 0.047)	0.496 (0.445; 0.546)	4748.64	< 0.001
Fagus sylvatica	1036	0.050 (0.048; 0.052)	-0.122 (-0.195; -0.049)	2381.48	< 0.001
Quercus robur	937	0.019 (0.018; 0.021)	1.460 (1.413; 1.506)	601.70	< 0.001

Figure S1

Figure S1. Variation of tree species' occurrence probabilities across the gradient of decreasing forest cover (note that PFC decreases to the right) in scenarios with very low (black curves) and moderate-to-high (grey curves) forest fragmentation (i.e. with rLPS >= 90% of PFC, and rLPS <50% of PFC, respectively). Thin lines represent 95% Confidence Intervals for each curve.



5. Species Distribution Models and Spatial Structure of Species

Daniel Montoya, Drew W. Purves, Itziar R. Urbieta & Miguel A. Zavala

Article published in *Global Ecology and Biogeography* (In Press)

Capítulo 5

Explican los modelos de distribución de especies la estructura espacial de los árboles dentro de sus rangos de distribución?

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Montoya, D., Purves, D. W., Urbieta, I. R. & Zavala, M. A. (2009). Do species distribution models explain spatial structure within tree species ranges?. Global Ecology & Biogeography (*In press*)

Resumen

Objetivo. Evaluar la capacidad de los Modelos de Distribución de Especies (MDEs) para predecir la estructura espacial de las especies de árboles dentro de sus rangos geográficos (cómo los árboles se distribuyen dentro de sus rangos).

Location. España Continental

Métodos. Empleamos una extensa base de datos consistente en ~90000 puntos de muestreo (1 punto/Km^2) donde la presencia/ausencia de 23 especies comunes de las regiones Mediterránea y Atlántica había sido registrada. En primer lugar generamos MDEs relacionando la presencia o ausencia de cada especie con un conjunto de 16 variables ambientales siguiendo un proceso de modelización progresivo ('stepwise') basado en métodos de máxima verosimilitud. La superposición de los correlogramas espaciales generados a partir de las predicciones de los MDEs sobre aquéllos obtenidos a partir de los datos crudos permitió una comparación entre observaciones y modelos sobre la naturaleza, escala e intensidad (nivel o grado de agregación) de la estructura espacial dentro de los rangos de las especies.

Resultados. Los MDEs predijeron con precisión la naturaleza y escala de la estructura espacial de los árboles. Sin embargo, para la mayoría de las especies, la intensidad de la estructura espacial observada (grado de agregación espacial de las especies) fue sustancialmente más alta que la predicha por los MDEs. En términos medios, la intensidad de la agregación espacial fue dos veces mayor que la predicha por los MDEs. Además, encontramos una correlación negativa entre la intensidad de agregación y el tamaño del rango geográfico de las especies.

Conclusiones principales. Las predicciones de los MDEs acerca de los patrones de estructura espacial difieren entre las especies. Los MDEs son aparentemente capaces de reproducir tanto la escala como la naturaleza de la estructura espacial de las especies dentro de sus rangos de distribución. No obstante, uno o más factores complementarios no incluidos en los MDEs hacen que las especies estén sustancialmente más agregadas en el espacio de lo que capturan los MDEs. Este resultado apoya las recientes llamadas para desarrollar una nueva generación de MDEs biológicamente más realistas. En particular, los futuros MDEs deberían incorporar procesos ecológicos que tiendan a aumentar la intensidad de agregación espacial, tal como dinámicas fuente-sumidero, heterogeneidad ambiental a pequeña escala, y desequilibrio.

Global Ecology & Biogeography (*In Press*)
Subject Editor: J.A.F. Diniz-Filho

Do species distribution models explain spatial structure within tree species ranges?

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Abstract

Aim. To evaluate the ability of Species Distribution Models (SDMs) to predict the spatial structure of tree species within their geographic ranges (how trees are distributed within their ranges).

Location. Continental Spain.

Methods. We used an extensive dataset consisting of ~90000 plots (1 plot/Km^2) where presence/absence data of 23 common Mediterranean and Atlantic tree species had been surveyed. We first generated SDMs relating the presence or absence of each species to a set of 16 environmental predictors, following a stepwise modelling process based on maximum likelihood methods. Superimposing spatial correlograms generated from the predictions of the SDMs, over those generated from the raw data, allowed a model-observation comparison of the nature, scale and intensity (level of aggregation) of spatial structure with the species ranges.

Results. SDMs predicted accurately the nature and scale of the spatial structure of trees. However, for most species, the observed intensity of spatial structure (level of aggregation of species in space) was substantially greater than that predicted by the SDMs. On average, the intensity of spatial aggregation was twice than predicted by SDMs. In addition, we also found a negative correlation between intensity of aggregation and species' range size.

Main conclusions. Standard SDMs predictions of spatial structure patterns differ among species. SDMs are apparently able to reproduce both the scale and intensity of species spatial structure within their ranges. However, one or more missing processes not included in SDMs results in species being substantially more aggregated in space that can be captured by the SDMs. This result adds to recent calls for a new generation of more biologically realistic SDMs. In particular, future SDMs should incorporate ecological processes that likely increase the intensity of spatial aggregation, such as source-sink dynamics, fine-scale environmental heterogeneity, and disequilibrium.

Introduction

Anthropogenic climate change is a major threat to the maintenance of biological diversity. Most modelling frameworks to predict its effects on species distributions rely on the bioclimatic 'envelope' approach, whereby present climate-species relationships are used to estimate distributions of species under future climate scenarios (Huntley *et al*., 1995; Peterson *et al*., 2002; Thomas *et al*., 2004; Thuiller *et al*., 2005). Despite that recent studies have demonstrated significant variability in model predictions (Segurado & Araújo, 2004; Pearson et al., 2006), Species Distribution Models (SDMs) constitute a general and widely used approximation to modelling geographic ranges of biological communities, on the basis that climate is the main driver of species distributions world-wide (Hawkins *et al*., 2003).

One of the main criticisms posed to SDMs, however, is that these models implicitly assume that biological communities are niche-assembled and not influenced by endogenous factors (Pearson & Dawson, 2003; Hampte, 2004). This assumption overlooks empirical evidence showing that spatial structure often emerges due to population-level factors (e.g. dispersal, biotic interactions, gregarious behaviour) as well as exogenous factors (e.g. aggregated environmental conditions; Tilman & Kareiva, 1997). Moreover, Bahn & McGill (2007) recently showed that environmental variables captured spatial structure of breeding birds of North America in a haphazard way, suggesting that population-level processes rather than exogenous factors are the main predictors of the spatial structure patterns of species. Although these findings do not exclude environment from models, they suggest that modelling species distributions must integrate diverse sets of explanatory factors from pure environmental variables (scenopetic; Soberón, 2007) to resource-related and biotic variables (bionomic; Soberón, 2007), because they together generate the spatial patterns observed in nature: scenopoetic variables may have broad spatial structures (i.e. climate), whereas bionomic variables probably tend to have much more fine-grained spatial structures (i.e. biotic interactions). Given that bionomic variables are difficult to obtain at broad geographic scales, modelling population-level processes represents a major challenge for SDMs, and attempts to incorporate processes such as competition and mutualistic interactions into the SDM framework are gaining in importance (Leathwick & Austin, 2001; Anderson *et al*., 2002; Gutiérrez *et al*., 2006; Araújo & Luoto, 2006). Although this research shows that including of population-level processes improves SDMs, a remaining question is to what extent SDMs predict the spatial structure of individual species within their distribution ranges. This is intriguing, since a knowledge of this spatial structure is likely to be critical to understanding the dynamics of forest communities, their interactions with the environment and other biological species, and their response to climate changes (Tilman & Kareiva, 1997).

In spatial ecology, the term 'spatial structure' refers to how species are organized (structured) within their distribution ranges, by reference to random (non-structured) null model which is usually assumed to be a homogeneous Poisson process. Spatial structure can be explored using spatial covariance-distance function (Solé & Bascompte, 2007), which provides measure of the direction and magnitude of deviation from randomness of a pair of locations as a function of their distance apart. This function reveals three important components of the spatial structure that we refer to here as intensity, nature, and scale. Intensity is a quantitative measure of the magnitude of spatial structure, i.e. the magnitude of the deviation between the observed pattern, and the null model. Intensity is associated to the level of aggregation/segregation of species in space, and gives information on how close in space are individuals from the same species. This magnitude is usually greatest at distance 0, and so in practice the intensity can usually be defined as the value of the covariance function at distance 0. Nature refers to the direction of the deviation (more aggregated than expected from the null model; less aggregated than expected) and how this changes with distance (e.g. more aggregated than expected at short distances, less aggregated than expected at intermediate distances, random at large distance). Scale refers to the distances in space over

which the deviation occurs: e.g. at what distance does the pattern first become non-structured? Therefore, nature and scale are qualitative measures of spatial structure that focus on questions such as whether species within a region are equally similar regardless of distance or differ as a function of distance.

Theory and evidence suggest that population-level processes affect species ranges (e.g. post-glacial dispersal limitation; Svenning & Skov, 2007) as well as spatial structure within these ranges (e.g. local dispersal leads to intraspecific aggregation; Pacala, 1997). However, little is known about what elements of the observed spatial structure in species distributions are more related to either environmental or population-level processes. The most likely reason for this is that current SDMs have commonly focused on understanding species ranges, and how these might alter under climate change; but have rarely examined how individual species are arranged within those ranges (e.g. random, regular/uniform, aggregated). A fundamental issue when exploring spatial structure is that we need models that allow a continuous probability of occurrence of a species given certain environmental conditions. Although most SDMs can potentially generate such probability maps, they usually convert *a posteriori* the continuous probabilities (range 0-1) into a binary prediction for presence/absence (0 or 1). This reduces continuous probability maps to discrete presence/absence predictions, and so spatial structure cannot be accurately studied because ecological properties such as spatial aggregation of individuals show no patterns of response along environmental gradients. Therefore, current SDMs have not yet shown how they can capture the nature, scale and intensity of spatial structure of individual species at finer scales.

Here, we investigate the performance of a SDM to capture the spatial structure of 23 common tree species of Mediterranean and Atlantic ecosystems. By using spatial structure analysis, we evaluate the performance of SDMs to describe the observed spatial structure for many species and at fine spatial scales. This is potentially important to understand species distributions because many suggested processes that may diminish the explanatory power of SDMs mainly operate at short to intermediate spatial scales (e.g. dispersal, biotic interactions, perturbation events, habitat loss and fragmentation; Pearson & Dawson, 2003; Hampte, 2004). For example, empirical dispersal kernels show high densities of seeds at short distances from the parent tree, demonstrating that local dispersal leads to intraspecific aggregation (Pacala, 1997). Also, perturbations such as habitat loss and fragmentation usually divide landscapes into a set of forest patches which, in turn, cause patchy aggregated distributions of species (Fahrig, 2003). Given that most of the population-level processes not considered by SDMs tend to result in more aggregated structures, we were interested in testing the hypothesis that spatial aggregation is the main unpredicted component of the spatial structure. Specifically, we address three questions: (1) To what extent can species' spatial structure be predicted by environmental conditions, (2) How does this predictive ability differ among different features of the spatial structure (intensity, nature, scale)? (3) How does this predictive ability differ among species?

Data and Methods

Study region

We analysed data from an extensive dataset carried out in Continental Spain (492173 Km2). This region houses a large altitudinal gradient (sea level - 3500 meters); it comprises a mosaic of different climates (from semiarid climates to Mediterranean and humid Atlantic climates), and a number of different landscapes. The Second Spanish Forest Inventory (Inventario Forestal Nacional 1986-1996, ICONA, 1995) surveyed this area, yielding a total of 89365 circular plots distributed across the forested surface of the Iberian Peninsula, with an approximate density of one plot per 1 Km2. Each plot was located in the field by giving its UTM coordinates, and was sampled for many attributes. We extracted the presence/absence data for 23 tree species commonly found in Mediterranean and Atlantic forests of the study region. These species comprise a wide range of niches and biological traits and include both native and introduced species (Table 1).

Environmental variables

To reduce the chance of missing environmental factors that may explain the observed patterns, environmental variability was characterized for each plot by a set of 16 variables which might be critical to plant physiological function and survival in the Mediterranean and Atlantic systems. We used annual, seasonal and monthly values of mean temperature (*T* [ºC]) and precipitation (*P* [mm]), and annual and seasonal values of mean radiation (*RAD* [Kw/m^2]), extracted from a digital atlas of the Iberian Peninsula (Ninyerola *et al*., 2005). From these variables, we generated mean temperature of the coldest month (*MTCM* [ºC]), mean temperature of the warmest month (*MTWM* [ºC]), thermal oscillation (*TO* [ºC] = *MTWM* - *MTCM*), Thornwaite's annual and monthly potential evapotranspiration (PET_{Th} [mm], estimated from temperature; Thornwaite, 1948), Jensen & Haise's annual and seasonal potential evapotranspiration (PET_{JH} [mm/day], estimated from solar radiation; Jensen & Haise, 1963), annual surplus (*AS*)

$$AS \text{ [mm]} = \sum_{i=1}^{12} (P_i - PET_{Th}) > 0$$

annual deficit (*AD*)

$$AD \text{ [mm]} = \sum_{i=1}^{12} (P_i - PET_{Th}) < 0$$

annual hydric index (*AHI*; Thornthwaite, 1957)

$$AHI = (100*AS - 60*AD)/PET_{Th},$$

drought length (*DL* = number of months where monthly precipitation is lower than PET_{Th}), and drought intensity (*DI* = Drought length / Wet length; where Wet length = 1 - Drought length). In addition, we considered topography and soil in the database. Topographic variables included altitude, aspect and slope, and were extracted from the Digital Elevation Model of the Iberian Peninsula (Ninyerola *et al*., 2005). Soil types extracted from the FAO soil map of the world (FAO, 1988) were included as a categorical variable.

Model description

We extended on a previous phenomenological statistical model (Purves *et al*., 2007) to predict the probability of presence or absence of each species *j* in survey plot *q*, $P_{j,q,\theta}$ given parameter set θ. $P_{j,q,\theta}$ was modelled as a product of Gaussian functions of two (or more) environmental variables associated to plot q.

$$P_{j,q,\theta} = 1/[1 + \exp^{-C(j,q,\theta)}] \quad (1)$$

$$C_{j,q,\theta} = \varepsilon_j + \sum \sigma_{x,j} \frac{[V_{x,j}(q) - \mu_{x,j}]^2}{\Delta_x} \quad (2)$$

where $V_{x,j}(q)$ is the value of variable *x* associated to plot *q*; Δ_x represents the range of variable *x* in the entire dataset; ε_j is a species-specific constant that sets the maximum probability that species *j* is present in plot *q*; $\mu_{x,j}$ and $\sigma_{x,j}$ are species-specific parameters for species *j* with respect to plot variable *q*. For a given species *j* and given set of predictor variables *x* (e.g. for a two-variable model, ***x*** could equal: mean annual temperature and drought length), these parameters make up the parameter set θ. The estimated values of $\sigma_{x,j}$ are negative for most variables and species. In such cases, the probability of occurrence of species *j* in plot *q* takes the maximum value ε_j when $V_x(q) = \mu_{x,j}$ and the relationship between $P_{j,q,\theta}$ and each predictor variable is approximately Gaussian in form. However, $\mu_{x,j}$ is allowed to take a value outside the range in the predictor variable, in which case the relationship between $P_{j,q,\theta}$ and each predictor variable is monotonic over the observed range in the predictor variable.

In contrast to the usual outcome of SDMs (0/1 predictions), this modelling approach directly provides a continuous variation in the probability of occurrence of a species given continuous variation in environmental conditions (0-1 predictions). This is crucial to assess spatial aggregation within geographical ranges of species because ecological properties of species such as spatial aggregation of individuals can show patterns of response along the environmental gradients.

We could define a SDM for any species *j* (bioclimatic 'envelope'), for any combination of predictor variables $V_{x,j}$. For each species, we followed a two-step process to generate a particular SDM for that species. First, we fit every possible two-variable model from the set of 16 environmental variables ([16 x 15] / 2 = 120 different models). Each species-specific model $\boldsymbol{x}$ was evaluated through maximum likelihood (Hilborn & Mangel, 1997). We denoted the observed presence/absence data for species *j* in survey plot *q* as $Z^{Obs}_{j,q}$. The total data set for species *j* is the vector $Z^{Obs}_{j,q}$ of 89365 ones and zeros for presence/absence in each survey plot. Given that each $Z^{Obs}_{j,q}$ is assumed to arise from an independent Bernoulli process, the log-likelihood function for $Z^{Obs}_{j,q}$ is:

$$L\{Z^{Obs}_{j,q} \mid \boldsymbol{x}, \grave{e}\} = \Sigma\, [Z^{Obs}_{j,q} \cdot \ln(P_{j,q,\grave{e}}) + (1-Z^{Obs}_{j,q}) \cdot \ln(1- P_{j,q,\grave{e}})] \qquad (3)$$

For two-variable models, $\boldsymbol{x}$ is a vector of size *D* whose components define the two predictor variables that are being used (*D* = 2). We used a simulated annealing algorithm (Metropolis-Hastings algorithm: Metropolis *et al*., 1953) to find the set of parameters θ that maximized the log-likelihood function $L\{Z^{Obs}_{j,q} \mid \boldsymbol{x}, \grave{e}\}$. Thus, for each species *j* and model $\boldsymbol{x}$, we could find the best-fit model parameters for different combinations of predictors, and compare the fit given by these combinations in terms of $L\{Z^{Obs}_{j,q} \mid \boldsymbol{x}, \grave{e}\}$. Note that models use information from every plot, irrespective of if the species *j* is present ($Z^{Obs}_{j,q}$) or absent ($1- Z^{Obs}_{j,q}$). This is in contrast to profile techniques that use only presences (e.g. BIOCLIM, DOMAIN, Ecological Niche Factor Analysis [ENFA], GARP, Maxent), in part because absence data is usually missing in large-scale datasets and expensive to collect. Presence-only techniques usually predict greater species' losses, resulting in a poorer fit to current observed distributions (Pearson et al., 2006).

Table 1. List of tree species included in the analyses. The origin of each species (native *Vs*. exotic) is indicated. Variables included in the best-fit species distribution models (SDMs) are provided. Proportion of spatial aggregation explained by SDMs is provided for each species as species' predicted aggregation at distance 0 (δ) and overall predicted spatial structure (pseudo-R^2).

Species	Origin	Factor 1 (*D*=1)	Factor 2 (*D*=2)	Factor 3 (*D*=3)	δ	Psedo-R^2
Abies alba	Native	MTCM	SumP		0.81	0.68
Castanea sativa	Exotic	AnP	MTCM		0.29	0.33
Ceratonia siliqua	Native	MTCM	AHI		0.53	0.66
Corylus avellana	Native	SumP	TO		0.32	0.68
Eucalyptus camaldulensis	Exotic	AMT	AHI		0.24	0.55
Eucalyptus globulus	Exotic	TO	MTCM	SumP	0.53	0.44
Fagus sylvatica	Native	SumP	TO		0.39	0.74
Ilex aquifolium	Native	SumP	TO		0.46	0.86
Juniperus thurifera	Native	MTCM	AnP		0.21	0.35
Olea europaea	Native	MTWM	AMT		0.31	0.47
Phyllirea latifolia	Native	MTWM	AnP		0.43	0.65
Pinus halepensis	Native	MTWM	AHI		0.42	0.54
Pinus nigra	Native	MTCM	MTWM		0.27	0.44
Pinus pinaster	Native	AMT	TO		0.32	0.68
Pinus radiata	Exotic	AR	MTCM		0.18	0.19
Pinus sylvestris	Native	AMT	SprP		0.27	0.33
Pinus uncinata	Native	MTCM	SumP	MTWM	0.89	0.92
Quercus faginea	Native	MTCM	AnP		0.39	0.49
Quercus ilex	Native	AnP	MTCM		0.05	0.06
Quercus petraea	Native	SumP	TO		0.20	0.27
Quercus robur	Native	TO	SprP		0.80	0.89
Quercus suber	Native	AMT	SprP		0.42	0.63
Rhamnus alaternus	Native	MTWM	SumP		0.43	0.73

MTCM = Mean Temperature of the Coldest Month (ºC); MTWM = Mean Temperature of the Warmest Month (ºC); TO = Thermal Oscillation (ºC); SumP = Summer Precipitation (mm); SprP = Spring Precipitation (mm); AnP = Annual Precipitation (mm); AMT = Annual Mean Temperature (ºC); AHI = Annual Hydric Index (adimensional); AR = Annual Radiation (Kw/m2). See main text for definitions and data sources.

Second, we went on to fit every possible three-variable model. The fit to data for each model $\boldsymbol{x}$ (D = 3) was defined as the maximum value of $L\{ Z_{j,q}^{Obs} \mid \boldsymbol{x}, \grave{e} \}$ found by the simulating annealing algorithm. When the best three-variable model was provided a significant improvement in fit compared to the best two-variable model (likelihood ratio tests; Hilborn & Mangel, 1997), the second-variable model was discarded. Although models could be expanded to more than three variables, we bounded the number of variables to three for simplicity. Moreover, the best models found, for all but two species, contained only two variables. Therefore increasing the model dimensionality was not justified in this case, because it did not provide further information, nor would it improve models' fit statistically. Multicollinearity was minimized by preventing SDMs from incorporating highly correlated variables (r > 0.6).

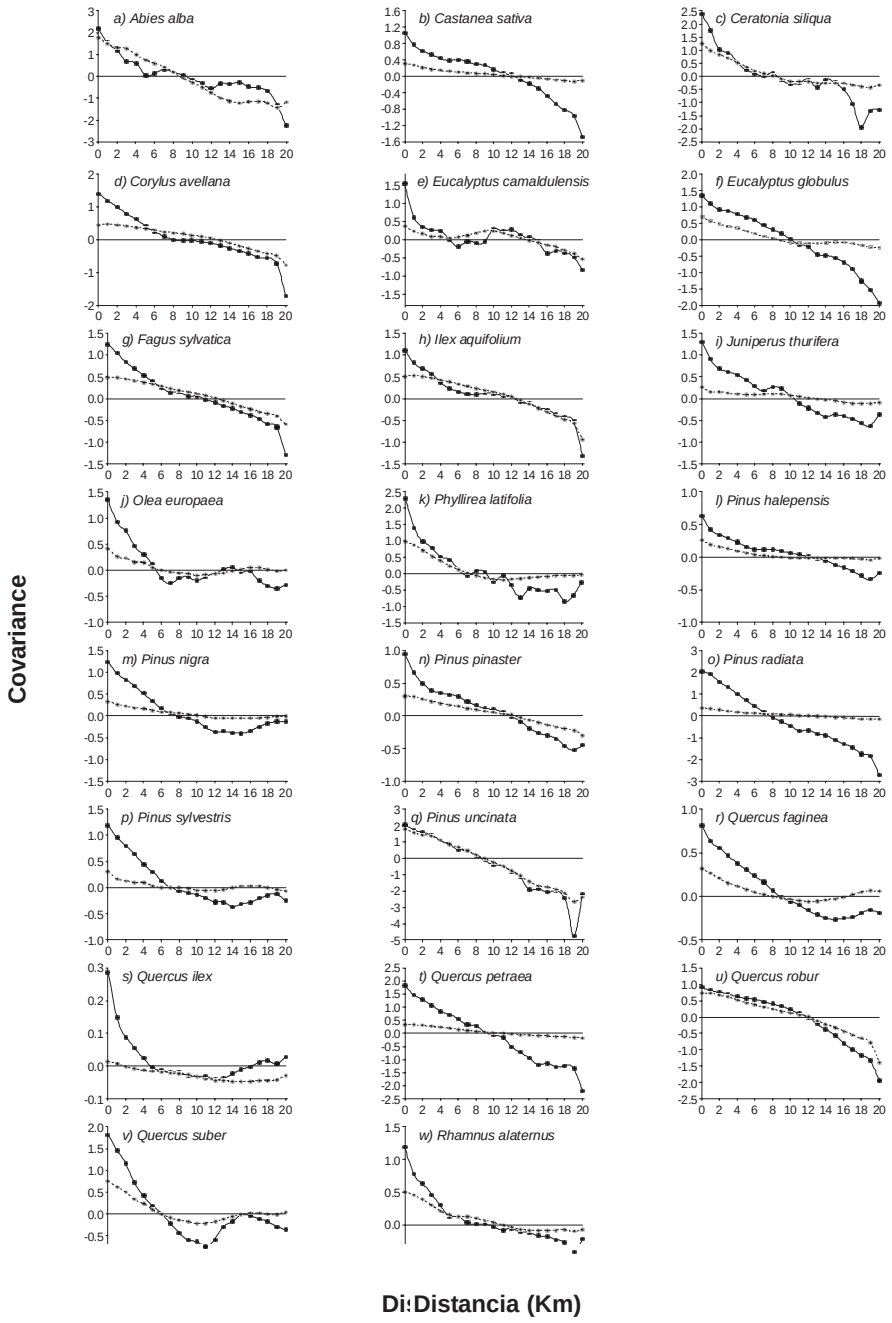
Spatial analysis

We used spatial correlograms, which give information on the spatial similarity of the samples *vs.* their distance apart (spatial covariance-distance function, Solé & Bascompte, 2007). Spatial structure was quantified using the spatial covariance functions given in Purves *et al.* (2007). These statistics give a value for the autocovariance of species j at a distance class r, $C_j(r)$, which we compare to the expected correlation under spatial randomness $E\{C_j(r)\}$. The ratio of these two quantities yields a dimensionless measure of departure from spatial aggregation $\Omega j(r)$ (Condit *et al.* 2000). A value of $\Omega j(r)>0$ indicates aggregation of species j at distance class r, $\Omega j(r)<0$ indicates segregation, and $\Omega j(r)=0$ indicates spatial randomness (no aggregation or segregation). The Ω statistic was used because it is simpler than the many alternative distance-based covariance functions (e.g., semivariance, Ripley's k [Ripley, 1981]); but it is likely to have yielded similar results to them. The estimates of Ω do not depend on the arrangement of survey plots.

We explored the spatial autocorrelation of the observations, and compared these to the spatial structure predicted by the SDMs. For each species, we calculated correlograms both from the observations and from the predictions of the best model. To do this we generated spatial correlograms using the spatial covariance functions calculated for original observations and predicted spatial structure after fitting each model at 20 distance classes. Thus, the lower the difference in spatial autocorrelation between observed and predicted values at any distance class, the greater the capacity of the model to explain spatial structure at that distance. In contrast, remaining spatial autocorrelation at a distance class indicates the inadequacy of the model to describe the spatial structure at that scale and, therefore, suggests that other processes not included in the SDMs are contributing to the observed spatial pattern. The estimation of spatial autocorrelation effects may thus help in detecting processes influencing species' spatial structure. For discussion, we divide spatial structure into three main components: nature, scale and intensity. The interpretation of residual autocorrelation in spatial structure between models and observations was performed for nature, scale, and intensity, so that possible mismatches could be associated to each of them.

To quantify the match between the predicted and observed spatial structure, we calculated two measures. The value δ is defined as the predicted aggregation at distance zero, as a proportion of the observed aggregation, i.e. δ = Predicted Cov [0] / Observed Cov [0]: thus, δ is a measure of observed *vs.* predicted intensity only. In contrast, pseudo-R^2 measures the overall match between the predicted and observed spatial structure at all distance classes, reflecting the overall match between the predicted and observed nature, scale and intensity of spatial structure. We expected *a priori* that values of pseudo-R^2 would be higher than values of δ, because pseudo-R^2 includes larger spatial scales where environmental conditions, especially climate, are thought to be the most critical determinants of species' spatial structure. Analyses were performed in C and STATISTICA (StatSoft, 2003).

Figure 1. Spatial autocorrelation of individual tree species. Observed (black circles) and predicted (dashed lines) correlograms for each species. As observed, for most species, environment (i.e. the Spatial Distribution Model) predicts accurately the nature and scale of the spatial structure, yet the intensity is poorly predicted for all species but *Abies alba*, *Pinus uncinata*, and *Quercus robur*.



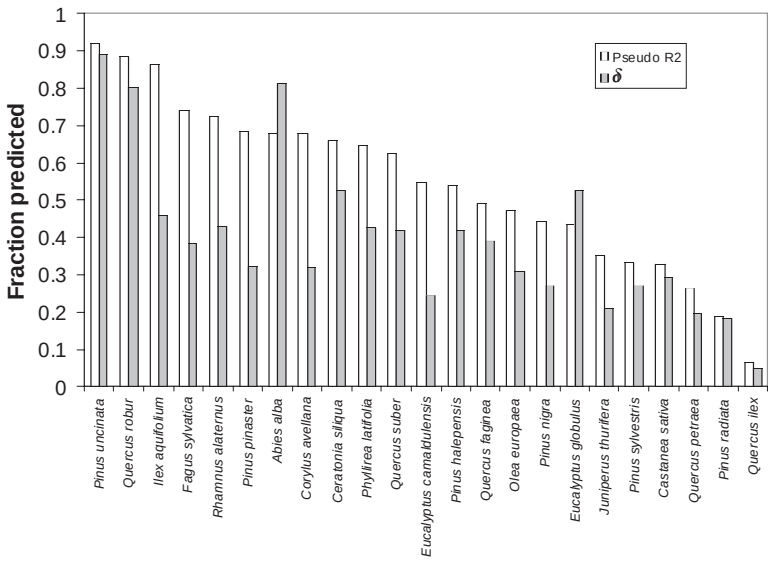
Results

For most species the best SDM included only two environmental predictor variables, the exceptions being *Eucalyptus globulus* and *Pinus uncinata*. Most of the selected variables (82.6%) were related to water and energy. Variables included in the SDMs are shown in Table 1 (model parameters are also provided: see Appendix S1 in Supporting Information).

The second step of our study involved the analysis of the relationship between the observed, and SDM-predicted, spatial structure. Superposition of the observed and predicted correlograms showed that the SDMs correctly predicted the nature, and scale, of spatial autocorrelation for most species (Fig. 1). Thus, mismatches between predictions and observations were mostly in intensity. For almost all species, pseudo-R^2 values were greater than values of δ (Fig. 2). This showed that, on average, the intensity of aggregation at short spatial scales was less predictable from environmental conditions than was the intensity of aggregation at larger spatial scales. However, across species, both measures were correlated (R^2 = 0.59; see Appendix S2). This showed that, on average, species showing a close match between the predicted and observed spatial intensity at short scales (measured by δ), also showed a better match overall (measured by pseudo-R^2). SDMs explained less than 50% of the short-scale aggregation (i.e. $\delta < 0.50$) for 18 out of 23 species. Of the 23 species considered, we consider that only three had spatial structure that was accurately predicted by the SDMs ($\delta > 0.8$, Pseudo-$R^2 > 0.8$; Figs 1 and 2).

Although SDM predictions differed greatly among species, the average values of the spatial covariance of all tree species - observed, and predicted - as a function of distance provides a simple average covariance function, measuring the overall ability of SDMs to reproduce the spatial structure of these species (Fig. 3). This shows a significant gap in the correlograms between the observed spatial structure, and the structure predicted by the SDMs. Consistent with the species-by-species comparisons, the nature and scale of spatial structure of this average pattern were predicted correctly, with the mismatch appearing in the intensity only.

Figure 2. Proportion of the spatial aggregation explained by species distribution models (Spatial Distribution Models, SDMs) for each species. Values of the two measures describing the match between predicted and observed spatial structure (δ and pseudo R^2) are provided.



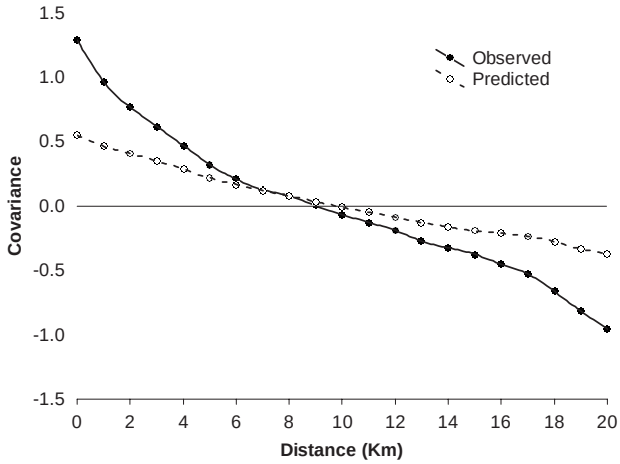


Figure 3. Average spatial autocorrelation over all species. Observed (solid circles) and predicted by environment (white circles). The environment (i.e. the Spatial Distribution Model) predicts the nature and scale of spatial structure, but does not predict the intensity.

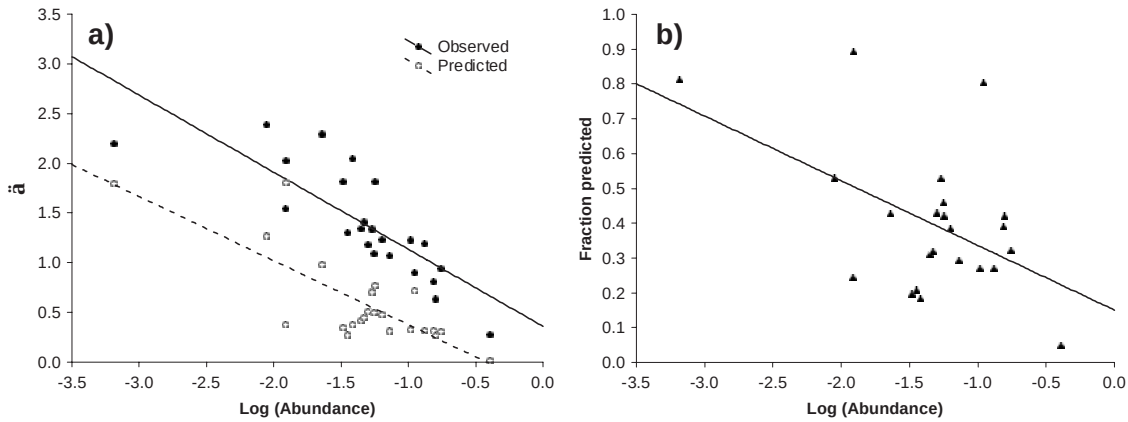
A first step to uncovering the mechanisms responsible for the higher-than-environmentally-expected aggregation documented here (see discussion), will be to find out which, if any, characteristics of species are correlated with the degree of mismatch between observed and predicted spatial structure. Although we did not attempt a complete search for such characteristics here, we did examine the influence of species' range size, and dispersal mode. We found that the covariance at distance 0 (δ) decreased with species' range size (Fig. 4(a)), indicating that less widely distributed species show more patchy distributions than widely distributed species (similar patterns have been observed in tropical forests: Condit *et al*., 2000). But this pattern was also captured by the SDMs, suggesting that the correlation between species' range size and spatial short-scale aggregation can be explained by the regional environmental dependency of the species. Because of this, the mismatch between predicted and observed spatial structure showed only a weak relationship with species' range size (Fig. 4(b)). In particular, the observed intensity of aggregation was, on average, one unit higher than predicted, over a wide range of species' range sizes (Fig. 4(a)). Thus, the weak and fragile pattern in δ *vs.* species' range size, results mostly from the fact that δ is a ratio, whereas the *difference* in predicted *vs.* observed intensity was independent of species' range size. No significant differences in spatial aggregation were found between qualitative dispersal mode groups (animal- *vs*. wind-dispersed species; see Appendix S3).

Discussion

We found that SDMs capture the nature and scale of spatial structure in trees, yet the intensity of such patterns fails to be predicted by the underlying environmental heterogeneity, consistently with previous spatial patch-occupancy models on three Mediterranean tree species (Purves *et al*., 2007). On the one hand, this provides evidence that exogenous environmental factors can account for not only the locations and shapes of species ranges, but also the qualitative features of spatial structure within those ranges. This in turn adds to the mounting evidence that environmental conditions strongly influences species' distribution patterns locally and regionally, as it does world-wide (Hawkins *et al*., 2003). Indeed, most of the selected variables were related to water and energy, which is consistent with the widely documented trend of plant species to be climatically driven by water-energy dynamics (see Field *et al*., 2005 and references therein)

However, we found that SDMs could not account for the intensity of the observed spatial structure within species ranges. For most species the SDMs predicted much less short-scale aggregation than was observed,

Figure 4. (a) Spatial covariance at distance 0 (Km) as a function of species range size. Species are ranked from less to more widely distributed in axis X. Predicted aggregation at distance 0 (δ) decreases with species range size, indicating that more widely distributed species are less aggregated in space (Observed $R^2 = 0.64$, $p < 0.05$; Predicted $R^2 = 0.62$, $p < 0.05$). (b) Fraction of the covariance at distance 0 predicted by species distribution models (SDMs) (δ) ($R^2 = 0.26$, $p < 0.05$). Removing the most and the lest widely distributed species gives a weak correlation between species range size and predictive ability (R2 = 0.026, $p < 0.05$) (see text).



suggesting that the observed imbalance between environment and species' spatial structure is associated to a higher-than-environmentally-expected spatial aggregation of tree species. However, substantial variation among species was detected, with some species having spatial structure that was close to that predicted by environmental conditions alone (*Abies alba*, *Pinus uncinata*, and *Quercus robur*). This indicates that there appears to be variation among species in the weight of influence of environmental dependency *vs*. other mechanisms (see below) in determining spatial structure within the range.

Although using different methods and data, the results reported here agree with those obtained by Bahn & McGill (2007). These authors concluded that 'the success of coordinates and contagion relative to environment in modelling species distributions suggests that we are missing fundamental ecological elements underlying distributions when we model them using environmental conditions only'. Given the imbalance between environment and spatial structure of species documented here, future SDMs will need to address ecological processes that tend to aggregate species in space in order to increase models' predictive power (see Leathwick & Austin, 2001; Araújo & Luoto, 2007). Indeed, most of the missing processes not considered by SDMs that have been suggested in the literature to this respect tend to aggregate biological species. These processes include short-scale environmental heterogeneity (e.g. microclimates, soil quantitative properties), local dispersal and source-sink dynamics (local dispersal leads to intraspecific aggregation; Pacala, 1997); biotic interactions across trophic levels that foster species coexistence or exclusion in different parts of the range (e.g. dispersal, polinization; Araújo & Luoto, 2007); and processes that tend to fragment space and create patchy aggregated distributions, such as recurrent perturbation regimes (e.g. fire events in Mediterranean ecosystems), and habitat loss and fragmentation (Fahrig, 2003). Although the assessment of each of these mechanisms is beyond the scope of this study, the patterns of aggregation detected in our study region and the suggestion of these processes are consistent with the hierarchical framework proposed by Pearson & Dawson (2003). Our results suggest that environmental/scenopoetic variables (Soberón, 2007) predict broad spatial structures (i.e. nature and scale of spatial structure), whereas population/bionomic variables tend to have much more fine-grained spatial structures and predict spatial patterns at lower scales (i.e. level of aggre-

gation of species).

Although there is a large variety of methods within the SDMs framework (see review of existing methods in Guisan & Zimmerman, 2000; Scott *et al*., 2002), most of them focus on understanding the location and extent of species distribution ranges, and have rarely paid attention to the spatial structure of individual species within these ranges. A fundamental issue when exploring spatial structure is that we need models that allow a continuous probability of occurrence of a species given certain environmental conditions. Although most SDMs can potentially generate probability maps (e.g. all regression-based SDMs, Neural Networks, Maxent, GARP), it is common practice to reclassify continuous probability of occurrence (range 0-1), into deterministic predictions of presence or absence (value 1 or 0). However, as this and other studies report (e.g. Condit *et al*., 2000), most species are very unlikely to show such deterministic spatial patterns, and instead have probabilistic patterns of occurrence, with the probabilities affected by many other factors in addition to exogenous environmental factors. Indeed, it has been argued that more robust predictions might be obtained by using estimates of change in the probabilities of occurrence rather than changes in the presences and absences of species (Araújo *et al*., 2005). Therefore, by applying reclassification, the exploration of ecological properties such as spatial aggregation of individuals is not possible because no patterns of response can be observed along the environmental gradients. In part, this explains why current SDMs have not yet shown how they can capture structure at finer scales.

An important limitation of our model is that soil properties are included as discrete categories (according to FAO classification), each of them comprising a set of different edaphic variables (e.g. pH, texture, moisture content, cation exchange capacity, etc). This indicates that our current model is not able to accurately estimate the influence individual soil variables, leaving open the possibility that some of the unexplained variation in the intensity of spatial structure is due to species responses to variation in soil. If so, this would not just be a case of an important exogenous environmental factor that has been missed. Rather, unlike most of the factors considered here, soil is heavily affected by the presence or absence of the species, over and above those aspects of soil that are defined exogenously (e.g. bedrock types). Because soil may determine spatial structure of biological communities (Coudun *et al*., 2006), especially for those species that are more substrate-dependent, it would be beneficial if future SDMs included high resolution soil datasets at large scales.

A potential problem with the model presented here assumes normal (Gaussian) responses between species occurrence and environmental variables. This is a common assumption in niche theory and SDMs (Austin, 2002) also made by our model. The functional response of species to environmental gradients is still a matter of debate: for example it has been argued that symmetric unimodal responses are rare whereas skewed curves predominate (see Austin, 2002). On the other hand, the real response curves of species to environmental variables can be quantified only when all other factors are non-limiting, an unlikely phenomenon in nature (Huston, 2002). It remains to be seen whether SDMs with alternative functional forms might reproduce spatial structure more accurately than those documented here: although the observed deviation in this case was so large (Fig. 1) that it seems unlikely that the mismatches can be attributed entirely, or even mainly, to this problem.

Another common and necessary assumption in large-scale distribution modelling is that tree populations are in pseudo-equilibrium with environmental conditions (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003). However, the validity of this assumption varies across different groups of organisms, and among species within the same group (Araújo & Pearson, 2005). This is the case for exotic species. Whereas some of the exotic species in the Iberian Peninsula have been naturalized over time since their first introduction (e.g. Castanea sativa), others (e.g. *Pinus radiata* and *Eucalyptus sp.*) have been recently introduced as plantations. The time for naturalization for these species has been really short since most plantations were made mostly in the second half of the 20th century (Blondel & Aronson, 1999). This

suggests that spatial distributions associated to recently introduced species do not fit with the pseudo-equilibrium assumption between species occurrence and environmental conditions. Indeed, in this case spatial structure is poorly explained by environmental conditions for most exotic trees, especially *Pinus radiata* (see Figure 2). This raises the possibility that, in other cases, a mismatch between predicted and observed fine-scale spatial structure might be a useful indicator of non-equilibrium. Results for introduced tree species should thus be taken cautiously because they may be reflecting their allochthonous nature.

Given the reported time lags in the recolonization of northern latitudes following Holocene warming in Europe (Araújo & Pearson, 2005; Svenning & Skov, 2004), the equilibrium between species distributions and environmental conditions may be associated to the distance to historical glacial refugia. Indeed, major biological regions in Europe are determined more by the location of these glacial refugia than by current climate gradients (Araújo & Pearson, 2005; Svenning & Skov, 2005, 2007). Because the last glacial episode affected more intensely the areas historically covered by ice than the southern ice-free regions of Europe (Montoya *et al*., 2007), and the Iberian Peninsula is located in a historical glacial refugia where trees were not excluded from (Hewitt, 2000; Carrión *et al*., 2003), it is reasonable to consider that tree species in Continental Spain are closer to equilibrium than tree species living in northern areas (except exotic species), simply because species have had more time and less dispersal distance to colonize suitable areas. The equilibrium assumption also depends on the dispersal abilities of individual species to colonize environmentally suitable regions (Tyre *et al*., 2001). For example, animal-dispersal of seeds is generally addressed to longer distances than wind-dispersal. 14 out of our 23 tree species are dispersed by animals, which suggests that, given enough time, at least these species might be at equilibrium with environment. However, previous studies have shown that the response of certain individual trees to glacial history indicates strong links between the location of glacial refugia and spatial patterns of trees in the Iberian Peninsula (Benito Garzón *et al*., 2007). Therefore, a reasonable conclusion is that, whereas spatial restrictions apply to a subset of species, others might be at equilibrium with current environmental conditions in our study region.

Finally, the equilibrium assumption is less apparent in disturbed ecosystems such as Mediterranean forests, where human influence is strong. In this case, the observed imbalance between environment and spatial aggregation of tree species might be explained by the lack of equilibrium between species and current environmental conditions. However, because attempts to incorporate population-level processes such as biotic interactions into the SDMs framework (Leathwick & Austin, 2001; Araújo & Luoto, 2007) have shown that combined population-environmental models have more predictive power than pure environmental models, it is reasonable to conclude that population-level processes at least explain in part the differences in spatial aggregation of tree species between SDMs and observations. Despite this, it is important to bear in mind that our results are restricted to tree species in Continental Spain, and thus we are not certain to what extent any patterns or results that we observe here may be extrapolated to other regions.

Patchiness, or the degree to which individuals are aggregated, is crucial to understanding the dynamics of forest communities, such as how a given species uses resources, how the species is used as a resource, and to describe the species' reproductive biology. Information on spatial aggregation of a species can be also critical to predict its distribution in a different region or future distributions following landscape changes (e.g. climate change). Moreover, the aim of reserve design is to select a small but efficient network of sites for conservation. In such a case, robust prediction of the distribution and spatial structure of the species in the selected network is crucial (Araújo & Williams, 2000; Araújo *et al*., 2002). However, given the high variation in the accuracy of SDM predictions (Segurado & Araújo, 2004; Pearson *et al*., 2006) and the species-specific nature of biological responses to landscape changes (e.g. climate change; Kerr & Kharouba, 2007), it seems clear that predicting

individual species' responses will often be difficult. A promising avenue is that recent studies suggest that species traits are behind these interspecific differences, and that species might therefore be aggregated into functional groups according to physiological and demographic traits. For example, Pöyry *et al*. (2008) have shown that the quality of SDMs for a set of 98 species of butterflies is shaped by processes operating at the population level. These authors found that the spatial distribution of species with low mobility and short flight periods were modeled more accurately than species with high mobility and long flight periods. Future studies should address empirically the question of which traits reduce the uncertainty associated with environmental models, and identify relevant traits to understand species' spatial distribution under global change.

In summary, although SDMs are a general and widely used approximation to modelling species distributions, future conservation strategies will require models that incorporate greater biological realism (Hampte, 2004; Keith *et al*., 2008). Spatial structure analyses within species' distribution ranges show that SDMs capture very accurately the nature and scale of the spatial structure of tree species, yet the intensity or level of aggregation of species in space is captured poorly. Species are more aggregated in space than environmentally expected, and so the development of more realistic SDMs should focus on those ecological processes that increase species aggregation.

Appendix. Appendix 1 provides the maximum likelihood estimates for each species-specific model. Appendix 2 gives the relatonship between predicted aggregation at distance 0 (δ) and overall predicted spatial structure (pseudo-R^2). Appendix 3 includes the permutation test on the relationship between spatial aggregation and qualitative dispersal mode. Appendix 4 provides the relationship between species' range size and overall predicted spatial structure (pseudo-R^2).

Acknowledgments

We thank the Ministerio de Medio Ambiente, Spain, and R. Vallejo and J. A. Villanueva for help with IFN2 data. We also thank M. A. Rodríguez for his useful comments on first versions of the manuscript, and three anonymous reviewers for their comments and suggestions. D.M. was supported by the Spanish Ministry for Education and Science (fellowship AP2004-0075). M.A.Z. was supported by the DINAMED project (grant CGL2005-05830-C03), and INTERBOS3 project (grant CDL2008-04503-C03-03). This research is part of the GLOBIMED (www.globimed.net) network of forest ecology.

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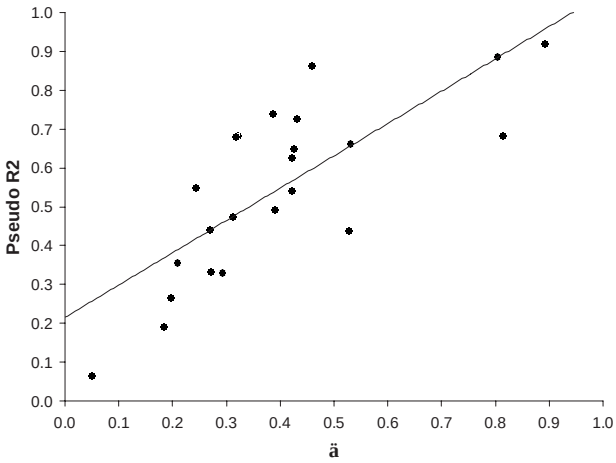
Appendix S1

MAXIMUM LIKELIHOOD ESTIMATES (MLE) FOR EACH SPECIES-SPECIFIC MODEL. ENVIRONMENTAL VARIABLES (FACTORS) ARE PROVIDED IN TABLE 1 (see main text)

Species		Factor 1		Factor 2		Factor 3	
	ε_j	$\mu_{x,j}$	$\sigma_{x,j}$	$\mu_{x,j}$	$\sigma_{x,j}$	$\sigma_{x,j}$	$\mu_{x,j}$
Abies alba	-5.604	89.353	4.204	289.78	-9.804		
Castanea sativa	-0.187	1552.843	-5.242	65.427	-9.905		
Ceratonia siliqua	-4.948	120.293	-9.914	1273.698	4.534		
Corylus avellana	-0.183	303.317	-5.208	135.076	-6.459		
Eucalyptus camaldulensis	-0.097	190.358	-9.962	1222.788	-6.508		
Eucalyptus globulus	-2.885	198.218	3.381	109.226	-9.891	733.882	-4.773
Fagus sylvatica	0.185	281.160	-6.799	145.175	-9.997		
Ilex aquifolium	-0.378	259.504	-5.990	131.657	-7.837		
Juniperus thurifera	1.258	-39.159	-4.312	355.889	-9.644		
Olea europaea	-0.164	226.267	-9.908	187.284	-9.865		
Phyllirea latifolia	-1.766	239.317	-9.215	1087.925	-7.520		
Pinus halepensis	1.060	254.588	-9.990	120.007	-9.602		
Pinus nigra	-0.298	11.263	-8.655	218.303	-9.921		
Pinus pinaster	-1.534	130.498	-9.985	164.934	3.948		
Pinus radiata	1.650	1.783	-9.204	71.652	-9.999		
Pinus sylvestris	0.891	65.349	-8.288	269.037	-7.706		
Pinus uncinata	1.438	-32.903	-8.899	439.617	-2.951	204.043	-3.158
Quercus faginea	-0.453	31.941	-8.277	826.867	-8.923		
Quercus ilex	0.917	738.250	-9.862	57.561	-7.010		
Quercus petraea	-0.844	290.558	-4.937	159.122	-8.711		
Quercus robur	0.811	98.116	-6.077	423.741	-3.086		
Quercus suber	0.720	181.962	-9.914	287.810	-9.734		
Rhamnus alaternus	-0.933	243.142	-9.880	161.682	-8.302		

Appendix 2

RELATIONSHIP BETWEEN PREDICTED AGGREGATION AT DISTANCE 0 (δ) AND OVERALL PREDICTED SPATIAL STRUCTURE (PSEUDO-R^2) ($R^2 = 0.59$, $P < 0.005$).



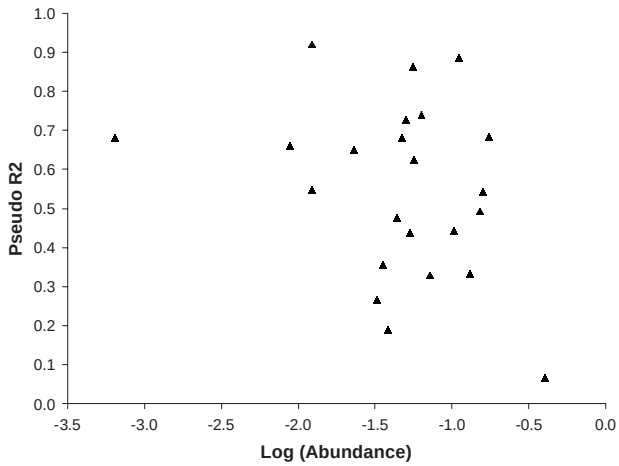
Appendix 3

PERMUTATION TEST ON THE RELATIONSHIP BETWEEN SPATIAL AGGREGATION AND QUALITATIVE DISPERSAL MODE.

Given that dispersal mode is a potential source of intraspecific aggregation (Pacala 1997), we ranked spe cies as a function of their observed spatial aggregation (species 1, species2,…, species 23), so the avera ge position of an animal- and wind-dispersed species in that list could be obtained. The difference betwe en the average position numbers was used as a test statistic to evaluate the probability of obtaining, by chance, the observed difference in average rank between wind- and animal-dispersed species. 10,000 sets of random species ranks were produced, where each species was assigned a rank (1-23) at random. For each of these 10,000 sets, the difference between the average rank for animal *vs.* wind-dispersed species was calculated. This yielded a frequency distribution of the difference between the groups, corresponding to a null hypothesis of no true difference in aggregation between the groups. We then noted where the observed value of the difference between the groups lay in the frequency distribution, which correspon ded to the probability of obtaining the observed difference without a true difference between the groups. We found no support for the alternative hypothesis, that is, we did not detect significant differences in spa tial aggregation of species between dispersal groups ($p = 0.48$ and $p = 0.31$, for δ and pseudo-R^2, respec tively). The permutation test was performed in C programming code.

Appendix 4

RELATIONSHIP BETWEEN SPECIES' RANGE SIZE AND OVERALL PREDICTED SPATIAL STRUCTURE (R^2 = 0.099, P = 0.14).



6. Conclusiones generales

1. Procesos espacio-temporales y riqueza de especies a gran escala

• La mayor disponibilidad de datos actual sobre presencia/ausencia, riqueza y abundancia de especies, su mayor calidad y el desarrollo de técnicas avanzadas de análisis espacial permiten replantearse viejas cuestiones de la Ecología que, en ocasiones, pueden arrojar resultados contrarios a los tradicionalmente obtenidos.

• Los '*Interim General Models*' (IGMs) constituyen una buena aproximación para estimar la riqueza de especies de árboles a nivel global.

• La 'huella' de la evolución del clima en tiempos recientes (últimos 14000 años) puede detectarse en los patrones de riqueza de las especies de árboles en Europa y Norte América. Esto refleja cómo un proceso con una estructura espacial y temporal concretas (retirada glaciar debido al calentamiento global post-Pleistocénico) puede determinar parcialmente la riqueza forestal observada en la actualidad.

• La comprensión de los gradientes de riqueza de especies actuales requiere de la consideración tanto de los patrones espaciales de cambio climático como de los patrones climáticos estáticos estimados en un determinado momento.

2. Pérdida de hábitat y riesgos de extinción de especies

• Existen diferencias a nivel inter-específico en la respuesta de los árboles a la pérdida de hábitat en su entorno.

• Estas diferencias vienen determinadas, al menos en parte, por el tipo de dispersión de las especies.

• La relación entre el grado de vulnerabilidad de las especies a la pérdida de hábitat y el tipo de dispersión dominante se basa en la estructura espacial asociada a cada vector de dispersión. Así, mientras que el viento genera una dispersión aleatoria y a corta distancia, la dispersión animal suele ser dirigida y cubre distancias más largas. En ambientes fragmentados, estas características ayudan a mantener demográficamente conectados fragmentos de bosque que se encuentran aislados físicamente.

• De este modo, las especies de dispersión anemócora se muestran globalmente más vulnerables que las especies de dispersión animal. No obstante, esto es solamente cierto si las especies dispersoras de semillas coexisten en el ecosistema. En caso contrario, las especies de dispersión zoócora serían más vulnerables a la pérdida de hábitat.

• Las políticas de conservación deberían, por lo tanto, dirigirse a la protección no solamente de especies individuales, sino de interacciones clave para la red ecológica.

3. Pérdida y fragmentación de hábitat y umbrales de extinción

• La fragmentación del hábitat puede distorsionar el umbral de extinción de las especies, aunque no siempre de la forma predicha por la teoría ecológica.

• La fragmentación del hábitat no tiene ningún efecto o tiene efectos positivos sobre la probabilidad de ocurrencia de las especies de árboles. Solamente las especies estrictamente forestales y con capacidades dispersivas limitadas se ven afectadas negativamente por la fragmentación del hábitat y parecen confirmar la hipótesis del umbral de extinción.

• Los patrones espaciales asociados a la fragmentación del hábitat ayudan a comprender algunos de los patrones de riqueza y presencia/ausencia de especies en paisajes fragmentados, así como a identificar especies más vulnerables a la fragmentación.

4. Modelos de Distribución de Especies y estructura espacial de las especies

• Las predicciones de la estructura espacial de las especies arbóreas dentro de sus rangos difiere a nivel inter-específico.

• Los Modelos de Distribución de Especies (MDEs) basados en relaciones especies-clima contemporáneas predicen varios aspectos de la estructura espacial de las especies dentro de sus rangos. No obstante, los MDEs no predicen un elemento importante de dichos patrones; las especies están espacialmente más agregadas que lo predicho por los modelos.

• La inconsistencia entre el grado de agregación espacial de las especies entre los modelos y la naturaleza pone de manifiesto que procesos no climáticos están detrás de los patrones de agregación observados, tales como la dispersión, las interacciones bióticas, la destrucción del hábitat y la falta de equilibrio entre el clima contemporáneo y las distribuciones actuales de las especies.

• Es necesario desarrollar una nueva generación de modelos biológicamente más realistas para predecir futuros cambios en la distribución y la estructura espacial de las especies ante el cambio global.