

Landscape properties affect biodiversity response to retention approaches in forestry

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Summary

1. Retention forestry, in which trees and tree patches are set aside at harvest to promote biodiversity, has been proven to have positive effects on biodiversity at the stand-level across different taxa. However, the effectiveness of retention approaches with regard to landscape composition remains unexplored.

2. We linked the effect sizes from two meta-analyses (31 case studies and 1050 comparisons from boreal and temperate regions), which quantified the effectiveness of biodiversity conservation as a result of retention practices, with the stand property of retention level (the percentage of trees retained after logging) and with Landsat-retrieved landscape data on forest cover and spatial configurations at three spatial scales (1, 3, and 5 km radii).

3. We found that, in addition to the fundamental importance of tree retention as a local-scale implementation for conservation, landscape properties were important in models to predict biodiversity responses. The effect sizes for species richness decreased with increasing patch contiguity within the landscapes at all spatial scales. Similar results were observed for abundance responses at the largest spatial scale. These results suggest that biodiversity responses to tree retention may be weaker in less fragmented landscapes, which is in agreement with theoretical and empirical findings from agricultural landscapes ('the intermediate landscape-complexity hypothesis').

4. The benefits of retention levels within a stand (percentage of trees retained) varied amongst species with different habitat requirements (forest-dependent, open habitat, and generalist species). Whilst this stand-level property was often an important determinant of biodiversity responses, models that included landscape properties as explanatory variables always performed better than those that were only based on the retention levels for all species groups. Thus, within-stand habitat conditions and landscape configurations likely have synergistic influences on biodiversity responses.

5. *Synthesis and applications.* In addition to the importance of stand-level properties, such as the action of retention harvesting itself and the number of trees retained, conditions in the surrounding landscape can simultaneously affect biodiversity in stands that are managed under retention forestry. Our study suggests that retention patches are particularly important in moderately fragmented landscapes. Retention practices could be less important in previously unlogged and less fragmented landscapes, where setting aside large reserves is a conservation priority. For highly fragmented landscapes, different actions of forest restoration, which are not limited to set-aside actions during logging, would be important. Our study emphasizes that carefully planned conservation schemes with a large-scale perspective, as well as local-scale actions, such as retention forestry, are critical for effective forest management and conservation planning.

Key-words: biodiversity, forest certification, habitat fragmentation, landownership, landscape heterogeneity, land-sharing, meta-analysis, nature-oriented forestry, retention forestry, set-aside action

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Introduction

Currently, numerous efforts aimed at halting the decline and loss of biodiversity and ecosystem services have been implemented at regional to intergovernmental scales (Butchart *et al.* 2010). Changes to land management and policies in response to the current biodiversity crisis have not always been successful, and the prospects for improving this situation in a global context are rather pessimistic (Kleijn *et al.* 2011; Tittensor *et al.* 2014). However, the recent substantial expansion of sustainable forest management has been evaluated, and it is seen as one of the most successful measures of human responses to the biodiversity crisis (Butchart *et al.* 2010; Tittensor *et al.* 2014). One of the notable cases in this context is retention forestry (Franklin *et al.* 1997), which is becoming widely applied, especially in temperate and boreal regions (Lindenmayer *et al.* 2012). Retention forestry is a practice that aims to maintain important elements of a stand during logging operations to ameliorate the post-disturbance structure over forest generations (Lindenmayer & Franklin 2002). That is, the important objectives of retention forestry are to provide 'lifeboats' of forest structure for forest biota and to maintain 'legacies' of older forest structure in regenerating stands (Franklin *et al.* 1997). Although requirements vary amongst different regions and its implementation is not exclusively aimed at conserving biodiversity, retention forestry is increasingly playing an important role in modern forestry practices (Gustafsson *et al.* 2012). As such, retention forestry provides an alternative way to satisfy the demands for both wood production and biodiversity conservation (Gustafsson *et al.* 2012; Lindenmayer *et al.* 2012).

Recently, two meta-analyses proved that retention forestry is effective at moderating the negative effects of logging on forest biodiversity (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014). However, these evaluations were based on the local stand-scale, and a large-scale perspective is lacking (Rosenvald & Löhmus 2008; Gustafsson *et al.* 2012). As analogues to retention forestry that adhere to the idea of land-sharing in terms of integration of intensification and reservation for land-use (Lindenmayer *et al.* 2012), agri-environmental schemes (primarily organic farming) are also becoming important (Butchart *et al.* 2010; Tittensor *et al.* 2014). Evaluations of such approaches have revealed mixed, but the overall positive effects (Batary *et al.* 2011; Tuck *et al.* 2014), and that such effects depend on the spatial scale (Bengtsson, Ahnstrom & Weibull 2005; Gabriel *et al.* 2010) and landscape complexity (Tscharntke *et al.* 2005; Batary *et al.* 2011; Scheper *et al.* 2013). In contrast to the numerous studies of agricultural systems, only limited numbers of large-scale analyses, particularly quantitative analyses, have examined the landscape-related effects of land-sharing approaches in forest landscapes (Gustafsson *et al.* 2012; Paul & Knoke 2015). Given the importance of the

landscape perspective (Lindenmayer *et al.* 2008), especially in the search for solutions to reconcile tradeoffs between conservation and development (Sayer *et al.* 2013; Tscharntke *et al.* 2015) and between multiple ecosystem services (Law *et al.* 2015; Knoke *et al.* 2016), further insight is required to evaluate how large-scale patterns may alter the effectiveness of conservation actions.

We revisited datasets that were provided by two meta-analyses of retention forestry (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014), which were compiled from studies of temperate and boreal forests. We used them to determine whether the effectiveness of the approach as a measure to safeguard forest biodiversity varies depending on the landscape context. In particular, we focused on connectivity, forest cover, and heterogeneity in a given landscape. A broad-scale perspective is important for several reasons. It remains unknown whether the effects of set-aside actions on biodiversity in production forests vary between landscapes with different histories and different degrees of modification. As an analogue to agricultural systems (Batary *et al.* 2011; Tuck *et al.* 2014), the effects of habitat retention on biodiversity in forest landscapes very likely depend on the conditions in surrounding areas. If so, retention forestry, which is mandatory in some countries (Gustafsson *et al.* 2012), but which is also often driven by forest certification (McDermott, Cashore & Kanowski 2010; Auld 2014), needs to be adopted and implemented whilst considering landscape configuration. Retention forestry is by no means a panacea to halt biodiversity declines; however, it can complement a scarcity of nature reserves (Lindenmayer *et al.* 2012; Mori & Kitagawa 2014). For this reason, careful assessment of the effectiveness of retention forestry from a landscape perspective can support policy making and thereby benefit society.

Materials and methods

DATA COLLECTION

We revisited literature datasets that were used in two recent meta-analyses (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014), including data on species richness and/or abundance in stands that were harvested using the retention approach (i.e. treatment units comprising cleared, open areas and areas with retained trees; henceforth 'retention cuts') and un-harvested (control) forests. Literature was retrieved using the Institute of Scientific Information Web of Science database (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014), Google Scholar, Scopus, and the Directory of Open Access Journals (Fedrowitz *et al.* 2014) with data collected through December 2012 (both studies). We used 31 case studies for which we could accurately identify the study location based on latitude/longitude information or other site descriptions (e.g. azimuth and distance from the nearest city). When photographs or illustrations of the study site (e.g. shape and size) were provided in the literature, we checked the landscape with Google Earth (<https://www.google.com/earth/>) to improve the

location accuracy. Our final dataset comprised 1057 comparisons (retention cuts/clear-cuts vs. un-harvested controls) from the 31 case studies, and it included eight taxonomic groups: amphibians, birds, bryophytes, fungi, invertebrates, lichens, mammals, and plants (Table S1, Supporting Information).

For the selected studies, we retrieved sample sizes, mean values, and standard deviations for biodiversity responses (species richness or abundance) of a focal taxonomic group related to the retention practice from the main text, tables, and figures (Table S1). We used WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>) to extract values from the figures. Then, we calculated the standardized mean difference, Hedges' d (Hedges & Olkin 1985; Gurevitch & Hedges 1999), as an effect size metric to compare the means between the retention cuts and the un-harvested controls. Positive values of Hedges' d indicate higher species richness or abundance in retention cuts compared with the control. We used Hedges' d because it adjusts for differences in the sampling effort amongst studies, and it corrects for a small sample size. We used R software 3.0.2 (<http://www.r-project.org/>) to calculate values. Furthermore, by reading through source papers, we also identified the retention type (aggregated retention, dispersed retention, aggregated + dispersed retention, unspecified retention, or clear-cut), the habitat preferences of species (forest-dependent, open habitat, generalist, or unspecified), the retention levels (percentage of trees retained), study plot size, and time-since-logging.

To quantify the landscape structure, we used Landsat Thematic Mapper/Enhanced Thematic Mapper Plus (TM/ETM+) images from the Global Land Cover Facility (<http://glcf.umd.edu/>). All pixels (30 m \times 30 m) were classified as 'forest' or 'other land-use types' (e.g. agricultural land, grassland, buildings, roads, or water) with supervised classification using ESRI ArcGIS ver. 10.1 (www.esri.com/) and with reference to Google Earth (<https://www.google.com/earth/>). Figure 1 provides an example of a Landsat TM/ETM+ image and the classified images used in this study. For each case study, we used the Landsat TM/ETM+ image with the smallest possible elapsed time since field research was conducted (ranging from 0 to 12 years, with a mean of 2.9 years). FRAGSTATS ver. 4.4 (<http://www.umass.edu/landeco/research/fragstats/fragstats>) was used to calculate several landscape indices: percentage forest cover, contiguity, fractal dimension, and perimeter-area ratio. Per cent forest cover is the percentage of forest area in the landscape, and it is a rough measure of land-use intensity. Contiguity is the spatial connectedness of forest fragments; a low contiguity score indicates small and isolated forest fragments, and a high score indicates large and contiguous fragments. The fractal dimension indicates the shape complexity of forest coverage; large and small values indicate an increase and a decrease, respectively, in patch shape complexity, which is associated with the degree of convoluted plane-filling perimeters in a two-dimensional landscape. The perimeter-area ratio represents the degree of complexity of planar shapes. Earlier studies that analysed agricultural landscapes evaluated landscape heterogeneity based on a proportion of natural habitats, such as forests within a landscape (Batory *et al.* 2011; Rader *et al.* 2014). However, as occurs with croplands, it is impossible to accurately distinguish managed forests and natural forests using satellite images; thus, we simply categorized land cover as forest or non-forest. We chose contiguity and fractal dimension as indices because we were, apart from forest cover, primarily interested in the effects of landscape connectivity and heterogeneity on forest biodiversity. Shannon's diversity index, an index that can also

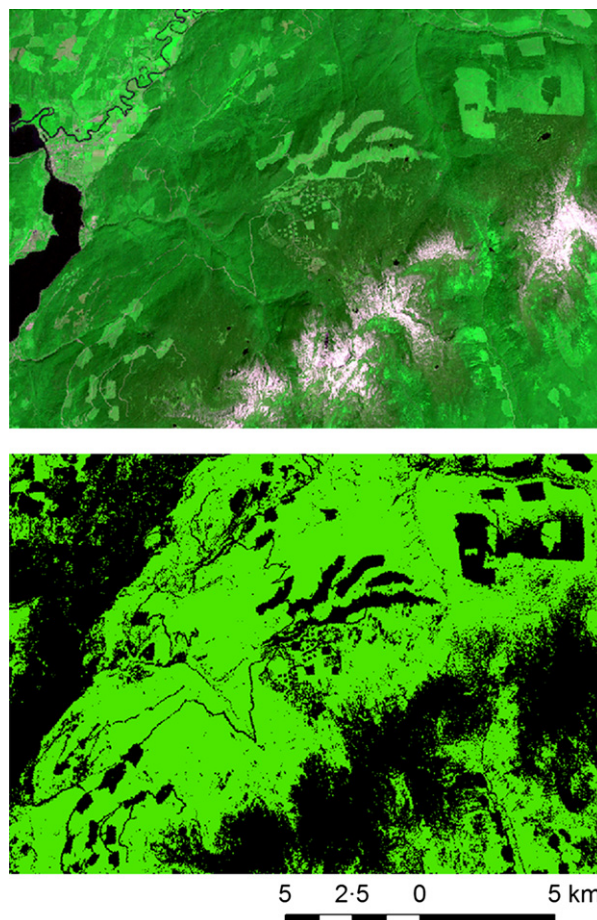


Fig. 1. A sample raw Landsat Thematic Mapper/Enhanced Thematic Mapper Plus (TM/ETM+) image (upper) and a classified image (bottom) used for the analysis. This example shows the surrounding landscape of the study site (located at the centre of the images) of Klenner & Sullivan (2003). The Landsat TM/ETM+ image is shown in true colour. Forested and non-forested areas are shown in green and black, respectively, in the classified image.

represent landscape heterogeneity (Perović *et al.* 2015), was significantly ($P < 0.05$) positively correlated with the fractal dimension in this study. For the measures of contiguity and fractal dimension, we relied on the area-weighted mean for patch characteristics, which gives a landscape-centric perspective of landscape structure (McGarigal, Cushman & Ene 2012). Another potentially important property is the edge length; fragmented landscapes have longer forest edges and, thus, may have more emigrants from surrounding forests. If this is true, edge length could be important in addition to the indices of forest continuity and forest cover. To account for possible differences in the responses of taxa to landscape structure amongst different spatial scales (Gabriel *et al.* 2010; Perović *et al.* 2015), the four landscape indices were calculated within three different radii (1, 3, and 5 km) that were centred on the study locations.

STATISTICAL ANALYSES

Following the procedures outlined by Mori & Kitagawa (2014), we preliminarily confirmed that the present datasets had no

publication bias (Fig. S1) and that the retention practice effectively conserved high levels of species richness (Hedges' d effect size: 0.456 ± 0.288 , $n = 27$) and abundance (Hedges' d effect size: -0.010 ± 0.149 , $n = 779$); the mean \pm 95% confidence intervals of the effect size were based on 9999 bootstrap iterations, and they were analysed for all taxonomic groups together. Note that our dataset includes data for clear-cuts (Table S1), but they ($n = 216$) were removed from the following analyses (except for Fig. S2). That is, comparisons were made between pairs of un-harvested controls and retention treatments, and, thus, zero values of Hedges' d effect size represent the diversity level in un-harvested controls.

To account for the nested complexity in our dataset resulting from possible differences in responses amongst different taxonomic groups and retention types, as well as repetitions within the studies, we used a linear mixed-effects model (LMM) to examine the effects of stand and landscape structure on the effect size (Hedges' d) on both species richness and abundance. In the LMMs, we used retention level, i.e. the percentage of the forest stand retained at the stand-scale, and the four landscape indices and other study-specific variables as explanatory variables. Taxonomic group identity (eight groups), retention type (four types), and habitat preference (four categories) were used as random terms. The percentage of forest area in the surroundings and the retention levels were arcsine-transformed, and the contiguity and fractal dimension indices were log-transformed to improve data normality. For each of the three radii, we used a backward stepwise selection to obtain the minimum models with fixed terms and random intercepts (Murtaugh 2009). Based on these models, we manually constructed all possible combinations of models with a random slope(s). This procedure resulted in more than 200 models with different explanatory variables, with random slope, random intercept, or both random slope and intercept for a given response variable. Using the lowest Akaike's information criterion (AIC) values amongst the candidate models, we determined which models were the most parsimonious. Note that our approach for variable selection aimed to be as objective as possible: model selection based on scientifically pre-informed hypotheses is not feasible because of many potentially important, but hard-to-measure, variables at both the stand- and landscape scale. Instead, we conducted variable selection by quantifying the values of log-likelihood, Δ AIC and Akaike weight for different candidate models with different explanatory variables (models with Δ AIC values <10). For fixed explanatory variables selected in the most minimum models, we also calculated the sum of Akaike weights. This helps us to further identify primary variables that explain biodiversity responses to retention practices. Then, to see how the various explanatory variables influenced the effect size, we excluded one of these variables from the most parsimonious model, and checked for an increase in the AIC value (Δ AIC). Furthermore, we separately repeated the above model selection for each of the species groups with different habitat preferences (for forest-dependent species, open habitat species, and generalist species). This was carried out only for the abundance metric, because it had sufficient information ($n = 779$ comparisons). For species richness ($n = 127$ comparisons), the majority of the studies did not specify the habitat preference for the species (Table S1). Note that our analyses relied on variables with different spatial perspectives: retention level, plot size, and time-since-logging were stand-scale metrics, whilst the other four metrics were based on the landscape scale. To separately evaluate the effects of these different scales on biodiversity responses, we

modelled abundance responses using only the retention level as an explanatory variable, which is known to affect Hedges' d values (Mori & Kitagawa 2014), and we compared the results based on the stand-level with those with the landscape effects. For all statistical analyses, we used R software 3.2.3.

Results

The results of the model selection to evaluate biodiversity responses to retention forestry are summarized in Table 1. The data, including all habitat preference categories, show that the differential responses of each species group to retention levels (percentage of trees retained within a retention cut) had the largest effect on determining biodiversity responses, regardless of the biodiversity metrics and spatial scales considered (Table 1). This indicates the fundamental importance of taxon-specific habitat preferences for determining biodiversity responses to retention forestry. For the landscape indices, the contiguity index for forest fragments within a landscape was, in general, the most important predictor determining the biodiversity responses to retention forestry (Tables 1 and S2), although fractal dimension and forest cover were also generally selected in the most parsimonious models (Table 1). Hedges' d values for species richness decreased significantly with increasing contiguity (Fig. 2a–c). Furthermore, the above responses of species richness to forest contiguity were more remarkable (i.e. the slope increased) when analysed at larger spatial extents (Fig. 2a–c). Hedges' d values for abundance similarly decreased with increasing contiguity, but the trend was weak and only marginally significant at a focal radius of 5 km (Fig. 2d–f). No significant changes in Hedges' d values for both species richness and abundance were observed in relation to the retention practice along the gradients of fractal dimension and forest cover (none of the standardized coefficients were significant at $P > 0.05$). Perimeter–area ratio as a landscape metric, and study plot size and time-since-logging as stand-level properties were not selected in the parsimonious models.

Biodiversity responses to retention logging varied across species groups with different habitat preferences (Table 1), and thus each species group was individually analysed for abundance responses (Tables 2, S3 and S4). The results showed that three of the four landscape indices remained in the best models at all spatial scales, and these models were always a better predictor than those that did not consider landscape effects (Table 2). That is, although responses varied amongst habitat preference categories, ignoring the landscape context generally decreased the goodness of the model fit for predicting biodiversity responses to retention forestry. Regarding the abundance of forest-dependent species, retention level was not a selected variable when considered with the landscape indices (Tables 2 and S3), and thus no change in their abundance was observed along the gradient of retention levels (Fig. 3a). Additionally, a

Table 1. Results of the linear mixed-effects models used to predict the responses of biodiversity to forest retention patches. The best models are based on the lowest value of the Akaike Information Criterion (AIC). For species richness responses, the best models included fractal dimension index (FD), percentage of forested areas (PFA), and contiguity index (CI) as an explanatory variable (fixed effects), individual study as a random intercept (1 | Study), and taxon-specific responses to percentage of forested areas (PFA | Taxon) and differential responses of each habitat preference category of species to retention levels (RL | Habitat) as a random slope, regardless of the radius size (1, 3, or 5 km) from a study site. The best models for abundance responses included fractal dimension and contiguity indices as explanatory variables, individual study as a random intercept, and differential responses of each habitat preference category of species to retention levels as a random slope, regardless of the radius size (1, 3, or 5 km) from a study site. An increase in AIC value (Δ AIC) represents how the fitness of a selected model decreases after removing a focal variable from the model. Fixed effects of the best models are shown (with standard deviation). See Table S2 for additional information about the relative importance of each explanatory variable amongst the different candidate models

Response variable	Focal radius	Model	K	log-likelihood	AIC	Δ AIC
Species richness	1 km	Best model [\sim CI + FD + PFA + (1 Study) + (PFA Taxon) + (RL Habitat)]	12	-165.1	354.2	0
		Fixed effects of the best model [CI: -14.3 ± 7.9 , FD: -6.2 ± 9.7 , PFA: 2.4 ± 2.7]				
		<i>Parameter excluded from the best model</i>				
		–(Retention levels Habitat preference)	9	-197.6	413.1	58.9
		–Contiguity index	11	-169.8	361.6	7.4
		–Fractal dimension index	11	-168.4	358.9	4.7
	3 km	–(Percentage of forest areas Taxon)	9	-170.3	358.6	4.4
		–Percentage of forest areas	11	-167.4	356.8	2.6
		Best model [\sim CI + FD + PFA + (1 Study) + (PFA Taxon) + (RL Habitat)]	12	-161.2	346.3	0
		Fixed effects of the best model [CI: -33.9 ± 11.6 , FD: -15.2 ± 10.2 , PFA: 4.4 ± 5.1]				
		<i>Parameter excluded from the best model</i>				
		–(Retention levels Habitat preference)	9	-194.0	405.9	59.6
	5 km	–(Percentage of forest areas Taxon)	9	-170.0	358.0	11.7
		–Contiguity index	11	-167.9	357.8	11.5
		–Fractal dimension index	11	-165.3	352.6	6.3
–Percentage of forest areas		11	-164.1	350.1	3.8	
Best model [\sim CI + FD + PFA + (1 Study) + (PFA Taxon) + (RL Habitat)]		12	-161.8	347.7	0	
Fixed effects of the best model [CI: -37.6 ± 16.5 , FD: -11.1 ± 10.4 , PFA: 7.5 ± 5.1]						
Abundance	1 km	<i>Parameter excluded from the best model</i>				
		–(Percentage of forest areas Taxon)	9	-196.4	410.8	63.1
		–(Retention levels Habitat preference)	9	-170.0	358.0	10.3
		–Contiguity index	11	-167.8	357.6	9.9
		–Fractal dimension index	11	-165.6	353.3	5.6
		–Percentage of forest areas	11	-165.4	352.9	5.2
	3 km	Best model [\sim CI + FD + (1 Study) + (RL Habitat)]	8	-1376.9	2769.8	0
		Fixed effects of the best model [CI: -0.3 ± 2.1 , FD: 1.4 ± 3.2]				
		<i>Parameter excluded from the best model</i>				
		–(Retention levels Habitat preference)	5	-1462.5	2935.1	165.3
		–Fractal dimension index	7	-1379.1	2772.1	2.3
		–Contiguity index	7	-1378.6	2771.1	1.3
	3 km	Best model [\sim CI + FD + (1 Study) + (RL Habitat)]	8	-1375.6	2767.1	0
		Fixed effects of the best model [CI: -3.5 ± 2.4 , FD: 0.1 ± 2.8]				
		<i>Parameter excluded from the best model</i>				
–(Retention levels Habitat preference)		5	-1375.6	2934.1	167.0	
–Contiguity index		7	-1377.5	2770.1	3.0	
–Fractal dimension index		7	-1462.0	2769.0	1.9	

(continued)

Table 1. (continued)

Response variable	Focal radius	Model	<i>K</i>	log-likelihood	AIC	Δ AIC
	5 km	Best model [\sim CI + FD + (1 Study) + (RL Habitat)] Fixed effects of the best model [CI: -3.6 ± 1.9 , FD: -0.9 ± 2.5] <i>Parameter excluded from the best model</i>	8	-1375.5	2767.0	0
		-(Retention levels Habitat preference)	5	-1462.6	2935.1	168.1
		-Contiguity index	7	-1378.8	2771.5	4.5
		-Fractal dimension index	7	-1377.4	2768.8	1.8

model including a fixed effect of retention levels, instead of the landscape indices, substantially decreased the model fit (Δ AIC = 10.4; Table 2). Regarding the abundance of open habitat and generalist species, retention level was a selected variable (Tables 2 and S3), and their Hedges' *d* values significantly decreased with increasing retention levels (Fig. 3b,c); however, the landscape

indices (especially forest contiguity) were relatively more important than the retention levels (Table 2). Results for the sum of Akaike weights also supported this trend (Table S3). Additionally, models without landscape consideration (models with a fixed effect of retention level only) showed larger increases in the AIC value (Δ AIC = 9.6 and 11.1) than those without retention level

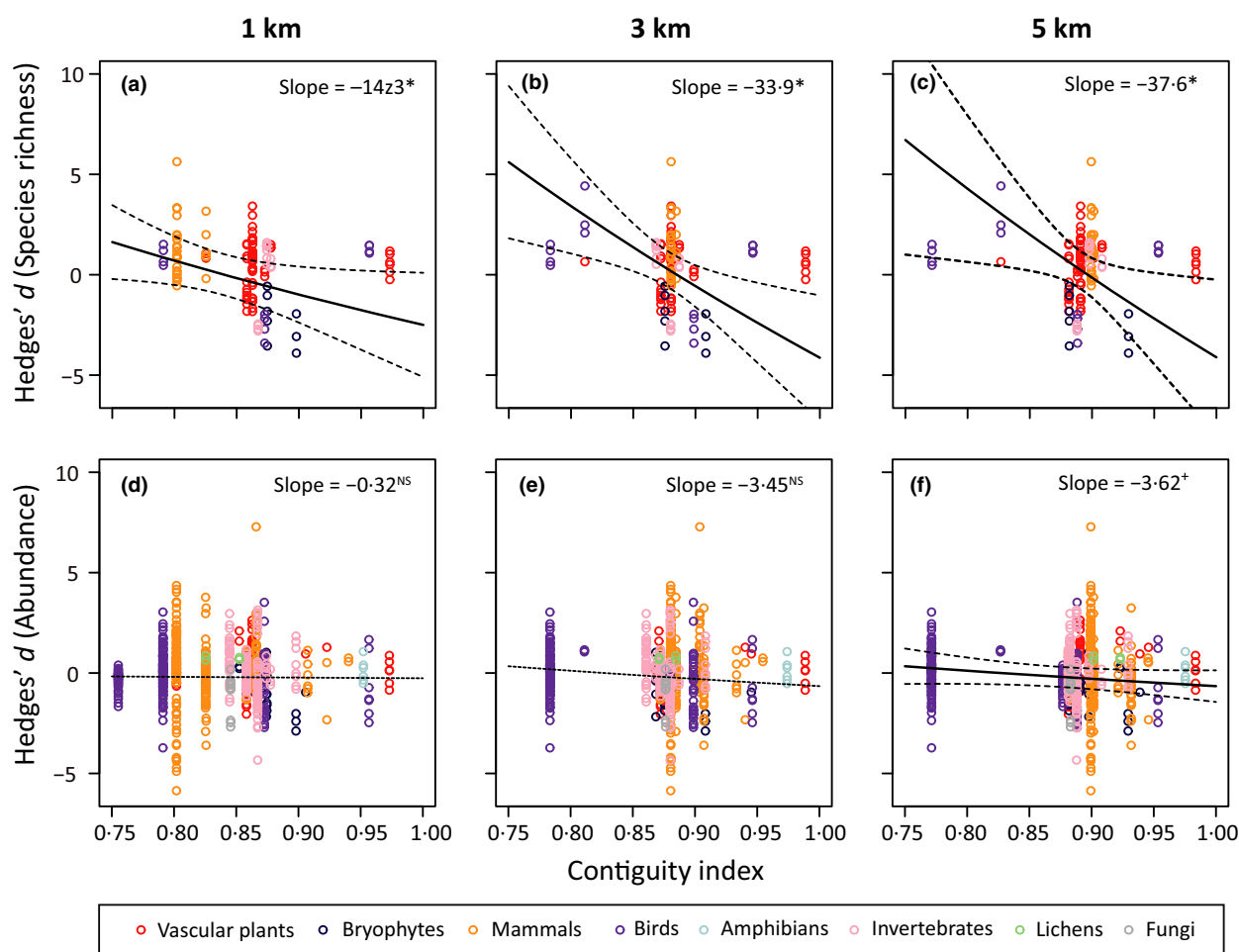


Fig. 2. Biodiversity responses to forest contiguity. The values of Hedges' *d* for species richness (a–c) and abundance (d–f) with a radius of 1 km (a and d), 3 km (b and e) and 5 km (c and f) are shown. Different colour symbols indicate different taxonomic groups. The solid lines indicate the linear mixed-effects model fit (Table 1 summarizes the best models), and dashed lines are 95% confidence intervals (a–c). The dotted (d–e) and solid (f) lines indicate the linear mixed-effects model fit (Table 1 summarizes the best models), and dashed lines are 90% confidence intervals (f). Slope values of the linear mixed-effects model fit are shown with significance levels; * $P < 0.05$, + $P < 0.1$, N.S. $P > 0.1$.

Table 2. Results of the linear mixed-effects models used to predict the responses of abundance to forest retention patches at the focal radius of 5 km. The best models are based on the lowest value of the Akaike Information Criterion (AIC). The best models for abundance responses included percentage of forested areas (PFA), fractal dimension (FD), contiguity indices (CI) and retention levels (RL) as explanatory variables (fixed effects), and individual study (1 | Study) as a random intercept, regardless of habitat preference category. Results at other spatial scales (1 km and 3 km of the radius) are shown in Table S4. An increase in AIC value (Δ AIC) represents how the fitness of a selected model decreases after removing a focal variable from the model. Fixed effects of the best models are shown (with standard deviation)

Habitat preference	Model	K	log-likelihood	AIC	Δ AIC
Forest	Best model [\sim CI + FD + PFA + (1 Study)]	6	-690.6	1393.2	0
	Fixed effects of the best model [CI: -5.1 ± 9.1 , FD: -1.9 ± 6.4 , PFA: -0.1 ± 2.3]				
	<i>Parameter excluded from the best model</i>				
	-Contiguity index	5	-693.9	1397.7	4.5
	-Fractal dimension index	5	-693.4	1396.8	3.6
	-Percentage of forest areas	5	-692.4	1394.7	1.5
Open	Best model [\sim CI + FD + PFA + RL + (1 Study)]	7	-327.0	668.0	0
	Fixed effects of the best model [CI: 8.9 ± 11.0 , FD: -4.7 ± 7.8 , PFA: -3.2 ± 3.4 , RL -1.0 ± 0.4]				
	<i>Parameter excluded from the best model</i>				
	-Contiguity index	6	-330.7	673.3	5.3
	-Fractal dimension index	6	-330.3	672.5	4.5
	-Percentage of forest areas	6	-329.8	671.7	3.7
General	Best model [\sim CI + FD + PFA + RL + (1 Study)]	7	-190.0	394.0	0
	Fixed effects of the best model [CI: -11.1 ± 16.2 , FD: -6.0 ± 14.3 , PFA: 2.8 ± 4.6 , RL -1.4 ± 0.6]				
	<i>Parameter excluded from the best model</i>				
	-Contiguity index	6	-194.0	399.9	5.9
	-Fractal dimension index	6	-193.7	399.4	5.4
	-Retention levels	6	-193.0	398.0	4.0
	-Percentage of forest areas	6	-192.7	397.3	3.3
	<i>Model with a fixed effect of retention levels only</i> [\sim RL + (1 Study)]	4	-198.6	405.1	11.1

as an explanatory variable (Δ AIC = 3.2 and 4.0) (with a focal radius of 5 km; Table 2). Similar results were obtained when the models were analysed with focal radii of 1 and 3 km (Table S4). Results for the sum of Akaike weights further showed that the landscape indices, especially contiguity index followed by fractal dimension, had larger influences on the model fit than retention levels (Table S3). In summation, in addition to the retention level as a stand-level property, the effectiveness of retention actions within the stands can be largely affected by the landscape properties, depending on the habitat preferences of species.

Discussion

The retention practice at harvest, which is oriented to emulate natural processes (Lindenmayer & Franklin 2002; Gustafsson *et al.* 2012; Lindenmayer *et al.* 2012), has been quantitatively proven to be effective for conserving local biodiversity at the stand-scale in forest landscapes (Fedrowitz *et al.* 2014; Mori & Kitagawa 2014). However,

insights into the effectiveness of tree retention in relation to landscape configuration are still lacking. Here, we found that removing the landscape indices largely reduced the goodness of the model fit (Tables 1 and 2), suggesting the fundamental importance of landscape properties.

We found that, amongst different influences of landscape properties, biodiversity can be especially affected by connectedness between forest fragments, i.e. landscape contiguity, although other landscape variables should have synergetic influences on biodiversity responses to retention practices (Tables 1 and 2). Interestingly, retention approaches were more effective in more fragmented landscapes, compared with less fragmented landscapes (Fig. 2). This was also the case for abundance, although the trend was rather weak (Fig. 2). The increase in the effectiveness of retention with increasing fragmentation may seem counterintuitive, but it is in agreement with theoretical expectations based on analyses of agri-environmental schemes. Several authors have suggested that management interventions for biodiversity are more effective in relatively simple landscapes than in complex

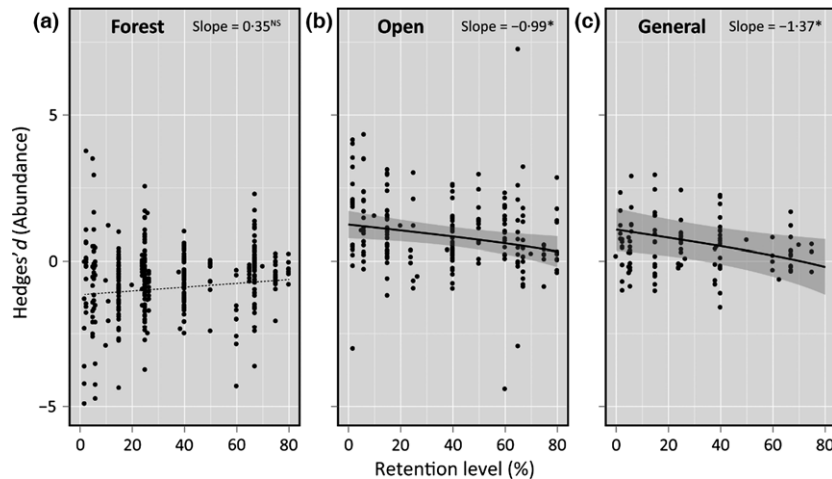


Fig. 3. Abundance responses to retention levels (percentage of trees retained within a retention cut). The values of Hedges' d for abundance of forest-dependent (a), open habitat (b) and generalist species (c) are shown. Solid black lines indicate mixed-effects model fit based on the best models (described in Table 2), and shaded areas represent 95% confidence intervals. Slope values are shown with significance levels; N.S. $P > 0.05$, $*P < 0.05$. For open habitat and generalist species, abundance responses to retention levels were significantly ($P < 0.05$) negative (b and c). For forest-dependent species, a dotted line based on the model fit with a fixed effect of retention levels only (Table 2) is shown as a reference (a). Also see Fig. S2 that tested abundance responses of these species categories to retention levels when data from clear-cut (i.e. zero values of retention levels) are included in the analyses.

landscapes ('the intermediate landscape-complexity hypothesis' Tscharntke *et al.* 2012, in which there is a hump-backed response curve of management effectiveness in relation to landscape complexity). Empirical support has been found mainly from studies of agricultural landscapes (Rundlöf & Smith 2006; Concepción, Díaz & Baquero 2007; Fischer, Stott & Law 2010) and, to a lesser extent, of forests (Pardini *et al.* 2010). The proposed mechanisms behind this response pattern are that in landscapes with large transformations of natural forests, species pools are depleted, implying that relatively few forest species are available for colonization. In landscapes in which natural forests are largely intact, biodiversity is already high and management actions have only marginal effects (Tscharntke *et al.* 2005, 2012). Further theoretical development has suggested that although habitat amount is often a stronger driver of population dynamics than habitat configuration (Fahrig 2013), spatial configuration should be observable in the mid-range of the habitat area gradient. This occurs because beta diversity (implying the coexistence of generalist and specialist species), as well as fragment variability (patch shape and size), is highest in landscapes of intermediate complexity (Villard & Metzger 2014). Another possibility is that fragmented landscapes have longer forest edges and more emigrants from forests into secondary habitats, although edge effects in fragmented landscapes can vary amongst species (Ricketts 2001; Hames *et al.* 2008). Note that we did not find a hump-backed response curve, but rather a linear relationship, between conservation effectiveness and landscape complexity. This probably occurred because the studies analysed here were made in landscapes with rather high connectedness, as indicated by a minimum contiguity index of approximately 0.75. That is, they were in the

right-hand side of the hump-backed curve. These results are consistent with meta-analyses of agri-environmental schemes (Batary *et al.* 2011; Scheper *et al.* 2013).

Importantly, we found that abundance responses varied according to the habitat requirements of different species (Fig. 3), likely resulting from differential responses of species to habitat fragmentation and degradation (e.g. Brosi *et al.* 2007; Jauker *et al.* 2009) and management interventions (including responses to retention actions; e.g. Matveinen-Huju *et al.* 2006). Thus, our results for the overall responses of forest taxa to set-aside actions (analysed with the LMM with random effects by different taxa) should be interpreted with this possibility in mind. Indeed, retention at harvest does not always promote or benefit biodiversity across different species groups in a similar manner (Fig. 3; Table 2). Unlike forest-dependent species, the abundances of open habitat and generalist species declined with increasing retention levels (Fig. 3). Note that the lack of change or response in the abundance of forest-dependent species along the retention levels (Fig. 3; Table 2) does not indicate that management should not consider the amount of trees retained within the stands. In fact, when analysing the biodiversity responses in clear-cut stands as well (provided in Table S1), retention levels were the most significant predictor of forest-dependent species (explained in the caption to Fig. S2), and their abundances significantly increased with increasing retention levels (Fig. S2a). In summation, although the responses vary across taxa according to habitat preferences, stand- and landscape-level properties have synergistic influences on the conservation outcome in retention forestry.

Because our study is the first to analyse the efficiency of retention practices in forestry in relation to stand and

landscape factors, further studies will be needed to achieve a more comprehensive understanding of their scale dependence. Our results reflect early responses to retention forestry because this type of practice was introduced only a couple of decades ago (Franklin *et al.* 1997), and thus older stands with legacies in the form of old trees and tree groups are not available for study. A limited number of studies that followed biodiversity over time in retention cuts, over a maximum of approximately 20 years, indicate rapid species dynamics (e.g. Halpern *et al.* 2012). Local extinctions are evident, but there are also clear processes of colonization (Lundström *et al.* 2013). Because the dispersal to retained trees most likely depends on species pools surroundings stands, landscape effects may become more pronounced with time. Thus, we found the time-since-logging variable to be less important; however, this result does not necessarily indicate that temporal scales are less influential, because uncertainties remain because of the limited number of case studies, as well as the relatively short study durations, in the present dataset. Testing spatial influences was possible in this study, but doing so in terms of temporal scales was not feasible because of the potentially lagging responses of taxa to anthropogenic influences. Thus, we call for further studies to address such uncertainties.

There are other caveats of our study. First, we found that species richness and abundance could be maintained at high levels by implementing a retention practice; however, these findings do not necessarily ensure the maintenance of other facets of biodiversity. Changes in species composition in response to retention forestry are still largely uncertain. Our results imply that species richness could be a summary index of rare species, rather than common species; that is, many rare species may be sensitive to landscape structure. Second, we did not separate managed and unmanaged forests in the landscapes analysed. Landscape effects on the outcome of retention actions could differ if analysed only for managed forests. Third, our dataset is largely biased to temperate forests (Table S1), and, thus, further empirical and experimental evidence are desired to test for possible differences in diversity responses to retention practices between biomes with different land-use histories and natural disturbance regimes. Lastly, because of data limitations, our results are based on linear models; however, it is possible that biodiversity responses to human influences could be nonlinear (Sasaki *et al.* 2015). If this is the case and certain thresholds for levels of retention and land-use intensification within a stand could be determined, such information would be useful for management planning and policy making.

Implications

Our results indicate that this environmentally adapted forestry model is effective for conserving forest biodiversity, particularly in landscapes with moderate levels of forest fragmentation. However, our study also suggests that the

application of retention forestry in areas with very large tracts of previously unlogged forests is less beneficial, and alternatives, such as setting aside large reserves, may be more desirable. Note that identifying the boundary between these two types of landscapes is not feasible, and thus further studies are necessary. It is also important to estimate the opportunity costs of retention practices and compare them with those of establishing nature reserves, which would be informative for policy-makers considering different land allocation options, although quantifying this is beyond the scope of the present study. Additionally, we suggest that the adoption of retention practices could be less effective in highly degraded landscapes. In such situations, urgent restoration actions would be needed, and localization close to core biodiversity areas will be an important consideration, in an effort to reduce the dispersal distance for various species. Our study does not fully discourage the actions of set-aside forestry as a small-scale measure for conservation, even in regions with high levels of landscape fragmentation, because any such actions would be, in reality, encouraged for restoration. Similar to the statement made by Batary *et al.* (2011), a one-size-fits-all approach to conservation is neither efficient nor desirable. Thus, we recommend that forest management should be flexible by considering landscape properties when implementing retention practices. Furthermore, similar consideration should be given to taxa that are of interest, as stand-level tree retention, which benefitted forest-inhabiting species regardless of the retention level (Fig. S2; Mori & Kitagawa 2014), was not necessarily favourable for some species, such as those that prefer open habitats (Fig. 3).

A retention practice is an example of land-sharing (Gustafsson *et al.* 2012), but as occurs in agricultural systems, a strict choice between land-sharing and land-sparing is seldom feasible (Green *et al.* 2005; Paul & Knoke 2015) because of the nature of historical land ownership patterns and other socioeconomic factors that restrict freedom of action (Fischer *et al.* 2008). Importantly, land ownership patterns, socio-political borders, and ecological boundaries are often spatially mismatched, which may impose additional management and conservation costs (Dallimer & Strange 2015; Gustafsson *et al.* 2015). Our findings suggest that biodiversity responses to the same local management action can have different consequences because of the landscape effects that can emerge beyond the land ownership pattern or management unit. Note that whilst our results are mainly from temperate forests, followed by boreal forests, our findings could be widely applicable to forests in other regions, such as tropical forests, although further studies are needed to test this possibility.

In some temperate and boreal regions, retention actions are often important requirements as a part of certification standards (Auld 2014), but they are often prescribed in a rather strict and quantitative way (McDermott, Cashore & Kanowski 2010; Johansson *et al.* 2013). Thus, the

integration of a landscape perspective into forestry management certification may need to be adjusted. We advise certification organizations to carefully consider new scientific knowledge when standards are revised, which requires good communication and participation of the scientific community. Current certification schemes are commonly negotiated at the national or sub-national levels (e.g. Keskitalo *et al.* 2009), but special occasions, such as meetings to enable trans-national coordination, may be needed to account for large-scale land-use patterns. Overall, to increase opportunities for local and regional adaptation, carefully planned conservation schemes with large-scale perspectives, as well as local-scale actions, will become critical for effective forest management and conservation planning.

Authors' contributions

A.S.M. designed the study and analysed data. A.S.M. and L.G. primarily wrote the manuscript. S.T. compiled data, conducted image and landscape analyses, and gave substantial inputs into the paper.

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Data accessibility

All data are available in Table S1.

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Data used for this study.

Table S2. Results of the candidate models with different fixed effects for each focal response variable and spatial scale.

Table S3. Results of the candidate models with different fixed effects to predict abundance responses for each species groups at different spatial scales.

Table S4. Results of the linear mixed-effects models used to predict the responses of biodiversity (abundance) to forest retention patches at different spatial scales.

Fig. S1. The relationships between sample size with the variance and the Hedge's *d* effect size for a) species richness and b) abundance.

Fig. S2. Abundance responses to retention levels (percentage of trees retained within a retention cut).