Global patterns of forest fragmentation: Impacts on species extinctions and climate change
Tesis Doctoral Milagros Ferrero Cedenilla

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Programa de Doctorado en Ecología, Conservación y Restauración de Ecosistemas

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TESIS DOCTORAL

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Universidad de Alcalá
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"Global patterns of forest fragmentation: Impacts on species extinction and climate change"

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La Tesis Doctoral que se presenta se desarrolla amparada con una beca FPI del Ministerio de Economía y Competitividad (BES-2011-048041) y todos sus objetivos se desarrollan en el marco del proyecto CGL2010-22119 “Fragmentación de bosques en España y Europa y probabilidades de extinción de especies forestales de animales y plantas”.

A mis padres:

D. Miguel Ferrero Bonilla y Dña. M^{a} Carmen Cedenilla Díaz

Agradecimientos

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Mi carrera investigadora comenzó en el CSIC, concretamente en IREC (Instituto de Investigación en Recursos Cinegéticos) sito en Ciudad Real, de la mano de Jorge Cassinello, quien me dio la primera oportunidad de tener contacto con la labor investigadora. En lo personal de allí me traje a Pedro Corell, el dueño del coto de caza “Los Claros” donde hacíamos los muestreos, que siempre fue tan amable conmigo, y a mi Luis y mi Paqui, matrimonio de guarda y cocinera, ejemplo de nobleza, que a día de hoy continúan formando parte de mi vida. Y cómo olvidarme de la primera irrupción en mi historia de Antonio el de la Alfonsa, guitarrista flamenco y mejor amigo, que después daría mucho que hablar en mi vida a mi regreso a Madrid, en la transformación de Mila Ferrero en Milana Real…

Tras este primer contacto lo la investigación, decidí embarcarme en la aventura de pedir una beca FPI del Ministerio para volver a Madrid y poder trabajar en lo que verdaderamente me gustaba, la Macroecología. A la bandeja de entrada del correo de Miguel Ángel Rodríguez llegó el email de una jovencita presentado currículum y credenciales para incorporarse a su proyecto, el cual he agradecido siempre que fuera tan gratamente recibido. Y aquí comenzó mi andadura por el departamento de Ecología (ahora Ciencias de la Vida) de esta maravillosa Universidad, la Universidad de Alcalá, donde he sido, puedo decir y digo, muy pero que muy feliz.

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Nunca sabes lo fuerte que eres
hasta que ser fuerte es tu única opción.

Y entonces te das cuenta de que no es fortaleza,
sino que es resignación.

No hay cosas buenas ni malas,
es cuestión de percepción…

(M. FERRERO)

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This current PhD Thesis is written in a bilingual format to meet the requirements to obtain the International Mention

CAPÍTULO 1

RESUMEN / ABSTRACT

Resumen

La pérdida y la fragmentación de hábitats son considerados unos de los principales causantes de la actual crisis global de biodiversidad. Estos fenómenos pueden tener además profundas consecuencias sobre los servicios ecosistémicos que sustentan la supervivencia y el bienestar humano, por lo que los esfuerzos para comprender sus efectos se han intensificado en las últimas dos décadas. Su estudio ha dado lugar a una de las áreas de investigación más activas dentro de la ecología aplicada y la biología de la conservación, destacando el estudio de la reacción de las especies a la alteración de su hábitat como una de las actuales líneas prioritarias.

La literatura sobre los efectos de la fragmentación de hábitats en la biodiversidad es muy abundante, pero también contradictoria, con diferentes estudios cuantificando la fragmentación de diferentes formas y alcanzando conclusiones dispares sobre la magnitud y dirección de sus efectos. En parte esto se debe a: (1) que la fragmentación suele analizarse indirectamente usando manchas de hábitat como unidades de análisis, en lugar de hacerlo de forma directa en paisajes (constelaciones de manchas) más o menos fragmentados; (2) la existencia de numerosos índices para medir fragmentación, a menudo redundantes y que no ayudan a distinguir entre efectos de pérdida de hábitat y de fragmentación; y (3) por la falta de métricas estandarizadas que permitan diferenciar niveles de fragmentación, lo que dificulta la comparación entre estudios.

En el capítulo III de la presente tesis abordamos estas cuestiones mediante el análisis de dos bases de datos que permiten analizar la fragmentación forestal a escala global y, con mayor resolución, dentro de la región mediterránea. Se generaron los correspondientes mapas de fragmentación y se exploró en ambos casos el potencial del índice rLPS (relative Largest Patch Size o porcentaje de hábitat concentrado en la mancha

más grande dentro de cada paisaje analizado) como medida sintética de fragmentación. Los resultados apoyan la capacidad de rLPS para diferenciar entre paisajes más y menos fragmentados, y además muestran que hay combinaciones de cantidad de hábitat y fragmentación que son empíricamente inexistentes, lo que tiene implicaciones para el diseño de experimentos realistas sobre los efectos de la fragmentación. También encontramos una alta correspondencia entre niveles de cobertura y fragmentación forestal, tanto en los bosques mediterráneos, como a escala global: los bosques con escasa cobertura solían estar muy fragmentados. Por tanto, las iniciativas para minimizar las ingentes pérdidas de superficie arbolada y sus consecuencias para la biodiversidad forestal no deben descartar la reducción de la fragmentación de los bosques.

Por otro lado, en la década de los ochenta, se acuñó el concepto de "umbral de extinción" (cantidad mínima de hábitat por debajo de la cual la población de una especie se extingue), argumentándose su posible dependencia de la fragmentación. Posteriormente distintos trabajos teóricos, a pesar de utilizar estrategias de modelización estocástica y determinística diferentes, encontraron umbrales de extinción mayores en presencia de fragmentación, lo que supuso un fuerte respaldo teórico a la hipótesis del umbral de extinción (HUE). En contraste, influyentes revisiones de la literatura existente concluyen que, mientras la pérdida de hábitat siempre afecta negativamente a la persistencia de las poblaciones, la fragmentación tiene efectos más débiles que pueden ser negativos, positivos o neutros dependiendo de la especie.

Ante esta disyuntiva, y siendo los test explícitos de esta hipótesis escasos, en la presente tesis doctoral (capitulo IV) se plantea un estudio de biogeografía de la conservación que tiene como objetivo evaluar la HUE para especies de vertebrados forestales en escala continental (Europa Occidental), concluyendo que aunque la cantidad de bosque es determinante para explicar la presencia de especies especialistas forestales, la fragmentación también es relevante para algunas de ellas, no pudiendo ser por tanto, obviada. La respuesta de las especies a la fragmentación dependía en gran medida de sus características biológicas (p.e. tamaño, dieta, nivel trófico), siendo útil considerar éstos como variables fundamentales para predecir e interpretar la respuesta de las especies a la fragmentación.

Por último, la proporción de carbono almacenado en los bosques asciende al 70-80% del carbono terrestre total, el cual es liberado a la atmósfera cuando los bosques son aclarados. Aproximadamente un cuarto del total de las emisiones de carbono de origen antrópico se debe a la deforestación, siendo la mayor fuente de CO_2 a la atmósfera (≈ 1,1 Gt). Sin embargo, los procesos resultantes de la misma, como la fragmentación, no han sido cuantificados en la mayoría de los casos. Por ello, en el capítulo V analizamos la contribución de la fragmentación, la cantidad de bosque y el clima sobre el secuestro de carbono, utilizando para ello una variable indicadora de biomasa, la altura de los árboles. Los resultados indicaron que la configuración espacial de los remanentes de bosque resultantes tras la deforestación es un factor más importante en la determinación de la altura de los árboles y el secuestro de carbono que la pérdida de hábitat *per se*, debido a la importante influencia del efecto borde. Dada la alta tasa de fragmentación forestal en los trópicos, tales emisiones pueden intensificar los efectos del calentamiento global más allá de los efectos debidos a la pérdida de bosque. La planificación de estrategias que minimicen la superficie de borde en paisajes manejados reduciría considerablemente las emisiones de gases de efecto invernadero.

En conjunto, los resultados de los tres trabajos de investigación que componen esta tesis tienen el potencial de incidir en el desarrollo de la teoría sobre la fragmentación (capítulos III y IV) y en su metodología de estudio

(capítulo III), así como en la conservación de especies en nuestras áreas de estudio gracias a los mapas de fragmentación obtenidos (capítulo III), indicando dónde acciones de reforestación y reducción de la fragmentación pueden tener mayor incidencia para la conservación de las especies, y mostrando la importancia de esta variable no solo sobre la biodiversidad y las probabilidades de extinción de las especies, sino también sobre el cambio climático (capítulo V).

Palabras clave: Fragmentación de hábitat, efecto borde, pérdida de hábitat, umbral de extinción, relative Largest Patch Size (rLPS), emisiones de carbono, efecto invernadero, calentamiento global, conservación de especies, extinción de especies.

Abstract

Habitat loss and fragmentation are considered one of the main causes of the current global biodiversity crisis. These phenomena can also have profound consequences on the ecosystem services that sustain human wellness and survival, thus, the efforts to understand their effects have intensified over the last two decades, leading to one of the most active research areas within applied ecology and conservation biology. This area highlights the study of species responses to the modification of habitat as one of its current priority research lines.

The literature on the effects of habitat fragmentation on biodiversity is very abundant, but also contradictory, with most studies quantifying fragmentation in different ways and reaching disparate conclusions about the magnitude and direction of its effects. This is in part due to: (1) fragmentation is generally measured indirectly, using habitat patches as analysis units, instead of directly quantifying it within more or less fragmented landscapes (i.e. constellations of patches) (2) the existence of multiples indexes to measure fragmentation, frequently correlated and unable to distinguish between the effects of habitat loss and fragmentation; and (3) the lack of clear standardized metrics allowing to differentiate fragmentation levels, which complicates comparison across studies.

In chapter III of this Thesis we addressed these issues by analyzing two databases that allow quantifying forest fragmentation at the global scale and, for a higher-detail resolution, within the Mediterranean region. We generated the corresponding fragmentation maps to each dataset and explored in both cases the potential of the rLPS index (relative Largest Patch Size or the percentage of habitat concentrated in the largest patch within each landscape analyzed) as a synthetic fragmentation measure. The results support the ability of rLPS to differentiate between more and less fragmented landscapes

and the existence of combinations of habitat amount and fragmentation that are empirically non-existent. This would have implications for the design of realistic experiments testing the effects of fragmentation at varying scales. We also found a high correlation between habitat coverage and forest fragmentation both, in Mediterranean and in global forest: forest with low coverage are often very fragmented. Therefore, initiatives to minimize the large losses of forest surface and its consequences for forest biodiversity should not rule out the need for reduction of forest fragmentation.

On the other hand, the concept of "extinction threshold" (minimum habitat amount below which the population of species would die out), was coined in the eighties arguing its potential dependence on fragmentation. Then, different theoretical works, found higher extinction threshold in presence of fragmentation despite using different stochastic and deterministic modeling strategies, which implies a strong theoretical support for the extinction threshold hypothesis (ETH). In contrast, influential reviews of the literature conclude that, while habitat loss always affects negatively populations persistence, fragmentation has weaker effects that can be negative, positive or neutral depending of the species.

Given the above controversy, and the scarceness of explicit tests of the ETH, in this doctoral thesis (chapter IV) we propose a conservation biogeography study aimed at evaluating the ETH for forest vertebrate species on a continental scale (Western Europe). It concludes that although the amount of forest is critical to explain the presence of forest specialist species, fragmentation was also relevant for some of them, and therefore it should not be ignored. The species´ response to fragmentation depended largely on their biological traits, which will ultimately be central to predict and interpret these responses to fragmentation.

Finally, the proportion of carbon stored in forests sums up to 70-80% of the total terrestrial carbon, which is released into the atmosphere when forests are cleared. Approximately one quarter of the total carbon emissions of anthropic origin are due to deforestation, being the largest source of CO_2 to the atmosphere (≈ 1,1 Gt). However, the effects of processes linked to deforestation, such as fragmentation, have only rarely been tested. Therefore, Chapter V analyzes the contribution of fragmentation, forest amount and climate on carbon sequestration, using tree height as a proxy for biomass. The results indicate that the spatial configuration of forest remnants resulting from deforestation is a more important factor in determining tree height and carbon sequestration than habitat loss *per se*, due to the influence of edge effects. Given the high rate of forest fragmentation in the tropics, such emissions may intensify the effects of global warming above and beyond the effects already attributable to forest loss. Planning clearing strategies to minimize habitat edges in managed landscapes will reduce considerably greenhouse gas emissions.

Together, the results of the three research chapters that make up this thesis have the potential to influence the development of the fragmentation theory (chapters III and IV) and methodological aspects of its study (chapter III). The results can also affect the conservation of biodiversity thanks to the fragmentation maps obtained (chapter III), indicating where reforestation and fragmentation reduction actions may have the greatest incidence for species conservation. Finally, the results from this Thesis confirm the importance of fragmentation not only for biodiversity and the likelihood of species extinction, but also for climate change (Chapter V)

Keywords: Habitat fragmentation, edge effect, habitat loss, extinction threshold, relative Largest Patch Size (rLPS), carbon emissions, greenhouse effect, global warming, species conservation, species extinction.

CAPÍTULO 2

INTRODUCCIÓN GENERAL

Introducción general

1. Pérdida de hábitat y fragmentación. Definición.

La pérdida de hábitat es el proceso mediante el cual el hábitat se destruye con el tiempo. La fragmentación de hábitat tiene que ver con la configuración espacial de los remanentes de hábitat que se encuentran en un paisaje. A igual cantidad de hábitat, un patrón más fragmentado presentará mayor cantidad de parches de hábitat de menor tamaño, así como una mayor cantidad total de borde en el conjunto del paisaje (Fig. 1) (Fahrig, 2017).

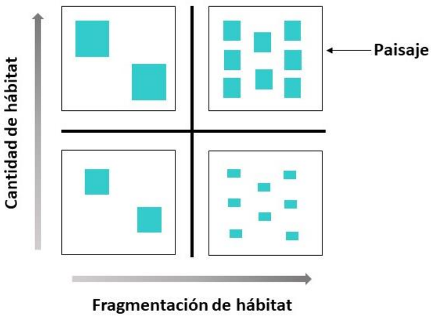

Figura 1: Ilustración de cómo a igualdad de cantidad de hábitat, un hábitat más fragmentado presenta un mayor número de parches de hábitat más pequeños (extraído de Fahrig, 2017). Los dos paneles superiores y los dos paneles inferiores muestran paisajes con la misma cantidad de hábitat, pero los paneles de la derecha están más fragmentados que los de la izquierda.

2. Parches de hábitat.

2.1. *Concepto de parche de hábitat. Definición y paradigmas.*

El concepto de parche de hábitat en ecología ha ido variando a lo largo del tiempo. Hasta los años 1970, los científicos asociaban el parcheado del hábitat con el concepto de heterogeneidad espacial, por lo que un incremento de parcheado implicaría una ganancia de hábitat y un incremento en la abundancia y diversidad de especies (Fig. 2a). Ejemplo de ello son los estudios clásicos de depredador-presa de Gause (1934) o Huffaker (1958), que señalaban que la división de los recursos alimenticios en una mayor cantidad de parches permite la persistencia del sistema depredador-presa, al proporcionar sitios temporales de refugio para las presas a lo largo del espacio y del tiempo. Otro ejemplo es el estudio de den Boer (1968), que mostró que la irregularidad del hábitat puede aumentar la persistencia de las especies en el largo plazo, el evitar la concentración espacio-temporal de las extinciones locales de especies de presas. En consecuencia, esa mayor cantidad de parches permitiría diluir el riesgo de extinción global entre una plétora de riesgos de extinción locales, evitando "poner todos los huevos en la misma cesta" (Fig. 2). Es más, den Boer (1968) también conectó la dinámica de extinciones locales con la creación de oportunidades para la permanencia o incorporación de otras especies en el paisaje, relacionando la noción de parches de hábitat con posibles aumentos de la diversidad (Fig. 2a). Sin embargo, esta perspectiva positiva decayó con la extensión, por parte de Levins (1970), de la teoría de biogeografía de islas (McArthur y Wilson, 1967) a los parches de hábitat. Desde entonces, los conceptos de parche y fragmentación del hábitat han quedado asociados al de pérdida de hábitat y, consecuentemente, con efectos negativos sobre la biodiversidad, dando lugar al paradigma dominante en la actualidad, que asume que la fragmentación suele reducir la probabilidad de persistencia de las especies (Fig. 2b) (Fahrig, 2017).

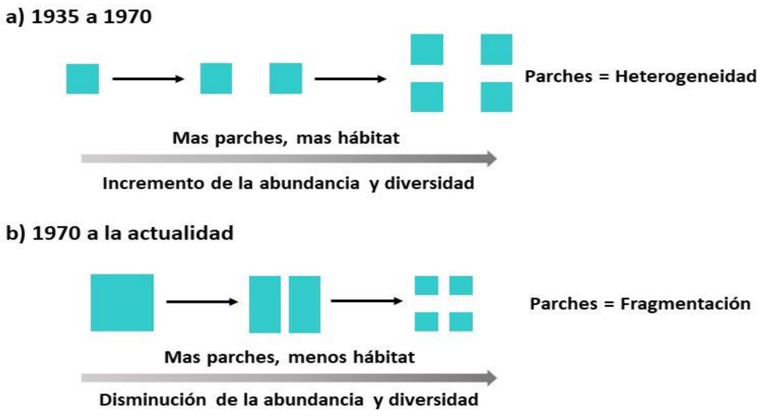

Figura 2: Cambio de paradigma en la concepción de los parches de hábitat en ecología. (a) De 1935 a aproximadamente 1970 el concepto de parcheado del hábitat se relacionaba con la heterogeneidad espacial, ganancia de hábitat e incremento de la abundancia y diversidad de especies. (b) A partir de 1970 y hasta la actualidad, el parcheado de hábitat se ha relacionado con el concepto de fragmentación de hábitat, asumiendo que presenta un efecto negativo sobre la biodiversidad (Fahrig, 2017).

3. Diseños experimentales para medir fragmentación de hábitat *per se*.

3.1. *Escala de parche vs Escala de paisaje.*

Los investigadores han usado varias formas de estimar las respuestas ecológicas a la fragmentación de hábitat: El enfoque de mancha, en el que las unidades de análisis son los parches de hábitat, y el enfoque de paisaje, en el que las unidades de análisis son celdas que contienen constelaciones de manchas.

En estudios a escala de parche, las variables predictoras son atributos espaciales de los parches individuales (ej. tamaño del parche, borde, forma, aislamiento) (Fig. 3a), en contraste, en los estudios a escala de paisaje, las variables predictoras son los atributos espaciales de paisajes (ej. fragmentación de hábitat, densidad de parches, porcentaje de hábitat) (Fig. 3b) (Fahrig, 2017).

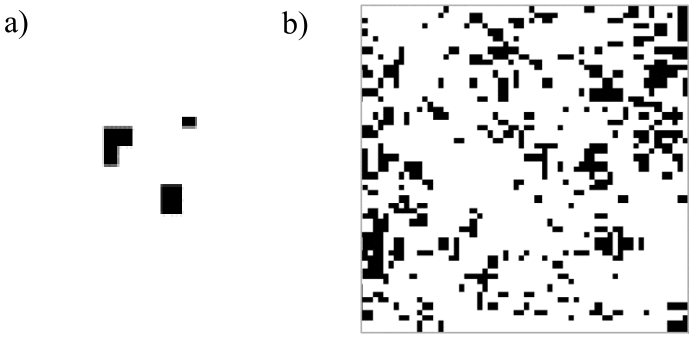

Figura 3: Ilustración de la diferencia entre estudios a escala de parche (a) y estudios a escala de paisaje (b). En el primero se estudian los atributos espaciales de los parches individuales (i.e. tamaño del parche, forma, perímetro, aislamiento), en el segundo las variables predictoras son los atributos espaciales de celdas con constelaciones de manchas (i.e. porcentaje de hábitat respecto al total del paisaje, fragmentación de hábitat).

En la literatura sobre fragmentación de hábitat existe un amplio predominio de estudios con enfoque de mancha, lo que resulta llamativo porque este enfoque no permite cuantificar la fragmentación de forma directa dado que ésta se manifiesta a escala de paisaje. Es más, de acuerdo con Farhig (2003, 2013), en estos estudios los efectos del tamaño del parche y de su aislamiento están intrínsecamente confundidos con los efectos de la cantidad de hábitat. Esto se debe a que parches más pequeños tienen menos hábitat que los parches más grandes, y los parches más aislados, precisamente lo están porque hay menos hábitat que pueda rodearlos (ver también Moilanene y Nieminen, 2002; Bender et al. 2003; Tischendorf et al. 2003; Prugh, 2009, Ranius et al. 2010; Thornton et al. 2011; Martin y Fahrig, 2012). En este sentido, McGarigal y Cushman (2002) concluyeron que, a diferencia de los enfoques de paisaje, los enfoques de mancha no son adecuados para identificar los efectos de la fragmentación de hábitat *per se* (v.g. independientes de la pérdida de hábitat).

3.2. Índices de fragmentación.

Cómo medir la estructura del paisaje es otro tema central en la literatura sobre fragmentación de hábitats. Por ejemplo, McGarigal et al. (2002) llegaron a describir más de 40 índices para medir fragmentación, muchos de ellos fuertemente correlacionados entre sí, lo que, unido a la creciente inflación de índices propuestos (Li y Reinolds, 1994; Ritters et al., 1995; Haines-Young y Chopping, 1996; O´Neill et al., 1999), ha constituido sin duda una fuente constante de confusión (Fahrig 2002). Por otro lado, ante la evidencia de que la relevancia ecológica de muchos de estos índices no ha sido investigada empíricamente, y la sospecha de que su proliferación y utilización responden más a la posibilidad de calcular cada métrica que a su potencial como indicadores de efectos biológicos relevantes, numerosos estudios se han centrado en determinar qué combinación de índices es más efectiva para analizar los patrones espaciales (Li y Reynolds, 1994; McGarigal y Marks, 1995; Ritters et al., 1995; Haines-Young y Chopping, 1996; O´Neill et al., 1999).

En relación con lo anterior, Fahrig (2002) abogó por generar métricas sintéticas para poder diferenciar razonablemente entre lugares más y menos fragmentados. Tal enfoque fue adoptado por Montoya et al. (2010), quienes, inspirándose en un trabajo teórico de Bascompte y Solé (1996), propusieron la métrica *rLPS* (acrónimo de *relative Largest Patch Size*) como indicador sintético de fragmentación, en un estudio pionero sobre relaciones entre fragmentación forestal y probabilidad de ocurrencia de especies arbóreas en España Peninsular. Para cada unidad de análisis, la métrica *rLPS* indica el porcentaje de hábitat representado por el parche de hábitat continuo de mayor tamaño; lo que, por ejemplo, permite diferenciar inmediatamente entre dos paisajes de igual forma, tamaño y cantidad de hábitat pero con distinta fragmentación: evidentemente, estará más fragmentado el que tenga el parche más grande con un tamaño menor, dado que, por obligación, los demás parches habrán de ser más pequeños y numerosos. Además de la simplicidad y fácil interpretación de esta métrica, Montoya et al. (2010) mostraron cómo con ella era posible separar estadísticamente relaciones atribuibles a la deforestación *per se* y a la fragmentación forestal *per se* sobre las especies estudiadas. Sin embargo, hasta la fecha no se ha realizado ningún análisis formal de las posibles virtudes y limitaciones de la métrica *rLPS* para medir niveles de fragmentación y de su relación con otras métricas.

4. Hipótesis del Umbral de Extinción: Relación con la fragmentación.

En la década de los ochenta, cuando Lande (1987) acuñó el concepto de "umbral de extinción" para referirse a la cantidad mínima de hábitat por debajo de la cual la población de una especie se extingue, este autor ya argumentaba sobre la posible relación de ese umbral con la fragmentación del hábitat. Posteriormente, trabajos teóricos como los de Bascompte y Solé (1996) y Fahrig (1997, 1998) (ver trabajos adicionales en la revisión de Fahrig 2002), utilizando estrategias de modelización estocástica y determinística diferentes, indicaron, por un lado, que la fragmentación actuaba agravando los efectos de la pérdida de hábitat sobre las poblaciones naturales, y, por otro lado, que la cantidad mínima de hábitat necesaria para la persistencia de la población era mayor en presencia de fragmentación. Estos resultados supusieron fuertes respaldos teóricos a la denominada Hipótesis del Umbral de Extinción (HUE) y su predicción de que cuanto mayor es el nivel de fragmentación, mayor es también la cantidad mínima de hábitat necesaria para la supervivencia (revisado por Fahrig 2002) (Fig. 4). Al mismo tiempo, dichos resultados supusieron el cuestionamiento de las hipótesis alternativas que sostienen que la persistencia depende de la cantidad de hábitat y que la fragmentación no es relevante (p.ej. Fahrig 2013).

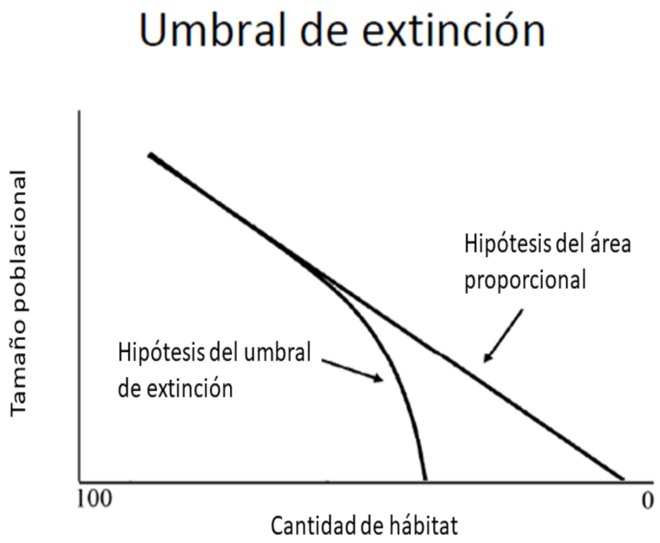

Figura 4: Ilustración de la hipótesis del umbral de extinción en comparación con la hipótesis alternativa del área proporcional. La hipótesis del área proporcional predice que el tamaño poblacional decrece de forma lineal con la pérdida de hábitat. La hipótesis del umbral de extinción señala la existencia de una cantidad de hábitat (umbral) por debajo de la cual la población decrece rápidamente hasta llegar a su extinción.

En contraste, la reciente revisión de Fahrig (2017) de 118 estudios empíricos con respuestas que indicaban efectos significativos de la fragmentación de hábitats (381 respuestas), mostró que un 76 % de los casos correspondían a efectos positivos, y un 24 % a efectos negativos. Las explicaciones a estos resultados incluían posibles incrementos de la conectividad funcional del paisaje, el aumento de la diversidad de hábitats, posibles efectos de borde positivos, incrementos de la estabilidad de los sistemas depredador-presa, reducciones de los niveles de competencia, reducciones de la propagación de riesgos, o efectos de complementariedad del paisaje asociados, por ejemplo, a la dispersión y dilución de los riesgos de extinción en el paisaje, en línea con la ideas pioneras avanzadas por den Boer (1968) (ver más arriba). Según Fahrig (2017), esta preponderancia de las respuestas positivas a la fragmentación pondría en cuestión el paradigma de que tanto la cantidad de hábitat como la fragmentación deben ser tenidas en cuenta en programas e iniciativas de conservación (como se deduce de la HUE), y da fuerza, por el contrario, a la visión alternativa de que sólo la cantidad de hábitat debe ser considerada (ver Fahrig, 2013).

No obstante, una perspectiva alternativa también es posible, conciliando las corrientes iniciadas por los trabajos de den Boer (1968) —y su énfasis en los posibles efectos positivos de la fragmentación por sus consecuencias para la heterogeneidad de hábitats y, a través de ésta, la persistencia y la diversidad—y Levins (1970) —y su visión inspirada en la teoría biogeográfica de islas que contempla la fragmentación como un proceso de creación de parches (o "islas hábitat") de tamaño y conectividad decrecientes, con consecuencias negativas sobre la persistencia— (ver más arriba). En efecto, la posibilidad de esta perspectiva conciliadora se hace más evidente cuando analizamos qué significa el término "hábitat" en las esferas conceptual, en la que es *específico de especie* (cada especie tiene el suyo) (Lindenmayer y Fischer, 2006), y operacional, en la que se trata de un *atributo asignado* por el investigador a las especies estudiadas en función de sus preguntas y objetivos (ver Didham et al., 2011). En este último contexto, los efectos esperables de la fragmentación sobre especies y biotas pueden ser de cualquier signo, y las perspectivas derivadas de las propuestas de den Boer (1968) y Levins (1970) se complementan y completan, haciéndose dependientes de cómo se haya hecho cada asignación.

5. Cambio climático y fragmentación.

5.1. Los bosques y el ciclo de carbono.

La proporción de carbono almacenado en los bosques supone entre el 70-80% del carbono total existente en los ecosistemas terrestres (Ma, 2017). Además, los bosques representan aproximadamente el 40% del intercambio de carbono entre la atmósfera y la tierra, desempeñando un papel clave en los ciclos biogeoquímicos mundiales, y en particular en el ciclo del carbono (Stephenson et al, 2014; Ma, 2017) (Fig. 5).

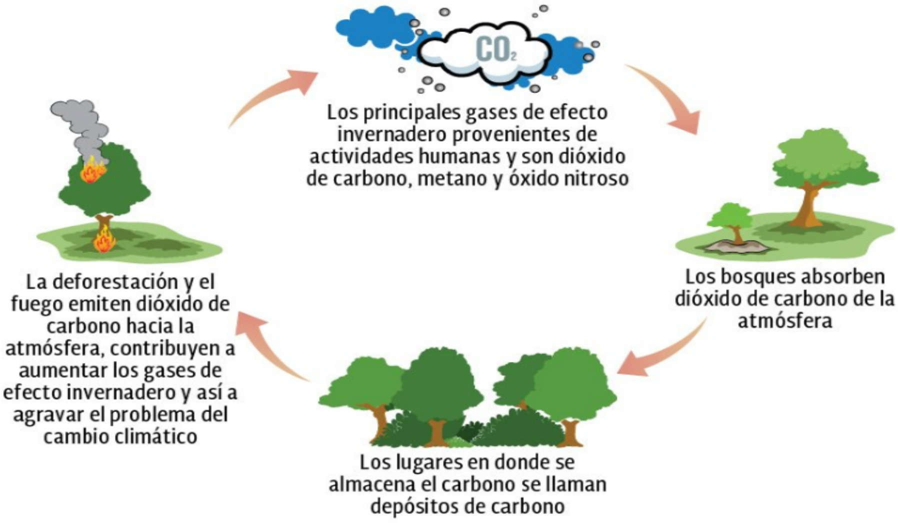

Figura 5: Ilustración de los flujos de carbono en los bosques. Los bosques absorben CO_2 de la atmósfera, actuando como depósitos o sumideros de carbono. La deforestación conlleva la emisión de CO_2 a la atmósfera, contribuyendo a aumentar los gases de efecto invernadero, agravando el problema del cambio climático (extraído de: Comisión Nacional Forestal: https://twitter.com/CONAFOR?lang=fi).

Cuando los bosques son aclarados, el carbono almacenado tanto en estructuras vegetativas (v.g. las hojas, ramas, troncos y raíces) como en el suelo, es liberado a la atmósfera (Baccini et al. 2012). Aproximadamente una cuarta parte del total de las emisiones de origen antrópico son debidas a la deforestación, siendo la mayor fuente de CO_2 a la atmósfera (≈ 1,1 Gt/año) (Laurance et al.,1998; Brinck, 2017). En consecuencia, incluso cambios leves en las reservas de carbono de los bosques podrían tener impactos sustanciales en el balance global de carbono (Ma, 2017).

5.2. *Fragmentación y cambio climático.*

En ausencia de perturbaciones, los bosques actúan como sumideros de carbono, mientras que los bosques fragmentados pueden ser vulnerables a la pérdida de carbono (Ma, 2017). Sin embargo, la mayoría de las estimas de flujo de carbono están basadas solamente en la deforestación (Laurance et al., 1998), mientras que las emisiones procedentes de otros procesos derivados de la deforestación, tales como la fragmentación, no han sido cuantificadas de forma habitual.

Como excepción a esta afirmación, Laurance et al. (1997) llevaron a cabo un experimento con fragmentos de bosque en la Amazonia, demostrando que los remanentes de hábitat de los bosques fragmentados perdían gran cantidad de biomasa aérea, debido a elevadas tasas de mortalidad y de daños causados en los fragmentos, como resultado de cambios microclimáticos y del incremento de las turbulencias del viento cerca de los márgenes del bosque (agravadas debido al mayor efecto borde en hábitats fragmentados). En un siguiente experimento, Laurance et al. (1998) estimaron que la fragmentación incrementaba en un 1-7% las emisiones de carbono a la atmósfera, y que las pérdidas de biomasa en los bordes de los fragmentos podrían derivar en unas emisiones de cerca de 150 millones de toneladas de carbono anualmente. Más recientemente, estudios como el de Benito-Garzón et al. (2013) señalaron que, bajo las futuras expectativas de cambio climático, el crecimiento de algunas de las especies de árboles podría aumentar, pero incluso en este caso, los rangos de las especies en el borde estarían limitados por un aumento en las tasas de mortalidad.

De estos resultados se deriva que la fragmentación forestal debería ser considerada al intentar comprender el papel de la vegetación en el balance global de carbono, y para ello, es crucial estudiar y comprender los mecanismos que regulan las relaciones entre fragmentación de hábitat y pérdida de biomasa forestal.

6. Objetivos e hipótesis

El **objetivo general** de la presente tesis doctoral persigue documentar los patrones geográficos de la fragmentación de hábitats forestales a escalas globales y regionales, y avanzar en el conocimiento acerca de cómo la fragmentación afecta a la biodiversidad y al cambio climático. Para alcanzar este objetivo, es además vehicular, definir un índice sintético capaz de medir la fragmentación de hábitat con independencia de la cantidad de hábitat.

6.1. Hipótesis y objetivos concretos.

H1: El índice rLPS (tamaño de la mancha más grande de hábitat dentro de la unidad de análisis) es un índice sintético de fragmentación efectivo para medir niveles de fragmentación independientemente de la escala de estudio.

- **Objetivo 1:** Analizar la capacidad indicadora y de síntesis del índice rLPS para diferenciar niveles de fragmentación y su dependencia de la escala (resolución, grano y extensión de análisis)

- **Objetivo 2:** Determinar cuál es la máxima fragmentación empírica posible para cada nivel de cobertura de bosque. Útil para el diseño de experimentos.

- **Objetivo 3**: Analizar el patrón de fragmentación de bosques a nivel global y del Mediterráneo. Generación de mapas.

H2: La fragmentación agrava los impactos de la reducción de hábitat, provocando una aparición más temprana del umbral de extinción en el gradiente de pérdida de hábitat (a mayor fragmentación, mayor cantidad de hábitat será necesario para sostener a la población).

- **Objetivo 1:** Investigar a escala europea si la fragmentación agrava los efectos de la reducción de la superficie de bosque sobre la probabilidad de ocurrencia de siete especies forestales de aves incrementando su umbral de extinción.

- **Objetivo 2**: Identificar posibles características diferenciadoras (fisiológicas y de historia de vida) de las especies sensibles a la pérdida y fragmentación de bosques, atributos que pueden determinar la sensibilidad de las especies a cambios en la estructura del bosque, que serán investigados a fin de encontrar posibles patrones generales en los grupos estudiados.

H3: La fragmentación y la deforestación tienen un efecto directo y negativo sobre la biomasa, contribuyendo negativamente al cambio climático debido a su efecto negativo sobre el secuestro de C.

- **Objetivo 1:** Analizar el efecto de la fragmentación, la cantidad de hábitat y el clima sobre la biomasa forestal (medida mediante la variable altura de los árboles) y sobre el secuestro de carbono a nivel global.

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CAPÍTULO 3

BIOGEOGRAPHIC PATTERNS OF FOREST FRAGMENTATION AT GLOBAL AND REGIONAL SCALES

Resumen

Objetivo: Existe un gran número de estudios dedicados a documentar y entender los efectos de la fragmentación de hábitat sobre la biodiversidad, pero los resultados obtenidos han sido contradictorios. Esto es principalmente debido a: (1) La fragmentación generalmente se mide de forma indirecta, utilizando parches de hábitat como unidades de análisis, (2) Existencia de múltiples índices para medir fragmentación, frecuentemente correlacionados e incapaces de distinguir entre los efectos de la pérdida de hábitat y los de la fragmentación, y (3) Falta de índices claros que permitan diferenciar niveles de fragmentación, lo que dificulta la comparación de estudios. En este trabajo analizamos el potencial del índice rLPS (tamaño relativo de la mancha más grande de hábitat) como medida sintética de fragmentación de hábitat. En segundo lugar, utilizamos este índice para determinar si existe un máximo empírico de fragmentación.

Localización: Global y Mediterráneo

Métodos: Para testar el potencial de rLPS como medida sintética de fragmentación y su respuesta a los cambios de escala, lo comparamos con tres métricas comúnmente utilizadas en la literatura (número de parches, densidad de borde y distancia media al vecino más próximo). En segundo lugar, determinamos el nivel de fragmentación máximo empírico posible a lo largo del gradiente de cobertura forestal, documentando las relaciones entre el porcentaje de cobertura forestal (PFC) y la proporción de ese porcentaje que ocurre en el parche más grande de hábitat (rLPS).

Resultados: El índice rLPS emerge como medida sintética de fragmentación, consistente a través de escalas distintas y capaz de discriminar esa fragmentación a diferentes niveles de cantidad de hábitat. Además, destaca

la existencia de un nivel máximo empírico de fragmentación que co-varía con la cobertura forestal y una alta correlación entre la cantidad de bosque y la fragmentación, independientemente de la medida de fragmentación utilizada.

Conclusiones principales: Proponemos el uso del índice rLPS como medida sintética efectiva para medir la fragmentación a lo largo de las escalas, y señalamos la necesidad de considerar la reducción de los niveles de fragmentación forestal en las iniciativas de conservación. Finalmente, destacamos la necesidad de tener en cuenta la existencia de un máximo empírico de fragmentación en el diseño de experimentos destinados a evaluar los efectos de la fragmentación sobre la biodiversidad.

Abstract

Aim: The abundant literature documenting the effects of habitat fragmentation on biodiversity has often provided contradictory results. This is largely due to: (1) Fragmentation is generally measured indirectly, using habitat patches as analysis units, instead of directly quantifying it in landscapes (constellations of patches). (2) There exist a myriad of indexes to measure fragmentation, frequently correlated amongst them and unable to discriminate the effects of fragmentation from those of habitat loss. (3) There is a lack of a standardized metric allowing to differentiate fragmentation levels and compare across studies. Here we test the indicator potential of rLPS index (relative Largest Patch Size) as a synthetic fragmentation measure across the global and Mediterranean scales. Secondly, we explore if there is a maximum of empirical fragmentation.

Location: Global and Mediterranean

Methods: To test the rLPS potential as a synthetic fragmentation measure we compared it against three common metrics of fragmentation (number of patches, edge density and mean nearest neighbor distance) at varying levels of habitat cover. Following we inspect relationships between the percentage of forest cover (PFC) and the proportion of this percentage occurring in the largest forest patch (rLPS), to determine the maximum empirical fragmentation level possible across the forest cover gradient.

Results: The rLPS emerges as an index able to measure fragmentation across the scales and to differentiate fragmentation levels. We also found an empirical maximum level of fragmentation, which co-varies with forest cover and a high correlation between forest quantity and fragmentation, regardless which metric is utilized.

Main conclusions: We propose the use of the rLPS index as an effective synthetic measure of fragmentation across scales, and suggest the convenience to consider forest fragmentation levels reduction in conservation initiatives. Finally, we recommend that experiment designs aimed at studying the effects of habitat fragmentation on biodiversity account for the existence of an empirical maximum of fragmentation.

Introduction

Habitat fragmentation—i.e. the breakup of continuous habitat into disconnected patches as a result of human activities—has attracted a fair deal of attention in the ecological literature, mostly focused on its effects on biodiversity (e.g. Hanski, 2005). Approaches to this topic have been varied and have lacked a standardized analytical framework. Thus, the myriad metrics proposed to measuring fragmentation have led to different conclusions regarding both the magnitude and the direction of its effects on biodiversity (Fahrig, 2003). Despite the many studies, methodological and conceptual issues have hindered our understanding of the fragmentation phenomenon. Debate persists about which metrics, scales or extents would be the most appropriate for its study (Zhang et al. 2013; Larrey-Lassalle et al. 2018; Taubert et al. 2018) and even, about whether or not fragmentation can affect biodiversity beyond the effects of habitat loss (Fahrig, 2017).

On the one hand, the debate about how habitat loss and fragmentation affect biodiversity is related to the difficulty to define habitat fragmentation. This is in turn related with the multiplicity of theoretical foundations and conceptual models used by research on fragmentation (Boutin & Hebert, 2002; Fahrig, 2003; McGarigal & Cushman, 2002). A chronological review of early models foundational for fragmentation theory would include, the models based on biogeographic island theory of McArthur & Wilson (1967) (see also the "island model"; Shafer, 1990), the metapopulations theory of Levin (1965) (Boutin & Hebert, 2002; Fahrig, 2003; Harrison & Bruna, 1999; McGarigal & Cushman, 2002), the patch-corridor-matrix model (Forman, 1995) or the percolation theory proposed by Stauffer (1985) (see Bascompte & Solé, 1996; Boswell et al., 1998; Hill & Caswell, 1999; Riitters et al., 2000; Solé & Bascompte, 2007). These models emphasize the roles of distance between habitat patches, their sizes, their connectivity as well as their geometric constrains, all central to the emerging concept of habitat fragmentation.

Later research included more sophisticated models. For example, the hierarchical patch dynamics model (Dunn & Majer, 2007; Wu & Loucks, 1995), which recognizes the crucial role of scale in ecological systems. The species-specific gradient models (Austin, 1999; Fischer et al., 2004; Fischer, 2006; Manning et al., 2004) based in the continuous model of Austin (1985) and focused in the relationship between landscape patterns and the underlying ecological processes. Or the most recent hierarchical causal model (Didham et al., 2011), based in the integrated community concept of Lortie et al. (2004). Approaches such as the latter, connect fragmentation-related characteristics of the habitat (e.g. patch area, shape complexity, matrix quality) with specific population-level responses (e.g. births, deaths, migrations) through known proximate mechanisms (e.g. resource availability, vegetation structure, microclimate) (Didham et al. 2012). While doing so may provide further insights on the effects of the different facets of fragmentation on biodiversity, fitting increasingly complex models comes at the cost of high demands of data (e.g. García-Valdés & Morales-Castilla 2016), which are rarely available and thus prevent an extended implementation. Instead of fitting exceedingly complex and data-hungry models, the use of proximal metrics may still provide valuable information on the effects of fragmentation.

Out of the above mentioned bodies of literature, the two most commonly used approaches are the island biogeographic theory and the metapopulation theory for patch scale analysis (Boutin & Hebert, 2002; Fahrig, 2003; Harrison & Bruna, 1999; McGarigal & Cushman, 2002), and the percolation theory for landscape scale studies (Bascompte & Rodríguez, 2001; McGarigal & Cushman, 2002; Montoya et al., 2010). The patch scale analysis has been useful to infer the mechanisms involved in the effects of fragmentation (Haila, 2002; Harrison & Bruna, 1999), but it does not allow quantifying the fragmentation directly, as this approach utilizes patches rather than landscapes as analysis units (Fahrig, 2003; McGarigal & Cushman, 2002). A shortcoming of this approach derives from the extrapolation of its results, which may not consistently scale-up and, thus, often leads to erroneous conclusions (Didham et al., 2011; Wiens et al., 1987).

In contrast, the landscape scale may be the most appropriate to carry on fragmentation studies as it allows direct quantification of fragmentation within a given landscape. Even though this is a well-known premise, there are few studies using this perspective, and even less conducted at large biogeographic scales suitable to inform conservation policies (Montoya et al., 2010; Haddad et al. 2015). Amongst the few works studying fragmentation at a global level, a first attempt was made by Riitters et al. (2000). The authors determined and mapped the different types of fragmentation that can be found at varying window size. However, this classification does not allow discriminating between more and less fragmented places, which would be critical to select the most appropriate conservation strategies. Then, Bregman et al (2014) evaluated the effects of fragment size on different functional components of the bird community in five continents, but only in certain locations, not globally and not at landscape scale. Highlights the study of Haddad et al. (2015), which measure the magnitude of forest fragmentation al global scale using the mean distance to forest edge as a fragmentation measure, or the study of Crooks et al (2017), which quantify and map global patterns of habitat fragmentation for the world's terrestrial mammals measuring as the amount of core habitat, and identifies regions that have been fragmented by human development specifically. See also Crooks et al. 2011 and Taubert et al, 2018 as additional information.

An additional barrier to standardize results from the fragmentation literature is due to the multiplicity of study scales used. This is, the fact that the resolution (i.e. sampling unit), the grain (i.e. analysis unit) and the extent (i.e. study area) of the analyses vary notably among fragmentation studies. The scale-dependence of landscape patterns is amply recognized in the literature (i.e. resolution and extent of analysis) (Gardner et al., 1987; Gardner, 1998; He & Legendre, 1994; Jelinski & Wu, 1996; Meentemeyer & Bos, 1987; Moody & Woodcook, 1995; O´Neill et al., 1991, O´Neill et al., 1996; Qi & Wu, 1996; Turner et al., 1989; Woodcock & Stralher, 1987; Wu et al., 2002). While most of these studies examined only a few fragmentation metrics or covered only a narrow range of scales, scale-dependence manifested in their landscape structure indexes. Thus, although we are well aware that changing grain size or extent affects landscape metrics, it is not clear whether these effects exhibit any general patterns (or scaling relationships) that are consistent across real landscapes (Wu et al., 2002). The difficulty to compare results from different sources highlights the importance of finding robust indexes to scale changes.

The overabundance of landscape structure indexes has been another element of debate. For example, McGarigal et al. (2002) described more than 40 variables or indexes of landscape structure. However, these indexes cannot be seen as independent metrics, as many of them are highly correlated (Haines-Young & Chopping, 1996; Li & Reynolds, 1994; Riitters et al., 1995; O´Neill et al., 1999). Further, the ecological relevance of many of them is often alleged rather than well founded, frequently lacking of the adequate empirical support (Li and Wu., 2004). In other words, some metrics are calculated because it is computationally possible, not because they are biologically meaningful. For this reason, numerous studies were focused on determining which combination of indexes was more effective to analyze the spatial patterns of fragmentation (Li & Reynolds, 1994; Haines-Young & Chopping, 1996; McGarigal & Marks, 1995; O´Neill et al., 1999; Riitters et al., 1995), but their results were contradictory. To tackle this issue, Fahrig (2002) advocated for generating synthetic metrics to differentiate between more and less fragmented places. Such an approach was adopted by Montoya et al. (2010) who used the relative Largest Patch Size (rLPS index hereafter) as unique fragmentation indicator, based on the theoretical work of Bascompte & Solé (1996). This metric indicates the percentage of forest cover within each analysis unit—i.e. generally an amount landscape of uniform shape and area—that formed the largest continuous patch of forest. Although these ideas had already been suggested, there are no formal tests analyzing and comparing the synthetic capacity of different fragmentations indexes.

The aims of the present study are, (1) to analyze the capacity of rLPS as an indicator able to quantify fragmentation levels across varying scales and to test its potential as a synthetic fragmentation measure in comparison with other common-use metrics; (2) to use rLPS to document fragmentation forest patterns at two scales, globally and in the Mediterranean; and (3) to determine if there exists a maximum empirical fragmentation level across the forest cover gradient. If rLPS proved useful to measure fragmentation and was robust to differing scales, the results of this work could potentially serve to the design of future experimental studies of fragmentation, as well as to inform policies and initiatives directed to forest conservation at large scale.

Methods

Data

Data sources obtained and processed for analyses performed at the global and the Mediterranean scales differed. For the global analysis, we used a global map of forest cover in raster format generated from remote sensing data (Defries et al., 2000), with a pixel size (i.e. resolution) of 1 km^2. Following Hansen and Sohlberg (2000), we considered as forest only those pixels with forest cover $\geq 40\%$, and subsequently we processed the raster by superimposing it to an equal area global grid, comprised of 42,114 grid cells of 50 x 50 km (i.e. the grain corresponding to this analysis). For the Mediterranean scale the data was extracted from a high resolution raster for the whole of Europe (Kempeneers et al., 2011) with a pixel size of 25 m, and which we processed to characterize the Mediterranean basin forests using grid cells of 5 x 5 km (48,562 grid cells). Note that scale-related components of this second analysis differed from the global analysis, namely, the resolution was more detailed (i.e. smaller pixel size), the grain was smaller (i.e. smaller size of analysis units) and the extent of the analysis was as well smaller since it was limited to Mediterranean Europe.

Fragmentation metrics

To measure fragmentation we quantified both the Proportion of Forest Cover (PFC hereafter) and the proportion of this percentage occurring in the largest patch (i.e. rLPS) within each grid cell—i.e. analysis unit (see Bascompte & Solé, 1996; Montoya, 2010; Solé & Bascompte, 2007). We used the Patch Analyst tool software (Rempel et al., 2012) implemented in ArcGIS (ESRI, 2009) to compute both metrics. The combined graphical representation of these two variables allowed us to clearly distinguish between empirical scenarios with different levels of fragmentation (Fahrig, 2002; Montoya, 2010). The underlying foundation under our hypothesis that rLPS would be capable to discriminate among fragmentation levels is based in the following: for any given PFC value, the higher the rLPS, the larger amount of habitat that will be contained in the largest patch within a grid cell. Also, the higher the rLPS, the less forest quantity will be available to form equal or smaller sized fragments than the largest patch, and thus fragmentation will necessarily be lower. In addition, rLPS has other characteristics that make it a suitable index to measure fragmentation. First, rLPS has a clear ecological meaning since it is related to the residential area (or home range), which is a key factor for the presence or absence of species in the territory.

The higher the rLPS, the larger amount of continuous habitat and hence, the higher number of species that a territory can harbor. Second, rLPS presents a fixed variation interval (%) and extremes within which it is possible to define a scale of fragmentation levels (i.e. from very low to very high fragmentation) that would facilitate the comparison and interpretation of results.

Apart from PFC and rLPS, we considered three other common-use indicators of forest structural characteristics. We compare rLPS against the number of patches (NumP hereafter, using the notation of Patch Analyst tool), edge density of forest (ED) related to the forest cover of the cell, and the mean nearest neighbor distance (MNN) between each forest patch, which informs of the degree of connectivity among patches. These three additional metrics were used to investigate their associations with rLPS and PFC, and to compare the capability of rLPS as a synthetic fragmentation index, in contrast with the synthetic ability of other metrics.

To determine the generalizability of our results, all fragmentation variables were generated for both the global and the European Mediterranean scales, allowing to test whether the patterns found for the global analysis would be robust to scale changes.

Results

The relationships between fragmentation (i.e. rLPS) and forest cover (i.e. PFC) showed very similar patterns both in the world and in the Mediterranean (Fig. 1). The fact that different spatial scales, grains and resolutions were used, is indicative that rLPS is stable to scale changes. Also, in both cases we observed that high fragmentation levels (i.e. rLPS ≤ 40 %) did not exist when the proportion of forest cover was high (i.e. PFC ≥ 60 %) (Fig. 1), which revealed the existence of an empirical maximum of fragmentation in co-variation with forest cover.

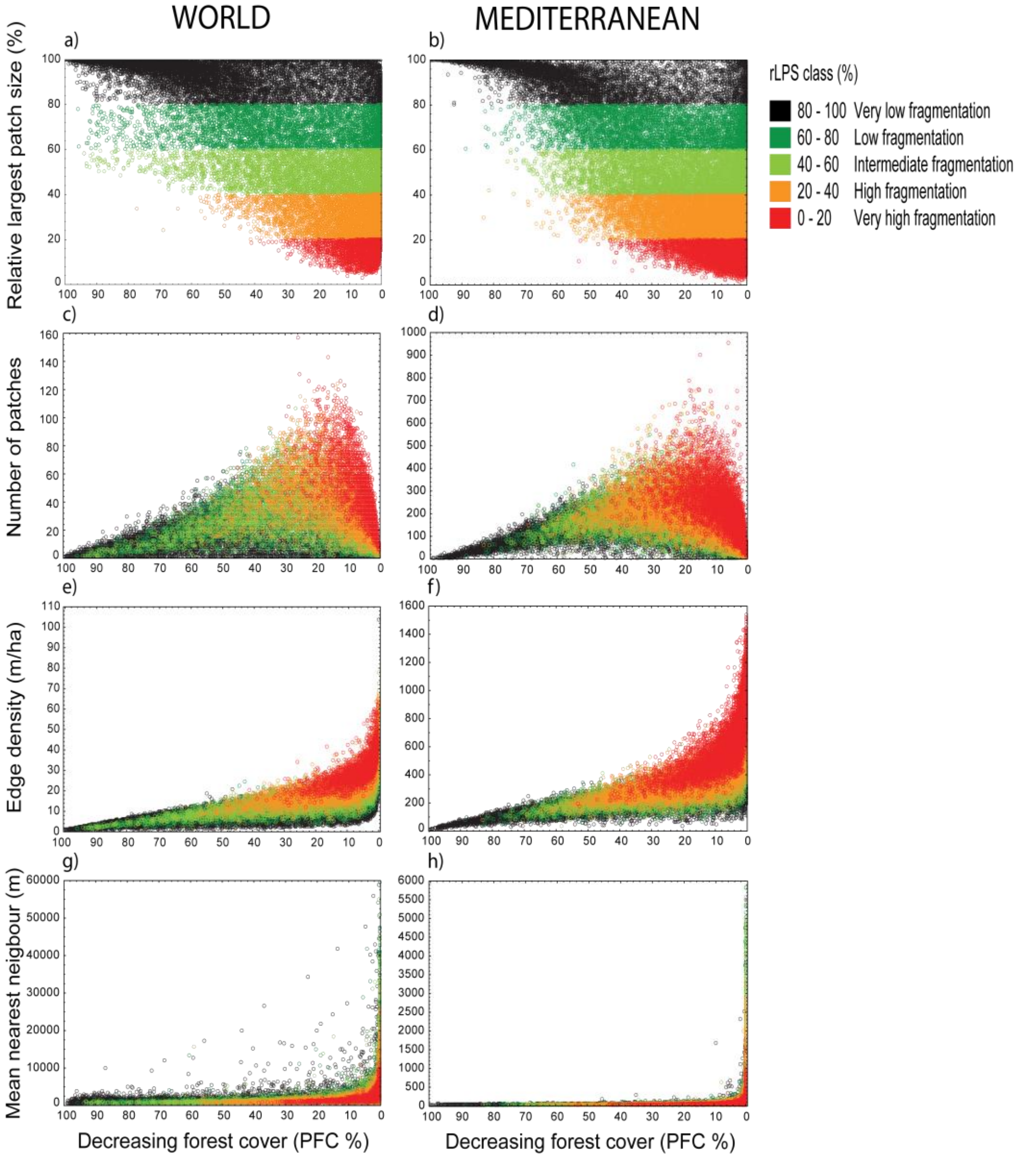


Figure 1: Forest fragmentation, measured as relative Largest Patch Size (rLPS) (a,b), Number of patches (b,c), ED (e,f) and MNN (g,h), as a function of proportion of forest cover (PFC) in the world and the Mediterranean. The colors indicate five fragmentation levels according to rLPS ranging from very low (black) to very high (red).

Regarding the rest of fragmentation indexes studied, we observed that at both scales, NumP and ED significantly increased with increasing fragmentation (i.e. rLPS decreasing) when forest cover values were below 50 % (Figs. 2a-d). For higher cover values the effects of fragmentation on these two variables were indistinguishable (Figs. 2a-d). This is, at a given value of high PFC (e.g. 70%) the number of patches or amount of edges can present from very low to intermediate fragmentation, indistinctly.

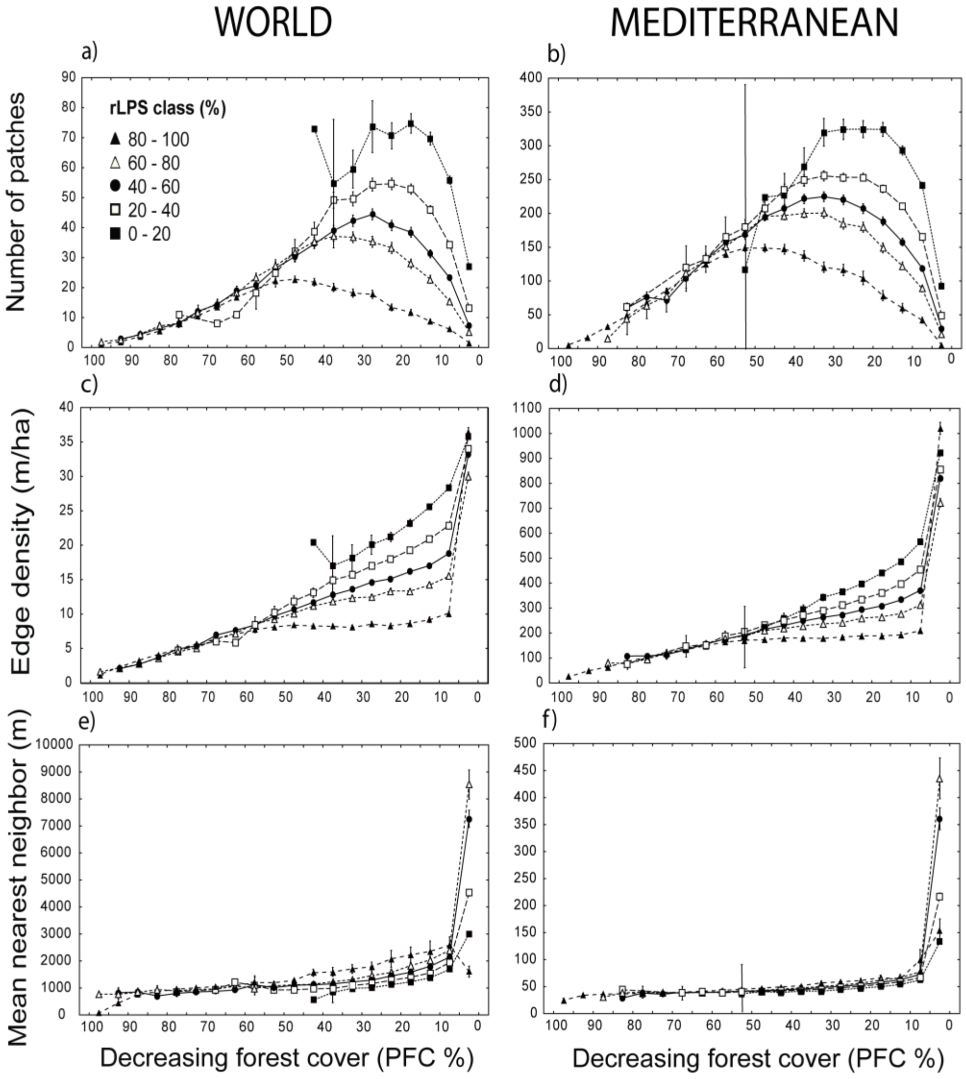


Figure 2: Mean values of number of patches (a,b), ED (c,d) and MNN (e,f), for 5% bins of proportion of forest cover (PFC) with 95 % confidence interval, for the world and the Mediterranean.

However, the variation relative to the amount of forest was different for both indexes, while the number of patches reached its maximum around values within the interval of 30-15% of PFC for each scale (Figs. 2a-b), edge density increased exponentially reaching its maximum value at minimum values of forest cover (i.e. PFC < 5%, see Figs. 2c-d). The MNN index also showed a tendency to increase exponentially with decreasing PFC, however, this metric shows rather limited non-significant variation except at very low forest cover levels (PFC < 10%, Figs. 2e-f). In addition, absolute values for NumP, ED and MNN are highly sensitive to scale changes—i.e. up to two orders of magnitude difference between the Global and Mediterranean—, which difficult direct comparison (Fig. 2).

In sum, the rLPS index would allow indirectly estimating patch abundance (i.e. a measure of dispersion) and edge quantity (i.e. a measure of habitat quality), and to a lesser extent the distances between patches (i.e. a measure of landscape configuration), and hence it could be regarded to as a suitable indicator for other facets of fragmentation.

An additional analysis showing the relative frequency distribution with which the different fragmentation levels occur across a forest cover gradient, showed similar patterns in the world and the Mediterranean (Fig. 3). In both cases, the most frequent grid-cells were the most deforested (i.e. PFC < 10%), and the frequency of cases with more fragmentation tended to increase with forest cover decrease (Fig. 3). However, while the cells with forest cover > 80 % were the second most frequent at the global scale (Fig. 3a), in the Mediterranean they were scarcely represented (Fig. 3b). This indicates a higher degree of alteration of Mediterranean forests, which can be related with the long history of human land use in this region. In addition, this analysis allowed quantifying the number of study units where previously identified extinction thresholds would be found, namely, the amounts of forest at which the fragmentation effects on biodiversity become stronger and which some authors have placed around 50-20% of remnant forest (Boutin & Hebert, 2002). The proportion of grid-cells with high or very high fragmentation levels located in this interval is low (4.7 % in the world and 10 % in the Mediterranean, Fig. 3). Together, this could explain the difficulties found for the empirical detection of the extinction thresholds.

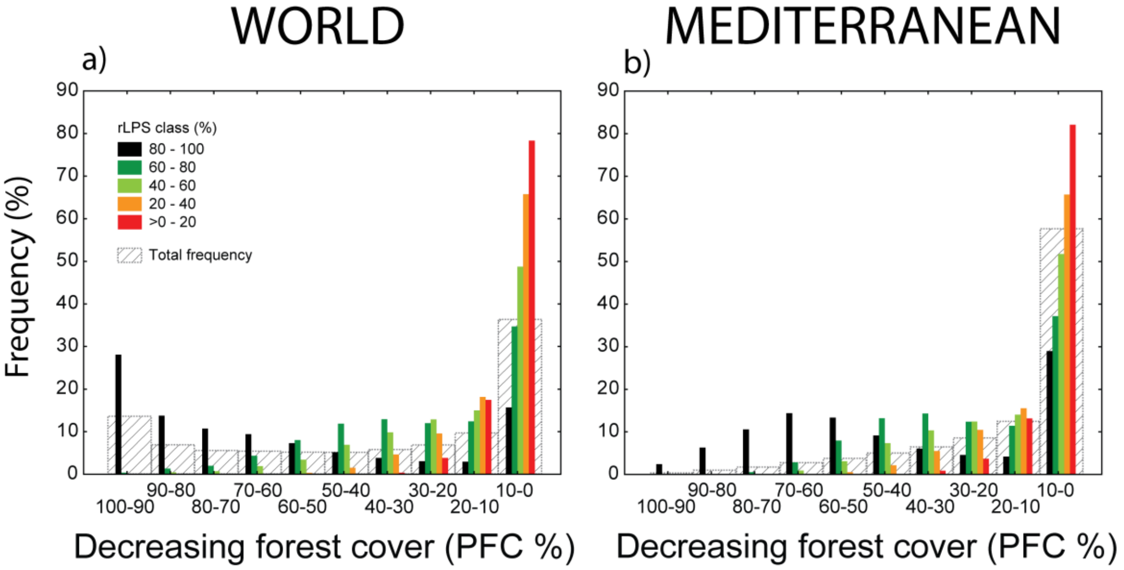
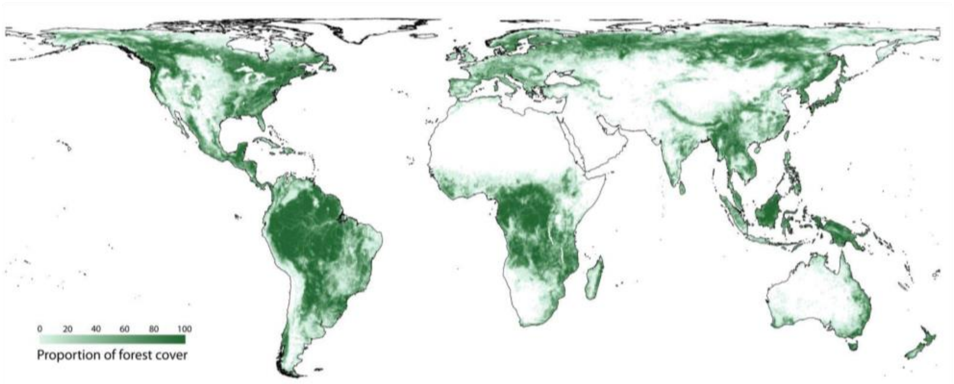


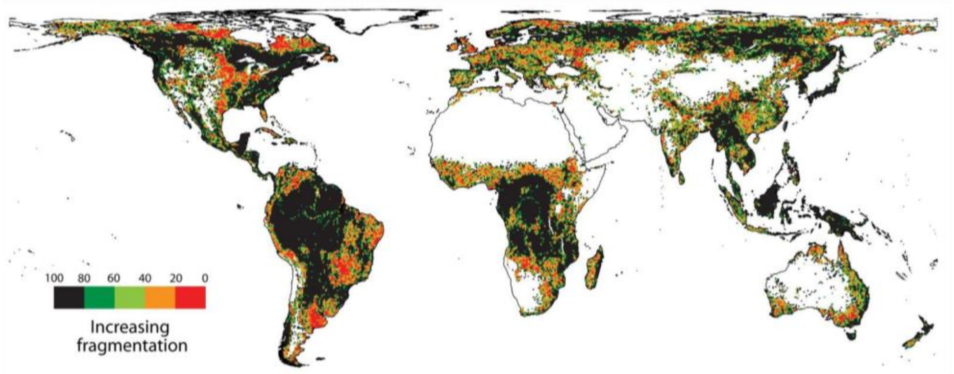
Figure 3: Total (dashed lines) and per rLPS (colored) level cell frequencies in the world (a) and Mediterranean (b) per forest cover intervals.

Finally, we observed interesting similarities between the geographic distribution of forest cover, fragmentation and their relationships, represented as maps of PFC, rLPS and PFC-rLPS (Figs. 4, 5). The predominance of extreme values is reflected by almost dichotomous maps. Specifically, the PFC-rLPS map showed two well-differenced situations in areas that were either densely covered and low fragmented forests or sparsely populated highly fragmented forests (Figs. 4c, 5c). This is indicative of the high correlation between forest amount and fragmentation, or the fact that the most deforested sites tended to be also very fragmented (Fig. 3). Intermediate situations had little representation and took place mainly in transitional regions between well preserved areas and highly degraded ones (Figs. 4c, 5c) (See supplementary material for more resolution).

a) Forest cover



b) Forest fragmentation



c) Combination of forest cover and forest fragmentation

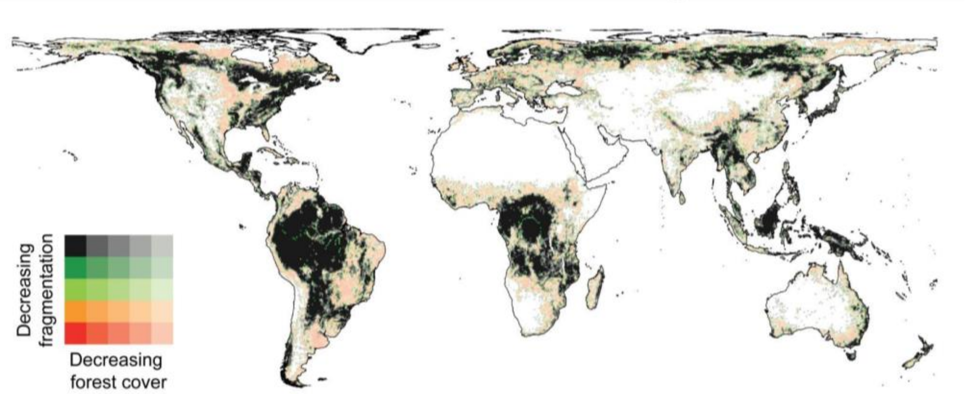
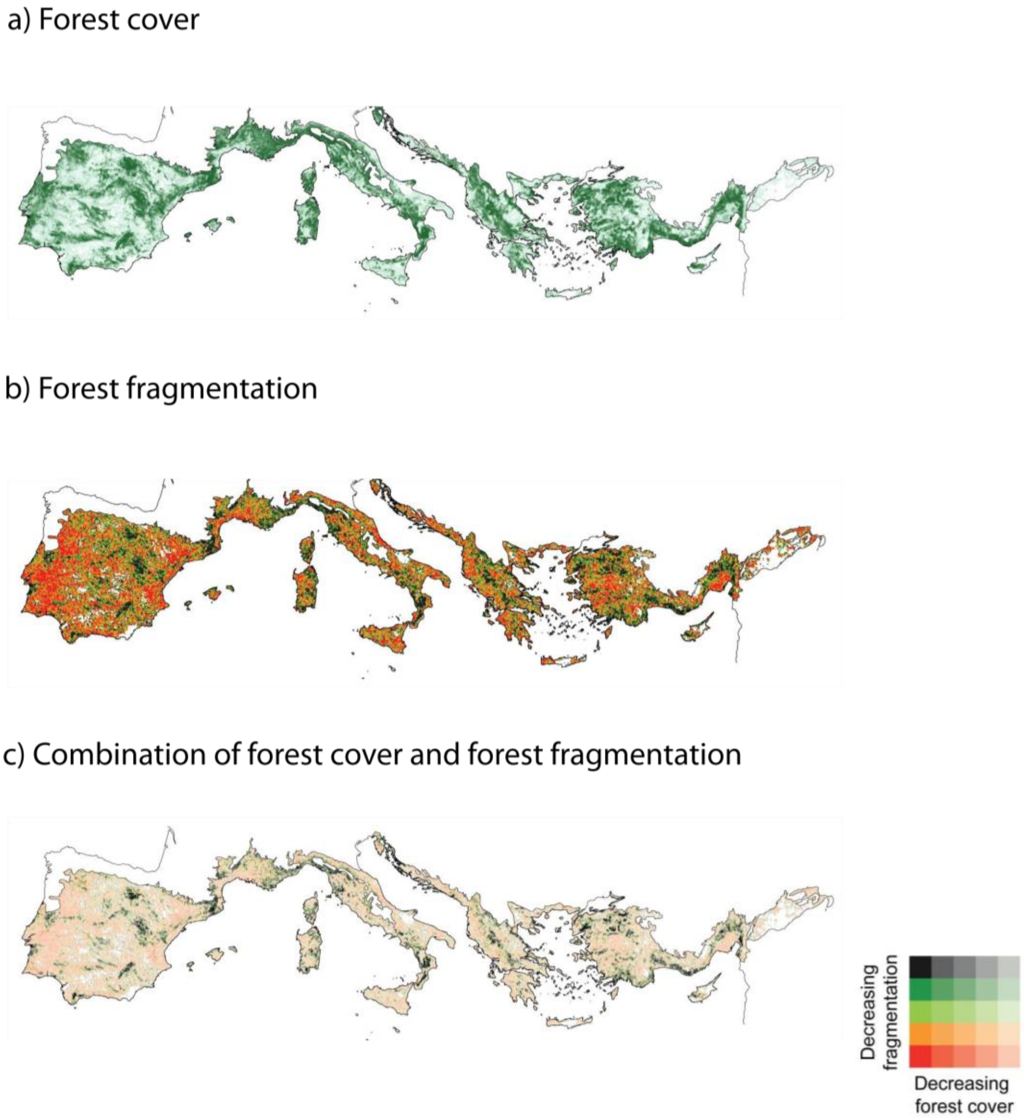


Figure 4: Global maps for the Proportion of Forest Cover (PFC) (a), fragmentation (measured as relative Largest Patch Size, rLPS) (b), and for both variables combined (c).



a) Forest cover

b) Forest fragmentation

c) Combination of forest cover and forest fragmentation

Figure 5: Maps of Proportion of Forest Cover (PFC) (a), fragmentation (measured as relative Largest Patch Size, rLPS) (b), and for both variables combined (c) for the European Mediterranean region (only areas with Mediterranean vegetation are included)

A comparison between the fragmentation patterns observed for the Mediterranean region utilizing two different scales and grain sizes shows consistent patterns but also informs that our perception of fragmentation may vary with grain and resolution. This is, a higher degree of fragmentation is more visible at finer scales (see Figs. 4b, 5b).

Discussion

Here we address some of the critical issues of studies on fragmentation such as how fragmentation is best measured, what are the scale-related effects on the study of fragmentation or what are the relationships between forest loss and fragmentation and how both factors co-vary geographically. Our analyses of fragmentation at the global and regional scales support the use of rLPS as a synthetic fragmentation index since it is correlated with other fragmentation metrics and is more easily comparable and more stable to scale changes. Finally, our results document the existence of an empirical maximum level of forest fragmentation, both globally and regionally.

Why rLPS is a suitable index to quantify fragmentation?

Our results show that the rLPS is robust to scale changes (see Figs. 2-3), supporting its suitability as a standard index to measure fragmentation. This is because it allows comparing results from different sources, and thus, it solves the cross-scales disparity issues amply covered in the literature (Gardner et al., 1987; Gardner, 1998; He & Legendre, 1994; Jelinski & Wu, 1996; Meentemeyer & Bos, 1987; Moody & Woodcook, 1995; O´Neill et al., 1991; O´Neill et al., 1996; Qi & Wu, 1996; Turner et al., 1989; Woodcock & Stralher, 1987; Wu et al., 2002). On the other hand, the pattern of covariation between rLPS and PFC is consistent and stable across scales and suggests the existence of an empirical maximum of fragmentation (see Fig. 1a-b). These relationships between forest cover and how that cover is spatially displayed is largely due to geometric constraints (O´Neill et al., 1996; Riitters, 2000). For example, whereas it is not possible to observe a low value of rLPS (i.e. high fragmentation levels) when PFC is high, it is possible to observe any level of rLPS at low forest cover (see Fig. 1a-b). The existence of this maximum limit of fragmentation might aid informing future experimental studies on fragmentation by avoiding the incorporation of unfeasible situations into the analysis.

The fact that rLPS allows to indirectly estimating patch abundance (i.e. measure of dispersion), edge amount (i.e. measure of habitat quality) and, to a lesser extent, the distances between them (see Fig. 2) supports the performance of rLPS as a synthetic fragmentation index. The difficulty of rLPS to discriminate across different levels of MNN is not surprising. Although many ecologists currently assume that certain metrics, particularly contagion, MNN, mean proximity index and mass fractal dimension can detect differences in landscape configuration (as supported by several publications, see McGarigal & Marks, 1995), currently there are no metrics to systematically quantify such landscape configuration (Hargis et al., 1998). In addition, there is a lack of knowledge about the existence of any indicator that effectively describes fragments disposition (Haines-Young, 1996; Hargis et al., 1998). In the particular case of MNN, we can find that a given landscape containing grouped patches could yield similar average values of MNN to those of a landscape with more dispersed patches (Hargis, 1998; Roger, 1993). This issue may be partially solved by reporting the standard deviation of the mean, which can serve as a measure of patch dispersion (Hargis, 1998; McGarigal & Marks, 1995), but it would only serve as an approximation. Therefore, it is likely that rLPS not detecting changes in landscape configuration had more to do with the limitations of MNN than with the sensitivity of rLPS to measure fragmentation.

In sum, our results endorse the suitability of rLPS as a fragmentation index, because of its ability to discriminate among fragmentation levels, its stability to scale differences and its ability to synthesize information contained in alternative fragmentation metrics.

Biogeographic patterns of forest fragmentation

The geography of the global patterns of forest fragmentation informs of a clear predominance of extreme values of both forest cover and fragmentation that were highly correlated, so that the most deforested sites tend to be very fragmented as well. This finding corroborates the spatial interdependence between habitat loss and fragmentation, already proposed by Didham et al. (2011). The authors noted that this dependence was not reciprocal, and that while habitat loss can occur without fragmentation, the latter is generally accompanied by a reduction in forest cover. Our results confirm this assertion (Figs. 1a-b,2) by showing that as habitat is lost higher fragmentation levels appear, but also that it is possible to find areas where habitat loss is not linked to fragmentation (although this is less common, see Fig. 3). Coinciding with Didham et al. (2011), our results suggest that habitat loss largely operates through changes in habitat disposition, and not independently of them. Therefore, we consider that initiatives directed to minimize losses of forested areas should bear in mind the need to reducing the associated degree of forest fragmentation as well.

By comparing global fragmentation patterns to the major biomes of the world (WWF terrestrial major habitat types), we found that regarding fragmentation of anthropogenic origin, the most affected forest were located in developed or developing countries, in climatically suitable areas with productive soils, ease of access and hence more susceptible to become disturbed and fragmented. This agrees with previous findings reported by Riitters et al. (2000), Haddad et al. (2015), Crooks et al. (2017) or Taubert (2018). The major well-preserved forests are frequently located coinciding with mountainous areas, as for example, the temperate conifer forest in the Rockies, the temperate broadleaf and mixed forest of the Appalachians in North America or the small and scarce well-preserved forest remnants of the Mediterranean region (see Fig. 4c, 5c). Also, large forested areas are found surrounding large river basins, such as the Amazon basin in Brazil or the Congo River, that due to its leafiness and location in developing countries with little access to roads have suffered less human impacts. Boreal forests are another example of well-preserved forests, probably due to the harsh climates and the reduced access from human settlements

(Riitters et al., 2000). A continental focus, allow concluding that forests in the Americas retain a considerable surface that is rather continuous, similarly to African forests and central savannahs.

Quite the contrary, in Europe and Asia the situation is critical. Only boreal forests have substantial density and continuity, in addition to a small temperate conifer forest extension in the Alps and temperate broadleaf and mixed forest in the north of Spain and moist broadleaf tropical and subtropical forest in Burma, Bangladesh and part of Indonesia, and tropical and subtropical dry broadleaf forest in Vietnam and Cambodia. In Australia, the situation is serious as well, containing only a narrow strip of temperate broadleaf and mixed forest in the east. Based on these patterns, we note the importance of maintaining the best-conserved forests, as well as of considering the need for broad scale restoration actions, mainly directed to Europe, Asia and Australia.

Finally, we draw two conclusions on the practical implications of our results in the experimental design of studies related to fragmentation. The first, coinciding with the results obtained by Nepstad et al. (1999a, b) and Riitters et al. (2000), reveals the existence of an effect of the grain and resolution on our perception of fragmentation since more fragmentation is apparent when studied at finer scales. Because of this, we note the importance of selecting adequately the two relevant scale components (i.e. resolution and grain) at the moment of designing a methodology according to the specific question to be addressed. The second conclusion appeals to the existing difficulty to establish the location of extinction thresholds in fragmentation studies, due to the low frequency with which those areas occur (4.7 % in the world and 10 % in the Mediterranean). This would explain the little accuracy with which the scientific literature has determined the empirical existence of extinction thresholds until today. Therefore, in these types of studies we recommend researchers to make an effort to previously select those areas with the suitable characteristics for correctly measuring the location of these thresholds.

Conclusions

We proposed the use of rLPS index as an effective synthetic measure of fragmentation across the scales, and signalized the necessity to consider forest fragmentation levels reduction in conservation initiatives. Finally, we mark the necessity to take into account the empirical fragmentation maximum in an experiment design.

Supplementary material

Figure S1

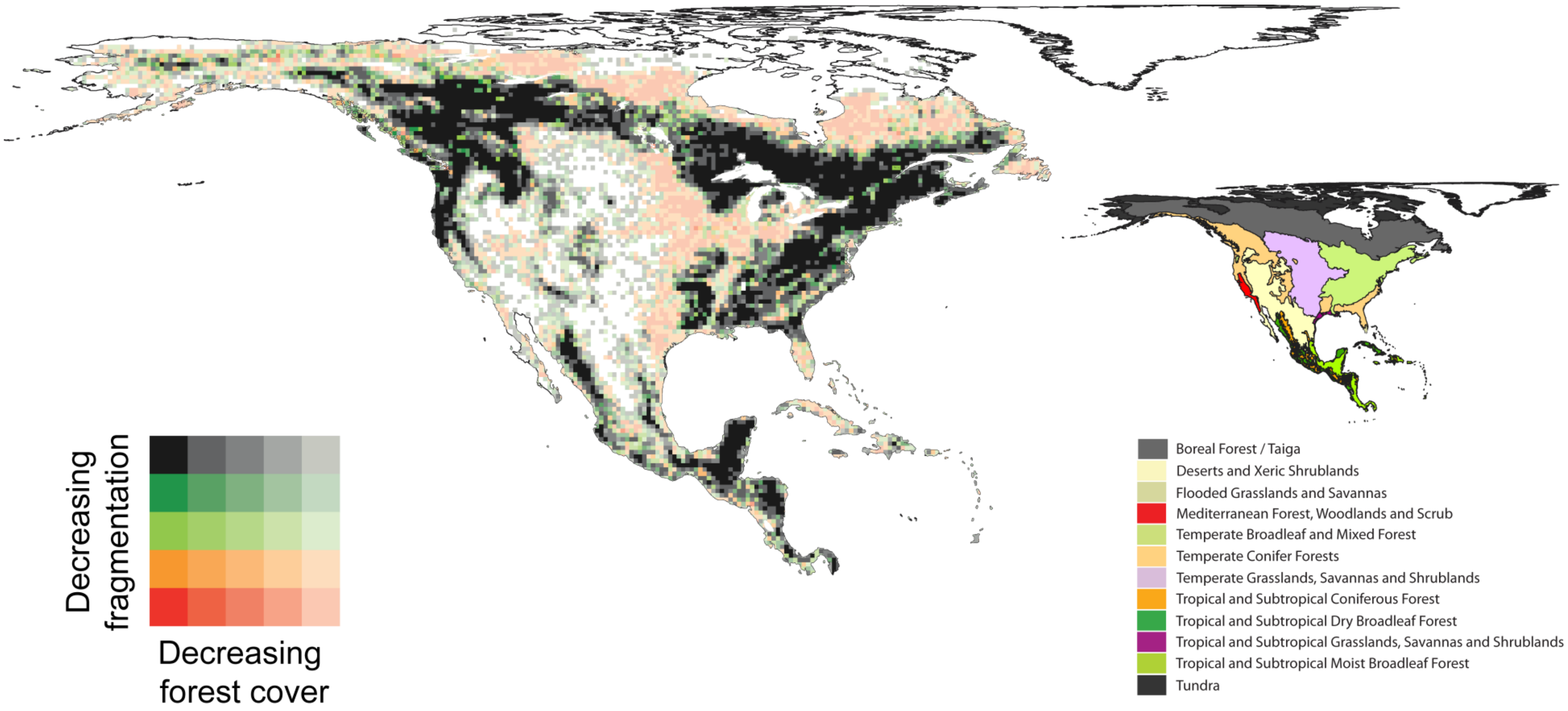


Figure S2

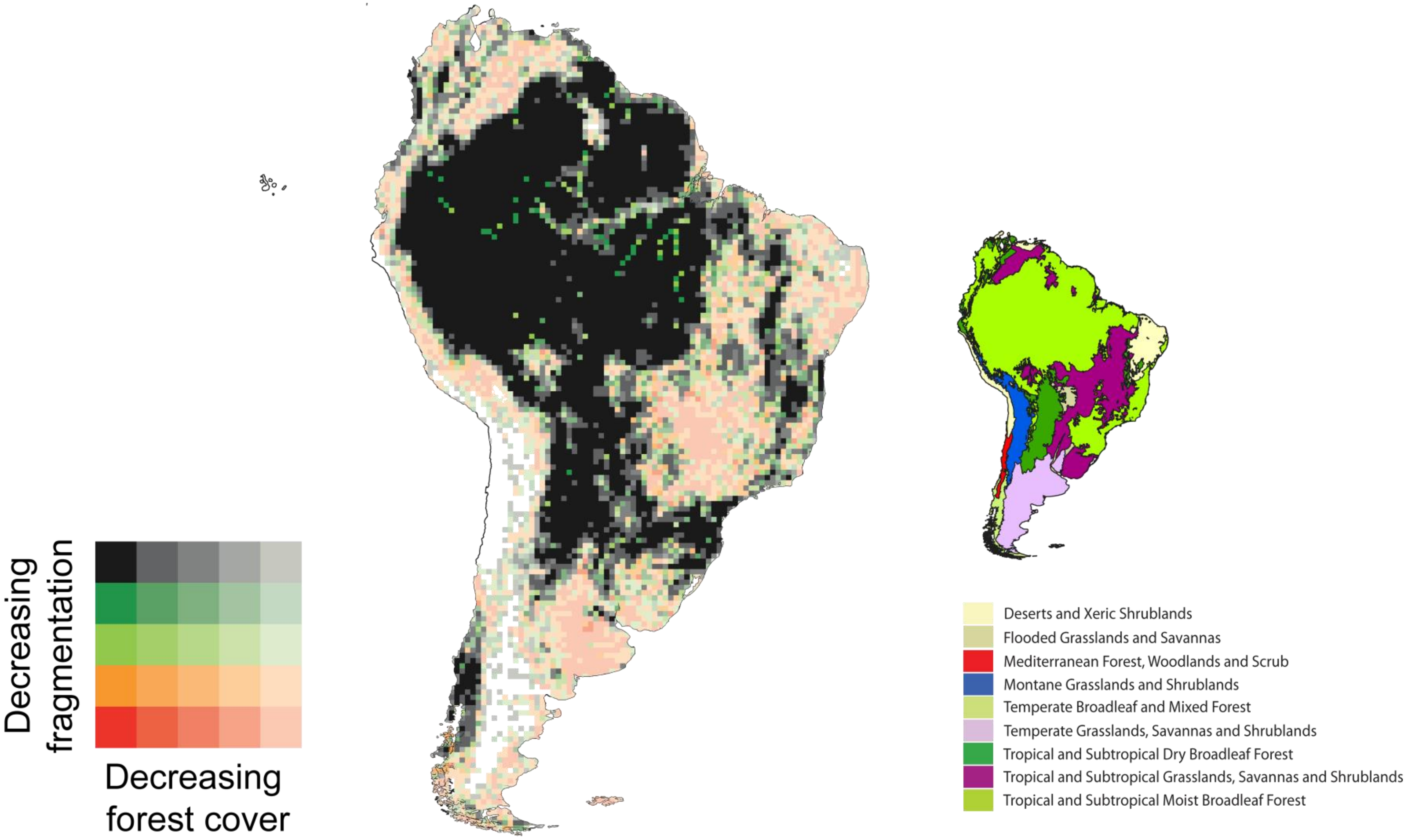

Decreasing fragmentation
Decreasing forest cover
Deserts and Xeric Shrublands
Flooded Grasslands and Savannas
Mediterranean Forest, Woodlands and Scrub
Montane Grasslands and Shrublands
Temperate Broadleaf and Mixed Forest
Temperate Grasslands, Savannas and Shrublands
Tropical and Subtropical Dry Broadleaf Forest
Tropical and Subtropical Grasslands, Savannas and Shrublands
Tropical and Subtropical Moist Broadleaf Forest

Figure S3

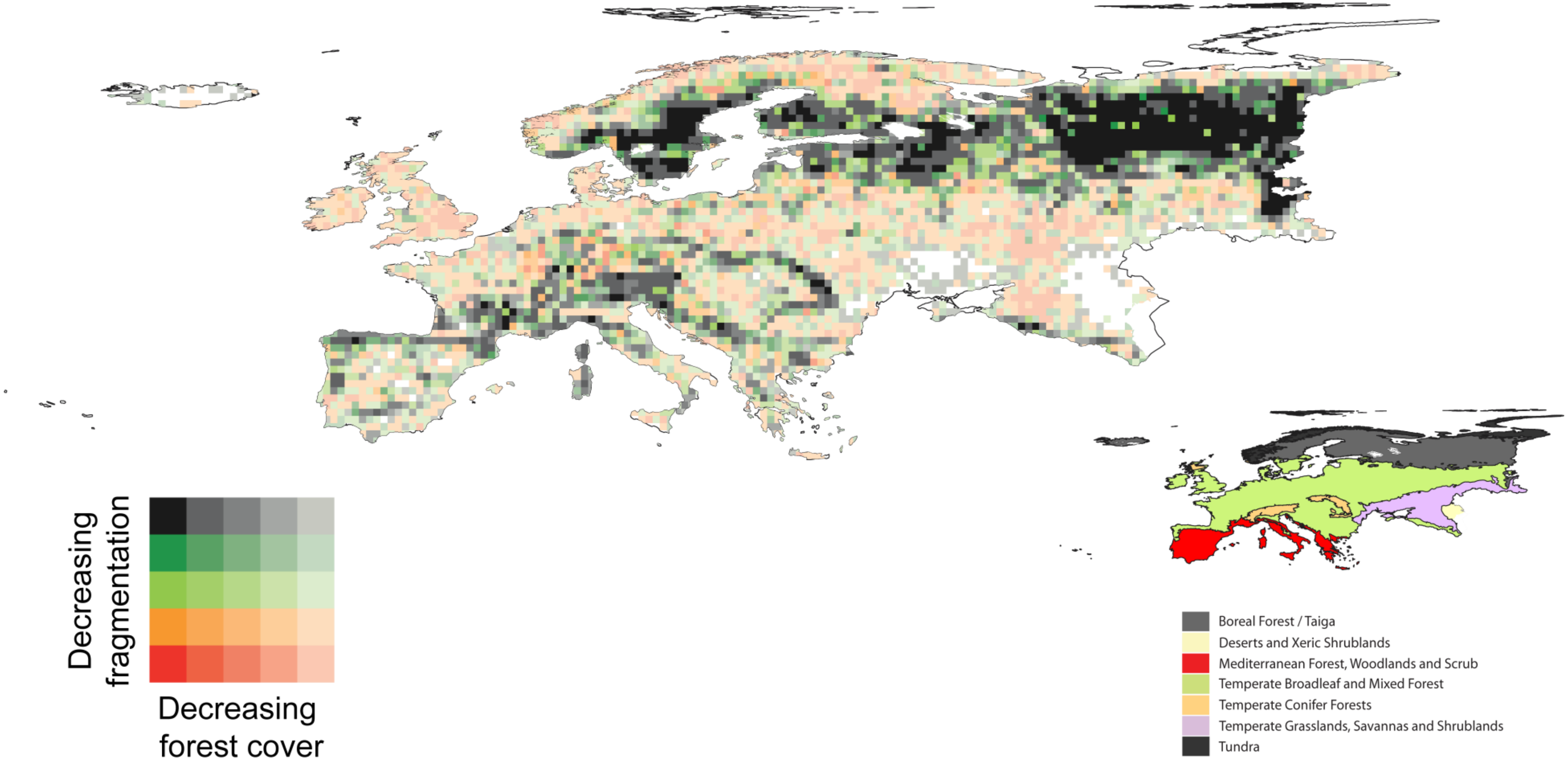
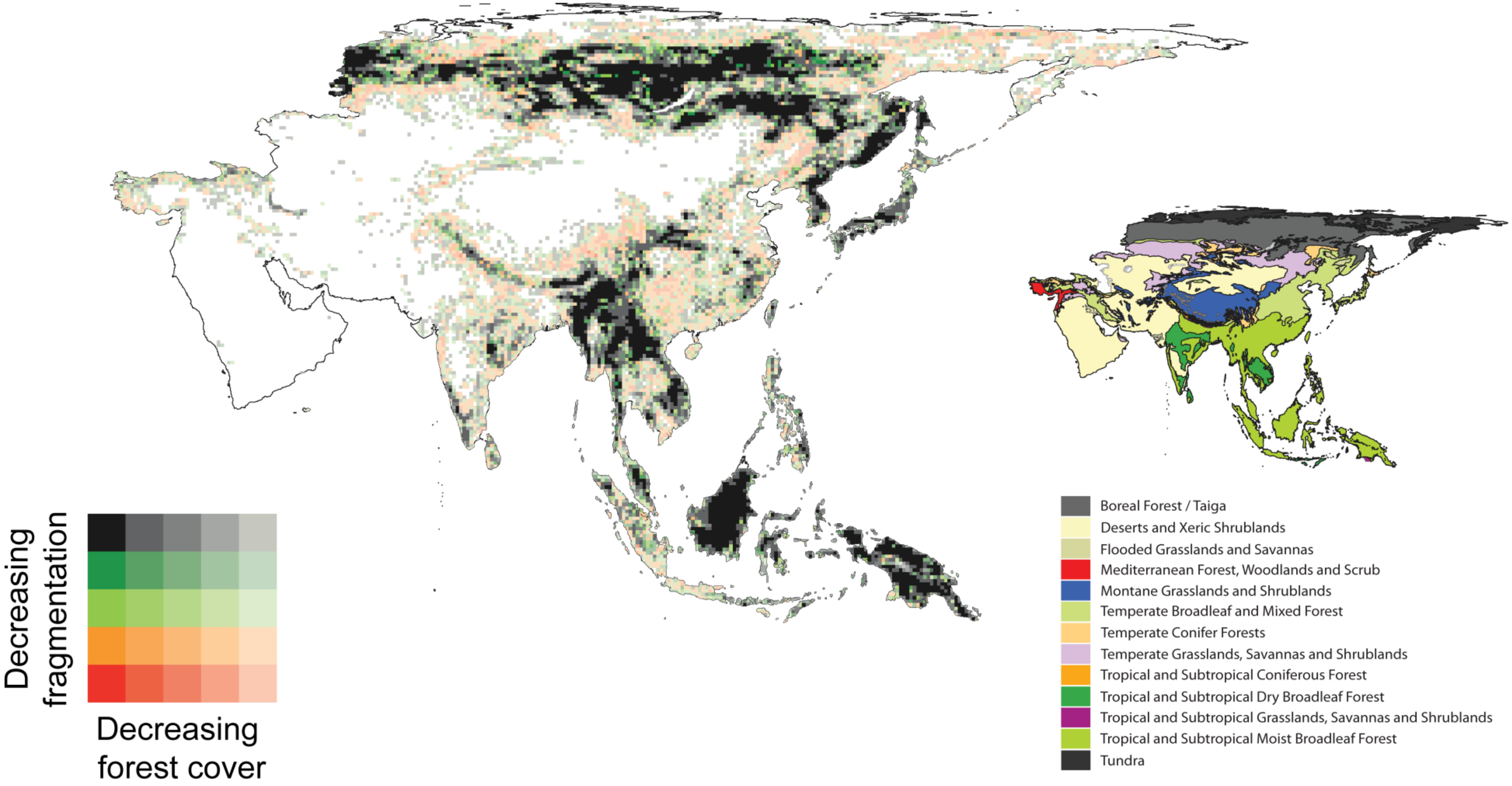

Decreasing fragmentation
Decreasing forest cover
Boreal Forest / Taiga
Deserts and Xeric Shrublands
Mediterranean Forest, Woodlands and Scrub
Temperate Broadleaf and Mixed Forest
Temperate Conifer Forests
Temperate Grasslands, Savannas and Shrublands
Tundra

Figure S4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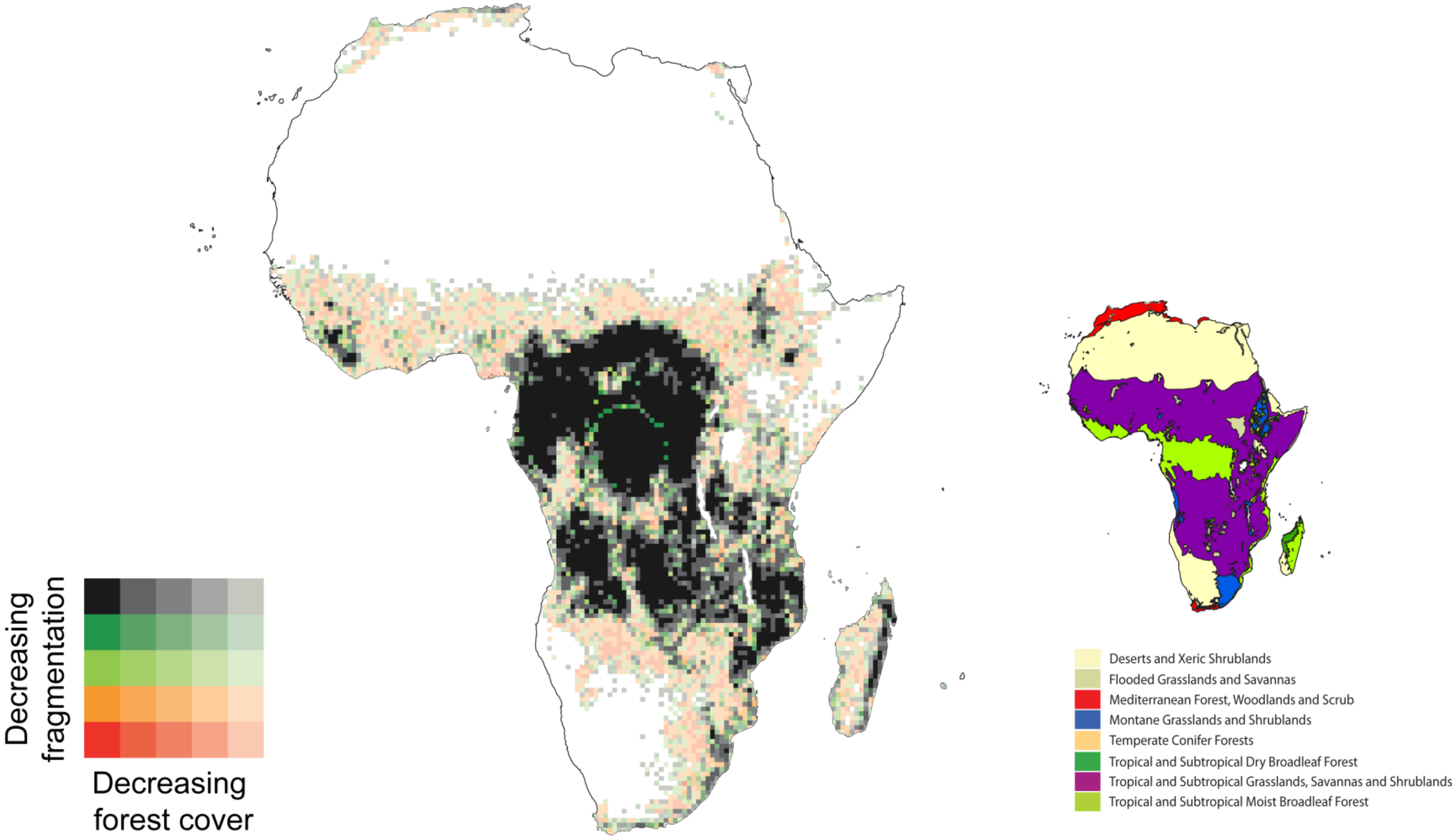
Mediterranean Forest, Woodlands and Scrub
Montane Grasslands and Shrublands
Temperate Broadleaf and Mixed Forest
Temperate Conifer Forests
Temperate Grasslands, Savannas and Shrublands
Tropical and Subtropical Coniferous Forest
Tropical and Subtropical Dry Broadleaf Forest
Tropical and Subtropical Grasslands, Savannas and Shrublands
Tropical and Subtropical Moist Broadleaf Forest
Tundra

Figure S5


Decreasing fragmentation
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Flooded Grasslands and Savannas
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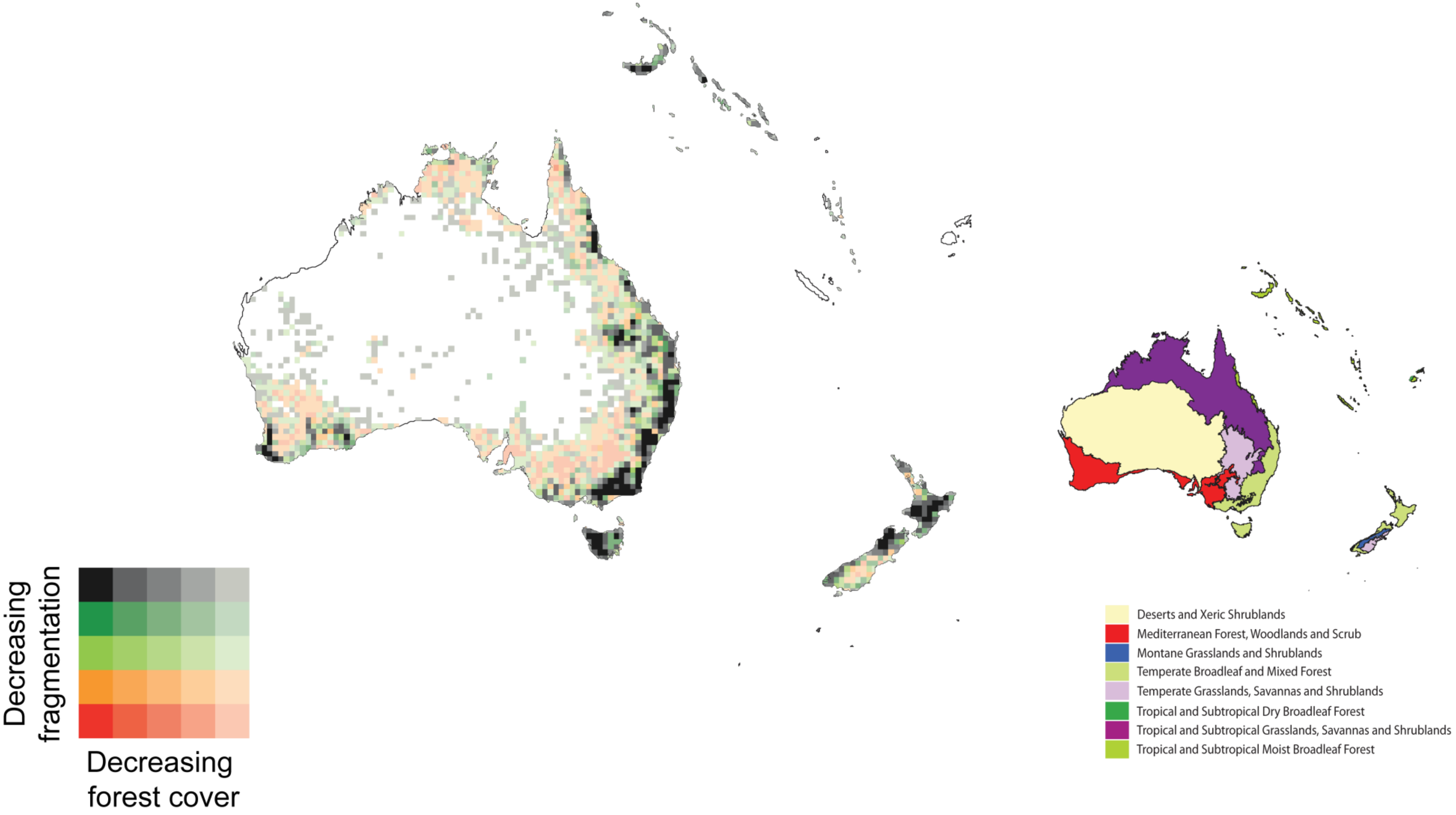
Tropical and Subtropical Grasslands, Savannas and Shrublands
Tropical and Subtropical Moist Broadleaf Forest

Figure S6


Decreasing fragmentation
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Deserts and Xeric Shrublands
Mediterranean Forest, Woodlands and Scrub
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Tropical and Subtropical Dry Broadleaf Forest
Tropical and Subtropical Grasslands, Savannas and Shrublands
Tropical and Subtropical Moist Broadleaf Forest

Acknowledgments

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CAPÍTULO 4

DOES FRAGMENTATION INCREASE EXTINCTION THRESHOLDS?

A EUROPEAN-WIDE TEST WITH SEVEN FOREST BIRDS

Resumen

Objetivo: La teoría predice que la fragmentación agrava los efectos de la pérdida de hábitat, incrementando el umbral de extinción de las especies especialistas de hábitat. Sin embargo, resultados empíricos contradictorios han alimentado la afirmación de que los efectos de la fragmentación han sido exagerados, y que debería dirigirse la atención a la pérdida de hábitat para la conservación de especies. En este estudio evaluamos las variaciones en la sensibilidad de las especies a la cantidad de hábitat y a la fragmentación, y evaluamos si la fragmentación está relacionada con los umbrales de extinción en siete especies de aves.

Localización: Europa

Métodos: Utilizamos el porcentaje de cobertura forestal y la proporción de cobertura de la mancha más grande de hábitat para separar los efectos de la cantidad de bosque vs fragmentación, y aplicamos regresión logística para modelar la presencia-ausencia de 17 especies de aves forestales. Obtuvimos modelos robustos para 7 especies. Definimos dos escenarios de fragmentación, mínimo y máximo, a lo largo del gradiente de cobertura forestal, y cuantificamos la sensibilidad de las especies a la pérdida de bosque sin fragmentación y con fragmentación a cobertura forestal constante. Finalmente, desarrollamos dos test para la hipótesis de umbral de extinción, comparando la probabilidad de ocurrencia de cada especie bajo los dos escenarios de fragmentación a diferentes coberturas forestales.

Resultados: Como esperábamos, la pérdida de bosque tenía un impacto negativo sobre la probabilidad de ocurrencia de las siete especies modeladas, pero -en línea con la teoría-, la fragmentación también condujo a un umbral de

extinción más alto para tres de ellas (urogallo occidental, urogallo y búho pigmeo euroasiático). Una especie (pájaro carpintero negro) exhibió el patrón opuesto, indicando que probablemente se beneficie de la fragmentación. Las diferencias entre las respuestas de las especies pueden reflejar las habilidades de dispersión, especialización en recursos/características del hábitat y/o sensibilidad a potenciales modificaciones en las relaciones interespecíficas.

Conclusiones principales: Aunque la cantidad de bosque es de primaria importancia para la persistencia de aves especialistas forestales, la fragmentación también relevante para algunas, y descuidar la fragmentación forestal sería un error para esas especies. Los rasgos específicos de las especies pueden ser de ayuda para interpretar la reacción de las especies a la fragmentación, y no debería asumirse que ésta siempre, o nunca, importa.

Abstract

Aim: Theory predicts that fragmentation aggravates habitat loss, increasing the extinction threshold of habitat specialists. However, contradictory empirical results have fueled claims that fragmentation has been overemphasized, and more attention should be given to habitat loss for preserving species. We assess variation in species sensitivity to forest amount and fragmentation and evaluate if fragmentation is related to extinction thresholds in seven forest bird species.

Location: Europe.

Methods: We use the percentage of forest cover and the proportion of cover occurring in the largest patch to partition effects of forest amount versus fragmentation, and apply logistic regression to model the presence–absence of 17 forest bird species. For seven species showing robust models, we define two fragmentation scenarios, low and maximum, across the forest cover gradient and quantify species sensitivity to forest contraction with no fragmentation, and to fragmentation under constant forest cover. Finally, we develop two tests of the extinction threshold hypothesis by comparing the occurrence probability of each species under the two fragmentation scenarios at different forest covers.

Results: As expected, forest contraction had negative impacts on the occurrence probability of all seven species modelled, but – in line with theory – fragmentation also led to a higher extinction threshold for three (Western capercaillie, Hazel grouse and Eurasian pygmy-owl). One species (Black woodpecker) exhibited the opposite pattern indicating that it probably benefits from fragmentation. Differences among species responses may reflect dispersal abilities, specializations in resources/habitat characteristics and/or sensitivity to potential modifications of interspecific interactions.

Main conclusions: Although forest amount is of primary importance for the persistence of forest specialist birds, fragmentation is also relevant for some, and neglecting forest fragmentation would be a mistake for these species. Species specific traits can be helpful for interpreting species reactions to fragmentation, and it should not be assumed that it always, or never, matters.

Introduction

Habitat destruction is the dominant threat affecting biodiversity in terrestrial ecosystems (Sala et al., 2000). Two key issues concerning conservation are the amount of habitat needed to achieve conservation goals and the importance of habitat fragmentation (Fahrig, 2001, 2002). Habitat fragmentation is an element of the pattern of habitat that differs from how much habitat there is (e.g. Haila, 2002). Nonetheless, the term has been used in many ways, commonly to illustrate human practices that destroy habitat, even though habitat might be removed without increasing fragmentation (e.g. Fischer & Lindenmayer, 2007). This loose use of the term has generated confusion, complicating understanding of the impacts of habitat amount and fragmentation on biodiversity. Haila (2002) and Fahrig (2003), among others, have argued for discrimination between habitat loss per se and habitat fragmentation per se, but the debate remains open, and although many studies have implicitly assumed independent effects of habitat loss and fragmentation, there is increasing awareness of their interdependence, recognizing that fragmentation is often a consequence of habitat loss (see Didham et al., 2012).

Theoretical results from both stochastic and deterministic models indicate that fragmentation *sensu strictu* aggravates the impacts of habitat loss on populations (Fahrig, 2002). Moreover, the models converge to predict that the greater the fragmentation, the earlier the appearance of the extinction threshold in the habitat loss gradient (*sensu* Fahrig, 2003); that is, of the minimum amount of habitat below which either the long-term population persistence probability is < 1 in stochastic models, or the equilibrium population size (or proportion of the landscape occupied) is 0 in deterministic models (Fahrig, 2002; see also Lande, 1987; Bascompte & Solé, 1996). Hereafter we refer to this as the extinction threshold hypothesis; although there are several explanations for relationships between critical thresholds and habitat amount, most focus on habitat fragmentation (Swift & Hannon, 2010).

Contrary to theory, the observed effects of fragmentation are generally weaker than those of habitat amount and can be negative, neutral or positive (e.g. Fahrig, 2003; Bennett et al., 2006), which led Fahrig (2002) to suggest that models are missing important processes. Indeed, since Levins (1966), it is accepted that generality, precision and realism cannot be maximized simultaneously in a model, and it may be that the extinction threshold hypothesis emerged from a lack of realism in the models that led to it (as suggested by Fahrig, 2002). However, Levins (1966) also claimed that a robust theoretical outcome is one that appears across a range of models, which is the case for the extinction threshold hypothesis. So, might problems lie in the structure of the empirical studies themselves or in the interpretation of their results?. Two lines of argument suggest that both could be influencing empirical evaluations of the importance of fragmentation.

Firstly, species can differ in their responses to the loss and fragmentation of habitats due to their specific characteristics and habitat needs. For example, highly dispersive species should be less likely to suffer from fragmentation than less dispersive species (e.g. Bascompte & Solé, 1996). Therefore, empirically observed differences in responses to habitat fragmentation among species that differ in their dispersal capabilities (e.g. Montoya et al., 2010) cannot be construed as discrediting the extinction threshold hypothesis. On the contrary, these differences are key for the interpretation of results. Moreover, in contrast to claims that species responses to the alteration of habitats should be viewed in an individualistic fashion (e.g. Fischer & Lindenmayer, 2006), Didham et al. (2012) argued for the existence of sets of traits generating 'interdependent' responses among them, generating common responses to fragmentation for species with similar resource or habitat requirements, dispersal capabilities, or sensitivity to fragmentation-driven altered interspecific interactions (see Angelstam, 1992; Andrén, 1995; Hanski, 1995). This opens a venue for investigation: to what extent are species responses to fragmentation (including extinction thresholds) related to traits?.

Secondly, empirical studies must cope with difficulties in measuring habitat characteristics. The habitat concept is species specific, with its precise meaning referring to the resources and conditions that permit occupancy for a particular species (Lindenmayer & Fischer, 2006). As theoretical studies model species and habitats with characteristics that researchers assign to them, a species-specific habitat definition is implicit. However, in empirical analyses, quantifying the conditions limiting the occurrence of every species might be impossible. Consequently, the common practice is to use human-perceived habitats, often based on vegetation type or land use, and assign these habitat proxies to groups of species as if all of them had identical needs (Fischer & Lindenmayer, 2007). Thus, it is not surprising that empirical analyses have found varying responses to habitat fragmentation and, hence, limited support for the extinction threshold hypothesis or other theoretical propositions (see Fahrig, 2002, 2003; but see Montoya et al., 2010).

Even if theory-derived predictions of species–habitat relationships do not always apply when using habitat proxies as defined above (e.g. types of vegetation or land use), investigating species reactions to changes in such proxies has the practical importance in that vegetation and land use types are commonly used for decision making in conservation (see also Fischer & Lindenmayer, 2007). Thus, if there were species for which fragmentation of the vegetation (or land use) type is found to worsen effects of habitat loss, conservation plans and initiatives involving these species should consider fragmentation. Moreover, if fragmentation is found to worsen effects of habitat loss in studies involving broad regions (see Montoya et al., 2010 for an example) or continents, specific policies could be devised for the conservation of fragmentation-sensitive species across these areas.

Here we present a broad-scale, grid-based analysis of the relationships between occurrences of forest bird species and forest amount and fragmentation across Europe. Because more than two-thirds of this region should be forested under present climatic conditions (Huntley & Birks, 1983), forest birds represent an important set of species to address our objectives. We concentrated on species that are associated with mature forest. Further, because long-term persistence of forest birds in landscapes depends on maintaining breeding populations, our analyses are based on the occurrence of breeding populations. Thus, for each species we used breeding bird atlas data covering Europe (Hagemeijer & Blair, 1997), which map the occurrence of at least one breeding pair at each site. Two key questions underpin this study: (1) How (positively or negatively) and to what extent is each species sensitive to forest loss and fragmentation, and (2) is fragmentation related to extinction thresholds? A third question is, if species respond differently to fragmentation, to what extent might this be due to differences in dispersal capabilities and/or habitat needs among them?. While responses to the first two questions are directly derived from the analysis of our database, the third can be surmised based on the biology and behavior of the species.

Methods

Bird data

The spatial distribution of birds and their nesting and foraging habits were taken from Hagemeijer & Blair (1997), which integrates 25 years of effort by volunteer ornithologists and specialists and describes the occurrence of species' breeding pairs in the 50 km x 50 km Universal Transverse Mercator grid system. Our analysis units comprised 1341 cells after excluding areas with insufficient bird or forest cover sampling, all islands except Great Britain, and all coastal cells containing < 50% of the landmass of inland cells (see Appendix S1 in Supporting Information). We focused on forest-specialists, which were defined as species primarily associated with forest habitat for nesting and feeding. According to descriptions provided by Hagemeijer & Blair (1997), 35 forest specialists exist in the study area (see Appendix S2), of which we excluded those with breeding pairs present in < 15% or > 70% of the cells, as statistical models and evaluations are less credible for them (Jiménez-Valverde et al., 2008). This resulted in 17 species for modelling (see Appendix S2).

We generated a 'potential distribution map' for each species that approximates the area in which it occurs or has likely occurred throughout the mid-20th century. This was done by superimposing the atlas maps and range maps provided by Petterson et al. (1957, 1967, 1982), Jonsson (1993) and Mullarney et al. (1999) to attain a synthetic map for each species that we considered its study area (i.e. the subset of cells for which we recorded the presence/absence of breeding pairs). All other cells were excluded; i.e. each species was analyzed using a unique set of cells.

Forest variables

We used the CORINE Land Cover CLC2000 and CLC90- Switzerland databases to quantify forest amount and fragmentation. CORINE Land Cover is a remotely sensed land cover classification covering Europe (except Norway and Serbia), of which we utilized the 250-m pixel resolution series (data available at http://www.eea.europa.eu/data-and-maps/; accessed November 2010). Of the 44 land cover classes, we identified all pixels belonging to broadleaved, coniferous or mixed forests. Forest amount and fragmentation for each cell was quantified as the percentage of cell's area covered by forest (percentage forest cover [PFC]) and the percentage of forest cover that corresponds to the largest patch (relative largest patch size [rLPS]). The latter has been used in theoretical (see Bascompte & Solé, 1996) and empirical studies (Montoya et al., 2010) and serves to distinguish between scenarios reflecting low and high fragmentation. For example, when PFC = 40%, weakly fragmented cells are those with most forest clumped in a single patch (e.g. with rLPS > 90%), as remaining forest is too small to represent additional fragments. Conversely, strongly fragmented cells would have very small rLPS (e.g. < 10%), as this indicates that all remaining forest is scattered in small, numerous patches (see Montoya et al., 2010 for discussion and utilization of rLPS).

Data analysis

Species distribution modelling

We used logistic regression with binomial errors to model presence/absence of breeding pairs of each species as a function of PFC and rLPS:

$$P(j, PFC_q, rLPS_q) = \frac{e^{k(j, PFC_q, rLPS_q)}}{1 + e^{k(j, PFC_q, rLPS_q)}} \qquad \text{(eq 1)}$$

$$k(j, PFC_q, rLPS_q) = M_j + C_j(PFC_q) + CC_j(rLPS_q) \qquad \text{(eq 2)}$$

where P(j, PFC_q, $rLPS_q$) is the probability of finding species j in cell q with forest cover PFC_q and relative largest patch size $rLPS_q$, and M_j, C_j and CC_j are species-specific parameters of the regression model for species j with respect to PFC_q and $rLPS_q$.

To ensure that interpretations were based on robust models, the 17 species were subjected to a second selection process based on the P-value of each model's chi-square and two additional model performance indexes, the area under the receiver operating characteristic curve (AUC) and McFadden's rho-squared (p^2). AUC ranges from 0.5 to 1 with values < 0.7 indicating por capacity of the model to predict presences and absences (Pearce & Ferrier, 2000). We thus discarded species whose models rated below this level. McFadden's rho-squared (p^2) approximates an ordinary least squares coefficient of determination (r^2) (McFadden, 1979). However, p^2 tends to be much lower than r^2, and p^2 values from 0.2 to 0.4 represent excellent fits (McFadden, 1979).We thus also excluded species with $p^2 < 0.2$.

Finally, the presence of spatial autocorrelation in model residuals can violate the assumption of independently distributed errors in regression models, so we also assessed spatial autocorrelation levels in model residuals with Moran's I coefficients (Diniz-Filho et al., 2003) computed using SAM 4.0 (Rangel et al., 2010). Logistic regression modelling was done in Matlab (version 7.0, MathWorks Inc., Natick, MA, USA), and AUC values were calculated with the 'PresenceAbsence' package (Freeman & Moisen, 2008) implemented in R Development Core Team (2008).

Sensitivity analysis to forest amount and fragmentation

To facilitate comparison among species, parameterized logistic models were used to generate scalar metrics of species sensitivities to changes in both forest cover at a constant fragmentation level ($\Omega_{j,cover}$), and fragmentation at a constant forest cover ($\Omega_{j,fragm}$). For the constant fragmentation scenario we fixed rLPS at 80%, a low fragmentation level found at most forest cover levels (see Fig. 1), and then computed the proportional reduction in occurrence due to a reduction in forest cover from a high value (PFC = 75%) to a low one (5%):

$$\Omega_{j,\mathrm{cover}} = \ln\left[\frac{P(j, PFC_q = 5, rLPS_q = 100)}{P(j, PFC_q = 75, rLPS_q = 100)}\right] \quad \text{(eq 3)}$$

where a positive or negative Ω_j, cover indicates that the species j responds positively or negatively to forest contraction.

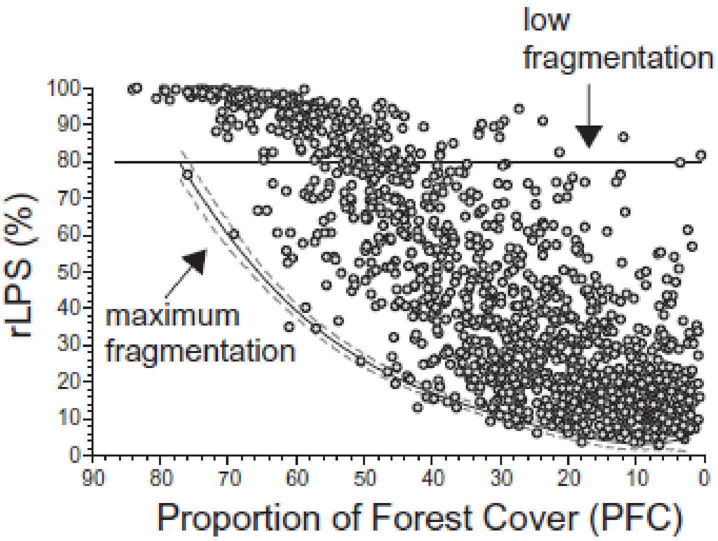


Figure 1: Forest fragmentation (measured as the percentage of forest occurring in the largest patch, rLPS) as a function of the proportion of forested area (PFC) in ≈ 50 km x 50 km cells in the study area. The upper solid line delimitates cells with low fragmentation (rLPS = 80%). The lower solid and discontinuous lines (95% CIs) correspond to a polynomial regression on 32 cells located at the lower edge of the cloud of points. We used this line to quantify maximum fragmentation in terms of rLPS at varying levels of PFC (see text). Note that PFC decreases to the right.

For the scenario of constant forest cover, we took into account that whereas cells with low fragmentation (e.g. with rLPS = 80%) can occur throughout the forest cover gradient, differences between minimum and maximum fragmentation (indicated by higher and lower rLPS values, respectively) increase as forest cover decreases (Fig. 1). Based on these relationships, we focused on a moderately low forest amount (PFC = 25%) and computed the proportional reduction in occurrence due to an increase from low to high fragmentation at this forest cover (i.e. for the rLPS values of 80 and 9%, respectively):

$$\Omega_{j,\,fragm} = \ln\left[\frac{P(j, PFC_q = 25, rLPS_q = 9)}{P(j, PFC_q = 25, rLPS_q = 80)}\right] \quad \text{(eq 4)}$$

where a negative $\Omega_{j,fragm}$ indicates a negative response of species j to increased fragmentation, whereas a positive $\Omega_{j,fragm}$ indicates that fragmentation favors occurrence of the species.

It should be noted that the logarithmic scale generates a nonlinear relationship of $\Omega_{j,cover}$ and $\Omega_{j,fragm}$ with proportional reduction in occurrence; for example, $\Omega_{j,\bullet} = -3$ represents a 95% reduction; $\Omega_{j,\bullet} = -1$ a 63% reduction; $\Omega_{j,\bullet} = -0.5$, a 39% reduction, and $\Omega_{j,\bullet} = +1$ represents a 170% increase.

We generated 95% confidence intervals (CI) for $\Omega_{j,cover}$ and $\Omega_{j,fragm}$ using a bootstrap procedure implemented in Matlab (version 7.0, MathWorks Inc.). We produced 1000 samples for each species by resampling with replacement triads of PFC_q, $rLPS_q$ and species occurrence (1 or 0) values from each original sample. Each bootstrap sample comprised the same number of cells as the original sample and was used to parameterize the logistic model (equations 1 and 2) and to compute $\Omega_{j,cover}$ and $\Omega_{j,fragm}$ as in equations 3 and 4, respectively. We generated 1000 ranked values per scalar metric, of which the values at the 25th and 976th positions corresponded to the lower and upper 95% CI.

We also computed $\Omega_{j,cover}$ and $\Omega_{j,fragm}$ substituting the rLPS values of 80% in equations 3 and 4 by 100%, assuming that fragmentation could be zero at any level of forest cover. We did this because although there were no cells with zero fragmentation (i.e. with rLPS = 100%) when PFC falls below ≈ 60% (see Fig. 1), this was found when we used a different source of forest data (DeFries et al., 2000; see details and patterns in Appendix S3). However, we obtained qualitatively similar results using either 80% or 100% rLPS, so we only report those for rLPS = 80%.

Testing the extinction threshold hypothesis

Formally, the extinction threshold is defined as the amount of habitat below which the probability of long-term population persistence is < 1 (see Fahrig, 2002). However, a shift from a probability of 1 to < 1 is of no value when utilizing logistic models, as probabilities of 1 (and 0) are approached asymptotically but never reached. Consequently, we tested the extinction threshold hypothesis following two alternative procedures.

First, we adopted a criterion analogous to the LD_{50} of a drug, the dose that kills half of a group of experimental subjects (see Woodroffe & Ginsberg, 1998 for a similar approach focused on carnivore extinction). We defined the extinction threshold of a species as the amount of habitat at which its logistic probability of occurrence falls to 0.5, so the prediction of the extinction threshold hypothesis of fragmentation theory is that this probability is reached at a higher habitat amount when the habitat loss occurs with fragmentation.

This was tested using the logistic model parameterized for each species to estimate P(j, PFC, rLPS) at nine levels of forest cover (PFC values of 85, 75, 65, 55, 45, 35, 25, 15 and 5%) for two fragmentation situations (low and maximum). The definition of the fragmentation scenarios was based on the empirical relationships between forest fragmentation and forest amount (Fig. 1). That is, we assumed low fragmentation to be the same at all instances (rLPS = 80%) and computed P(j, PFC, rLPS) for each of the resulting nine pairs of PFC and rLPS; (85,80), (75,80), (65,80), . . ., (5,80). For maximum fragmentation, we examined the cloud of points and selected 32 cells that delimited it from below (i.e. cells representative of higher fragmentation at different levels of forest cover). Then we generated a fourth order polynomial regression of rLPS on PFC with these cells and computed the maximum empirical fragmentation for each of the selected forest cover values. This provided rLPS values of 80, 75, 52, 34, 22, 14, 9, 4 and 3%, so that P(j, PFC, rLPS) was computed for the PFC and rLPS pairs of (85,80), (75,75), (65,52)… (5,3). To obtain a 95% CI for each P (j, PFC, rLPS), we repeated all calculations for the 1000 bootstrap samples generated for each species.

As for the case of the sensitivity analyses, we repeated this test of the extinction threshold hypothesis using the same maximum fragmentation scenario (i.e. with the same paired levels of PFC and rLPS) but no fragmentation (i.e. rLPS = 100%) at all levels of PFC. Again, the results did not differ and are not shown to reduce redundancy.

Our second test defined the extinction threshold as the location in the PFC gradient of the lower inflection point of the logistic curve (i.e. the PFC value at which the second derivative is greatest). Specifically, for each species and fragmentation scenario – i.e. low (with rLPS = 80%) and maximum (rLPS values generated with the polynomial regression described above) – we computed the second derivative of the logistic curve at decreasing 0.1% intervals between the PFC levels of 85 and 5%, identified the maximum value and retained that PFC point. Statistical differences between the extinction thresholds found for each fragmentation scenario were again established based on bootstrapped 95% CIs. If a species occurrence was negatively affected by fragmentation, its extinction threshold should occur at significantly higher levels of PFC for the maximum fragmentation scenario. We also computed the 95% CIs for the probability of occurrence at which each extinction threshold was found. A lack of significant differences between fragmentation scenarios would support the robustness of our definition of the extinction threshold for this test. Still, a potential limitation of this method is that the inflection point could occur outside of the range of PFC values included in the analysis, in which case the test would be uninformative.

Second derivative values of the logistic curve were generated with the 'e1071' package for R.

Results

Of the 17 bird species selected initially for modelling, we obtained robust models for seven (Table 1), which were used for further analyses. The two-factor habitat models reduced the spatial autocorrelation at all distance classes (see Appendix S4). The largest amount of residual positive spatial autocorrelation remained in the shortest distance class, but with Moran's I-values lower than 0.2 in all cases. Thus, despite the simplicity of the models, they described effectively the occurrence patterns of all seven species.

Table 1. Sample sizes (N) and goodness-of-fit statistics for the logistic regressions (the area under the ROC curve [AUC], and McFadden's rho-squared [ρ^2]) of 17 forest specialist bird species in Western Europe. All models were significant at Chi-squared p-value < 0.0001. The models of the first seven species (in bold) met all three quality criteria described in the Methods (i.e. significant p-value, AUC ≥0.7 and McFadden's $\rho^2 \geq 0.2$) and were selected for further analysis. Parameter estimates (and their 95% CIs) of the logistic models Mj, Cj, CCj are provided.

Common name	Scientific name	N	AUC	ρ^2	*Mj* (lower; upper)	*Cj* (lower; upper)	*CCj* (lower; upper)
Western capercaillie	***Tetrao urogallus* (Linnaeus, 1758)**	**793**	**0.87**	**0.35**	-3.913 (-4.456;-3.346)	0.084 (0.064;0.102)	0.012 (0.003;0.022)
Three-toed woodpecker	***Picoides tridactylus* (Linnaeus, 1758)**	**517**	**0.87**	**0.35**	-4.281 (-4.991;-3.468)	0.103 (0.077;0.130)	-0.0002 (-0.013;0.013)
Hazel grouse	***Tetrastes bonasia* (Linnaeus, 1758)**	**798**	**0.83**	**0.28**	-2.647 (-3.097;-2.174)	0.068 (0.050;0.085)	0.012 (0.003;0.022)
Eurasian pygmy-owl	***Glaucidium passerinum* (Linnaeus, 1758)**	**648**	**0.83**	**0.27**	-3.255 (-3.819;-2.691)	0.068 (0.048;0.089)	0.009 (-0.0009;0.020)
Tengmalm's owl	***Aegolius funereus* (Linnaeus, 1758)**	**858**	**0.83**	**0.27**	-2.694 (-3.130;-2.257)	0.079 (0.062;0.096)	0.002 (-0.005;0.011)
Black woodpecker	***Dryocopus martius* (Linnaeus, 1758)**	**1063**	**0.81**	**0.21**	-0.110 (-0.478;0.256)	0.094 (0.075;0.113)	-0.014 (-0.025;-0.003)
Ural owl	***Strix uralensis* (Pallas, 1771)**	**345**	**0.74**	**0.26**	-4.160 (-5.089;-3.061)	0.103 (0.066;0.140)	-0.010 (-0.028;0.008)
Red crossbill	*Loxia curvirostra* (Linnaeus, 1758)	1217	0.81	0.13	-0.991 (-1.346;-0.636)	0.048 (0.033;0.064)	0.004 (-0.003;0.012)
Willow tit	*Poecile montanus* (Conrad, 1827)	858	0.70	0.08	1.000 (0.640;1.359)	0.062 (0.044;0.081)	-0.021 (-0.033;-0.010)
Brown creeper	*Certhia familiaris* (Linnaeus, 1758)	1124	0.69	0.08	0.154 (-0.119;0.427)	0.053 (0.040;0.067)	-0.014 (-0.022;-0.005)
Firecrest	*Regulus ignicapilla* (Temminck, 1820)	1022	0.69	0.07	0.204 (-0.098;0.508)	0.052 (0.037;0.067)	-0.004 (-0.013;0.004)
European pied flycatcher	*Ficedula hypoleuca* (Pallas, 1764)	1182	0.68	0.07	-0.175 (-0.415;0.065)	0.056 (0.044;0.069)	-0.020 (-0.028;-0.012)
Grey-faced woodpecker	*Picus canus* (Gmelin, 1788)	803	0.66	0.02	0.251 (-0.068;0.571)	0.033 (0.019;0.047)	-0.013 (-0.022;-0.004)
Middle spotted woodpecker	*Dendrocopos medius* (Linnaeus, 1758)	860	0.64	0.04	0.771 (0.466;1.076)	0.035 (0.022;0.049)	-0.028 (-0.036;-0.020)
Collared flycatcher	*Ficedula albicollis* (Temminck, 1815)	504	0.62	0.04	-0.663 (-1.084;-0.241)	0.043 (0.026;0.060)	-0.021 (-0.031;-0.011)
Spotted nutcracker	*Nucifraga caryocatactes* (Linnaeus, 1758)	620	0.62	0.03	-0.317 (-0.723;0.087)	0.030 (0.014;0.046)	-0.004 (-0.014;0.004)
Red-breasted flycatcher	*Ficedula parva* (Bechstein, 1792)	503	0.61	0.06	-0.356 (-0.783;0.069)	0.038 (0.018;0.058)	-0.001 (-0.013;0.010)

Sensitivity to forest amount and fragmentation

As expected for forest specialists, all species responded negatively to decreased forest cover under low fragmentation (a negative $\Omega_{j,cover}$ with 95% CIs not including zero), with $\Omega_{j,cover}$ values ranging from -1.18 for Black woodpecker to -4.50 for Ural owl (Fig. 2a). This meant that, under the modelled scenario of decreasing forest cover from 75% to 5%, the proportional reduction in the occurrence probability ranged between 72% and 98% across all species.

In contrast, for the scenario of high fragmentation (i.e. from $rLPS_q$ = 80% to 9%) at a constant forest cover (PFC_q = 25%) three species showed significantly negative $\Omega_{j.fragm}$ values (Fig. 2b), the two grouse (Western capercaillie and Hazel grouse) and the Eurasian pygmy-owl, although the owl had a weaker negative response to fragmentation as indicated by the closer proximity of its upper 95% CI to zero (see Fig. 2b). One species, the Black woodpecker, responded positively and, hence, is more likely to be found in more fragmented cells, and the occurrence of three species was not significantly affected by fragmentation (Tengmalm's owl, Ural owl and Three-toed woodpecker).

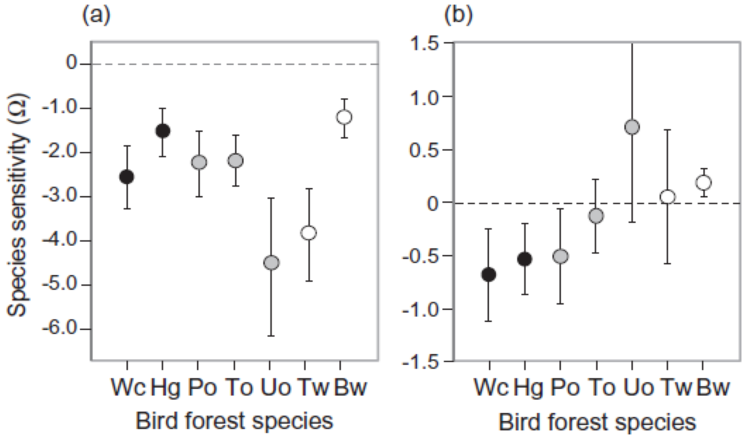


Figure 2: Sensitivity (Ωj) (± 95% CIs) of seven forest-specialist birds to forest cover reduction (a) and forest fragmentation (b). Colours of the circles represent the family to which species belong: black (Phasianidae), grey (Strigidae) and white (Picidae). Wc = Western capercaillie; Hg = Hazel grouse; Po = Eurasian pygmy-owl; To = Tengmalm's owl; Uo = Ural owl; Tw = Three-toed woodpecker; Bw = Black woodpecker.

Fragmentation and extinction thresholds

Relationships between occurrence probabilities and forest cover are shown in Fig. 3 for the low and maximum scenarios of forest fragmentation. Our first test of the extinction threshold hypothesis focused on where in the gradient of decreasing forest amount occurred the first overlap between an occurrence probability (or its 95% CI) and the critical probability of 0.5 (i.e. at which the presence or absence of the species become equally likely), as we took this level as indicating an elevated chance of extinction. Thus, if this occurred at a higher forest cover for the scenario of maximum fragmentation, then fragmentation leads to a higher extinction threshold, as predicted by the hypothesis. This was the case for the three species negatively affected by fragmentation. For both Western capercaillie and Eurasian pygmy-owl, the first overlap with the critical probability of 0.5 occurred at a forest cover of 45% under maximum fragmentation, and at 35% under minimum fragmentation (see Fig. 3a & c), whereas, for Hazel grouse, the 0.5 probability was first found at a forest cover of 35% and 25% for maximum and minimum fragmentation, respectively (Fig. 3b). Additionally, if we compare both fragmentation scenarios, the distance between the confidence intervals of their corresponding curves is generally higher for the two grouse (see Fig. 3a & b) than for Eurasian pygmy-owl, in which intervals overlapped at all instances, and only in two occasions the overlap did not include the mean occurrence probability values (i.e. at PFC levels of 45% and 35%, see Fig. 3c). This indicates that significant differences only occurred at these forest cover levels for this species. Overall, these results indicate that although the extinction threshold hypothesis was supported for three species, support was stronger for the two grouse than for Eurasian pygmy-owl, consistent with the weaker negative sensitivity to fragmentation detected for the latter.

The results for the remaining species were also consistent with the sensitivity analysis. Tengmalm's owl, Ural owl and Three toed woodpecker had no significantly different occurrence probabilities between the scenarios of maximum and minimum fragmentation at any forest cover level (Fig. 3d–f), consistent with their neutral sensitivity to fragmentation. For the Black woodpecker, we found the converse response to that predicted by the hypothesis

(Fig. 3g). Again, Black woodpecker probably benefits from fragmentation, particularly where the amount of forest habitat is moderate to low.

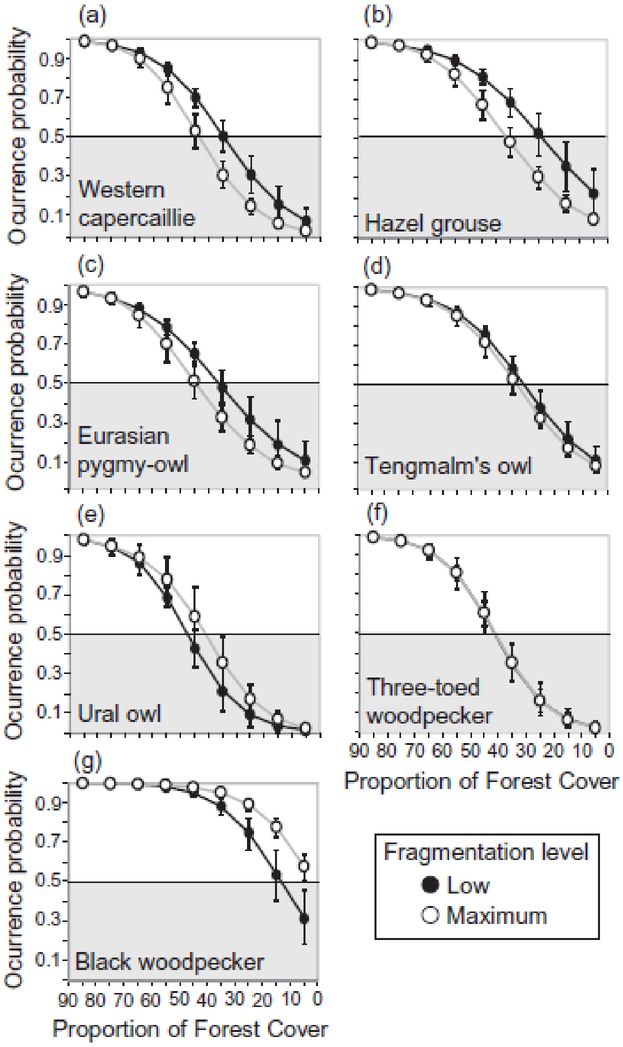


Figure 3: Occurrence probabilities of the seven forest-specialist birds (a–g) averaged over nine values of forest cover (from 5% to 85%) under the two scenarios of forest fragmentation, low (in black) and maximum (in white) (see Methods). Bars represent 95% confidence intervals. Note that proportion of forest cover decreases to the right.

Our second test compared both fragmentation scenarios looking for the PFC value at which the lower inflection point of the logistic curve is reached, which was assumed to correspond with the extinction threshold. Consistent with the previous results, this threshold was significantly higher for maximum fragmentation for the two grouse and Eurasian pygmy-owl (Fig. 4a–c), whereas no differences were found for Tengmalm's owl, Ural owl and Three-toed woodpecker (Fig. 4d–f). For Black woodpecker the test was uninformative, as the lower inflection point of its logistic curves was below meaningful PFC values (i.e. < 0%).With the exception of this species, occurrence probabilities at the extinction threshold did not differ across species and scenarios, P(j, PFC, rLPS)~0.2 in all cases (see Fig. 4), indicating that the results are not artefacts generated by the method.

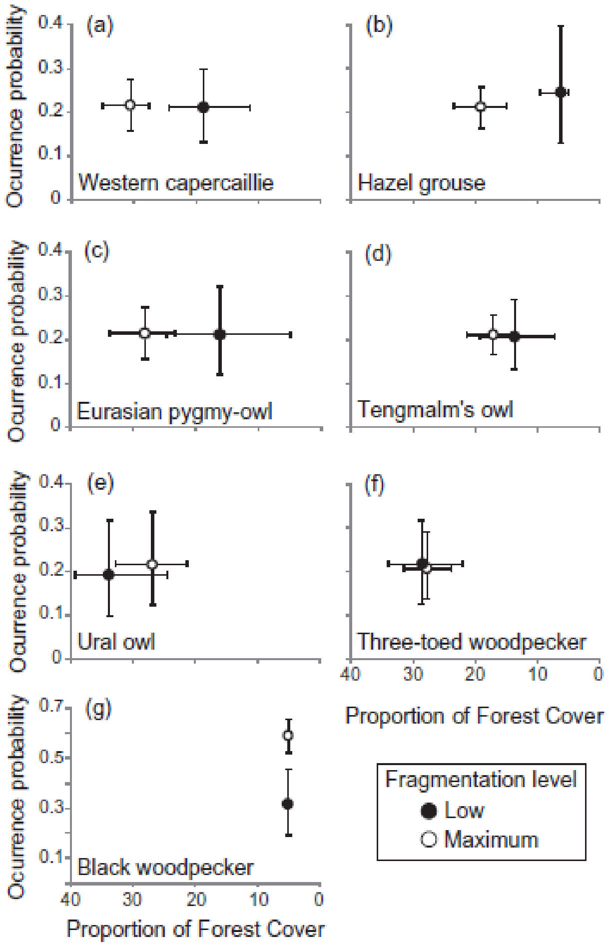


Figure 4: PFC extinction thresholds for the seven forest-specialist birds (a–g) under low (black) and maximum (white) fragmentation scenarios. Each extinction threshold reflects the PFC value coinciding with the lower inflection point of its corresponding logistic curve (i.e. that at which the second derivative of the curve is maximal). Bars are for 95% confidence intervals for extinction thresholds (horizontal) and occurrence probabilities at each threshold (vertical). Significantly different extinction thresholds between both fragmentation scenarios are indicated by lack of overlap in the horizontal direction, whereas similar extinction probabilities in both cases are indicated by overlaps in the vertical direction. Note that because no lower inflection point was found for any of the logistic curves of the Black woodpecker within the range of meaningful PFC values (>= 0%), points in panel (g) do not reflect extinction thresholds, but occurrence probabilities at 5% PFC.

Discussion

A long-standing tenet of fragmentation theory is that extinction thresholds occur earlier in the habitat loss gradient if habitat contraction takes place in concert with its fragmentation. This has received much attention due to its implications for biodiversity conservation. But debate about the validity of this hypothesis continues, fueled by empirical results that have been interpreted as discrediting it. For the seven bird species that can be categorized as forest specialists, we found, as expected, that forest contraction has negative effects on the occurrence probability of all of them. However, we also found that responses to fragmentation vary across species. This might reflect to some extent that, instead of defining and measuring habitat characteristics taking into account the specific needs of each species (a difficult task, particularly in broad scale studies), we used a general definition of habitat for all species (forests), which is common practice in fragmentation studies. Irrespective, we cannot conclude that the lack of conformity with the extinction threshold hypothesis of each species means that the hypothesis is incorrect. Rather, we can ask what aspects of the species biology influence the outcomes under the study constraints.

Two forest-specialist herbivores, Western capercaillie, the world's largest grouse, and Hazel grouse, were negatively affected by fragmentation and supported the extinction threshold (see Figs 3 & 4). Both species are widely accepted as being severely impacted by forest fragmentation (Storch, 1991; Saari et al., 1998), which can be directly related with several species-specific traits that predispose them to be vulnerable in fragmented habitats; they are sedentary, territorial habitat specialists that require extensive home ranges and have low dispersal ability (Åberg et al., 2000; Pakkala et al., 2003).

For the three owls, negative effects of forest fragmentation and support for the extinction threshold hypothesis were found for Eurasian pygmy-owl but not for Tengmalm's owl and Ural owl (see Figs 2–4). In this case, neither low dispersal ability nor habitat specialization seem to be behind the Eurasian pygmy-owl's sensitivity to fragmentation; females and juveniles of this species (and also Tengmalm's owl) can migrate up to 600 km – a behavior not observed in Ural owls (Lehikoinen et al., 2011) – and the Eurasian pygmy-owl can be classified as a generalist forager (Kullberg, 1995). A more likely explanation relates to indirect effects of fragmentation through alteration of inter-specific interactions. Due to its smaller size (c. 60 g), Eurasian pygmy-owls are preyed upon by a number of larger predators, including the other two owls (Mikkola, 1983). This has been thought to explain the affinity of this species for mature forests, as cleared and fragmented forests increase its exposure to predators (Strøm & Sonerud, 2001), and in turn could explain the support we found in Eurasian pygmy-owl to the extinction threshold hypothesis.

Positive effects of forest fragmentation were detected for the Black woodpecker, whereas the Three-toed woodpecker had a neutral response (see Figs 2–4). Although both are found in mature forests (Cramp, 1985), the more specialized Three-toed woodpecker is limited by the availability of conifer bark beetles (Fayt, 2006), and can suffer from intensive forest management (Angelstam & Mikusin´ ski, 1994). In contrast, the weakly territorial Black woodpecker has high dispersal capability, a broader diet and may use a wide spectrum of forest habitats, which makes this species more of a forest generalist (Mikusin´ ski, 1995). Moreover, lower predation pressure on this species in cutover and open forests compared with old forest stands (Rolstad et al., 2000), and an increase of the density and diversity of invertebrates in forest edges (Peltonen & Heliövaara, 1998) can influence the persistence of Black woodpecker in fragmented forests (Tjernberg et al., 1993). This may also explain why forest fragmentation only increased the occurrence probability of Black woodpecker at relatively low forest cover levels (<= 35%; see Figure 3g).

Thus, species' biology coupled with our results suggest that dispersal ability, degree of specialization (in resource and/or habitat use) and sensitivity to interspecific interactions may be key determinants of species' reactions to fragmentation (see Angelstam, 1992; Andrén, 1995; Hanski, 1995). The importance of these traits also suggests that, even though habitat needs are expected to differ across species (Lindenmayer & Fischer, 2006), there exist common'themes' (sensu Lawton, 1992, 337) or 'interdependences' (*sensu* Didham et al., 2012) in species' responses to fragmentation, which can be used to identify potentially sensitive species in conservation.

Didham et al. (2012) also proposed a type of interdependency, to refer to the entanglement of habitat loss and fragmentation and emphasizing that fragmentation is most often a consequence of habitat reduction. Although following Fahrig's (2003) suggestions, we devised a technique to measure species sensitivities to one process separately from the other (see Fig. 2), finding that fragmentation effects that only occur within particular forest cover ranges (see Fig. 3) are consistent with Didham et al.'s (2012) propositions. This can be explained by the observation that not all fragmentation levels are possible for any amount of forest cover, with greater cover allowing only low to moderate fragmentation (see Fig. 1). This should be taken into account in future tests of the extinction threshold hypothesis, and more generally in studies examining fragmentation effects.

Our study has potential limitations that may have led to underestimating forest amount and, specially, fragmentation effects. Firstly, our database comprised species presence/absence data, and potential effects on population density could not be investigated. Secondly, the coarse resolution of our species occurrence data (~50 km) precluded matching spatially each species' presence with a particular type of forest (i.e. broadleaf, conifer or mixed forests) and, hence, we could not conduct separate tests for different forest types, which might have obscured the signals found in some cases (e.g. for the Three-toed woodpecker, as this occurs primarily in coniferous forests). And thirdly, although we were able to differentiate between less and more fragmented cells by using a single fragmentation metric (rLPS), this could not capture all spatial subtleties of the configuration of habitat patches (e.g. number, size, physical connectivity or inter-patch distances) that might affect species' occurrences (see Montoya et al., 2010). Thus, our analysis should be viewed as a conservative test of fragmentation effects. These limitations may also account for the fact that we obtained robust models for only 7 out of 17 bird species initially investigated, and leave open the possibility that future, finer datasets will detect stronger reactions to fragmentation, even for those species that appeared to be insensitive to it in the present analysis.

To conclude, although we followed common practice when dealing with real world conservation issues and have used a habitat proxy, we detected broad-scale, fragmentation-driven, increased extinction thresholds in three out of seven European forest specialist birds, much in line with what has been proposed by theory. Although our results have emphasized the primary importance of habitat amount per se effects on species persistence, they also highlight that there is a risk in neglecting fragmentation, at least for some species. Sensitive species are likely characterized by low dispersal ability, specialization in resources/habitat characteristics and/or elevated sensitivity to interspecific interactions. This is an important message for future tests of fragmentation theory.

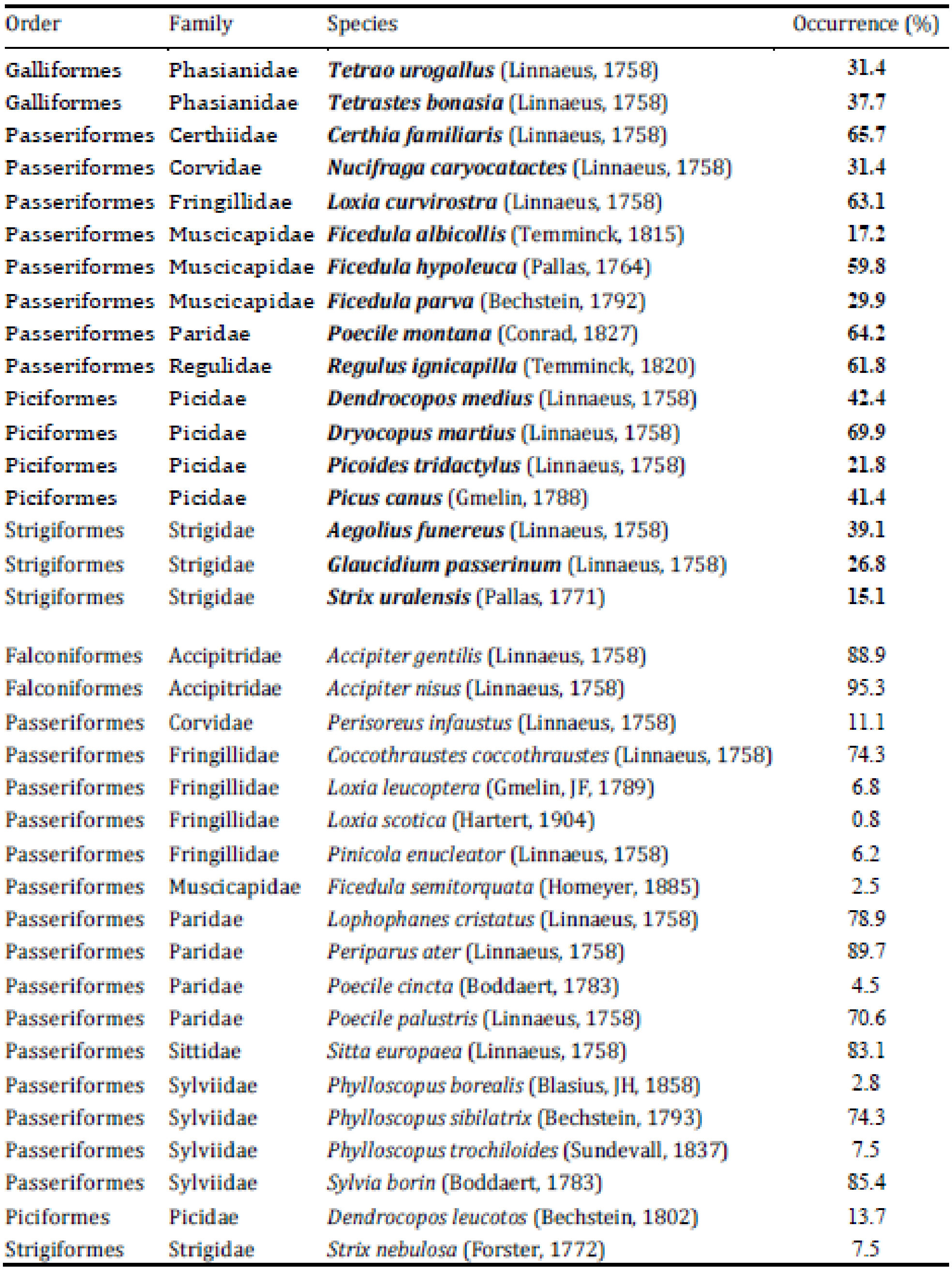
Conclusions

Although forest amount is of primary importance for the persistence of forest specialist birds, fragmentation is also relevant for some, and neglecting forest fragmentation would be a mistake for these species. Species specific traits can be helpful for interpreting species' reactions to fragmentation, and it should not be assumed that it always, or never, matters.

Supplementary material

Figure S1: Map of the survey area showing the 1341 grid cells used as our analysis units.

Figure S2: List of the 35 European bird species that nest and feed primarily within forest habitats (forest specialists) and occur in any of the 1341 cells used for analysis. The first 17 species (in bold) occurred between 15 and 70% of the cells and were selected for the study.



Order	Family	Species	Occurrence (%)
Galliformes	**Phasianidae**	***Tetrao urogallus*** **(Linnaeus, 1758)**	**31.4**
Galliformes	**Phasianidae**	***Tetrastes bonasia*** **(Linnaeus, 1758)**	**37.7**
Passeriformes	**Certhiidae**	***Certhia familiaris*** **(Linnaeus, 1758)**	**65.7**
Passeriformes	**Corvidae**	***Nucifraga caryocatactes*** **(Linnaeus, 1758)**	**31.4**
Passeriformes	**Fringillidae**	***Loxia curvirostra*** **(Linnaeus, 1758)**	**63.1**
Passeriformes	**Muscicapidae**	***Ficedula albicollis*** **(Temminck, 1815)**	**17.2**
Passeriformes	**Muscicapidae**	***Ficedula hypoleuca*** **(Pallas, 1764)**	**59.8**
Passeriformes	**Muscicapidae**	***Ficedula parva*** **(Bechstein, 1792)**	**29.9**
Passeriformes	**Paridae**	***Poecile montana*** **(Conrad, 1827)**	**64.2**
Passeriformes	**Regulidae**	***Regulus ignicapilla*** **(Temminck, 1820)**	**61.8**
Piciformes	**Picidae**	***Dendrocopos medius*** **(Linnaeus, 1758)**	**42.4**
Piciformes	**Picidae**	***Dryocopus martius*** **(Linnaeus, 1758)**	**69.9**
Piciformes	**Picidae**	***Picoides tridactylus*** **(Linnaeus, 1758)**	**21.8**
Piciformes	**Picidae**	***Picus canus*** **(Gmelin, 1788)**	**41.4**
Strigiformes	**Strigidae**	***Aegolius funereus*** **(Linnaeus, 1758)**	**39.1**
Strigiformes	**Strigidae**	***Glaucidium passerinum*** **(Linnaeus, 1758)**	**26.8**
Strigiformes	**Strigidae**	***Strix uralensis*** **(Pallas, 1771)**	**15.1**
Falconiformes	Accipitridae	*Accipiter gentilis* (Linnaeus, 1758)	88.9
Falconiformes	Accipitridae	*Accipiter nisus* (Linnaeus, 1758)	95.3
Passeriformes	Corvidae	*Perisoreus infaustus* (Linnaeus, 1758)	11.1
Passeriformes	Fringillidae	*Coccothraustes coccothraustes* (Linnaeus, 1758)	74.3
Passeriformes	Fringillidae	*Loxia leucoptera* (Gmelin, JF, 1789)	6.8
Passeriformes	Fringillidae	*Loxia scotica* (Hartert, 1904)	0.8
Passeriformes	Fringillidae	*Pinicola enucleator* (Linnaeus, 1758)	6.2
Passeriformes	Muscicapidae	*Ficedula semitorquata* (Homeyer, 1885)	2.5
Passeriformes	Paridae	*Lophophanes cristatus* (Linnaeus, 1758)	78.9
Passeriformes	Paridae	*Periparus ater* (Linnaeus, 1758)	89.7
Passeriformes	Paridae	*Poecile cincta* (Boddaert, 1783)	4.5
Passeriformes	Paridae	*Poecile palustris* (Linnaeus, 1758)	70.6
Passeriformes	Sittidae	*Sitta europaea* (Linnaeus, 1758)	83.1
Passeriformes	Sylviidae	*Phylloscopus borealis* (Blasius, JH, 1858)	2.8
Passeriformes	Sylviidae	*Phylloscopus sibilatrix* (Bechstein, 1793)	74.3
Passeriformes	Sylviidae	*Phylloscopus trochiloides* (Sundevall, 1837)	7.5
Passeriformes	Sylviidae	*Sylvia borin* (Boddaert, 1783)	85.4
Piciformes	Picidae	*Dendrocopos leucotos* (Bechstein, 1802)	13.7
Strigiformes	Strigidae	*Strix nebulosa* (Forster, 1772)	7.5

Figure S3: Forest fragmentation (*rLPS*) as a function of the proportion of forested area (*PFC*) in 2061, 50 x 50 km cells covering all continental Europe and Great Britain (i.e. all the area shown in appendix S1 map). The data were extracted from the global forest cover database by Defries *et al*. (2000), which has a lower resolution (pixel size is of 1000-m) than CORINE Land Cover (i.e. the database we used for analyzing bird responses to forest cover and fragmentation; see Methods), but a global coverage. This allowed us to explore relationships between *rLPS* and *PFC* without excluding any European country (note that Norway and Serbia were not covered by CORINE Land Cover) and, as can be seen in the figure, confirm that cells with near zero fragmentation (see upper solid line indicating *rLPS* ≈100%) occur at all levels of *PFC* within our study region. Note that *PFC* decreases to the right.

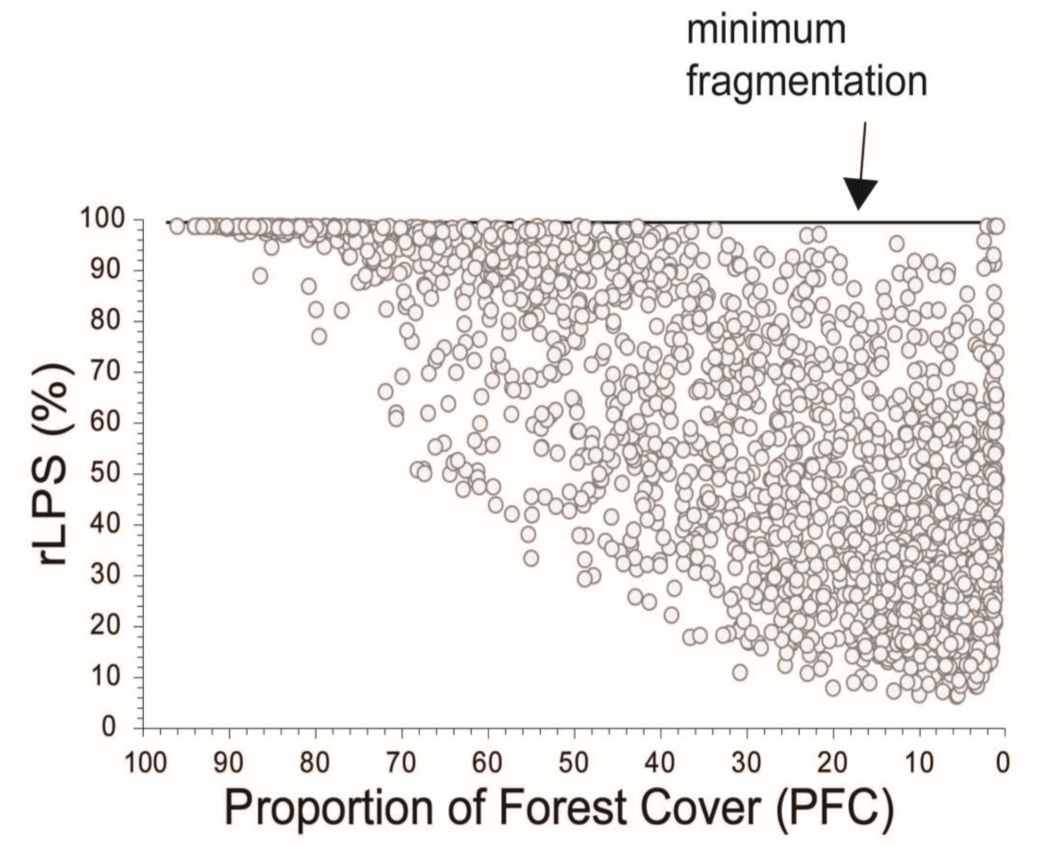
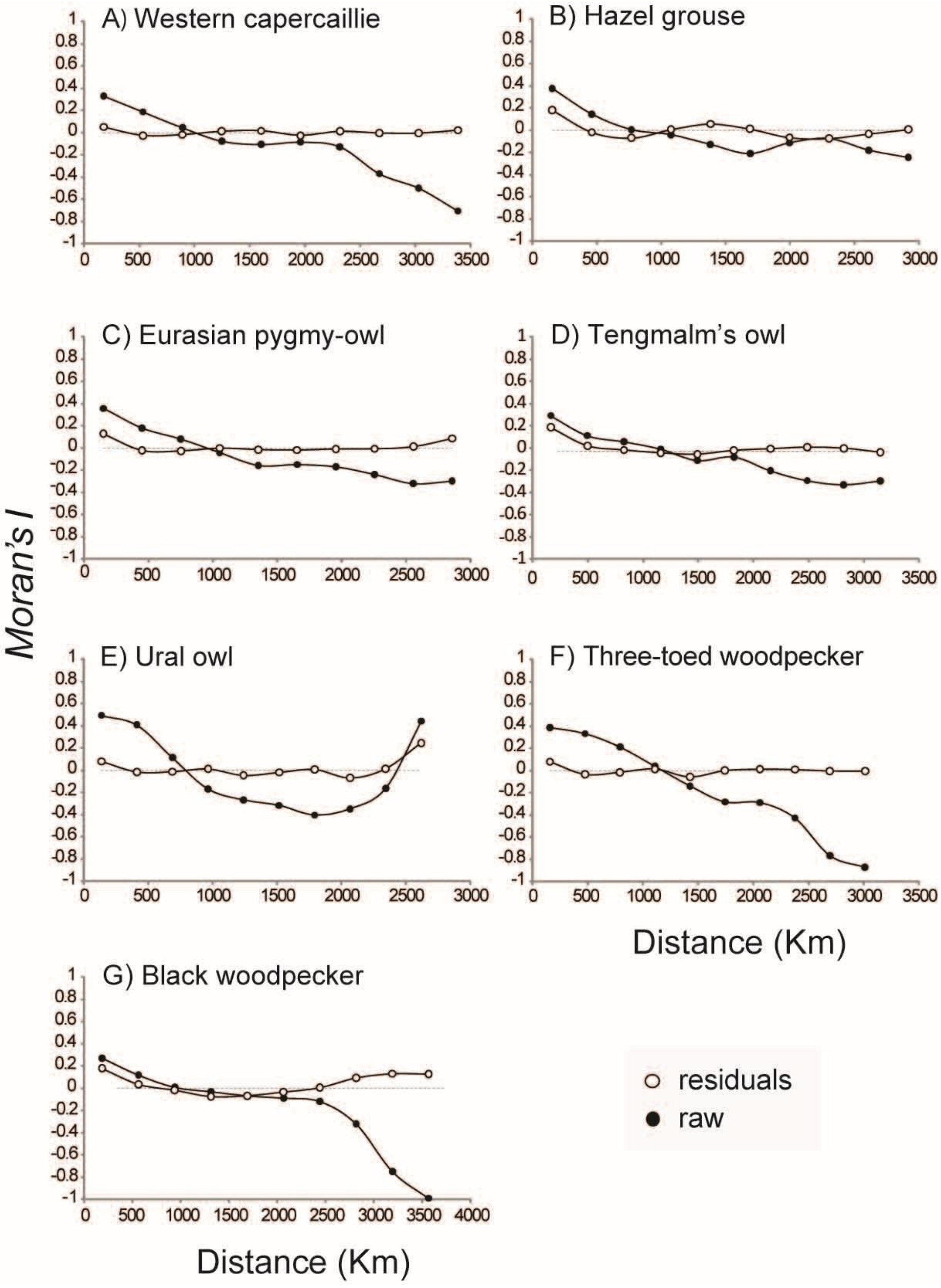


Figure S4: Spatial correlograms for the seven species selected for modelling.



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CAPÍTULO 5

CAN FOREST FRAGMENTATION IMPACT CLIMATE CHANGE?

A GLOBAL ASSESSMENT

Resumen

Objetivo: Aproximadamente una cuarta parte del total de las emisiones de gases de efecto invernadero de origen antrópico son debidas a la deforestación. Sin embargo, la contribución de los procesos derivados de la misma, tales como la configuración espacial de los remanentes de hábitat, no han sido cuantificados en la mayoría de los casos. Aquí lo hacemos, documentando las relaciones de la altura de los árboles y el secuestro de carbono con la cantidad de bosque y la fragmentación a nivel global.

Localización: Global

Métodos: Para determinar la contribución de la fragmentación, la cantidad de hábitat y el clima en la variación de la altura media de los árboles y el secuestro de carbono, utilizamos modelos de regresión lineal (OLS). Además, se tuvo en cuenta la autocorrelación espacial, mediante el uso de modelos autorregresivos, ajustados para cada variable respuesta (altura media de los árboles y secuestro de carbono) y unidad de vegetación. Por último, para establecer las relaciones causales entre variables ajustamos modelos de ecuaciones estructurales o *path analysis*.

Resultados: El clima, sumado a la cantidad de hábitat y su grado de fragmentación, explican dos tercios (66.8%) de la variación en la altura media los árboles. La fragmentación explicó el -29.41% (-20.62% debido al efecto borde), la cantidad de bosque el 11.79% y el clima el 18.07%. El modelo para el secuestro de carbono explicó el 74.6 % de la varianza. En este modelo la altura media de los árboles y el clima explicaron el 32.25 % y el 29.79 % de las variaciones en el secuestro de carbono respectivamente. Fragmentación y cantidad de bosque contribuyeron a la altura de los árboles un 9.5% y un 3.8% respectivamente. La

relación entre la fragmentación y el secuestro de carbono fue indirecta, a través de sus efectos sobre la altura de los árboles, mediada principalmente por el efecto borde.

Conclusiones principales: La configuración especial de los remanentes de bosque resultante tras la deforestación es un factor mucho más importante que la pérdida de hábitat per se en la determinación de la altura de los árboles y el secuestro de carbono, debido a la importante influencia negativa del efecto borde. Dada la rápida tasa de fragmentación forestal en los trópicos, tales emisiones pueden exacerbar fuertemente los efectos del calentamiento global mucho más allá de los causados por la tala de bosques *per se*. Planear claras estrategias para minimizar los bordes de hábitat en paisajes manejados reducirá considerablemente las emisiones de gases de efecto invernadero.

Abstract

Aim: About a quarter of total anthropogenic emissions are due to worldwide deforestation. However, the contribution of derivative processes therefrom, such as forest remnants configuration, has not been quantified in most cases. Here, do so by documenting the relationships of tree height and carbon storage with forest amount and fragmentation at global level.

Location: Global

Methods: To determine the contribution of fragmentation, forest amount and climate to variation in mean tree height and carbon storage, we computed ordinary least square (OLS) linear multiple partial regression. To account for spatial autocorrelation we calculated a pure autoregressive model for each response variable (mean tree height and carbon storage) and vegetation unit. To know the causal relationships between variables we made a path analysis.

Results: Mean tree height multiple partial regression model explained 66.8 % of the variance. Fragmentation explained the -29.41 % (-20.62 % due to edge effects), forest amount the 11.79 % and climate the 18.07 %; Carbon storage model explained 74.6 % of the variance. In this model mean tree height and climate explained 32.25% and 29.78% of carbon storage variations. Fragmentation and forest amount contribution through tree height was 9.5 % and 3.8 % respectively. Relationship between fragmentation and carbon storage was indirect through its effects on tree height, mediated principally by edge effects.

Main conclusions: The resulting spatial configuration of forest remnants after deforestation is a much more important factor than habitat loss per se to determine tree height and carbon sequestration, due to the important negative

influence of edge effects. Given the rapid rate of forest fragmentation in the tropics such emissions may exacerbate strongly the effects of global warming above and beyond that caused by forest clearing *per se*. Planning clearing strategies to minimize habitat edges in managed landscapes will reduce considerably greenhouse gas emissions.

Introduction

The proportion of carbon stored in forests comprises 70–80% of total terrestrial carbon (Baccini et al., 2012). Tropical forest account for 50% of the carbon stored in the global vegetation (350-600 Gt), rivalling the amount of carbon in the atmosphere (750 Gt) (Brinck et al., 2017). When forests are cleared, carbon stored in them is released to the atmosphere (Baccini et al., 2012), being the largest source of CO2 emissions (about a quarter of total anthropogenic emissions, contributing roughly 1,1 Gt annually) (Brinck et al., 2017).

Most estimates of carbon flux are based solely on deforestation (Laurance et al., 1998; Morton, 2016; Mitchard, 2018). The additional or complementary contribution to carbon fluxes of other processes associated to deforestation such as forest fragmentation and the subsequent spatial configuration of forest remnants, have received much less attention, particularly in extratropical forests (see Brink et al., 2017). Biomass tends to decline in forest fragments, especially towards the edges of the fragments, due to higher wind exposure and border effects leading to higher mortality and biomass loss (Brinck et al. 2017). Thus, emissions of CO_2 and other greenhouse gases are determined not only by the deforestation level, but also by the spatial pattern of clearing and remnant forest (Laurance et al., 1998). It stems that metrics of spatial fragmentation such as, the amount and shape of edges, the number, size and shape of the patches, or the isolation of such patches should be able to inform carbon storage and carbon emissions. If so, it should be possible to quantify the contribution of fragmentation to warming gas emissions and, ultimately, to climate change.

As an example of research concerned with the effects of fragmentation on greenhouse gas emissions, Laurance et al. (1997) demonstrated in their experiment in Amazonian forest fragments, that forest remnants lose substantial aboveground biomass. This would be due to elevated rates of tree mortality and damage in fragments, as a result of microclimatic changes and increased wind turbulence near forest edges (Kapos, 1989; Ferreira & Laurance, 1997). In a subsequent simulation model (Laurance et al., 1998), they reported that the importance of considering fragmentation might range between 1-7% of flux carbon estimates and estimated that biomass loss around forest edges could generate up to 150 million tons of carbon emissions annually. More recently, Brinck et al. (2017) quantified the contribution of fragmentation to carbon release to the atmosphere as 0.34 Gt per year, or 31% of the annual releases due to tropical deforestation. These works support an effect of forest fragmentation on carbon emissions. Yet, wider-focus studies outside the tropics and using more comprehensive descriptions of forest fragmentation are lacking.

There are multiple mechanisms able to explain why biomass would be lost with increased permeability to external factors derived from increased edges of forest remnants. Examples include: damage to vegetation, tree mortality, appearance of fast-growing pioneer species, microclimatic stress and increased vulnerability to fire and alterations of herbivore density, all bearing direct relation with the amount of tree biomass (Laurance, 2008; Laurance, 1998). However, measuring the above aspects might be cumbersome or even not feasible at macroecological scales, particularly when biotic interactions are involved (Morales-Castilla et al. 2015). In this respect, some authors reported the direct and positive relationship between tree height and aboveground biomass (Saatchi et al., 2011; Lefsky et al., 2010; Drake et al., 2002), which accounts for 70–90% of forest biomass carbon (Long et al., 2001). Hence, tree height would be a good predictor of the forest biomass carbon stock at macroecological scales. Besides, tree height has also been regarded to as an important predictor of primary productivity and biodiversity (Goetz et al., 2007), due to the niche differentiation derived from large strata variation (Orians, 1969; Terborgh & Weske, 1969; Marra & Remsen, 1997). So, tree height alterations can have an important effect on carbon sequestration, but also on other important processes and properties of ecosystems.

In this work, we conduct a global scale study of the relationships of tree height and carbon storage with forest amount and, specially, forest fragmentation. Our working hypothesis is that tree height can be negatively affected by forest fragmentation, and more specifically by edge effects. The reasons why involve five potential mechanisms: 1) microclimatic stresses such as desiccation or sunlight excess which can decrease growth 2) appearance of competitors able to grow faster than native species lower in the canopy; 3) emergence of structural parasites that can lead to reduced tree growth; 4) tree damages due to wind and air circulation that would reduce tree growth effectiveness; and 5) decrease of net primary productivity due to increased herbivore density (Laurance et al., 1997; Kapos, 1989; Ferreira & Laurance, 1997; Londré et al. 2006). If fragmentation and forest cover amount did have a measurable effect on biomass (Laurance & Delamonica, 1998; Laurance & Curran, 2008; Brinck et al., 2017), they can be expected to also have an indirect effect on carbon sequestration, which could be estimated through tree height as a proxy. Beyond fragmentation and forest cover, the geographical variation of aboveground biomass also depends on key factors for tree growth such as climate, soil and topographical space (Baccini, 2012; Myneni et al., 2007; Rennó et al., 2008). Thus, we also estimate the magnitude of the combined direct and indirect effects of potentially relevant predictors associated with these factors. Our findings suggest that fragmentation has an important and negative effect on tree height and, consequently, an important indirect negative effect on carbon fixation.

Methods

Forest cover, tree height and carbon storage data

We used a global raster of forest cover generated from remote sensing data (Defries et al., 2000), with a resolution of 1 km². Following Hansen & Sohlberg (2000), we considered as forest only those pixels with forest cover ≥ 40%, and subsequently we processed the raster by superimposing it to an equal area global grid, composed of 42.014 cells of 50 x 50 km. To measure fragmentation metrics, we used the Patch Analyst tool software (Rempel et al., 2012) implemented in ArcGIS (ESRI, 2009). We quantified the Proportion of Forest Cover (PFC hereafter), the proportion of this percentage occurring in the largest patch (i.e. rLPS) within each grid cell (i.e. analysis unit) (see Bascompte & Solé, 1996; Montoya et al., 2010; Ferrero et al. unpublished data), edge density (ED), double log fractal dimension (DLFD), mean neighbor distance (MNN) and the number of patches (NumP).

Mean tree height was obtained from the tree height raster by Simmard et al. (2011) at a resolution of 1 km² (see figure 1 supplementary material), and the carbon storage from the carbon storage dataset by Ruesch et al. (2008), also at a 1 km² resolution (see figure 2 supplementary material). The carbon data set presents estimates of above- and below-ground (root) biomass, and was the first to apply consistently the IPCC Good Practice Guidance (Penman et al., 2003) to the whole terrestrial surface. These variables were again superimposed against our 50-km² equal area global grid and processed for each grid cell.

Climate and soil data

We downloaded all 19 bioclimatic variables from the Worldclim database (Hijmans et al., 2005), 10 soil variables from the Harmonized World Soil Database v1.2 (HWSD, FAO/IIASA/ISRIC/ISSCAS/JRC, 2012), as well as additional variables important to tree growth (Svenning et al., 2010; Slik et al., 2013) such as, growing degree days (New et al., 1999), water balance (WBAL), mean annual potential evapotranspiration (PET), and actual evapotranspiration (AET) (see Table 1 for more information on data source).

Table 1: Data sources for bioclimatic and soil variables.

Variables	Data source
Biolimatic variables (BIO1-BIO9)	Bioclim (1950-2000) http://www.worldclim.org/bioclim
Growing degree days (GDD)	University of Wisconsin (Madison). Nelson Institute for Environmental Studies (data: 1961-1990) http://www.sage.wisc.edu/atlas/maps.php?datasetid=31&includerelatedlinks=1&dataset=31
Water balance (WBAL)	EDIT GEOPLATAFORM (MNCN-CSIC) (data: 1920-1980). EDIT: http://edit.csic.es/Climate.html Data sets were developed by AHN Chung-Hyun and Ryutaro TATEISHI (Remote Sensing and Image Research Center, Chiba University) and downloaded from Global Resource Information Database - United Nations Environment Programme (UNEP/GRID).
Mean annual potential evapotranspiration (PET), Actual evapotranspiration (AET)	CGIAR-CSI. CONSORTIUM FOR SPATIAL INFORMATION http://www.cgiar-csi.org/data
% Sand, % Gravel, pH, CEC.	Harmonized World Soil Database v1.2 (HWSD) (FAO-IIASA/ISRIC-ISSCAS/JRC) (2012) http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/HWSD_Data.html?sb=4

All variables were processed and extracted for the 50x50 km grid following the above-mentioned procedure. To reduce the number and co-linearity amongst variables, we ran two principal components analyses (PCA) (StatSoft Inc., 2007), one including the climate data and the other the soil data. We retained the PCA axes with eigenvalues larger than 1, resulting in four climate and four soil related axes. The four climate and four soil axes explained 92.97% and 68.62% of data variability, respectively. Out of these eight PCA axes we selected the ones with the highest loadings—i.e. with higher correlations with the climatic and soil variables, namely, $r > 0.90$ and $r > 0.65$, respectively—for further analyses. This resulted in including in our models the following climatic and soil variables: Precipitation of the wettest month (WMP), minimum temperature of the coldest month (CMMT), water balance (WBAL), mean temperature of driest quarter (DQMT), cation exchange capacity (CEC), pH, % of sand and % of gravel. Although it would be possible to work with PCA axes directly, it was easier to interpret the original variables and, because of the very high correlation between these variables and PCA axes, the results were qualitatively the same.

Statistical analysis

To determine the association of global variation in mean tree height with fragmentation, climate and soil variables we computed an Ordinary Least Square (OLS) partial regression model using three sets of predictor variables—i.e. fragmentation and forest cover, climate, and soil variables. Prior to fitting partial OLS models, we tested whether univariate relationships between the response variables and each of the predictors met the assumptions for regression analysis, making the appropriate transformations—e.g. log-transformation—when necessary. The results of linear partial regressions informed of rather weak associations (adj-R^2 ≥0.047) with soil variables, DQMT, and DLFD, so these predictors were excluded from the models. Then, we fitted a second partial regression model to determine the contribution of mean tree height and climate variables to global variation in carbon storage. Additionally, although variation partitioning is, in itself, an explicit way of evaluating colinear effects among explanatory variables, we also computed the variation inflation factor (VIF) associated to each predictor (or meaningful combination of predictors) as a complementary check. As a rule of thumb, VIFs > 5 are considered too high to trust p-values and advise to focus interpretations on e.g. amounts of variance explained the regression's coefficients of determination.

To account for spatial autocorrelation in our OLS models, we first fitted an autoregressive model for each response variable and each vegetation unit (Olson et al., 2001). This autoregressive model takes the form:

$$Y = \rho Wy + e \tag{eq. 1}$$

Where, W is the pairwise matrix of spatial weighting among grid cells, and ρ is the autoregressive coefficient. The estimated values of the response variables estimated by the autoregressive model (ρWy, spatial filter hereafter) were then added as a predictor variable in the partial regression model. This procedure allows to correct for the effects of spatial autocorrelation while comparing how autocorrelation would affect the direction, strength and significance of the OLS regression coefficients without spatial filter (Hawkins et al. 2007; Diniz-Filho et al. 2003). Statistical modelling was conducted in R (R Core Team, 2020), and autoregressive models were fitted in SAM v.4.0. (Rangel et al. 2010).

Causal structure among variables

We are mainly interested in unveiling potential independent effects of fragmentation and forest amount on carbon fixation. In order to simplify and optimize the model, we previously performed a partial regression model with fragmentation variables as predictors, first using tree height and then using carbon storage as a response variable. The results showed that LnED was the variable with the highest R^2, while the contributions of NumP, MNN and LPI were non-significant. Thus, we chose LnED as our proxy for fragmentation in the subsequent analysis. The underlying assumption is the existence of a direct effect of fragmentation on carbon fixation mediated by edge effects. Our hypothesis is that in fragment edges there is a strong exposure to external environmental factors such as microclimatic changes, wind turbulence or fire, which elevate tree mortality rates and tree damages, producing a substantial loss of aboveground biomass (Laurance et al., 1997; Laurance et al., 1998; Kapos, 1989; Ferreira & Laurance, 1997). We also hypothesize that the most important effect of fragmentation on carbon storage would be indirect rather than direct, mediated through alterations in tree growth, probably through five possible mechanisms. First, through microclimatic stress such as desiccation or sunlight excess which can decrease growth. Second, through the emergence of fast-growing pioneer species, with maximum growth under the canopy than forest native species, and thus, with lower ability to store carbon (Laurance et al., 2008). Third, through the emergence of structural parasites that would affect tree fitness and reduce tree growth (Nenzen et al. 2017). Fourth, through tree damage due to wind and air circulation that reduce tree growth effectiveness. And fifth, as a consequence of increased levels of herbivore density derived from the loss of large predators in small fragments, resulting in a decrease of growth and net primary productivity.

Meanwhile, we consider that PFC would have a direct effect on carbon storage because biomass increases with increasing forest amount, and carbon storage increases with increasing biomass. Decrease in forest amount is often accompanied by forest fragmentation (Ferrero et al. umpublished data; Fahrig, 2017; Hanski, 1995) so that carbon storage could also be affected through this indirect route. In addition, areas with the highest amount of forest frequently correspond to old and mature well-conserved forests, with taller trees, probably due to the presence of a greater quantity of intact forest. This could be a third pathway for direct effects of forest amount on carbon storage.

While others factors such as soil or topography variation are known to condition the spatial variation of aboveground biomass (Baccini, 2012; Myneni et al., 2007; Rennó et al., 2008), these variables were discarded for our models due to their global weak associations with carbon storage. However, we did account for the direct contribution of climate on forest amount, tree height and carbon stock.

Partial regression techniques can inform about the relative contribution of explanatory variables to the model, but they do not allow establishing causal relationships between variables—i.e. quantifying direct and indirect effects of predictors on other predictors and on response variables. This information would be useful to determine the direct and indirect effects of predictors on each other and on the response variable, and can be approximated using a path analysis approach (Steiger, 1995; Mitchell, 1992) also known as structural equation modelling. This analysis, as multiple regression, quantifies partial correlations between independent variables and provides the percent of explained variance of the response variable by explanatory variables, and allows evaluating potential causal models of relations between variables. In our study case, we designed a path diagram to represent our hypothetical causal model assuming linear relationships among the explanatory variables (see Fig. 2). These included two variables of forest cover and fragmentation (i.e. PFC and LnED) and three climate predictors (water balance, precipitation and temperature) to model canopy height, and the same predictors plus canopy height (now being introduced as an extra explanatory variable) to model carbon fixation. After removing no significant relationships —i.e. with path coefficients lower than 0.1 – we calculated direct and indirect effects for each variable (Mitchell, 1992) using the Normed-Fit Index (NFI) goodness fit parameter to check model performance (Bentler & Bonnet, 1980).

Results

Partial regression models explained 66.8% of the variation in mean tree height at the global scale. Variation partitioning analyses showed that fragmentation together with forest amount explained a substantial amount of mean tree height variation (28.87%) independently of all other explanatory variables, whereas an additional 16.25% was explained along with climate, 6.88% along with our spatial filter, and 5.11% along with this filter plus climate (Fig 1a, Table 1 supplementary material). In contrast, the amounts of tree height variation independently explained by either climate or space were much lower (7.39% and 1.96%, respectively), thus suggesting secondary roles for them.

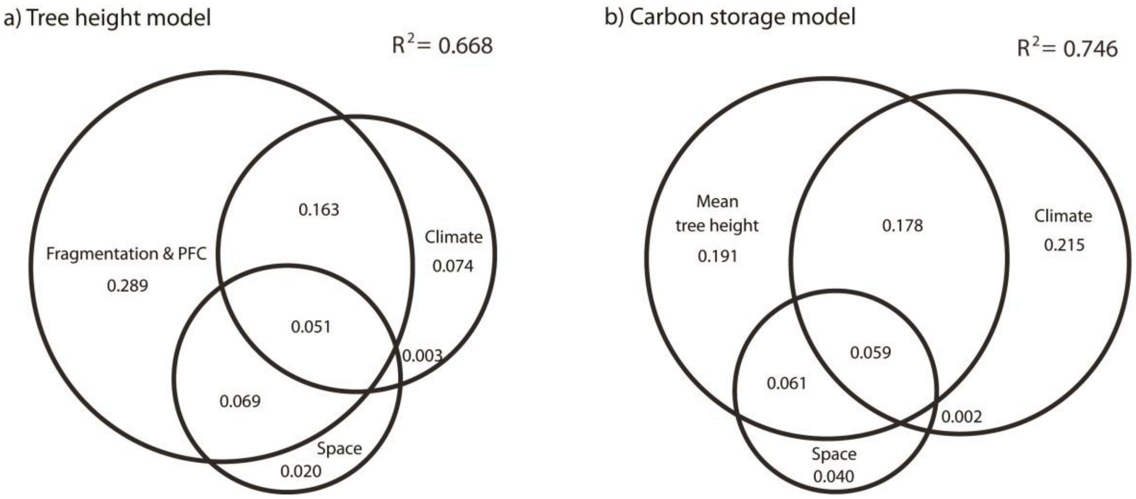

Figure 1: Venn diagrams for 3-way variation partitioning, for multiple regression OLS models using mean tree height (a) and carbon storage (b) as response variables. The tree height model shows the independent and shared contributions of fragmentation & PFC (proportion of forest cover), climate and space, which explained 66.8% of the total variation. The carbon storage model shows how mean tree height, climate and space explained up to 74.6% of its variation.

OLS regression coefficients ranked the fragmentation variable LnED as the first predictor of tree height, with which it was negatively associated, followed by forest cover (i.e. PFC) and water balance (WBAL), both with positive relationships (Table 2). Remarkably, LnED explained almost twice as much variation in tree height as PFC, and over twice the variation explained by all climatic variables together (Table 2). Looking at shared variable contributions to explaining tree height variation, fragmentation and PFC accounted for 41.20% of the total variation—i.e. with 29.41% attributed to fragmentation, and 11.79% to forest amount. The strong associations of fragmentation with tree height were largely due to edge effects (20.62%). Climate, explained 18.07% of the variation in tree height, and the spatial autoregressive predictor accounted for 7.55% of the variation in tree height—i.e. most of it, overlapped with what is already explained by fragmentation, forest amount, and climate. Altogether, these results confirm that forest cover and, specially, fragmentation play stronger roles than climate and unaccounted for spatial nuances in explaining the geographic variation of tree height, globally.

Table 2: Results of OLS model for mean tree height as a response variable, including standardized regression coefficients, their significance as well as variation partitioning indicating the variation explained by each predictor individually and shared with other predictors (model R^2adj= 0.668). Fragmentation was the most important variable to determine mean tree height, driven by the major contribution of edge density.

Variable	Std. coeff.	VIF	Std. Error	P-Value	Individual effect		Shared effect		Total effect	
Constant	0	0	0.293	<0.001	%	%	%	%	%	%
MNN	-0.01	1.284	<0.001	0.001	20.61	0.36	8.80	0.15	29.41	0.51
NumP	-0.079	1.722	0.002	<0.001		2.83		1.21		4.04
rLPS	-0.083	2.864	0.001	<0.001		2.67		1.27		3.94
LnED	-0.404	8.939	0.08	<0.001		14.45		6.17		20.62
PFC	0.231	8.377	0.002	<0.001	8.26	8.26	3.53	3.53	11.79	11.79
Wbal	0.279	1.169	<0.001	<0.001	7.39	5.82	10.68	8.56	18.07	14.38
T min	0.066	1.124	<0.001	<0.001		1.35		2.02		3.37
Precipitation	0.009	1.066	<0.001	0.002		0.19		0.28		0.47
Space	0.148	1.109	0.023	<0.001	1.96	1.96	5.59	5.59	7.55	7.55

Our model for carbon storage explained almost three quarters—i.e. 74.6%- of its variation (Fig. 1b, Table 2 supplementary material). Tree height and climate similarly contributed to explain carbon storage variation independently, 19.11% and 21.52%, respectively. The overlapped explained variation between these two variables was of 17.77%. The contribution of our proxy for spatial structure explained only 3.97% of the variation in carbon storage. According to OLS standardized regression coefficients, the most important predictors were mean tree height (β = 0.54; p-value ≤ 0.001) and the mean temperature of the coldest month (β = 0.47; p-value ≤ 0.001), both positively correlated with carbon storage (see Table 3).

Table 3: Results of variance partition model with carbon storage as a response variable (model r^2adj= 0.746).. The table shows the individual and shared contribution of each group of variables, the magnitude of effect of the each variable independently and the total effect of each. Mean tree height and climate were the most important variable to determine carbon storage, both with similar contribution. Fragmentation contributed on a 9.5 % to the carbon storage variations, being its effect 2.5 times bigger than forest amount effect (PFC).

Variable	Std. coeff.	VIF	Std. Error	P-Value	Individual effect		Shared effect		Total effect	
Constant	0	0	0.274	<0.001	%	%	%	%		%
Tree height	0.536	1.503	0.02	0	19.11		13.14		Frag.	9.49
									PFC	3.80
									Climate	5.83
									Space	2.43
									Unknown	10,71
Wbal	0.008	1.381	<0.001	0.004	21.52	0.35	8.26	0.13	Climate	0.48
T min	0.470	1.086	<0.001	<0.001		20.43		7.84		28.27
Precipitation	0.017	1.066	<0.001	<0.001		0.74		0.28		1.02
Space	0.209	1.098	0.170	<0.001	3.97		8.60		Space	12.57

These results indicate a balanced contribution of tree height and climate on carbon storage, since both predictors explain similar proportions—i.e. 32.25% and 29.78%, respectively—of carbon storage (Table 3). The indirect effects on carbon storage of other determinants—i.e. fragmentation, PFC, and climate—via their effects on tree height, suggest a major contribution of forest fragmentation, followed by climate and PFC—i.e. explaining 9.5%, 5.83% and 3.8% of carbon fixation, respectively (Table 3). Besides this, 12.57% of the variation in carbon storage was spatially structured—i.e. explained by our spatial filter—and 3.97% of such structuring would correspond to spatially structured processes not represented by our set of predictors. Overall, these results show how climate variables (temperature in particular) emerge as the most influential on carbon storage, followed by fragmentation –i.e. through edge amount—, which is 2.5 times more important than the effect of forest amount once their indirect effects via tree height are accounted for.

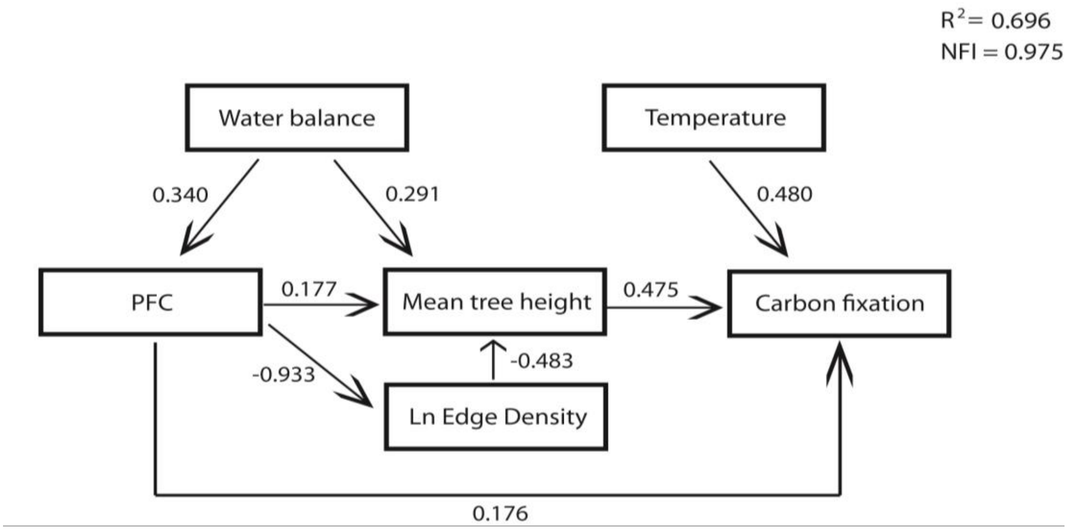

Figure. 2: Path model for carbon fixation, including all direct and indirect effects among predictors. Links with coefficients lower than 0.1 were removed. Model goodness-of-fit as measured by R^2 and NFI is noted.

Table 4: Direct, indirect and total effects of each predictor on carbon fixation, obtained from path model coefficients.

EFFECTS OF PREDICTOR VARIABLES ON CARBON FIXATION			
Variable	**Direct association**	**Indirect association**	**Total association**
PFC	0,176	0,299	0,474
Ln Edge Density	0,000	-0,230	-0,230
Canopy height	0,475	0,000	0,475
Water balance	0,000	0,300	0,300
Temperature	0,480	0,000	0,480

Path model (see Fig. 2) explained the 69.6% of the carbon model variance and the goodness-of-fit parameter NFI scored a high value that can be categorized as 'good' since NFI > 0.95. Path model showed the direct and indirect influence of the variables on carbon storage. Direct effects were mediated mainly by temperature (β = 0.48) and canopy height (β = 0.475), and secondarily by PFC (β = 0.18). Indirect effects were chiefly mediated by water balance and PFC, with positive overall coefficients of 0.3 and 0.299, respectively, and by an overall negative indirect effect of edge density of -0.23 (see table 4). Total associations show the similar and positive effect of canopy height, PFC and temperature on carbon storage, with weights of 0.475, 0.474 and 0.48 respectively, followed by water balance with weight of 0.3 and by edge density, with a negative effect with weight of -0.23 (table 4).

Discussion

Worldwide, deforestation is estimated to contribute roughly 1,1 Gt of carbon emissions annually, which make for about a quarter of the total anthropogenic emissions (Brinck, 2017). Most of these estimates of carbon fluxes are solely based on the amount of forest clearing (Laurance et al., 1998), but the contribution of other processes derived therefrom, such as the spatial configuration of forest remnants due to fragmentation, have not been comprehensively quantified globally (but see Brinck et al. 2017; Morton et al. 2016; Mitchard et al. 2018). Here we tested the importance of forest fragmentation and forest amount on tree height and carbon storage, finding a prevalent role of these factors to determine carbon storage either directly in the case of forest amount or indirectly *via* its effects on canopy height, in the case of fragmentation.

Our findings indicated that forest fragmentation is a major driver for tree height—i.e. explains almost a third of its variation: 29.41%—, which is negatively affected by the increased edge effects on forest remnants as fragmentation increases. The association of tree height with either climate or forest amount were weaker than those with fragmentation—i.e. 18.07% and 11.79%, respectively. This suggests that the resulting spatial configuration of forest remnants after deforestation is a much more important factor than habitat loss to determine tree height and, as a consequence, the amount of aboveground tree biomass (see Table 2). Nevertheless, forest amount also plays a detectable role as a determinant of tree height (Table 2; Fig. 2) and thus, it should not be ignored. The reason why tree height would be linked to fragmentation stems from the negative influence of edge-effects on tree growth, consistent with has been reported by previous work (e.g. Didham et al. 1999; Magnago et al. 2015).

For instance, our results coincide broadly with those by Laurance et al. (1997) who, in a fragmentation experiment in Amazonia, determined that the aboveground tree biomass loss and tree mortality was largest within 100 meters of fragments edges. Forest edges were shown to experience microclimatic changes, elevated wind turbulence as well as increased amount of liana-like vegetation—i.e. acting as structural parasites—in the transition areas (Laurance et al., 1997; Kapos, 1989; Ferreira & Laurance, 1997; Londré et al. 2006). These authors registered losses of forest biomass of up to 36% in the first 10 to 17 years after fragmentation. Regarding biomass loss due to tree damage, Ferreira & Laurance (1997) estimated that it was nearly as high (within 100 m from the edges, 2.82% per year) as tree mortality (3.04% per year). Other authors have pointed out the important effect of crown damages on maximum height of conifer trees (Ishii et al, 2010). They found that the height of damaged conifer trees was 16–17% shorter than that of intact trees, and as much as 16–28% shorter than the potential maximum height estimated from the diameter–height relationship of the tallest intact trees. While our analysis does not measure tree damage, our finding of a major negative association of forest edge amount with canopy height (see Table 2; Figs. 1a, 2a) suggests a mechanism whereby fragmentation leads to increased damage, which would in turn limit tree growth (and thus carbon storage).

Altered biotic interactions might also be involved in complementary or alternative mechanisms accounting for fragmentation effects on tree growth. For example, Feeley et al. (2005) related larger herbivore density observed in recent tropical forests fragments with increases in tree growth and aboveground plant productivity. However, these effects could be overshadowed by subsequent later changes in community composition, possibly resulting in a predominance of non-preferred plant species for herbivores and in the decrease of nutrient availability and primary productivity. Indeed, as indicated by Oliveira-Filho et al. (1997) old-growth trees in fragments tend to be replaced over the long term by shorter, shrubby forest with lower volume and biomass. Related to this, fragmentation may induce remarkably rapid changes in tree communities as well, favoring fast-growing early successional trees with low wood density, small seeds, abiotic seed dispersal and low shade tolerance (Tabarelli et al., 1999). Moreover, many old-growth species, especially slow-growing, shade-tolerant subcanopy trees that have obligated outbreeding and rely on mammals or larger birds for seed dispersal, are especially disadvantaged (White et al., 2004; de Melo et al., 2006). Given this link between forest patch dynamics and observed declines in aboveground tree biomass and tree height, the magnitude of biomass loss with deforestation will ultimately depend on the spatial pattern of forest remnants, which is characterized by the number, sizes and shapes of these forest patches (Laurance et al., 1997), and, according to our results, also by how much edge they have.

Concerning carbon storage, early simulation-based studies estimated an effect of fragmentation of 1-7% decline in carbon fluxes (Laurance et al., 1998). Our results exceed this figure and indicate that, at the global scale, fragmentation could be linked to 9.49% (6.65% due only to edge effects, proportion value calculated from explained variation of total fragmentation and edge variable individually obtained in table 2) of the variation in carbon storage, which decreases as tree biomass is limited by increasing fragmentation (see Table 3). Thus, due to fragmentation large amounts of carbon would not be assimilated by the forest biomass, remaining as CO_2 in the atmosphere. The effect of fragmentation, and in particular of edge effects, acts indirectly through its negative effects on tree height and on aboveground biomass. Fragmented forests exhibit an accelerated carbon cycling and have a substantially reduced ability to store carbon (Nascimiento & Laurance, 2004). In addition, these reductions in carbon storage could be an important source of greenhouse gas emissions (Laurance et al, 2008). Laurance et al. (2000) noted that fragmentation affects large trees more severely because they are more vulnerable to uprooting, infestation by parasitic woody vines and desiccation. The authors detected near the edges a *ca.* 40% increase in mortality over what would be expected, and with large trees dying nearly three times faster when they were within 300 m of distance from the edges. In this regard, our results point to that these effects might be particularly important in warmer regions, as climate—i.e. mostly through effects of warm winters—explained over one third of the variation in carbon storage (see Fig. 2b) so that there is more carbon stored in warmer forests.

Given the rapid rate of fragmentation in the tropics and, considering the indirect effect of fragmentation on carbon storage, reduced carbon uptake and CO_2 emissions derived from fragmentation (Laurance et al, 2008) may have implications for global warming beyond what is caused by forest clearing *per se* (Laurance et al., 1997). While most research on this topic has been conducted on tropical forests leading to acceptance that edge effects would affect negatively carbon uptake, recent research on temperate forests shows that forest edges are themselves relevant in storing carbon but, at the same time, particularly vulnerable to climate change and, thus, prone to be heavily affected in providing this service (Reinman & Hutyra 2017). Along these lines, our global results are clearly consistent with a negative effect of fragmentation on carbon storage, and thus, suggest a potential role of fragmentation in worsening climate change. Taking into account the influence of fragmentation on the release or failure of capturing of greenhouse gases, and the links between atmospheric CO_2 and global temperatures, we could think that these variables could feedback each other. In one hand, fragmentation constrains tree height and aboveground tree biomass, resulting in a reduction of carbon forest stock and potentially, in an increase of greenhouse gas emissions. On the other hand, increased greenhouse gas concentrations lead to increasing temperatures, and our results point to that the higher the minimum temperature of the coldest month, the larger the forest carbon fixation. However, under the ongoing high rates of deforestation and fragmentation, it is unlikely that such buffering mechanism—i.e. self-regulating feedback—will be fast enough to compensate absolute emissions derived from fragmentation and deforestation.

Conclusions

The resulting spatial configuration of forest remnants after deforestation is a more important factor than habitat loss *per se* to determine tree height and carbon sequestration, due to the relevance of the negative influence of edge effects. Given the rapid rate of forest fragmentation in the tropics, such emissions may exacerbate strongly the effects of global warming above and beyond those caused by forest clearing *per se*. Implementation of restoration strategies aimed at minimizing habitat edges in managed landscapes might lead to significant increases in the amounts of carbon captured by forests.

Supplementary material

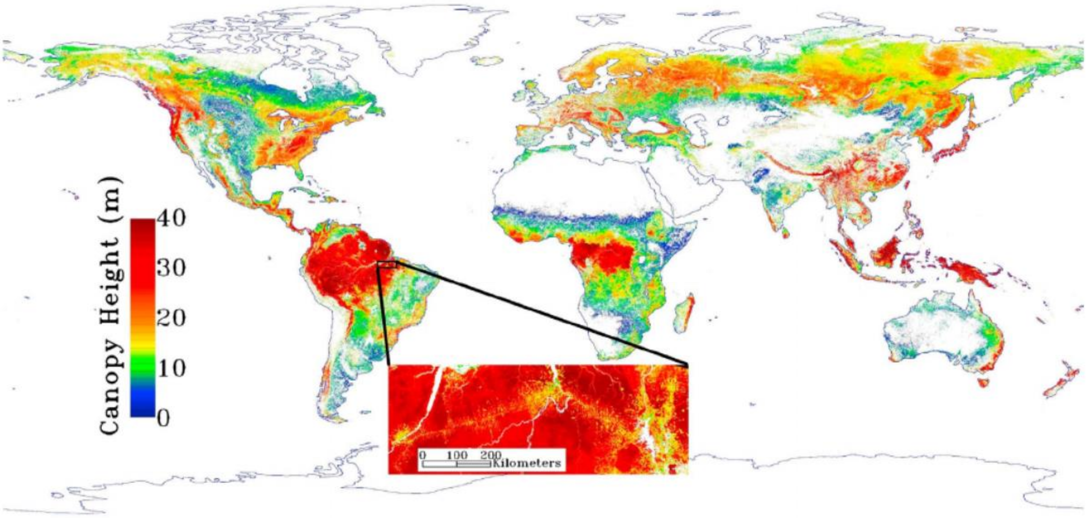

Figure. 1: Canopy height map of Simmard et al. (2011).

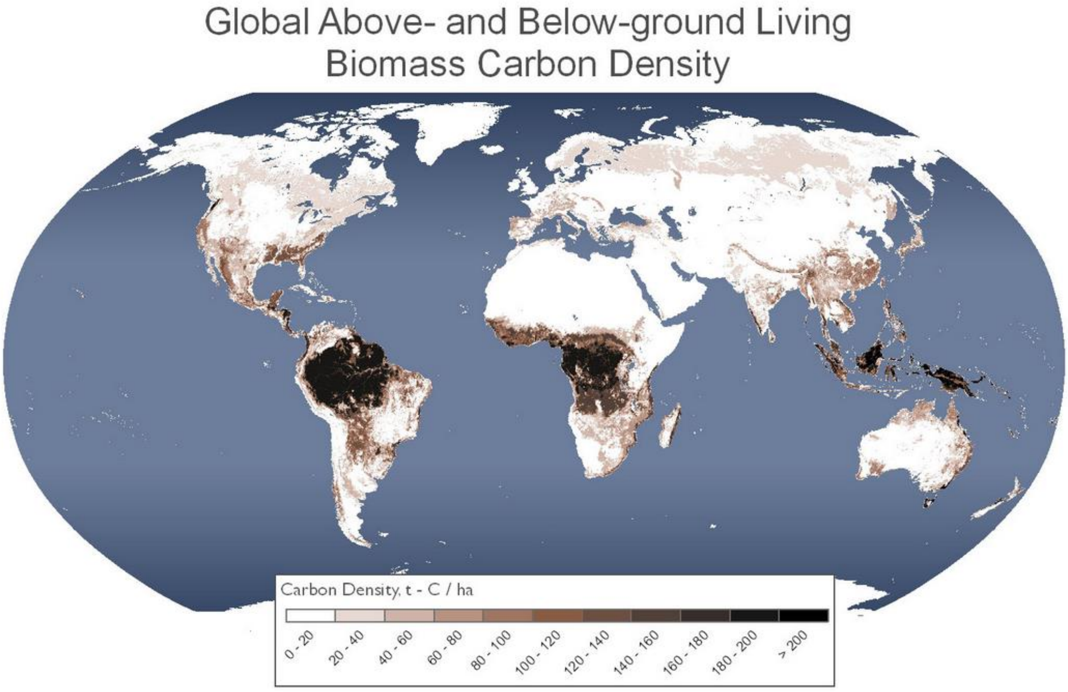

Figure. 2: Global above -and below- ground living biomass carbon density map of Ruesch, A.S. & Gibbs H.K. (2008).

Table 1: Data source of climatic and soil variables.

PARTITION: HEIGHT MEAN AS A RESPONSE VARIABLE

Individual fractions

	Df	**R.square**	**Adj.R.square**	**Significance**
Fragmentation	5		**0,28872**	0,005***
Climate	3		**0,07389**	0,005***
Space	1		**0,01964**	0,005***
Fragmentation + Climate	0		0,16248	
Climate + Space	0		0,00366	
Fragmentation + Space	0		0,06878	
Fragmentation + Climate + Space	0		0,05111	
Residuals			**0,03317**	
Total explained variance	10	0,66834	**0,66834**	

Table 2: Results of variance partition model with carbon storage as a response variable. The table shows the individual contribution of each group of variables (mean tree height, climate and space) and their shared contribution of them.

PARTITION: CARBON AS A RESPONSE VARIABLE

Individual fractions

	Df	**R.square**	**Adj.R.square**	**Significance**
Mean tree height (MTH)	1		**0,19115**	0,005***
Climate	3		**0,21522**	0,005***
Space	1		**0,03969**	0,005***
MTH + Climate	0		0,17772	
Climate + Space	0		0,00167	
MTH + Space	0		0,06125	
MTH + Climate + Space	0		0,05949	
Residuals			**0,25382**	
Total explained variance	5	0,74621	**0,74618**	

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CAPÍTULO 6

CONCLUSIONES GENERALES
GENERAL CONCLUSIONS

FUTURAS LINEAS DE INVESTIGACIÓN

CONCLUSIONES GENERALES

Capítulo 3

1. La pérdida de cobertura forestal suele ir acompañada de fragmentación de hábitat.
2. Existe un máximo empírico de fragmentación que varía en función de la cobertura forestal, factor a tener en cuenta de cara al diseño experimental de estudios de fragmentación.
3. El índice rLPS -tamaño relativo de la mancha más grande de hábitat-es estable ante los cambios de escala y presenta una elevada capacidad de síntesis de distintos aspectos de la fragmentación: estima indirecta de la abundancia y el tamaño de las machas (medida de dispersión) y de la cantidad de borde (medida de calidad de hábitat). Además, presenta un intervalo de variación fijo (de 0 a 100) y tiene un significado ecológico claro, lo que se traduce en sencillez y facilidad a la hora de interpretarlo y en una relevancia ecológica superior a la de índices alternativos.
4. Los umbrales de pérdida de biodiversidad (localizados en áreas con un 50-20% de cobertura forestal) son difíciles de detectar debido al escaso tamaño muestral existente.
5. A escala global y regional, sería conveniente que las medidas destinadas a recuperar cobertura forestal fueran acompañadas de medidas dirigidas a minimizar la fragmentación, generando zonas con mayor rLPS, ya que ambos descriptores de la cantidad y calidad de los ecosistemas forestales están fuertemente asociados geográficamente.

Capítulo 4

6. La pérdida de hábitat tiene efectos negativos sobre la probabilidad de ocurrencia de las siete especies de aves forestales objeto de estudio.
7. La fragmentación de hábitat tiene efectos negativos sobre la probabilidad de ocurrencia de tres de las especies de aves forestales

estudiadas (Urogallo occidental y Urogallo Hazel y Búho pigmeo euroasiático), efectos positivos sobre el pájaro carpintero negro y efectos neutros sobre el búho de Tengmalm, búho del Ural y pájaro carpintero de tres dedos.

8. Los rasgos biológicos específicos de cada especie pueden ser de ayuda para interpretar como dichas especies responden a la fragmentación del hábitat. Las diferencias entre las respuestas a la fragmentación pueden reflejar las capacidades de dispersión, especialización en recursos/características del hábitat y/o sensibilidad a potenciales modificaciones en las interacciones interespecíficas (p. ej. riesgo de depredación).

Capítulo 5

9. La configuración espacial de los remanentes de hábitat es un factor más importante que la pérdida de hábitat per se en la determinación de la altura de los árboles y su consecuente capacidad para el secuestro de carbono. Esto se debe a la importante influencia negativa del efecto borde sobre la altura.
10. Dado el rápido ritmo de fragmentación forestal en los trópicos, las emisiones de CO_2 asociadas (debidas a la disminución del almacenamiento de carbono en forma de biomasa, lo que supone una mayor cantidad de carbono disponible en forma de CO_2 en la atmósfera), podrían exacerbar el efecto del calentamiento global, más allá de los efectos sobre el calentamiento derivados de la deforestación per se.
11. La planificación de estrategias de reforestación y restauración forestal dirigidas a minimizar la superficie de borde en paisajes forestales manejados, tiene el potencial de reducir considerablemente las emisiones de gases de efecto invernadero.

GENERAL CONCLUSIONS

Chapter 3

1. Forest cover loss is often accompanied by habitat fragmentation.
2. There is an empirical fragmentation maximum, which varies along the forest cover gradient, a factor to be considered in the experimental design of fragmentation studies.
3. The rLPS -relative Largest Patch Size- index is stable across spatial scales and is appropriate to synthesize different aspects of fragmentation: indirect estimation of abundance of patches and patch size (dispersion measure) and the amount of habitat edge (a measure of habitat quality). In addition, it ranges between a fixed variation interval (from 0 to 100), and has a clear ecological meaning, which translates into simplicity, ease of interpretation and ecological relevance.
4. Biodiversity extinction thresholds (located in areas with 50-20% of forest cover) are difficult to detect due to the small existing sample size.
5. At the global and regional scales, it would be convenient that measures aimed at recovering forest cover were joined by measures aimed at minimizing fragmentation –generating areas with larger rLPS- given that both descriptors of forest habitat amount and quality are strongly associated across the geography.

Chapter 4

6. Habitat loss has negative effects on the probability of occurrence of the seven forest species of birds under study.
7. Habitat fragmentation has negative effects on the probability of occurrence of three forest species studied (Western Grouse, Hazel Grouse and Eurasian Pigmy Owl), positive effects on the Black

woodpecker and neutral effects on the Tengmalm´s owl, Ural owl and Three-toed woodpecker.

8. Specific species traits can be useful to interpret the species responses to fragmentation. Differences among species responses may reflect their dispersal abilities, their specializations in resources or habitat characteristics and/or their sensitivity to potential modifications of interspecific biotic interactions -e.g. predation risk.

Chapter 5

9. The spatial configuration of habitat remnants is more important than habitat loss *per se* in determining tree height and subsequent carbon sequestration, due to the important negative influence on tree height shown by edge effects.
10. Given the rapid rate of forest fragmentation in the tropics and its associated CO_2 emissions (due to the decrease of carbon storage in the form of biomass, which means a greater amount of carbon available in the form of CO_2 in the atmosphere), such emissions may exacerbate strongly the effects of global warming above and beyond the warming that is already caused by forest clearing *per se*.
11. Planning clearing strategies to minimize habitat edges in managed forest landscapes will reduce considerably greenhouse gas emissions and should have a number of ecological benefits.

FUTURAS LÍNEAS DE INVESTIGACIÓN

De los trabajos realizados en esta tesis surgen una serie de preguntas o cuestiones, cuya respuesta contribuiría a aumentar el conocimiento del impacto de la fragmentación de hábitat sobre las especies. En futuros estudios sería interesante abordar las siguientes cuestiones derivadas de esta tesis:

Una línea de investigación sería, partiendo de la base de los mapas de fragmentación obtenidos en nuestros trabajos, estudiar la conectividad de los remanentes de hábitat y su relación con la biodiversidad a escala macroecológica, cuantificando la importancia de las áreas de hábitat y los enlaces para el mantenimiento o mejora de la conectividad como herramienta de apoyo para la toma de decisiones de cara a la planificación del paisaje y la conservación del hábitat, elaborando mapas de áreas críticas para la conectividad ecológica.

Además, en nuestro estudio encontramos respuestas variables de las distintas especies a la fragmentación. Estos resultados dispares podrían estar relacionados con las limitaciones de nuestro estudio para testar la Hipótesis del Umbral de Extinción (HUE), debido al uso de una definición general de hábitat para todas las especies (bosques) en lugar de medir las características del hábitat teniendo en cuenta las necesidades de cada especie. Por ello, en futuras líneas de investigación sobre la HUE sería adecuado tener en cuenta las características concretas de cada especie, así como sus necesidades específicas, tales como la capacidad de dispersión, grado de especialización o la sensibilidad a la modificación de las interacciones interespecíficas, entre otras.

Por otro lado, el efecto invernadero ocasionado por las emisiones de gases produce un incremento de la temperatura global. De entre las variables climáticas que hemos incluido en nuestro modelo, en el caso concreto de la temperatura mínima del mes más frio nuestros resultados mostraron que cuanto mayor era ésta, mayor era también la fijación de C, por lo que los propios gases de efecto invernadero producidos por fragmentación actuarían a su vez como un mecanismo de amortiguación que permitiría reiniciar el proceso de fijación de carbono. Futuras líneas de investigación podrían ir dirigidas hacia tratar de dilucidar y cuantificar este mecanismo de retroalimentación y hacia el estudio de las variables climáticas y sus posibles efectos amortiguadores sobre el calentamiento global.

Otras líneas de investigación interesantes y novedosas podrían ser:

- Respuestas co-evolutivas de las especies a la fragmentación.
- Efectos de la fragmentación sobre la probabilidad de expansión de especies invasoras.
- Interacción entre fragmentación y evolución a través de cuellos de botella genético-ecológicos (endogamia, deriva genética…).
- Relación entre la fragmentación y los brotes de enfermedades infecciosas.

CURRICULUM VITAE

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Septiembre 2011 – Actualidad: **Cursando Doctorado en Biología**. Universidad de Alcalá.

Julio 2010: **Postgrado de Especialista en Sistemas de Información Geográfica aplicada a la Gestión Ambiental**. Universidad Politécnica de Madrid (U.P.M): Análisis Vectorial y Análisis Raster.

Septiembre 2010: **Máster Oficial en Biología de la Conservación**. Universidad Complutense de Madrid (U.C.M.)

Junio 2009: **Licenciada en Biología**. Universidad Complutense de Madrid (U.C.M.).

IDIOMAS

Becaria MEC 2010: Curso de inglés en el extranjero (3 semanas) en Inglaterra. Dos meses en California. Tres meses en Reino Unido.

INGLÉS: B1. (C.S.I.M., 2010. Universidad Complutense de Madrid)

PORTUGUÉS: A2 (C.S.I.M., 2008. Universidad Complutense de Madrid). Tres meses en Brasil.

INFORMÁTICA

Sistemas de Información Geográfica: **ArcGis 10.1**. Nivel alto.

Programas de estadística y análisis de datos: **Statgraphics, Statistica y R**. Nivel intermedio.

Otros programas: **Stella, Estimates 8.2**. Nivel medio.

CURSOS

Título	Autores	Lugar	Fecha	Nª créditos
Introducción a los modelos de distribución de especies	Isabel Cabra	Universidad de Alcalá	3-5 julio 2013	6 horas
Landscape genetics and connectivity modeling	Samuel Cushman	Universidad Politécnica de Madrid	Marzo 2013	14 horas
Introducción al análisis multivariado	Jaime Madrigal	Universidad de Alcalá	Febrero 2013	6 horas
Herramientas para el análisis de la conectividad del paisaje: fundamentos metodológicos y ejemplos de aplicación	Santiago Saura	Universidad Politécnica de Madrid	Marzo 2012	20 horas
Modelos mixtos en R	Luis Cayuela	IREC-CSIC	Mayo 2011	20 horas
Introducción a R	Luis Cayuela	Universidad de Alcalá	Febrero-Marzo 2011	24 horas
Evaluación de Impacto Ambiental (EIA)	Asociación Española de EIA	Universidad Politécnica de Madrid	2005	40 horas

SEMINARIOS IMPARTIDOS

1) Tectónica de placas y fauna (Facultad de Biología, Universidad Complutense de Madrid)

2) Importancia del tamaño y la forma en la evolución (Facultad de Biología, Universidad Complutense de Madrid)

3) Edafología Ibérica (Facultad de Biología, Universidad Complutense de Madrid)

4) Modificación del régimen de caudales y sus efectos sobre la fauna y la vegetación riparia (Facultad de Biología, Universidad Complutense de Madrid)

5) Patrones globales de fragmentación forestal (Facultad de Ciencias, Universidad de Alcalá)

6) Padroes globais de fragmantaçao florestal (Insituto Ciencias Biológicas, Universidad Federal de Goiás, Goiania, Brasil)

7) Influencia de la fragmentación forestal en el cambio climático. Un estudio global (Facultad de Ciencias, Universidad de Alcalá)

DOCENCIA

UNIVERSIDAD DE ALCALÁ				
Curso académico	**Asignatura**	**Titulación**	**Curso de la titulación**	**Numero horas impartidas**
2014-2015	Educación Ambiental	Grado en Ciencias Ambientales	4º	42
	Gestión y conservación de áreas naturales protegidas	Grado en Ciencias Ambientales	4º	18
2013-2014	Evaluación Impacto Ambiental	Grado en Ciencias Ambientales	3º	18
	Ecología	Grado en Biología	2º	16
	Gestión y conservación de los recursos naturales	Grado en Ciencias Ambientales	3º	14
	Gestión y conservación de áreas protegidas	Grado en Ciencias Ambientales	4º	12
2012-2013	Evaluación Impacto Ambiental	Grado en Ciencias Ambientales	3º	9
	Ecología	Grado en Biología	2º	36
	Métodos en conservación y biodiversidad	Grado en Biología	1º	15
2011-2012	Degradación ambiental y restauración de ecosistemas	Máster oficial interuniversitario de Restauración de Ecosistemas	1º	16
	Bases biológicas de la conservación	Grado en Biología	4º	24
	Evaluación Impacto Ambiental	Grado en Ciencias Ambientales	3º	20
			TOTAL	**240 horas**

COMUNICACIONES EN CONGRESOS

Título	Autores	Congreso	Lugar	Fecha	Tipo participación
Can forest fragmentation impact climate change?. A global study.	Mila Ferrero, Luis Mauricio Bini, José Alexandre Felizola Diniz-Filho Ignacio Morales-Castilla, Miguel Á. Rodríguez	IV Iberian Ecological Congress	Coimbra (Portugal)	16-19 junio 2015	Póster
Influencia de la fragmentación forestal en el cambio climático. Un estudio global.	Mila Ferrero, Luis Mauricio Bini, José Alexandre Felizola Diniz-Filho Ignacio Morales-Castilla, Miguel Á. Rodríguez	V Jornadas de Jóvenes Investigadores de la Universidad de Alcalá	Madrid (España)	1-3 dic 2014	Comunicación oral estándar

Caracterización de los niveles de fragmentación forestal a escala global y del Mediterráneo	Mila Ferrero, Ignacio Morales-Castilla, Marta Rueda, Juan Carlos Moreno, Miguel Á. Rodríguez.	XI Congreso Nacional de la Asociación Española de Ecología Terrestre (AEET)	Pamplona (España)	6-10 mayo 2013	Comunicación oral estándar
Biogeographic patterns of forest fragmentation at global and regional scales	Mila Ferrero, Ignacio Morales-Castilla, Marta Rueda, Juan Carlos Moreno, Miguel Á. Rodríguez	6th Biennial Conference of the International Biogeography Society (IBS).	Florida (USA)	9-13 enero 2013	Póster (internacional)
Cuantificando la cobertura y fragmentación de los bosques globalmente y en la vegetación mediterránea.	Mila Ferrero, Ignacio Morales-Castilla, Marta Rueda, Juan Carlos Moreno, Miguel Á. Rodríguez	IV Jornadas de Jóvenes Investigadores de la Universidad de Alcalá	Madrid (España)	28-30 nov 2012	Comunicación oral estándar
Influence of forest fragmentation on biodiversity: Consequences for green and transport infrastructures	José V. de Lucio, Mila Ferrero, Ignacio Morales-Castilla, Jesús Martínez-Fernandez & Miguel Á. Rodríguez. 2012	Infra Eco Network Europe (IENE)	Potsdam (Alemania)	21-24 oct 2012	Póster (internacional)

PUBLICACIONES

Título	Autores	Revista
Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds.	Marta Rueda, Bradford A. Hawkins, Ignacio Morales-Castilla, Rosa M. Vidanes, Mila Ferrero & Miguel Á. Rodríguez	Global Ecology and Biogeography (2013), 22, 1282-1292.
Biogeographic patterns of forest fragmentation at global and regional scales	Mila Ferrero, Ignacio Morales-Castilla, Marta Rueda, Juan Carlos Moreno & Miguel Á. Rodríguez.	Pte. envío
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Can forest fragmentation impact climate change?. A global estudy.	Mila Ferrero, Luis Mauricio Bini, José Alexandre Felizola Diniz-Filho Ignacio Morales-Castilla, Miguel Á. Rodríguez	Pte. envío
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CAPÍTULOS DE LIBRO

GUERRERO ORTEGA, Antonio; ROS MAGÁN, Germán; HIDALGO MORENO, Miguel A.; AGUADO MOLINA, Jesús. V Jornadas de Jóvenes Investigadores de la Universidad de Alcalá. **2015**. Colección Obras Colectivas en Ciencias. ISBN: 978-84-15834-15-1. CAPÍTULO: **Influencia de la fragmentación forestal en el cambio climático. Un estudio global.**

GUERRERO ORTEGA, Antonio; ROS MAGÁN, Germán; HIDALGO MORENO, Miguel A.; AGUADO MOLINA, Jesús. IV Jornadas de Jóvenes Investigadores de la Universidad de Alcalá. **2013**. Colección Obras Colectivas en Ciencias. ISBN: 978-84-15834-15-1. CAPÍTULO**: Cuantificando la cobertura y fragmentación de los bosques globalmente y en la vegetación mediterránea.**

ESTANCIAS EN CENTROS EXTRANJEROS

14/5/14-11/8/14: **Imperial College of London** (Londres), Reino Unido. Faculty of Natural Sciences. Life Science department.

20/9/13-18/12/13: **Universidad Federal de Goiás** (Brasil). Instiuto de Ciencias Biológicas. Departamento de Ecología.

11/4/12-11/06/12: **University of California** (Irvine), EEUU. Biological Science Center. Ecology and Evolutionary Biology department.

PARTICIPACIÓN EN PROYECTOS

Título del Proyecto: Fragmentación de bosques en España y Europa y probabilidades de extinción
de especies de animales y plantas.
Referencia: CGL2010-22119/BOS.
Organismo financiador: Ministerio de Ciencia e Innovación.
Fechas de inicio y finalización: 01/01/2011-31/12/2013
Entidades participantes: Universidad de Alcalá, Universidad Autónoma de Madrid
Número de investigadores del proyecto: 7
Nombre del IP: Miguel Ángel Rodríguez Fernández

Título del proyecto: Ungulados exóticos y nativos de interés cinegético: análisis de la competencia por los recursos entre el muflón y el ciervo ibérico
Tipo de contrato: Contrato por obra o servicio determinado en el marco de proyectos de investigación del CSIC, con categoría de Titulado Superior
Investigador contratado: Milagros Ferrero Cedenilla
Duración del contrato: 1/3/2011 - 31/8/2011

Organismo financiador: Junta de Comunidades de Castilla-La Mancha, Ref. POII10-0321-9389
Centro de ejecución: Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM)
Investigador principal: Dr. Jorge Cassinello Roldán
Nº investigadores participantes: 6
Ayuda concedida: 180.000 €
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EXPERIENCIA LABORAL

- **Septiembre 2011- Actualidad:** Beneficiaria de una **beca FPI** de investigación del Ministerio de Economía y Competitividad en la Universidad de Alcalá. Proyecto: **Fragmentación de bosques de España y Europa y probabilidades de extinción de especies forestales de animales y plantas.**

- **Septiembre 2010 – 2014:** Universidad Complutense de Madrid. Proyecto**: Efecto de la estructura espacial sobre la distribución de la comunidad reproductora de aves.**

- **Marzo 2011 – Septiembre 2011:** Instituto de Investigación en Recursos Cinegéticos (CSIC-IREC-JCCM). Proyecto: **Ecological effects of invasive species: Comparative use of resources by the exotic African aoudad and the Iberian ibex in sympatry and allopatry, and effects on native flora in southeastern Spain.**
  Proyecto: **Etología del muflón** (*Ovis orientalis musimon*).

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