Current Landscape Ecology Reports (2023) 8:23–33
https://doi.org/10.1007/s40823-022-00082-7

REVIEW

Does a Species' Mobility Determine the Scale at Which It Is Influenced by the Surrounding Landscape Pattern?

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Accepted: 7 December 2022 / Published online: 16 January 2023

Abstract

Purpose of Review Species at a site interact with environmental variables of the surrounding landscape, but the spatial extent (scale) at which such interaction is strongest ("scale of effect," SOE) varies among species. SOE is hypothesized to be driven mainly by species' mobility, as a more mobile species should interact with environmental variables across larger scales. Yet, previous reviews found little evidence for this expectation. This may be because the actual SOE is often outside the assessed range of scales, as suggested by the fact that the estimated SOE frequently equals the smallest or largest scale investigated. We conducted a systematic review of studies published during the last decade to assess whether SOE can be predicted by mobility-related species traits. We controlled for the effects of several study attributes, and repeated all analyses excluding the SOE values that equaled the smallest or largest scales investigated.

Recent Findings We found 70 studies reporting 1059 SOE values for 291 species, but ~ 50% of SOE values were not scale sensitive. SOE was weakly related to six mobility-related traits, independently of the taxonomic group, especially after controlling for study attributes. They remained weak after excluding the SOE values that equaled the smallest or largest scales investigated.

Summary Our results imply that SOE cannot be predicted a priori from mobility-related traits. Therefore, we suggest that multi-scale analyses covering a wide range of scales should become standard practice to ensure we are not missing landscape context effects due to studying them at the wrong scale.

Keywords Animal movements · Buffer · Landscape size · Multi-scale analysis · Scale dependency · Species dispersal

Introduction

Understanding the drivers of biological communities is paramount in ecology, as well as for accurately predicting and preventing damage to ecosystems given the current environmental crisis. This is, however, a challenging task, as each driver can operate across different spatial and temporal scales, and can be undetected if assessed at the wrong scale [1]. This is particularly evident in landscape ecology studies, as environmental variables associated with landscape structure depend on the spatial extent ("scale" hereafter) at which such variables are measured. Thus, to make accurate

Topical Collection on Scale-Measurement, Influence, and Integration

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and confident inferences on the role played by landscape variables in shaping ecological patterns and processes, we should measure landscape variables at different scales to identify the correct one [2, 3••, 4].

The scale at which a given landscape variable best predicts a given response is called the "scale of effect" (SOE), and has important ecological and applied implications [5]. From an ecological point of view, the SOE sheds light on the scale at which the processes that shape the studied response variables act, and thus, on the way species and ecological processes perceive (and interact with) the surrounding landscape [6••, 7••]. For example, plant restoration success in degraded lands increases with increasing forest cover in 10-km radius landscapes, suggesting that seed dispersal and other ecological processes involved in forest restoration act at this scale [8•]. From an applied point of view, this information can guide management and conservation practices at the landscape scale, as the SOE indicates the scale at which such practices can be more effective [8•]. Although these implications have led to increasing attention on the SOE, the patterns and predictors of SOE remain so poorly understood that the topic is still in its infancy [6••, 9].

Several variables may predict the SOE, but species' mobility is the most frequently cited one [3••, 4, 6••, 10•]. This is because, logically, the farther a species moves within and between territories, the larger the scales across which it will interact with (and depend on) environmental variables [6••]. Some modeling studies support this expectation. For example, using an individual-based multigenerational model of movement, Jackson and Fahrig [10•] found that SOE increases with increasing average dispersal distance of individuals. Ricci et al. [11] also found that SOE is positively related to dispersal distance in a simulation study. However, previous reviews [3••, 6••] found that the effects of species traits on SOE are highly variable among empirical studies and the expected positive association between mobility-related traits (e.g., territory size, home range size, dispersal distance) and SOE is only weakly supported.

The lack of empirical support for the expected effect of species' mobility on SOE may be related to suboptimal study design [3••]. If SOE depends on mobility then to identify the true SOE and make accurate inferences on a given species–landscape relationship, researchers should base their range of investigated scales on relevant species traits (e.g., dispersal distance, see [12, 13]). Yet, most multi-scale studies tend to use too few scales over a too small range to adequately identify the true SOE [3••]. In fact, 44% of reported SOE values equaled the smallest or largest scale evaluated, which suggests that a better scale (true SOE) is outside the assessed range [3••] (Fig. 1). This is not trivial as it suggests that most studies are assessing species–landscape relationships at the wrong scales, and therefore, they are likely missing or underestimating such relationships.

Here, we took advantage of the fact that since 2011—the year that Jackson and Fahrig [3••] made their literature review—there have been an increasing number of multi-scale ecological studies. We compiled the studies published in the last decade (2012 to 2021) on species–landscape relationships across multiple scales, and assessed whether the observed SOE values can be predicted by mobility-related species traits and study attributes. Regarding species traits, following Jackson and Fahrig [3••], we first evaluated whether SOE increases with home range size and territory size, because they are positively related to dispersal distance in mammals and birds [14, 15]. We also assessed whether SOE increases with body mass, as larger animals are expected to move more and over larger distances than small-bodied species [16–18]. Trophic level could also matter [6••], as carnivores can require more space than equally sized herbivores [19]. We also assessed whether SOE increases with increasing wing length, as this species trait is expected to be positively related to mobility [6••]. Finally, we tested the effect of migratory status on SOE because there is evidence that SOE is significantly higher in migrant birds than residents [3••], although the opposite pattern (migrant < residents) could also be possible [6••]. As SOE values could also differ among

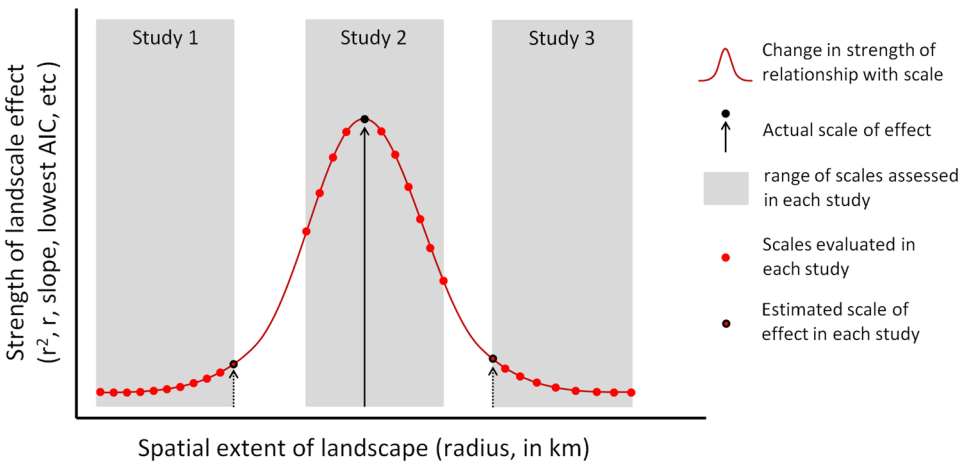

Fig. 1 Illustration of three study scenarios, in two of which (study 1 and 3) the estimated scale of effect differs from the actual scale of effect. All studies assessed the influence of landscape structure at multiple spatial scales, but in study 1 and 3, the estimated scale of effect equaled the largest or smallest scales investigated, respectively. Only study 2 estimated the actual scale of effect. Other possible scenarios are indicated in Fig. 2 of Jackson and Fahrig [3••]

taxonomic groups, we assessed the effects of each trait separately for each taxonomic group [3••].

As our findings and conclusions could be affected by different attributes of the reviewed studies [3••], we included in the models cofactors describing the study attributes. In particular, following Jackson and Fahrig [3••], we included the response variable (abundance or occurrence), region (tropical, subtropical, or temperate), and focal habitat (forest, open, or wetlands) in each study. SOE is predicted to be smaller for abundance than occurrence because the former response is expected to be more strongly shaped by local-scale processes (i.e., those affecting the fitness of individuals) than the latter, which is expected to depend more on processes operating across larger spatial and temporal scales (e.g., extinction; [6••, 45]). Tropical and subtropical species are thought to move less than temperate species because of their narrower geographic ranges compared to temperate counterparts [20]. And, as resource availability can be more ephemeral in open areas (e.g., grasslands) and wetlands than in forests, animals likely move more and farther across open areas and wetlands than forests (reviewed by [21]).

As a novel contribution here, we also included the landscape metric (i.e., predictor variable) assessed in each study because each landscape variable can regulate processes that operate at different scales, and can therefore have different SOE values [6••, 9]. In particular, as landscape compositional variables such as habitat amount are directly related to landscape connectivity [5], they are hypothesized to affect large-scale processes, such as dispersal-related mortality and dispersal success [6••]. Although landscape connectivity can also depend on configurational variables, such as patch density and edge density, Miguet et al. [6••] argue that these variables likely affect more strongly local processes (e.g., breeding and/or foraging) because they determine the relative amount of core and edge habitat within a species home range. Therefore, we classified landscape variables as compositional or configurational variables predicting larger SOE for compositional than configurational ones [6••].

Finally, to determine whether the lack of SOE ~ mobility relationship detected in previous reviews was due to inaccurate estimation of SOE's, we repeated all analyses using the subset of SOE values that were not the largest or smallest evaluated scales. In other words, we omitted SOE values that were at the edges of the ranges of values studied, as in those cases the true SOE was likely outside that range [3••] (Fig. 1).

Methods

Literature Review

We replicated the search protocol used by Jackson and Fahrig [3••], but using the Scopus database (accessed 18th November 2021) instead of the ISI Web of Knowledge, because Scopus offers a more extensive list of modern sources. In brief, we searched for studies assessing the effect of landscape structure at multiple scales on the presence or abundance of populations in focal sites (i.e., focal site multi-scale studies, sensu [13]). We used the same search string as Jackson and Fahrig [3••]: ((“spatial scale*” OR “spatial extent*” OR “landscape size” OR “multi-scale” OR “landscape area” OR “buffers” OR “focal patch*” OR “focal point*”) AND (“surrounding landscape*” OR “landscape context” OR “habitat loss” OR “habitat fragmentation” OR “habitat amount” OR “landscape structure” OR “landscape composition” OR “habitat area”) AND (abundance OR occupancy OR incidence)). We obtained 503 studies published from 2012 to our search date, and used the following criteria for selecting relevant studies for our review. First, the landscape variables assessed in each study should be measured in at least two scales surrounding central sample areas (e.g., 1 and 10 km radius), and these scales should be the same for all sample areas. Second, the effort per sample area should be standardized (e.g., the same number of camera traps) or statistically controlled in models (e.g., including sample area as a random factor). Third, the resolution (e.g., 10×10 m pixel) of the image used to quantify the landscape variables should be the same for all scales. Fourth, the study should assess the effect of the landscape variable(s) on each species separately (i.e., we excluded community-level responses, such as species richness or total abundance of several species) (see Jackson and Fahrig [3••] for more details on study selection).

Data Extraction

We also followed Jackson and Fahrig [3••] for data extraction, but a brief overview is given here. First, we recorded the SOE reported in each study (i.e., in tables, figures, or main text), with the SOE being the scale at which landscape variables best predicted the presence or abundance of a given species, i.e., the scale at which the models had the lowest AIC value, highest R^2, or highest correlation coefficient. As proposed by Jackson and Fahrig [3••], we recorded “scale sensitivity,” with “true” indicating that the model at the SOE was markedly greater than the model at the weakest scale (e.g., $\Delta\text{AIC} > 2$, $\Delta R^2 > 0.01$, $\Delta r > 0.1$). We also recorded whether the observed SOE values were equal to the smallest or largest scale [3••]. Furthermore, we determined whether authors justified the selected range of scales. We also recorded whether there was spatial overlap among study landscapes at the largest scale tried in each study, and if overlapped, we recorded whether the study controlled statistically the potential lack of independence in the models [3••]. The sample size (number of sample areas), response (abundance or occurrence) and predictor variables

(composition or configuration variables), habitat type in sample areas (forest, open, or water), and region (temperate, tropical, or subtropical) were also recorded.

Regarding the species traits, we reviewed published papers, species guides, and online databases to obtain two direct estimates of mobility, home range size (in ha) and territory size (in ha) [14]. Home ranges are areas normally used by animals for feeding, resting, and reproduction [22], and are estimated with all available location data [23]. Territories are measured by delineating the location of territorial-defense events (e.g., aggressive behavior, escape/avoidance responses of competitors) exhibited by the territory holder [23, 24]. Territories may or may not coincide with the home range area, and can also be called "defended home ranges" [25]. We also recorded other coarser measures of mobility including (i) body mass (in g); (ii) migration status (migrant or resident); (iii) wing length (in cm); and (iv) trophic level (herbivore, omnivore, or carnivore). Furthermore, we recorded the major taxonomic group (amphibian, arthropod, bat, bird, ground mammal, or reptile), and whether arthropods have flight ability (yes or no) to assess whether flying arthropods have larger SOEs [3••]. However, as the database was extremely unbalanced (91% flying vs 9% non-flying species), we could not include this cofactor in our analyses. The final database with the reviewed sources is available in Appendix S1.

Statistical Analyses

We first assessed the relative influence of each mobility-related trait on SOE, for each relevant taxonomic group, using linear mixed-effects models with the "lme4" package [26] for R version 4.1.1 (R-Core Team 2022). In all models, the SOE value was log10 transformed for normality, and we included the mobility-related trait as a fixed factor, and study as a random effect. Following Jackson and Fahrig [3••], we assessed the effects of each trait separately for each major taxonomic group. For categorical traits, we limited the analyses to taxa that showed at least two levels of that mobility-related trait, and at least ten samples per level. After this filtering, we were able to test SOE ~ trait relationships (where "trait" is short for "mobility-related trait"), for 18 taxon-trait combinations. We used the Akaike Information Criterion (AIC) and likelihood ratio tests (using REML) to assess whether the full models (i.e., with both fixed and random factors) were a better fit for SOE than the null models (i.e., with only the random factor) [27].

We also assessed the effects of study attributes in predicting the SOE values. In particular, for each SOE ~ trait relationship for each taxon, we built six alternative models, each including the given trait and one of the following study attributes as a fixed effect covariate: (i) response variable (i.e., abundance or occurrence); (ii) landscape predictor (i.e., landscape configuration or composition); (iii) region (i.e., tropical or subtropical, or temperate); and (iv) habitat type in the sample site (i.e., open or wetland, or forest). We then used AIC and likelihood ratio tests to compare the full models (i.e., with the fixed trait and the fixed study attribute) with the model in which the study attribute was removed. We estimated both the marginal and conditional R^2 values of all models using the "MuMIn" package [28], with marginal values indicating the variance explained only by fixed effects, and conditional values providing the variance explained by the entire model. We estimated the 95% confidence intervals of the fixed effects parameters using the *confint.merMod()* function available in the "lme4" package [26], and used the "lsmeans" package [29] to examine pairwise comparisons with Tukey tests for fixed categorical factors.

Finally, to determine whether any relationship between SOE and mobility is masked by an inadequate range of scales investigated (Fig. 1), we repeated the analyses above using the subset of SOE values that were not the largest or smallest investigated. Note this is different from the approach of Jackson and Fahrig [3••], who included in their models the radius of the smallest and largest scales evaluated in each study. Because the recorded SOE must be necessarily located in that range of scales, it is not surprising that SOE is strongly predicted by the smallest and largest scales. By including this strong covariate, Jackson and Fahrig [3••] may have missed important mobility effects (high type II statistical error). However, as our approach decreased the sample size to less than half, i.e., only 44% of SOE values in our review were not at the smallest or largest scales investigated, we combined our SOE estimates with the subset of estimates from Jackson and Fahrig [3••] that were also not at the largest or smallest scales investigated (i.e., 327 SOE estimates from 257 species, representing 56% of assessed SOE values in their review; see Appendix S2). Thus, the total number of SOE values including those at the largest and smallest scales investigated (from 2012 to 2021) was 1059 (Appendix S1), and the total number of SOE values excluding those at the largest and smallest scales (across all years, 1997–2021) was 781 (Appendix S2). As Jackson and Fahrig [3••] did not record the wing length, we did not include this species trait in the analyses of the SOE's that were not at the smallest or largest scale investigated. Furthermore, as we found that including a cofactor (i.e., a study attribute) only weakly affected model fit (see the "Influence of Study Attributes on the Scale of Effect" section below), in the set of analyses excluding SOE's at the smallest or largest scale investigated we only assessed whether the models including a mobility trait were better than the null models with only the random factor for study ID, following the protocols described above (i.e., using Akaike Information Criterion and likelihood ratio tests).

Results

Overview of the Database

A total of 70 studies met our criteria and provided 1059 SOE values for 291 species on four continents (Appendix S1; Fig. 2). Most SOE values were provided for species using forested habitat in temperate regions, with arthropods ($n=357$ SOE values, 101 species), birds (281 values, 106 species), bats (222, 38), and ground mammals (115, 23) being the best represented taxonomic groups in the database (Appendix S1). The available information for amphibians (74, 13) and reptiles (10, 10) was notably scarcer, with amphibian samples coming from a few temperate regions of Canada and USA, and all reptile samples coming from a single Australian subtropical region (Appendix S1; Fig. 2). Most SOE values ($n=760$) assessed the effect of landscape pattern on the abundance of individuals (as opposed to species occurrence, $n=299$ SOE values; Appendix S1). Regarding the predictor variables, most SOE values ($n=729$) assessed the effect of landscape composition variables (as opposed to landscape configuration variables, $n=330$). Importantly, although most SOE values (78%) came from studies using non-overlapping landscape replicates, almost half of the observed SOE values ($n=527$) cannot be considered scale sensitive (Appendix S1). Also, more than half of observed SOE values ($n=605$, 56%) were equal to the smallest or the largest scales assessed in the reviewed studies, and 44% did not provide any biological justification for the selected range of scales (Appendix S1).

Mobility-Related Trait Predictors of the Scale of Effect

The observed SOE values ranged from 0.01 to 32 km, and differed significantly among taxonomic groups (Fig. 3). The contrast tests indicated that the taxonomic differences were driven mainly by larger SOE values for bats than arthropods (see a complete output in Appendix S3). Only 2 of the 18 SOE ~ trait relationships for individual taxa (≈11%) were significant, and indicated that birds with larger home ranges and larger wingspans had larger SOE values (Fig. 4), but the explanatory power of home range size was low, as this fixed trait explained only 6% of the SOE variance (Appendix S3). SOE also tended to be higher in mammals with larger home ranges, in small-bodied arthropods, in smaller bats, in migrant birds than residents, and in carnivorous mammals than in herbivores (Fig. 4). However, in all these cases, the fixed traits explained a small portion of SOE variance (marginal $R^2<0.07$ in all cases; Appendix S3).

Influence of Study Attributes on the Scale of Effect

The Akaike Information Criterion and the likelihood ratio tests indicated that in most (12 of 18) taxon-trait combinations (63%), the inclusion of a study attribute (i.e., response variable, predictor variable, region, or local habitat) did not change significantly the fit of the models (Table 1, Appendix S4). Where model fit did improve, SOE values were higher: in wetland than forest when assessing the effects of bird migration status, wingspan, and trophic level; in forest than open areas when assessing the effects of bat body mass and trophic level (Table 1, Appendix S5); for abundance than occurrence when assessing the effect of bat migration status and trophic level; and for landscape configuration than composition when assessing the effect of bird territory size (Table 1, Appendix S5).

Effect of Mobility-Related Traits on the Scale of Effect for SOE Estimates that are Not at the Largest or Smallest Scale Assessed

After combining our findings with those of Jackson and Fahrig [3••], we found 109 studies providing 781 SOE

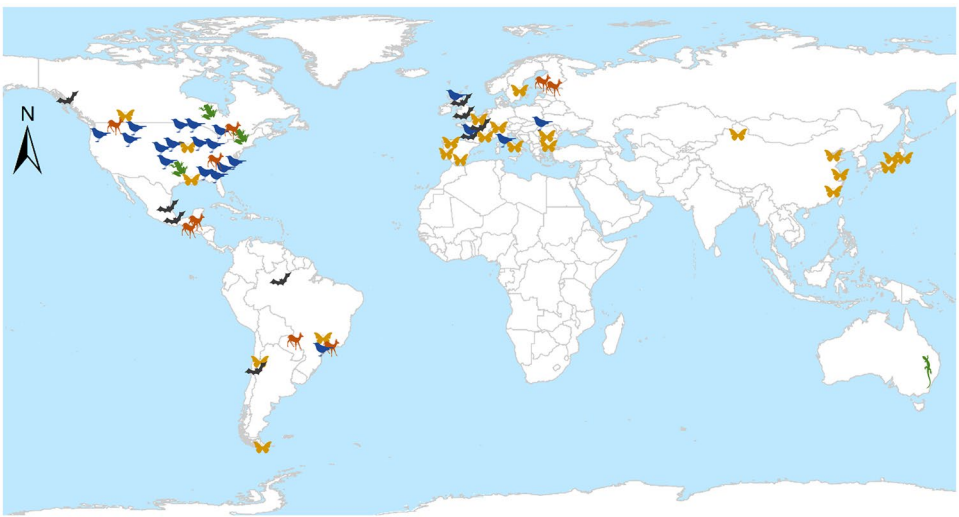

Fig. 2 Distribution of the 70 studies on the scale of landscape effect on species' occurrence or abundance. Symbols indicate the major taxonomic groups surveyed in each study (arthropods, birds, bats, ground mammals, amphibians, and reptiles)

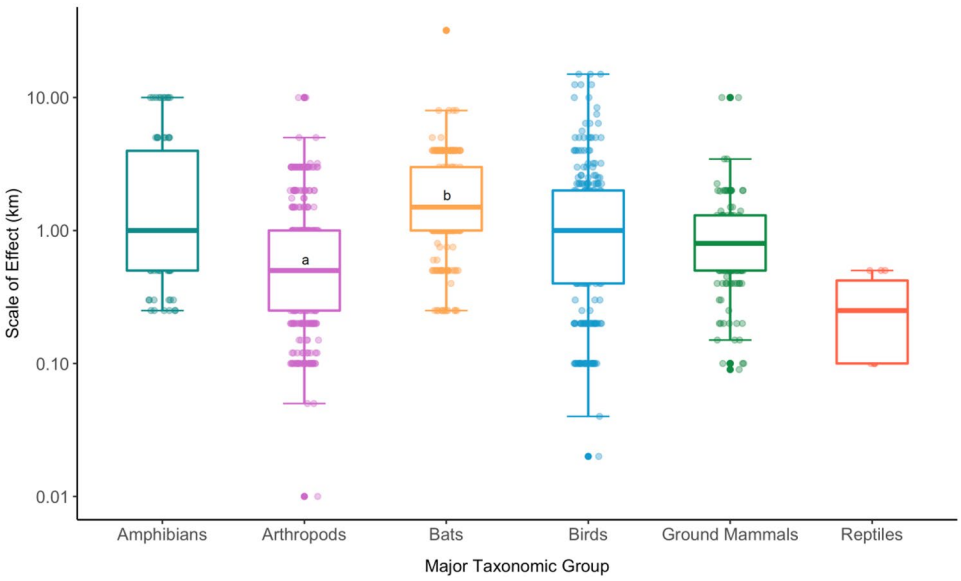

Fig. 3 The scale of landscape effect (in log10 scale) on species occurrence or abundance for six major taxonomic groups. Only the groups indicated with "a" and "b" letters differ significantly between each other (contrast tests; $p < 0.01$). The boxplots show the median (thick lines), the first and third quartiles (boxes) and 1.5 times the interquartile range (whiskers). Dots are the data points

values for 404 species that were not the largest or smallest scales tried in the reviewed studies (Appendix S2). With this database, we found the same significant differences in SOE estimates among taxonomic groups as above, being larger for bats than arthropods (see Fig. S1 and complete output in Appendix S6). However, the rest of SOE ~ trait relationships remained weak and non-significant after excluding the SOE values that equaled the smallest or largest scales investigated ($p > 0.05$ and marginal $R^2 < 0.06$; in all cases; Appendix S6).

Discussion

Does species' mobility determine the scale at which they interact with the surrounding landscape pattern? Our extensive quantitative review of empirical evidence, including 70 studies reporting 1059 scale of effect (SOE) values for 291 species, suggests the answer is no, at least not predictably so. We assessed how SOE responds to two direct measures of species mobility (home range size and territory size) and four coarser measures of mobility (body mass, migration status, wing length, and trophic level) in six major taxonomic groups (amphibians, arthropods, bats, birds, ground mammals, and reptiles) and found that most SOE ~ trait relationships were weak. This was particularly evident after controlling for the effects of four study attributes that could also affect SOE values (i.e., response variable, predictor variable, regional realm, and focal habitat). Finally, the SOE ~ trait relationships remained relatively weak after excluding the SOE estimates that are likely not true SOE values, namely those that were the smallest or the largest scales assessed in each study [3••]. As these findings agree with previous reviews [3••, 6••], the evidence indicating that species' mobility is a poor predictor of SOE is more extensive than ever. This does not imply, however, that SOE is independent of species' mobility, but that such dependence cannot be generalized across species and landscapes. Among other potential causes of our findings, we highlight two alternative but non-exclusive ones. First, the traits we evaluated could be inaccurate or ambiguous indicators of species mobility. Second, we could be using inadequate models, as even with our large sample of SOE values we were not able to simultaneously model all the factors that might affect SOE. Below, we discuss these factors and propose some guidelines for future research.

To adequately assess any SOE ~ trait relationship, the trait needs to be accurately estimated. This is not an easy task, as species trait values can be highly variable among individuals and populations [30–32]. For example, in social animals that live in groups, larger groups typically deplete food patches faster, so individuals in larger groups may be forced to visit more patches each day, increasing their daily ranges, and even increasing their home ranges [33–35]. Habitat quality also matters, as organisms can be forced to compensate for the scarcity of resources in low-quality habitats by foraging across larger areas [36], and the opposite can also be true as an energy-saving strategy [37]. Landscape structure is also important. For example, Leal-Ramos et al. [38] found that birds in the Brazilian Atlantic Forest fly larger distances in less forested landscapes.

Whatever the causes of such variation in trait values, the consequences are critical: there are large intraspecific variations in mobility-related trait values [32, 39]. For example, the home range size of a given primate species can vary by one to two orders of magnitude among studies (e.g., 100 to 3700 ha in Chacma baboons, 12 to 2200 ha in Tibetan macaques, and 42 to 963 ha in Central American spider monkeys; [39]). Therefore, as mobility-related trait values

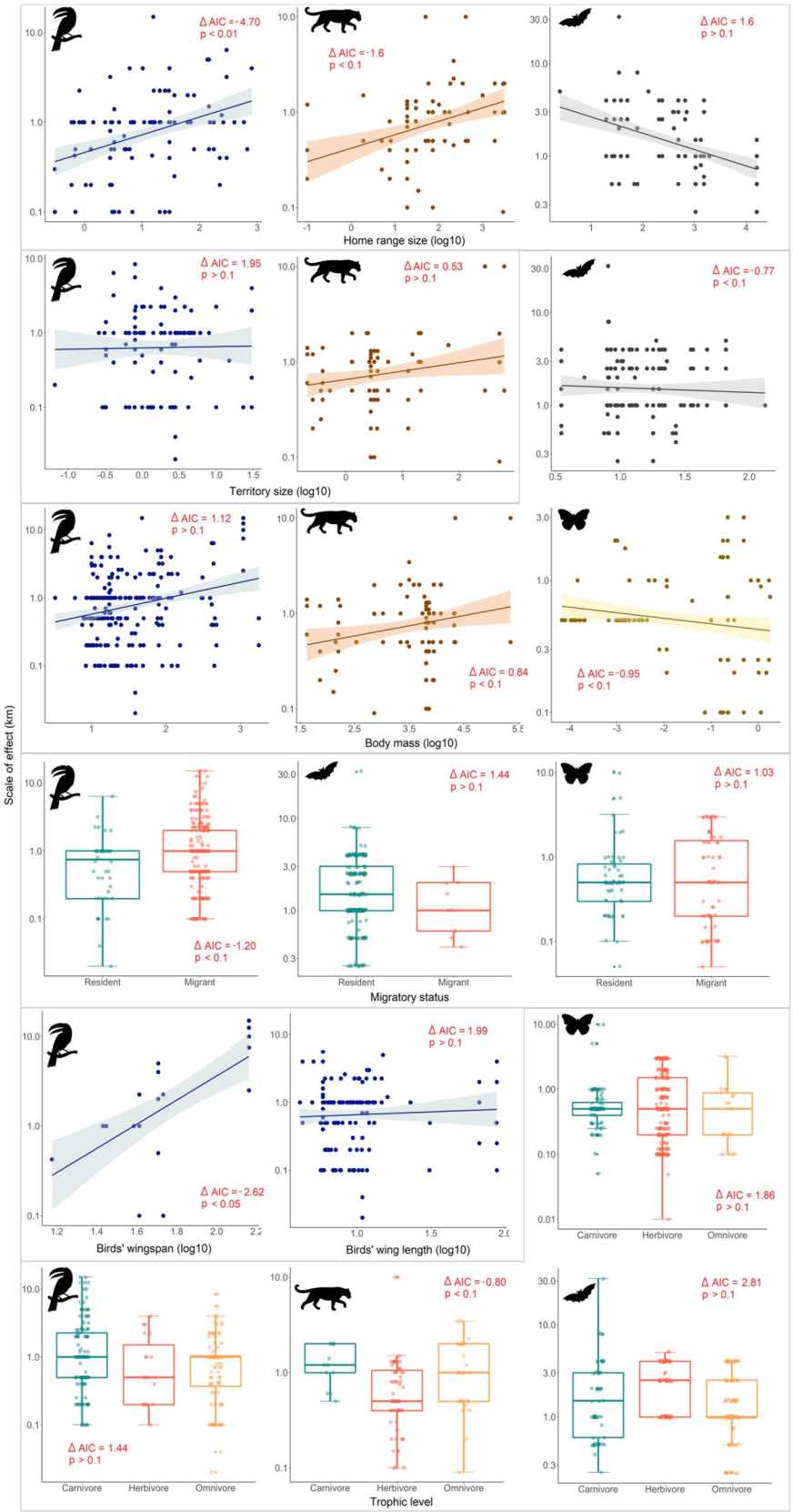

Fig. 4 Influence of mobility-related species traits on the scale of landscape effect (SOE, in log10 scale) for different taxonomic groups, indicated by silhouettes (i.e., birds, ground mammals, bats, and arthropods). Two statistics (in red) assessed whether the full models (i.e., including the fixed trait and random factor for study ID) were a better fit for the scale of effect than the null models (i.e., including only the random factor): (i) difference in the Akaike Information Criterion (ΔAIC) between the full model and the null model (negative values indicate that the full model has higher information value, and positive values indicate the opposite), and (ii) the *p* values of likelihood ratio tests comparing the full and null models. Note that as the available measures of wing length differed among species, we show the results separately for each type of measure. Complete model outputs are in Appendix S3

Table 1 Influence of four study attributes (cofactors) on the scale of landscape effect. We compared linear mixed models including the effect of each mobility-related trait alone, with four alternative models, each including the trait and one of the following cofactors: (i) response variable; (ii) landscape predictor; (iii) region; and (iv) habitat type in the sample site. Two complementary statistics are provided, the difference in Akaike Information Criterion (ΔAIC) between the full models (i.e., with both a mobility-related trait and a covariate) and the model in which the cofactor was removed), and the significance (*$p < 0.05$, **$p < 0.01$, ns ≥ 0.1) of the likelihood ratio tests comparing the models. Negative ΔAIC values indicate that the full model has higher information value, and thus, that the study attribute increases the fit of the model relative to the mobility-related trait alone. In the few cases (in boldface) where the increased fit was significant, we indicate in parentheses how the scale of effect differed among cofactor levels, i.e., a > b indicates the scale of effect was larger for a than for b. Complete model outputs (including parameter estimates) are in Appendix S4 and S5. Note that there are some empty cells because some taxon-trait combinations were not available for some study attribute categories (e.g., bird home range sizes were available only for temperate regions), so we were not able to evaluate all study attributes for all taxon-trait combinations

Species trait/group	Response	Predictor	Region	Habitat
Major taxonomic groups	0.01 ns	−0.8 ns	1.8 ns	2.4 ns
Home range				
Birds	1.7 ns	−1.0 ns		3.8 ns
Mammals	1.8 ns	0.06 ns	1.9 ns	
Bats	−1.4 ns	2.0 ns	0.1 ns	−1.0 ns
Territory size				
Birds	2.0 ns	**−2.5*** (configuration > composition)		2.4 ns
Mammals	0.9 ns	1.3 ns	0.7 ns	
Body mass				
Arthropods	1.6 ns	−0.8 ns		1.8 ns
Bats	−0.01 ns	2.0 ns	−0.3 ns	**−2.2*** (forest > open)
Birds	1.9 ns	−0.1 ns		−1.6 ns
Mammals	1.6 ns	0.9 ns	1.5 ns	
Migration status				
Birds	2.0 ns	0.5 ns	0.5 ns	**−2.6*** (wetland > forest)
Bats	**−5.3**** (abundance > occurrence)	2.0 ns	−1.4 ns	−0.8 ns
Arthropods	1.9 ns	0.4 ns	1.4 ns	3.8 ns
Wings length				
Birds (wingspan)	0.8 ns	1.9 ns		**−2.6*** (wetland > forest)
Birds (wing length)	0.8 ns	−0.9 ns		3.55 ns
Trophic level				
Arthropods	0.5 ns	1.5 ns	3.0 ns	4.0 ns
Bats	**−4.9**** (abundance > occurrence)	2.0 ns	−0.6 ns	**−2.7*** (forest > open)
Birds	2.0 ns	0.5 ns		**−2.2*** (wetland > forest)
Mammals	2.0 ns	0.5 ns	1.8 ns	

can depend on where and when they are measured (for temporal variation see, e.g., [40]), we cannot assume that traits are consistent for a species in space and time (i.e., the "species robustness assumption" [41]). Although for some traits intraspecific variability is smaller than the interspecific variability [41], this does not seem to be the case for continuous mobility-related traits. Therefore, the weak SOE ~ trait relationships could be simply caused by inaccurate/ambiguous trait values.

The weak SOE ~ trait relationships could also be caused by the exclusion of other important determinants of SOE from models, thus masking the effect of mobility-related traits. SOE is hypothesized to depend on a complex set of factors acting across different spatial and temporal scales [6••]. Miguet et al. [6••] provide the most comprehensive summary of the drivers of SOE, and propose five general hypotheses, from which they derive 14 predictions. However, only two of these hypotheses are related to species mobility (i.e., H1: local movements and

H2: dispersal movements) and involve seven species traits (i.e., home range or territory size, dispersal distance, body size or mass, flight ability, trophic level, migration status, and habitat specialization). Both this study and Jackson and Fahrig [3••] found that these traits have weak effects on SOE. Evidence is also weak for the other predictors of SOE in Miguet et al. [6••], when tested in isolation. For example, Galán-Acedo et al. [42] and Martínez-Ruiz et al. [43] found that habitat specialization plays a minor role in predicting the SOE of primates and diurnal raptors, respectively. Furthermore, the predicted effect of response variable—species fecundity, abundance, occurrence, or genetic diversity—is not well supported [7••, 9, 42–44].

Our models are slightly more complex than single-factor models. In particular, we also included in the models some cofactors related to some of the non-mobility hypotheses in Miguet et al. [6••]. However, adding these cofactors did not result in strong models. In 2 of 18 cases, including the response variable significantly increased model fit, but the observed patterns were opposite to that predicted by Miguet et al. [6••]. In only 1 of 18 cases, the type of landscape metric (landscape composition or configuration) increased the fit of the model, and the observed patterns (i.e., larger SOE for configuration than composition) also did not follow the expected pattern (see also [43, 44]). Finally, two of our covariates were related to inter-regional variability (prediction 14 in [6••]), the regional realm (tropical, subtropical, or temperate) and the focal habitat (forest, wetland, or open). While focal habitat seemed to play a role in predicting SOE (Table 1), the patterns were not consistent with expectations (i.e., wetland > forest) in 3 of 18 cases, and were opposite to expected (i.e., forest > open) in 2 of 18 cases. Thus, overall there is little support for effects of individual predictors (mobility-related traits) or pairs of predictors on SOE.

This leaves open the possibility that simultaneous consideration of many factors might provide a stronger predictive model. Such a model might also involve interaction effects, which could be explored with tree-based models, and non-linear or threshold effects. However, obtaining sufficient information for building such a model would require a very large research effort, involving estimation of many more SOE values across wide ranges of conditions, to allow simultaneous modeling of multiple factors. Alternatively, given the apparently idiosyncratic responses of SOE to mobility-related species traits, we could rather focus on improving case studies, correcting for potential confounding factors to have more reliable information at least for some particular species and regions.

Conclusions

Landscape ecologists have realized for decades that species–landscape relationships could depend on the scale at which landscape variables are measured. Yet, the condition under which such dependency is strongest is still an open question, as consistent with previous reviews [3••], we found that almost half of observed SOE values were not scale sensitive. This means that scale dependency is not ubiquitous among species, biological responses, and landscape predictors.

Scale dependency is however frequent, and not trivial, as it implies that strong landscape-species relationships can be overlooked if assessed at an inappropriate scale. Therefore, predicting the scale at which species respond most strongly to changes in landscape structure (i.e., the SOE) has become a key topic in landscape ecology research [2, 3••, 4, 6••, 7••, 9, 10•, 16, 45], as it is not only relevant to understand how species interact with the surrounding landscape context [5], but to implement conservation actions at the most effective spatial scale [8•]. However, despite the growing body of knowledge about the topic, predicting SOE is extremely challenging, and this is confirmed in our review.

Although species' mobility is the most intuitive driver of SOE, all mobility-related traits assessed in the present review showed weak relationships to SOE. We suggest this is partly related to high spatial and temporal within-species variability in mobility. This variability means that to predict the SOE based on mobility, we would need mobility estimates for the time and location of the particular study. Such information is very difficult to obtain, which means that it will almost always be more feasible to estimate the scale of effect directly using a multi-scale study [3••]. Doing this effectively will require selecting the range of scales for investigation based on a biological justification and ensuring that range will be wide enough to encompass the actual scale of effect in that particular place and time [12]. We acknowledge that future research may reveal a strong predictive model of the scale of effect, likely including a large number of interacting variables. However, until that time, we suggest that multi-scale analyses should become standard to ensure we are not missing landscape context effects due to studying them at the wrong scale.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s40823-022-00082-7.

Acknowledgements We thank A. Martin for the invitation for writing this paper and two anonymous reviewers for their constructive comments. MM-R thanks the Dirección General de Asuntos del Personal Académico (DGAPA)-UNAM for a postdoctoral scholarship. CG-A received a postdoctoral scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC).

Data Availability The data used in the present review is available as Supplementary material (Appendix S1 and S2)

Compliance with Ethical Standards

Conflict of Interest Víctor Arroyo-Rodríguez, Marisela Martínez-Ruiz, Jakelyne S. Bezerra, Carmen Galán-Acedo, Miriam San-José, and Lenore Fahrig declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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- •• Of major importance

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