



Habitat configuration influences mammal populations at a wider spatial extent than habitat composition: a meta-analysis of forest mammal datasets

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Abstract

Context The spatial extent at which landscape variables most strongly influences wildlife populations (i.e., scale of effect) is of key importance to ecology and conservation. Many factors can influence scales of effect, but these relationships are poorly understood. In particular, the way scales of effect vary with different landscape metrics has not been extensively tested.

Objectives Our study tested whether metrics of landscape configuration have wider or narrower scales of effect than habitat composition. We also examined how species traits and landscape context influence the magnitude of differences in scales of effect between metrics.

Methods We calculated scales of effect for four metrics of habitat configuration and one metric of composition directly from species presence/absence data in online repositories including 102 species of forest mammals from 33 studies across the globe. We then

compared the magnitudes and variability of scales of effect using Hedge's g .

Results Two metrics of configuration (flux and patch density) had significantly wider scales of effect than habitat composition, while the differences between the other two metrics of configuration and composition were not statistically significant. The magnitude of the difference between metrics varied among samples, but none of the factors tested explained this variability.

Conclusions For forest mammals, the scale of effect of a configuration metric can be expected to be 15–20% wider than a composition metric. However, this pattern may not hold for metrics of configuration that do not quantify attributes of the landscape that mediate species dispersal or that are correlated with the metric of composition.

Keywords Scale of effect · Spatial extent · Dispersal · Landscape metric

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Introduction

The relationships between attributes of the landscape and species' distributions and population dynamics are often scale dependent (Wines 1989; Levin 1992), making the scale at which researchers measure these landscape attributes important for ecological research, land management, and conservation. Landscape connectivity is one of these scale-dependent

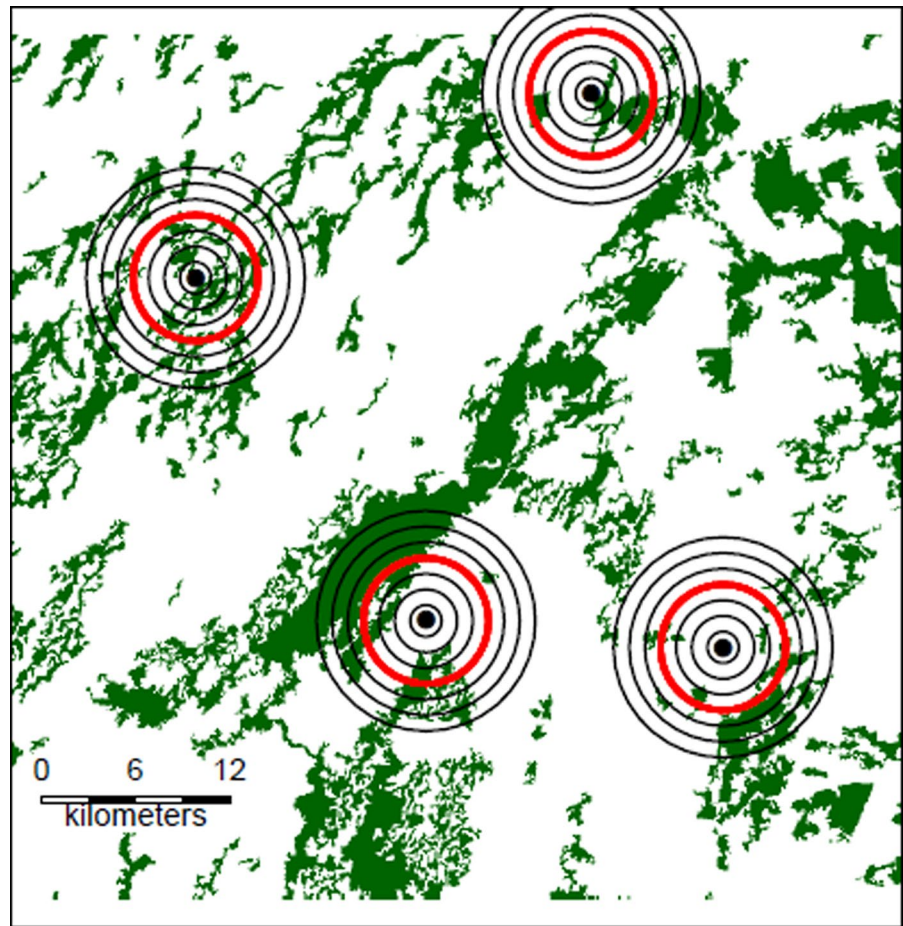
attributes that mediate movement and dispersal of wildlife across heterogeneous landscapes (Taylor et al. 1993; Crooks and Sanjayan 2006). Landscape connectivity can promote movement that expands individuals' access to resources across their home ranges and across wider scales by contributing to successful dispersal, demographic rescue, and patch colonization (Hanski 1998; Elmhagen & Angerbjorn 2001). Structural connectivity of a landscape is commonly measured with metrics of habitat composition and configuration (Calabrese & Fagan 2004; Prugh 2009), which can be refined to represent functional connectivity by incorporating movement information that is specific to a species (Crooks and Sanjayan 2006). Habitat composition describes the proportion and diversity of land cover types (e.g., percent forest cover); whereas configuration describes the shape and spatial arrangement of this cover (e.g., average inter-patch distance). Habitat composition can increase landscape connectivity by increasing the proportion of suitable habitat, and consequently the number of traversable paths on the landscape and the probability of an individual's survival during dispersal (Fahrig 2013). Habitat configuration can increase landscape connectivity independently of habitat composition by influencing the spatial arrangement of patches that can ultimately form corridors, stepping stones, and redundant paths (Bierwagen 2007; Fletcher et al. 2014; Herrera et al. 2017). As such, metrics of habitat configuration and composition provide complementary perspectives on the relationship between landscapes and the population dynamics and distributions of organisms occupying these landscapes. However, the scale (i.e., spatial extent) at which these metrics are quantified is crucial to understand and accurately assess how aspects of the landscape, such as connectivity, shape ecological processes (Jackson & Fahrig 2015). Thus, measurements of the landscape need to be made at an appropriate scale. This scale may differ in response to numerous factors, including between metrics of habitat configuration and composition.

The spatial extent at which a landscape attribute most strongly correlates with a biological variable of interest is known as the "scale of effect" (Holland et al. 2004; Fig. 1). In the context of scale of effect, these biological variables can include occurrence, abundance, or genetic diversity; however other variables such as community-level biodiversity can also be biological variables of interest. The assessment

of a landscape attribute at a scale other than its scale of effect can decrease the statistical strength or even change the nature of this landscape-wildlife relationship (De Knegt et al. 2010; Martin et al. 2016). For example, the correlation between patch isolation and the proportion of woody matter in the diet of howler monkeys varied from minor ($r^2 < 0.2$) to strong ($r^2 > 0.8$) depending on the scale at which patch isolation was measured (Ordóñez-Gómez et al. 2015). Even studies that test multiple scales can miss the scale of effect by testing a range of scales that does not extend near or far enough from the focal locations or has too wide of gaps between scales (Jackson & Fahrig 2015). The quantification of landscape metrics at too small a scale likely will fail to account for the influence of factors and processes occurring at broader scales such as access to distant resources, immigration from distant sources, or distant anthropogenic pressures (Jackson & Fahrig 2015). Similarly, the quantification of landscape metrics at too wide a scale will likely include extraneous information thereby increasing the uncertainty in the observed relationship between the landscape metric and biological response variable (Jackson & Fahrig 2015). The ability to approximate scale of effect a priori would improve studies aimed at evaluating how landscape attributes mediate ecological processes by reducing the chance of quantifying landscape attributes at an incorrect scale. Similarly, a priori approximations would support key landscape level decisions (e.g., in the design of corridors or reserve networks) when empirically derived scales of effect are lacking. However, current understanding of the main factors that mediate scale of effect is nascent, and many have not been assessed empirically.

Factors related to species traits and landscape attributes (i.e., regional context) are predicted to mediate scales of effect (Miguet et al. 2016) because the scale of effect relates to the spatial extent over which species perceive and interact with the landscape (Nathan et al. 2008). The species traits predicted to mediate scale of effect are predominantly associated with mobility (e.g., dispersal distance, home range size, and body size) and demography (e.g., reproductive rate; Jackson and Fahrig 2012; Miguet et al. 2016). For example, large bodied species are predicted to have larger scales of effect than smaller species across response variables (e.g., demographic trends, species occurrence, genetic diversity)

Fig. 1 Simulated representation of scale of effect. Green areas represent forested patches; white background indicates non-forest habitat. Black points indicate sample locations where a biological response variable was measured (e.g., species distribution, abundance, biodiversity). Black concentric circles represent different spatial extents at which a landscape explanatory variable could be quantified (e.g., patch density, percent forest cover, interpatch distance). The red circle indicates the spatial extent at which the explanatory landscape variable most correlates with the biological response variable



because they interact with a wider extent of the landscape via larger home ranges and longer dispersal distances (Thornton & Fletcher 2014). Simulation studies provide strong support for the influence of species traits on scale of effect (Jackson & Fahrig 2012; Ricci et al. 2013), but most empirical studies fail to detect this pattern (Jackson & Fahrig 2012, 2015; Miguët et al. 2016; Galán-Acedo et al. 2018). Reviews of empirical studies largely attribute this failure to suboptimal measurement of scales of effect, for example testing too narrow a range of scales or too few scales (Ricci et al. 2013; Jackson & Fahrig 2015; Miguët et al. 2016). However, other factors that influence scale of effect such as the regional context of the study site, the biological response variable researchers selected (e.g., species occurrence vs. species richness), and the landscape variable the researchers measured also could complicate detecting a relationship between species traits and scales

of effect in across-study comparisons (Martin 2018; Moraga et al. 2019; Amiot et al. 2021). A variety of factors related to regional context such as geographic location, regional fragmentation, or climate could increase or decrease scale of effect for biological response variables, in particular occurrence, because these factors influence processes such as dispersal and population dynamics that mediate species' distributions. For example, scales of effect are predicted to be wider in regions with a greater proportion of habitat because increased habitat facilitates longer dispersal movements (Miguët et al. 2016). Scale of effect also may vary with the landscape attribute used as an explanatory variable. For example, metrics that describe landscape attributes that promote long-distance dispersal (e.g., via enhancing landscape connectivity) are predicted to have a wider scale of effect than a metric that describes a landscape attribute that primarily impacts smaller-scale movements

within home ranges related to foraging and breeding (Miguet et al. 2016). This difference between scales of effect occurs because dispersal movements are often substantially longer than home range diameters. Although the effects of species traits on scale of effect have been examined across a range of taxa, considerably less is known about how scales of effect differ among landscape attributes such as habitat composition and configuration (Jackson & Fahrig 2015; Miguet et al. 2016).

Some researchers have hypothesized that the scale of effect of habitat amount (a metric of habitat composition) should be larger than that of habitat fragmentation (i.e., metrics of habitat configuration) across biological response variables (Miguet et al. 2016). This hypothesis is rooted in the idea that increasing habitat amount improves dispersal success by reducing mortality during dispersal; whereas increasing habitat fragmentation alters resource availability at the scale of an individual's home range by determining the amounts of core and edge habitat (Fahrig 2013). Simulations support this hypothesis (Jackson & Fahrig 2012), but empirical data are equivocal (Jackson & Fahrig 2015; Miguet et al. 2016). Alternatively, habitat configuration could have a wider scale of effect because habitat configuration could more directly promote species dispersal via corridors, stepping stones, and providing redundant pathways (O'Brien et al. 2006; Ferrari et al. 2007; Saura & Rubio 2010; Fletcher et al. 2018a, b), whereas habitat composition more directly promotes breeding and foraging success at the home range level via resource abundance. Finally, due to the multifaceted nature of configuration, whether configuration or composition have a wider scale of effect could vary depending on which metrics are being compared. A previous review of five empirical studies containing 26 comparisons between scales of effect of composition (primarily habitat amount) and configuration (primarily patch density) reported a nearly equivalent number of cases of configuration having a wider scale of effect than composition and vice versa (Miguet et al. 2016). These results may be inconclusive because the empirical studies reviewed might have tested an insufficient range and precision of scales, thus potentially missing the scale of effect. Also, these studies varied by many factors important for predicting scale of effect such as biological response variable (Miguet et al. 2016; Martin 2018), landscape metrics (Miguet et al. 2016),

and land-cover maps (Amiot et al. 2021). Overall, uncertainty remains as to whether habitat configuration or composition has a wider scale of effect.

We compare these competing hypotheses by conducting a meta-analysis of primary data to answer the question: do metrics of habitat configuration or composition have a wider scale of effect on species occurrence? Answering this question could support one of three competing hypotheses: (1) metrics of composition have wider scales of effect, (2) metrics of configuration have wider scales of effect, or (3) the metric assessed determines whether configuration or composition has a wider scale of effect. Corollary to our primary research question, when there was a significant difference between two metrics' scales of effect, we conducted an ad-hoc assessment to identify factors that could potentially explain this difference. Our experimental design overcomes common issues in studies of scale of effect in that we tested a wide range of scales, used consistent methods to estimate all scales of effect, and assessed a wide range of geographic locations.

Materials and methods

Study system

To assess the extent that metrics of habitat configuration and composition differ in their scales of effect, we conducted a meta-analysis of mammal distributions in fragmented forest landscapes. Mammals are appropriate taxa to test our hypothesis because they are well studied, many published datasets are available for meta-analysis, and the mechanisms by which landscapes mediate their demographic processes are relatively well-known compared to other taxa (Presley et al. 2019). Mammals also vary widely in species traits, facilitating the analysis of how these traits might mediate the magnitude of the difference between scales of effect (Supplementary Information (SI), Appendix 1).

We narrowed our analysis to forest mammals, namely those with forest listed as suitable habitat in IUCN Redlist (SI, Appendix 1; IUCN 2021), because they are more sensitive to changes in habitat composition and configuration than species with other habitat preferences (Keinath et al. 2017). Additionally, our analysis required calculation of scales of effect using

a consistent source of land cover information for all datasets (Amiot et al. 2021). The availability of a global forest cover database contributed to our selection of forest species, as opposed to other habitat preferences for which land cover data are less available. We excluded migratory species (i.e., most individuals regularly migrate large distances) because their distributions are influenced by landscapes not included in our analysis. We determined migratory behavior from IUCN information (SI, Appendix 1).

Literature review and data extraction

We calculated a standardized difference between scales of effect of configuration and composition directly from primary data. Extraction of effect sizes from existing literature was unfeasible because few studies compare scales of effect between metrics of landscape composition and configuration. Additionally, studies use different methods such as landscape metrics, buffer size ranges, and explanatory variables. Calculation of scale of effect directly from primary data allowed us to analyze the difference between scales of effect with a consistent set of methods to reduce among-study variability (Simmonds et al. 2005; Koricheva et al 2013). Our study is the first to compare a large number of scales of effect from wildlife populations around the globe using consistent methods.

We searched for primary data in January 2021 in Dryad, Web of Science (“Data Papers” only), and Knowledge Network for Biodiversity repositories. We used the search terms “wildlife”, “mammal”, “camera trap”, and “habitat fragmentation” in separate searches. “Camera trap” was included because these studies are particularly well suited for scale of effect analysis due to their ability to detect mammals (Tobler et al. 2008), and because they often include numerous sample locations. We found 2129 datasets combined across the three repositories. In primary data meta-analyses such as ours, the term “dataset” is equivalent to “study” in the traditional meta-analysis of published effect sizes. From the initial 2129 results, we selected datasets that reported a measure of distribution (i.e., presence/absence, abundance, or sign detection rate) and had greater than 10 sample locations for at least one species of forest mammal. Also, we selected datasets that occurred in landscapes fragmented at the scale of the study area (e.g., the

forest cover surrounding all study sample locations did not comprise one forest patch) because many metrics of habitat configuration or composition would not vary in a homogeneous landscape. Finally, we selected datasets for which geographic coordinates of sample locations could be obtained directly from the dataset or by contacting the authors. The type of biological response variable can influence scales of effect (Miguet et al. 2016; Moraga et al. 2019). Therefore, we converted abundance and sign rate to presence/absence in datasets that reported these metrics. A species was considered present if it had more than one detected individual or sign and absent otherwise. We excluded species that were present in all sample locations, and species present or absent in only one sample location in a dataset because calculating scale of effect requires variability in the response variable (i.e., species presence/absence). From the initial 2129 datasets, 33 met our criteria for inclusion (SI, Appendix 2, Appendix 3). Of these 33 datasets, 25 reported information for multiple species (mean = 5.1; range = 1, 16). A total of 107 unique species was represented with 26 species measured in multiple datasets. We assessed species that were included in multiple datasets separately because sampling methods and landscape contexts (which can affect scale of effect) differed among these datasets. Thus, the basic unit of analysis for our study was species per dataset, totaling 163.

For each dataset, we obtained a binary forest/non-forest map from Google Earth Engine (Gorelick et al. 2017), specifically, the Global PALSAR-2/PALSAR Forest/Non-Forest Map (Shimada et al. 2014). This map has 25-m pixel spatial resolution, defines forest as more than 10% canopy cover, and represents forest cover at year 2010. Among the datasets in our study, forest loss between 2010 and dataset publication year averaged 4% and never exceeded 8%. Forest cover loss was low in our selected datasets because these areas were located in previously deforested/fragmented regions, not on frontiers of deforestation. We did not assess forest cover gain due to the lack of accessible data past the year 2012, but we expect it to be similarly low or lower than forest cover loss because total forest area is decreasing globally (d’Annunzio et al. 2015). Therefore, we expect that forest cover information from a more precise date would not significantly change our measured metric values. We used the PALSAR map because of its accessibility, global

coverage, and fine-scale spatial resolution. Using one consistent source of land cover information to generate scale of effect estimates across all datasets was important as different land cover maps could add variability to scale of effect estimates (Amiot et al. 2021). Thus, even though calculating scale of effect with more detailed forest cover maps would be preferable for assessing individual species, we prioritized comparability between species and datasets by using one common source of land cover data.

Scale of effect calculation

We selected five metrics for scale of effect comparison. Four of these were metrics of habitat configuration: flux, patch density, mean Euclidean nearest neighbor distance (mean ENN), and cohesion. We tested multiple metrics of configuration because configuration is multifaceted and no one metric can capture all aspects of configuration. In contrast, percent forest cover captures habitat composition in a binary forest/non-forest landscape.

Flux is the summed probability of dispersal between all patches in a landscape by a species (Urban & Keitt 2001). We selected flux because it incorporates movement information specific to a species (i.e., represents functional connectivity). Flux utilizes graph theory to effectively quantify the contribution of each stepping stone on the landscape to overall connectivity (Foltête 2019). Patch density is the number of forest patches per square kilometer. We selected patch density as a computationally efficient index of habitat fragmentation (Trani & Giles 1999). Patch density is also one of the most widely used metrics of habitat configuration in scale of effect research (Miguet et al. 2016). Mean Euclidean nearest neighbor (mean ENN) is the average of the shortest edge-to-edge distance between a forest patch and its nearest neighboring patch for all patches across a landscape. Mean ENN measures an aspect of landscape configuration that is not well captured by the other metrics in our study. Cohesion represents the extent that forest pixels are clustered together versus evenly spread out (McGarigal 2015). We selected cohesion as a metric of habitat aggregation that has been shown to predict animal dispersal (Schumaker 1996). Percent forest cover is the proportion of a focal landscape that is covered by forest. We selected percent forest cover as our only metric of habitat composition because it

is the only meaningful metric of habitat composition in a binary landscape (SI, Appendix 4). Additionally, other scale of effect studies often use percent forest cover as the only metric of habitat composition (Bosco et al. 2019; Miguet et al. 2016; D. H. Thornton & Fletcher 2014). These five metrics resulted in four scale of effect comparisons: flux with forest cover, patch density with forest cover, mean ENN with forest cover, and cohesion with forest cover.

To make these scale of effect comparisons, we first calculated each of the five metrics in 63 concentric buffers of increasing radii surrounding all sample sites in each dataset. The first buffer was set at a 100-m radius surrounding a sample site, a buffer size much smaller than is typically considered for calculating scale of effect. An excessively small buffer size was chosen to minimize the risk of missing the true scale of effect. The radii of the subsequent nine buffers increased by 100-m intervals. After the first ten buffers (i.e., up to 1000-m radius), we increased the buffer radii to 500-m intervals because in larger landscapes smaller changes in buffer sizes (i.e., 100-m radii intervals) would produce nearly identical metric values as the previous buffer size. Similarly, we increased the buffer radii intervals to 1000-m starting at 25,000-m until a final buffer radius of 30,000-m. Thus, we used a total of 63 buffers (range = 100–30,000-m) around each sample location in every dataset to calculate our five landscape metrics. These buffer sizes ensured a sufficient range and precision of scales with which to identify a scale of effect and could be computed in a reasonable amount of time. This range of 63 buffer sizes is much wider and has a finer resolution than most other efforts to identify scale of effect (Thornton & Fletcher 2014; Jackson & Fahrig 2015; Miguet et al. 2016). Sample locations in a dataset were often within 30,000-m of each other; however overlapping buffers do not affect calculation of scale of effect (Zuckerberg et al. 2012).

To select a buffer size as the scale of effect for each species within a dataset, we compared the AIC scores of 63 generalized linear models with binomial distributions (Huais 2018). These models contained species presence/absence as the response variable and the landscape metric measured at the different buffer sizes as the explanatory variable. The buffer radius that produced the model with the lowest AIC score was identified as the scale of effect (SI, Appendix 4; Holland et al. 2004). We produced a measure

of variability for each scale of effect estimate by bootstrapping sample locations. First, we randomly selected sample locations from a dataset with replacement until we had as many sample locations as the original dataset (SI, Appendix 4; Efron and Gong 1983). As such, some sample sites were repeated and others excluded for a given iteration. We then used this set of random sample sites to generate one scale of effect estimate. To avoid including random sample location combinations for which a given landscape metric did not have a significant relationship with species presence/absence, we only considered buffer sizes for which the beta-coefficient of the landscape metric had a p -value < 0.05 . If an iteration did not produce any buffer sizes with a p -value < 0.05 , that iteration was skipped. We repeated this process until a total of 1000 statistically significant scales of effect were recorded for each species in each dataset (SI, Appendix 4). Post hoc analysis did not reveal any correlation between the number of repetitions needed to achieve 1,000 statistically significant scales of effect and the variability in a sample's scale of effect (SI, Appendix 7).

Scale of effect analysis

We used the mean and standard deviation from the 1,000 scales of effect produced by bootstrapped combinations of sample sites to calculate Hedge's g . A value of Hedge's g was calculated for each of the four comparisons between scales of effect of configuration and composition. Hedge's g is the difference between two means divided by their pooled standard deviation (SI, Appendix 4). As a rule of thumb, a Hedge's g of 0.2 represents a small effect, 0.5 a medium effect, and 0.8 a large effect (Cohen 1988); however, this should be interpreted in the context of what is being compared (e.g., a Hedge's g of 0.2 reducing child mortality is an important effect; Durlak 2009).

We assessed whether a metric of habitat configuration had a wider scale of effect than composition by calculating the overall effect and associated 95% confidence interval of meta-analysis models. These models contained Hedge's g as the response variable and no explanatory variables. We created a separate model for each of the four combinations of configuration/composition. To account for potential lack of independence among effect sizes for multiple species within the same dataset (e.g., shared regional context

and sampling methods), we compared three-level mixed effect models designed for meta-analyses that account for variance at three levels: sample, within dataset, and between dataset against similar models that account for variance at two levels: sample and between dataset, and selected the model structure with the lowest AIC score (SI, Appendix 4; Cheung 2019; Gucciardi et al. 2021). Once we selected a model structure, we considered the difference between two metrics' scales of effect as significant if the 95% confidence interval of a model's overall effect did not include zero.

We also tested the influence of seven explanatory variables on the magnitude of the difference between scales of effect in cases where the difference between scales of effect was significant. This was an exploratory hypothesis generating analysis rather than a hypothesis testing approach (i.e., detailed examination of the effect of one variable; Tredennick et al. 2021). We tested five species traits: body mass, habitat preference, trophic level, volant/non-volant, and home range size; and two variables related to the study area: geographic location and regional forest cover. We obtained body size from the PanTHERIA database (Jones et al. 2009), or from published literature in the rare instances a species' body mass was not present in PanTHERIA. We obtained home range sizes from the literature and averaged home range estimates if multiple studies existed. We designated a species as a forest specialist if forest was the only habitat listed as suitable in the IUCN Redlist (IUCN 2021), and as a generalist if other habitat types were suitable. These are not strict definitions, but rather indicate a species' ability to survive in multiple habitat types. We calculated regional forest cover as the percent forest cover across the entire study region for a dataset (i.e., 30-km buffer surrounding all sample points), and thus all species in a dataset shared the same value. Because regional forest cover is bound by an upper and lower limit (0 and 100), we tested a quadratic form of this variable. We compared AIC scores of two models containing only regional forest cover: one with a linear form, and another with the quadratic form. If the AIC score of these models differed by > 2 , we used the form with the lowest AIC for the full model of regional forest cover containing all explanatory variables. We selected the simpler linear form if models did not vary by > 2 AIC. For the geographic location of the study area, we

incorporated a binary variable indicating whether the dataset was collected in tropical or temperate latitudes (i.e., $\pm 23^\circ$ from the equator). The continuous variables in our study (i.e., body mass, home range, and regional forest cover) were centered and scaled. We considered a variable to have a significant influence on the magnitude of the difference between configuration/composition scales of effect if its beta coefficient p -value was < 0.05 . We used separate models for the four configuration/composition combinations.

Results

Difference between configuration and composition scales of effect

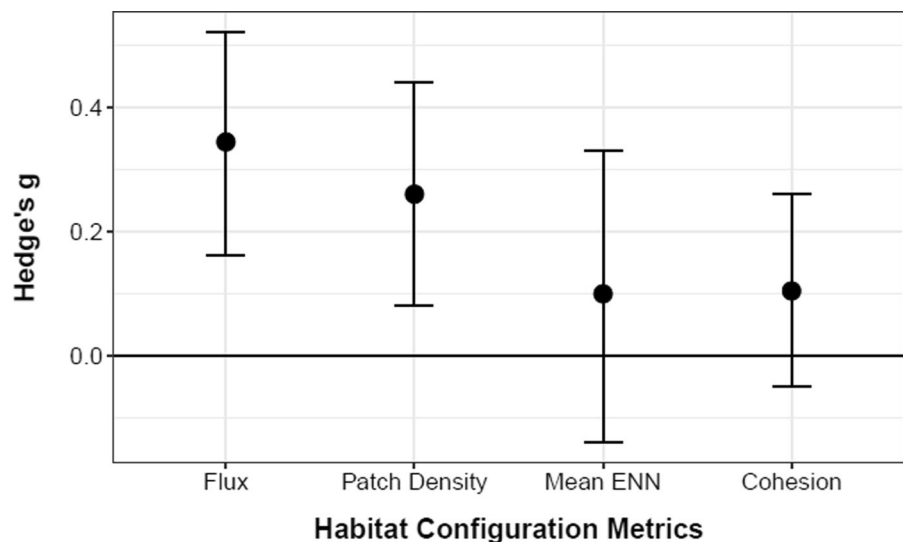
Habitat configuration had a significantly wider scale of effect than habitat composition in some cases, depending on the metric used for configuration. Flux and patch density had significantly wider scales of effect than forest cover (Hedge's g (g) = 0.34 ± 0.09 standard error (SE), and $g = 0.26 \pm 0.09$ SE, respectively; Fig. 2). In contrast, scales of effect of mean ENN and cohesion were not significantly different from the scale of effect of forest cover ($g = 0.10 \pm 0.12$ SE and 0.10 ± 0.08 SE; Fig. 2). In these four comparisons, we estimated overall effects with models that incorporated heterogeneity at three levels (i.e., sample, within dataset, and between datasets) because this model

structure was more strongly supported than models incorporating heterogeneity at two levels (i.e., samples and between datasets; $\Delta AIC > 1,000$). Tests of heterogeneity among these datasets indicated that variation was significantly greater than expected from sampling variance alone and, thus, adequate for these meta-analysis models (Cochran's Q_{flux} (Q) = 4.6×10^4 , $Q_{\text{pd}} = 5 \times 10^4$, $Q_{\text{mean ENN}} = 5.4 \times 10^4$, $Q_{\text{cohesion}} = 3.3 \times 10^4$; all four $p < 0.0001$).

Factors influencing the magnitude of the difference between scales of effect

Neither species traits (i.e., body mass, habitat preference, trophic level, volant/non-volant, home range size) nor regional context (i.e., geographic location and regional forest cover of the study area) explained the magnitude of the difference between scales of effect of metrics of flux and patch density and forest cover (all coefficients $p > 0.05$; Appendix 5). This is further revealed by non-significant tests of moderators (F) for both models ($F_{\text{flux-forest cover}} = 0.67$, $p = 0.72$; $F_{\text{pd-forest cover}} = 0.71$, $p = 0.69$). In both models, the variance (σ^2) of samples within studies ($\sigma^2_{\text{flux-forest cover}} = 0.74$; $\sigma^2_{\text{pd-forest cover}} = 0.77$) was greater than the variance among studies ($\sigma^2_{\text{flux-forest cover}} = 0.11$; $\sigma^2_{\text{pd-forest cover}} = 0.12$). We made inferences from meta-analysis models containing only a linear term for regional forest cover because adding

Fig. 2 Overall effects (mean $g \pm 95\%$ CI) for the differences in scales of effect of four metrics of habitat configuration compared to one metric of habitat composition (i.e., percent forest cover; $N = 163$ samples from 33 datasets). A positive Hedge's g value indicates a wider scale of effect for the metric of configuration than for composition



a polynomial term did not improve any model by > 2 AIC units.

Discussion

Metrics of habitat configuration and composition provide complementary information on attributes of the landscape, including connectivity, and there are competing hypotheses regarding which of these categories of metrics have the wider scale of effect. Our results showed that for mammals associated with forest habitat configuration has a wider scale of effect than composition, but only when flux and patch density were used to quantify configuration. The metric of configuration used to compare scales of effect matters because different metrics contain information about different aspects of the landscape. Our study provides empirical evidence that fills a previous knowledge gap regarding whether landscape metrics significantly vary in their scales of effect and which kinds of metrics tend to have wider scales of effect (Miguet et al. 2016). Based on our results, if a researcher knows the scale of effect of a metric of composition used to explain species occurrence, they can expect the scale of effect of certain metrics of configuration to be wider, particularly metrics that quantify aspects of the landscape important for dispersal and do not correlate with composition.

Difference in scale of effect of composition and configuration

The difference between the scales of effect of habitat configuration and composition (i.e., forest cover) depends on which metric of configuration is selected for comparison. Of the four metrics of configuration, flux had the greatest difference from forest cover in scales of effect. Flux likely had a wider scale of effect than forest cover because flux measures aspects of the landscape that more strongly mediate dispersal. Metrics related to dispersal are predicted to have a wider scale of effect than metrics that quantify landscape attributes that are more related to breeding and foraging success within a home range. This is because dispersal movements usually are longer than home range diameters (Miguet et al. 2016). Compared to the other metrics in this study, flux is more effective at measuring aspects of the landscape that influence dispersal

because it incorporates species-specific movement information (i.e., home range diameter) to estimate probable rates of dispersal for that species, making flux the only metric of functional connectivity in our study (Crooks and Sanjayan 2006). Also, flux is the only metric in our study to use graph theory to incorporate patch arrangement to quantify the extent a stepping stone corridor promotes dispersal (Calabrese & Fagan 2004; Foltête et al. 2012). Thus, unlike all other metrics, flux can distinguish between habitat patches that contribute to connectivity, and those that do not.

Of our three metrics of structural connectivity, only patch density had a significantly wider scale of effect than forest cover. A direct link between patch density and dispersal is not as clear as this link for flux. However, landscapes with lower patch density may promote dispersal by being less fragmented and more contiguous, thus allowing more movement without the need to interact with the matrix (Schtickzelle et al. 2006; Van Houtan et al. 2007; Thornton et al. 2011; Fletcher et al. 2018a, b; Fletcher et al. 2018a, b; Fahrig et al. 2019). In other circumstances a landscape with higher patch density may promote dispersal by having an increased number of stepping stones, thus providing more pathways across the landscape (Andreassen & Ims 2001; Coulon et al. 2010; Fahrig 2017; Karnatak & Wollrab 2020). These opposing mechanisms by which patch density can positively or negatively mediate dispersal might act simultaneously to diminish the extent patch density contributes to species dispersal, and could in part explain why previous comparisons of the scales of effect of patch density and forest cover produced mixed results regarding which was significantly wider (Ethier & Fahrig 2011; Feagan 2011; Flick et al. 2012; Ordóñez-Gómez et al. 2015; Galán-Acedo et al. 2018; Bosco et al. 2019; Gestich et al. 2019). However, by assessing 163 comparisons of scale of effect from numerous species and contexts using consistent methods, our study has produced empirical support that patch density has a wider scale of effect than forest cover. Similar to flux, the most likely reason for this difference is that patch density measures aspects of the landscape that more strongly mediate dispersal (either positively or negatively) than forest cover. However, across all datasets in our study, the values of flux and patch density were highly correlated across scales ($R^2 = 0.77$, Appendix 6). Thus, it is

possible that the information provided by patch density served as a proxy for the information provided by flux, resulting in similar scale of effect estimates. To assess this, we tested the correlation between Hedge's g for patch density-forest cover and a dataset's average correlation between patch density and flux across all 163 samples and found the correlation to be low (-0.07). This result suggests that samples with a low correlation between patch density and flux were not generally more likely to have lower Hedge's g , nor were samples with high correlation between patch density and flux more likely to have generally higher Hedge's g values. Furthermore, we re-fit the three-level meta-analysis models using a subset of the datasets for which the average correlation between flux and patch density was <0.7 . We chose 0.7 as it is a rule-of-thumb for determining if two correlated variables should both be included in an analysis. We found that both flux and patch density still had significantly wider scales of effect than forest cover (SI, Appendix 7). Thus, these post-hoc analyses show that patch density has a wider scale of effect than forest cover in its own right, rather than by serving as a proxy for flux. Still, it is possible that some of the strength of the relationship between patch density's scale of effect and forest cover's scale of effect results from the correlation between flux and patch density.

Regarding mean ENN and cohesion, at least two mechanisms may be responsible for the lack of difference between their scales of effect and forest cover. First, these two metrics of configuration measure attributes of the landscape that are weakly related to species dispersal compared to flux and patch density, and thus would not be expected to have a significantly wider scale of effect than forest cover. Mean ENN measures the average distance between a patch and its single nearest neighbor, and thus, may not capture details about the landscape important to long range dispersal which likely involves traversing multiple patches or making long distance movements between patch clusters (Fletcher et al. 2013). In other empirical studies, mean ENN has been a poor predictor of wildlife distributions (Moilanen & Nieminen 2002; Calabrese & Fagan 2004; Prugh 2009). Cohesion measures aggregation of forest pixels, which primarily relates to patch size and edge density. These attributes promote resource diversity at the scale of an individual's home range (Bender et al. 1998; McIntyre 1999). Thus, compared to flux and patch density,

cohesion may measure aspects of the landscape more relevant to breeding and foraging success than dispersal, causing it to have a scale of effect similar to forest cover.

Second, both mean ENN and cohesion were more strongly correlated with forest cover compared to flux or patch density's correlation with forest cover ($R^2 = 0.43, 0.73, 0.05, \text{ and } -0.2$ respectively, Appendix 6). Generally, as percent forest cover increases the average distance between forest patches (i.e., mean ENN) decreases. The similarity in information content between the two metrics likely diminishes the difference between their scales of effect. Cohesion captures information even more similar to that of forest cover. When percent forest cover increases, more forest pixels are bordered by other forest pixels, thus increasing cohesion. This degree of correlation could make these two metrics of configuration reasonably good proxies of habitat composition at these scales. Thus, because they represent much of the same information, their scales of effect are more similar. Together, the weak relationship between mean ENN and cohesion with mammal dispersal and their statistical correlation with forest cover could explain why the scales of effect of these two metrics of habitat configuration were not significantly wider than the scale of effect of forest cover. Post-hoc analysis revealed that flux and patch density did not have similarly high levels of correlation with forest cover at any of the 63 scales tested (Appendix 7).

Although our study is the first to synthesize numerous comparisons of scales of effect of configuration and composition among multiple species, other empirical studies also have found metrics of configuration to have wider scales of effect than composition (Feagan 2011; Galán-Acedo et al. 2018; Bosco et al. 2019; Gestich et al. 2019). These results combined with ours indicate that certain metrics of habitat configuration, particularly those that effectively predict wildlife dispersal/distributions and are not correlated with composition, have wider scales of effect than metrics of habitat composition, in our case, forest cover. Based on the average scale of effect across all 163 samples, scales of effect of flux and patch density were roughly 15–20% wider than those of forest cover. These specific results are most applicable to forest mammals; however, they could possibly apply to other taxa in other contexts. In particular, our study included volant mammals (i.e., bats) which followed

similar scale of effect trends as the other mammal species. This suggests that bird species could follow similar trends, or at least are not excluded from these trends based on their volant habits. Mammals and birds living in other non-forest ecosystems could follow similar trends, provided that the preferred habitat is fragmented. Still, the differences between mammals and birds extend beyond their volant habits, and the extent to which these results apply to non-mammal taxa remains to be tested. More broadly, our results confirm that different landscape metrics can have significantly different scales of effect, and thus it is important to consider what landscape metric is used when assessing scales of effect.

Factors influencing the difference between scales of effect

No species traits or factors related to landscape context that we tested explained the magnitude of the difference between scales of effect for flux and forest cover or patch density and forest cover. The lack of any significant relationship was likely in part because scales of effect are influenced by a complex mix of direct and indirect factors (Amiot et al. 2021; A. E. Martin 2018; Miguet et al. 2016), resulting in high variability in the relationship between scales of effect and explanatory variables (SI, Appendix 5). For example, the scales of effect of all five metrics were sometimes smaller for large species like black bear and jaguar (*Ursus americanus* and *Panthera onca*, respectively), than for similar but smaller species like lynx and ocelot (*Lynx rufus* and *Leopardus pardalis*, respectively). Also, the same species sometimes had scales of effect that varied by as much as an order of magnitude between studies. For example, we found that tyra (*Eira barbara*) had a scale of effect for patch density of 3700-m in one study, and 16,255-m in another. A possible explanation that contributes to the weak empirical relation between species traits and scales of effect is that regional context may be a stronger driver of scales of effect than species traits (Tittler 2008; Jackson & Fahrig 2015; Miguet et al. 2016; Galán-Acedo et al. 2018). This is supported by evidence that landscape composition, configuration, and other regional factors (e.g., level of human disturbance) significantly mediates wildlife movement which can in turn influence scale of effect (Renken & Wiggers 1989; Taylor & Merriam 1995; Hein

et al. 2004; Van Houtan et al. 2007; Van Beest et al. 2011; Delattre et al. 2013). Overall, there were highly variable relationships between explanatory variables and scales of effect for both configuration and composition, inhibiting our ability to identify factors that determined the difference between scales of effect for these two aspects of the landscape.

Furthermore, no factors explained the magnitude of the difference in scales of effect because in many cases explanatory variables exhibited relationships that were similar for scales of effect of configuration and composition (i.e., a positive, negative, or quadratic relationship). As such, the magnitude of the difference between scales of effect remained relatively constant across the range of variation of an explanatory variable. For example in a separate study, we found scales of effect for all five metrics had positive relationships with home range (Gengler, Acevedo, and Branch, unpublished). The same was also true for study area geographic location (i.e., all scales of effect tended to be wider in tropical latitudes; SI, Appendix 5), which was generally a strong predictor of scale of effect (Gengler, Acevedo, and Branch, unpublished). For these two reasons, the high variability and similar trends present for both composition and configuration, we did not identify any factors that influenced the magnitude of the difference between scales of effect. Rather, the difference between two metrics' scales of effect seems to be an inherent difference that is relatively consistent across contexts.

Study limitations

Studies of scale of effect are limited by numerous methodological issues (Jackson & Fahrig 2015; Miguet et al. 2016). We were able to address some, but not all, of these. Foremost, testing an inadequate range and number of scales can result in erroneous identification of the scale of effect. For example, in many previous studies the observed scale of effect was the smallest or largest scale tested, and the correct scale of effect may have been on either side of this tested range (Jackson & Fahrig 2015; Martin 2018). By analyzing primary data, we were able to generate large numbers of buffers with high resolutions that allowed us to limit this bias. All but four of the 815 scales of effect in our study were more than 1000-m medial to the endpoint buffers, suggesting

that our large range of buffers was sufficient to identify the true scale of effect.

A second common issue we were able to address is that low spatial resolution of landscape data biases the estimate towards wider scales of effect (Mendenhall et al. 2011; Miguet et al. 2016). In our study, landscape data were constrained by the highest spatial resolution available for all study sites (25-m pixels). Although finer resolution may have been preferable, we expect this resolution was adequate to identify the scale of effect for mammals because their perceptual ranges (i.e., the distances from which animals can detect landscape elements; Lima and Zollner 1996) exceeds 25-m. Perceptual ranges, which affect species' ability to move across fragmented landscapes, generally are 100-m or more for small mammals and much greater for larger mammals (Mech & Zollner 2002; Pe'er & Kramer-Schadt, 2008; Bracis & Mueller 2017; Rocha et al. 2021).

Despite addressing these methodological issues common to scale of effect studies, our ability to identify factors that explain the magnitude of the difference between scales of effect remained limited. Part of this limitation could be related to other methodological problems. One common limitation is that a landscape metric at a given scale correlates with itself at similar scales (Miguet et al. 2016). Such correlations can result in models that predict a species' distribution almost equally well across several scales. This increases the variability in scales of effect because a range of scales might be equally likely to be identified as the scale of effect, and by random chance values at the high or low end of this range might be selected as the scale of effect. Although this issue is largely unavoidable when selecting scales of effect, the wide range of scales tested in our study reduced this problem by allowing scales to take extremely different values, thus, facilitating the lack of correlation between the largest and smallest possible scales. Alternatively, our ability to detect significant explanatory variables may have been limited by the enormous complexity of factors that produce a scale of effect, especially indirect effects. Indirect effects arise when a landscape variable influences a factor that in turn affects the biological response variable of interest, creating one or more degrees of separation between the landscape variable and the biological response variable of interest. For example, patch density may promote predator populations, confounding the scale of effect

of patch density for prey species. Even though we assessed seven factors predicted to influence scales of effect via plausible biological mechanisms (Miguet et al. 2016), these factors may have exhibited a relatively small influence on scale of effect compared to indirect effects or the combined effects of many factors with weak direct effects. Finally, our study was limited by using a generalized measure of forest cover that might not accurately reflect all species' habitat preferences. For example, dry secondary forest was indistinguishable from mature humid forest in our landcover maps, yet for some species in our study (e.g., the Indian squirrel *Ratufa indica*) mature forest could be preferable. This lack of habitat detail could increase the variability of our scale of effect estimates by confounding a species' response to, for example, mature forest with their response to forest in general. However, the total amount of forest habitat in an area likely correlates with the amount of preferred forest habitat in most cases. Furthermore, this was a necessary simplification to allow comparisons across species and studies. Our extensive range of scales and consistent methodology across all species and datasets overcomes many of the barriers that impeded previous comparisons of different metrics' scales of effect.

Conclusion

Our analysis of 163 comparisons of scale of effect that represent 107 mammal species from 33 datasets supported the hypothesis that the difference between scales of effect for configuration and composition depends on the metrics selected. In the two cases where there was a significant difference (i.e., flux and patch density), the metrics of configuration were wider than composition, suggesting that these two metrics measure attributes of the landscape that contribute more strongly to dispersal than forest cover does, likely via mediating landscape connectivity. Previous research predicted that different landscape metrics have different scales of effect, but empirical support was limited (Miguet et al. 2016). Our study confirmed this prediction, but contradicted the specific prediction that metrics of habitat configuration should have smaller scales of effect than composition.

If the scale of effect of a metric of composition is known from previous research, then a metric of

configuration's scale of effect would be expected to be roughly 15–20% wider, and vice-versa, at least for forest mammals. However, this pattern may not hold for metrics of configuration that do not measure attributes of the landscape that mediate species dispersal or are correlated with the metric of composition. Our results strengthen our empirical understanding of scale of effect and are a step towards the ability to form a priori approximations of scale of effect.

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Data availability The datasets generated during and/or analyzed during the current study are available in the Appendices found in the Supplementary Information, and from the corresponding author upon reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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