

# What determines the spatial extent of landscape effects on species?

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## Abstract

**Context** Landscape ecologists are often interested in measuring the effects of an environmental variable on a biological response; however, the strength and direction of effect depend on the size of the area within which the environmental variable is measured. Thus a central objective is to identify the optimal spatial extent within which to measure the environmental variable, i.e. the “scale of effect”.

**Objectives** Our objectives are (1) to provide a comprehensive summary of the hypotheses concerning what determines the scale of effect, (2) to provide predictions that can be tested in empirical studies, and

(3) to show, with a review of the literature, that most of these predictions have so far been inadequately tested. **Methods** We propose 14 predictions derived from five hypotheses explaining what determines the scale of effect, and review the literature (if any) supporting each prediction. These predictions involve five types of factors: (A) species traits, (B) landscape variables, (C) biological responses (e.g. abundance vs. occurrence), (D) indirect influences, and (E) regional context of the study. We identify methodological issues that hinder estimation of the scale of effect.

**Results** Of the 14 predictions, only nine have been tested empirically and only five have received some empirical support. Most support is from simulation studies. Empirical evidence usually does not support predictions.

**Conclusions** The study of the spatial scale at which landscape variables influence biological outcomes is in its infancy. We provide directions for future

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research by clarifying predictions concerning the determinants of the scale of effect.

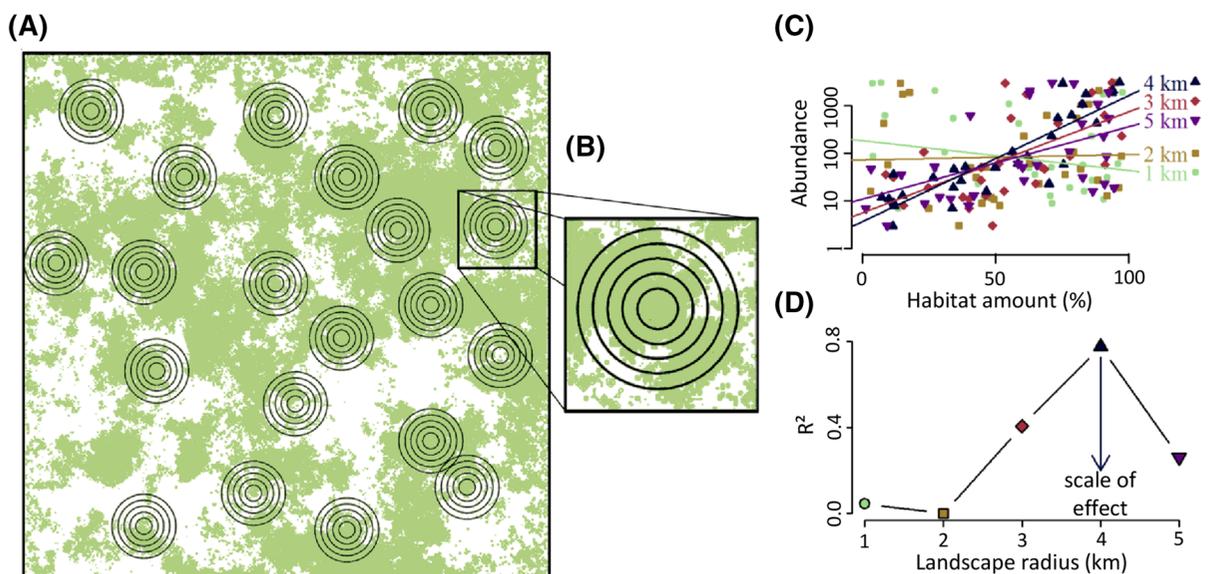
**Keywords** Biodiversity · Habitat fragmentation · Landscape size · Multi-scale model · Scale of response · Spatial scale

## Introduction

A common goal for landscape ecologists is to relate a biological response at a given location (e.g. abundance of a species) to environmental variables in the surrounding area, i.e. the landscape. The relationship between a biological response and surrounding environmental variables depends on the spatial extent (hereafter referred to as scale) at which environmental variables are measured. In particular, this spatial scale can influence (a) the strength of effect and whether it is considered biologically or statistically significant (Holland et al. 2004; Smith et al. 2011); (b) conclusions about the relative importance of different environmental variables on the biological response (Smith et al. 2011), and (c) the direction (positive or

negative) of effect (Holland et al. 2004; Smith et al. 2011). Thus, to ensure that we uncover an important relationship between a response and an environmental variable, we must measure that variable at the scale at which the relationship is strongest, i.e. the “scale of effect” (Jackson and Fahrig 2012). We usually assume that the scale of effect is related to the scale at which the species perceive and interact with the landscape.

We do not usually know the best scale for a given environmental variable and biological response. One way to find the scale of effect is to estimate it using empirical data in a multi-scale study (Fig. 1). In this approach, the environmental variable is measured at a range of spatial extents around each location where the biological response is sampled. Although species may interact with the landscape in areas that are not circular, we usually calculate landscape variables in circular areas because we do not have a priori knowledge to predict a more complex shape. Then a statistical model relating the environmental variable to the biological response (usually using linear regression) is fitted for each spatial extent. The scale of effect is estimated as the spatial extent that gives the best



**Fig. 1** Design of a hypothetical focal site multi-scale study: **a** the biological response, e.g. abundance of a species, is sampled in focal sites (not necessarily distinct patches) across the region of interest; **b** landscape structure is measured at multiple spatial extents centered on the focal site, each extent including landscape at smaller extents. Landscape structure is any measure of landscape composition or configuration (McGarigal et al. 2012). In this example, percent habitat amount

is measured, where habitat is represented in green; **c** the relationship between the biological response and landscape structure is evaluated for each spatial extent; **d** the scale of effect is the spatial extent at which landscape structure best predicts the response. In this example, the scale of effect is 4 km, where the  $R^2$  is highest and the slope is steepest (c). Modified with permission from Jackson and Fahrig (2015). © 2014 John Wiley & Sons Ltd

model according to a given criterion, e.g. Pearson's correlation coefficient ( $r$ ),  $R^2$ , or Akaike Information Criterion (AIC) (Fig. 1d). This method does not take into account the direction of the relationship between the landscape variable and the biological response (i.e. whether it is positive or negative), because the direction of effect does not influence the scale at which the relationship is strongest.

Landscape management and research would be easier if the scale of effect did not have to be estimated empirically in a multi-scale study, but could be predicted a priori. The multi-scale study (Fig. 1) requires to sample multiple landscapes and provides little help to a landscape manager with a single parcel to manage. With a good prior knowledge of scale of effect, landscape managers could identify the appropriate scale over which to implement a land management action. Research would be easier because researchers could optimally space their samples, i.e., far enough apart to allow the sampling of independent landscapes, but close enough to avoid the travel costs associated with excessively large distances among sample points. Additionally, researchers would not have to collect and analyse the large quantity of environmental data required when measuring environmental conditions at multiple scales. Some methodological concerns with the multi-scale method may also be dealt with by choosing the scale a priori. For example, analyses at many scales may increase the chance of Type I error, i.e. the probability of finding a significant effect at at least one scale.

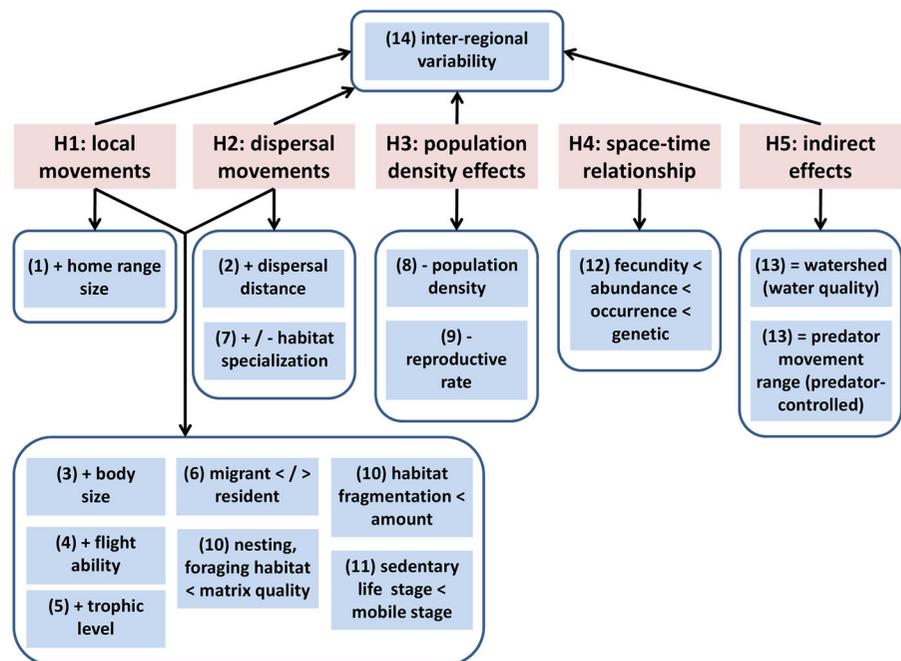
In a recent meta-analysis, Jackson and Fahrig (2015) explored whether certain species traits were predictive of the scale of effect across a range of organisms and found that most studies did not include a wide enough range of scales to even evaluate this question. This result suggests that current data are generally insufficient to adequately predict scales of effect a priori based on species traits. We also lack a comprehensive survey of other parameters, besides species traits, that may influence the scale at which species interact with the landscape. Most studies that investigate correlates of the scale of effect only consider one or two factors, and currently no conceptual framework exists for evaluating which factors to investigate, how these factors may shape the scale of effect, or how these factors may relate to one another.

In this paper, we thus expand on Jackson and Fahrig (2015), which was restricted to the effect of species traits on the scale of effect. Our goal is to compile and organize the hypotheses and predictions regarding the possible mechanisms that influence scale of effect and to review to what extent these predictions have been investigated and supported. This summary will provide a useful guide for the design of future empirical studies aiming to predict the scale of effect and will help us to move beyond the mechanism-blind approach of the multi-scale study. Specifically, our objectives are (1) to provide as comprehensive as possible a summary of the hypotheses concerning what determines the scale of effect; (2) to develop predictions that could be tested in empirical studies; and (3) to review the literature addressing these predictions, as a way to show that most of these predictions have been inadequately tested. We have identified five types of factors that may influence the scale of effect, and devote a section to each: (A) species traits, (B) landscape variables, (C) biological responses (e.g. abundance vs. occurrence), (D) indirect influences on the scale of effect, and (E) regional context of the study. We have included an additional section that considers (F) factors that can influence the estimated (as opposed to the actual) scale of effect. In each section, we formulate relevant predictions derived from hypotheses (summarized in Fig. 2), explain their basis, and summarize the current empirical and theoretical evidence for each prediction (if any). None of these predictions discussed is exclusive; several factors can simultaneously influence the scale of effect.

### Relationships between species traits and the scale of effect

Among the factors that may influence the scale of effect, species traits are the ones most commonly considered in theoretical (e.g. Jackson and Fahrig 2012; Ricci et al. 2013) and empirical (e.g. Thornton and Fletcher 2014; Jackson and Fahrig 2015) studies. Predictions of relationships between species traits and the scale of effect generally depend on an assumption that the trait is an indicator of either mobility (e.g. dispersal distance, home range size, body size, wing shape) or demography (e.g. reproductive rate) (Table S1).

**Fig. 2** Predictions about what determines the spatial extent of landscape effects on species (in *blue*) derived from five hypotheses (in *red*). The numbers in parentheses refer to the numbers used to index predictions in the text. H1 to H5 refer to the numbering of the hypotheses used in the text. The signs +/− refer to the predicted directions of the effects on the scale of effect. The signs </> refer to the predicted differences in the scale of effect. See the text for an explanation of each hypothesis and prediction. (Color figure online)



### Mobility-related predictions

The scale of effect should be larger for more mobile species because they interact with (and are affected by) environmental conditions over a larger spatial extent. This is the most intuitive hypothesis, and the one that researchers most frequently consider. When researchers conducting multi-scale studies provide justification for the scales at which they conduct their studies, all of their explanations are related to species mobility (i.e. home range size or dispersal distance; Jackson and Fahrig 2015). There are actually two distinct hypotheses for the proposed relationship between mobility and the scale of effect, one about local movements (Hypothesis H1) and one about dispersal movements (Hypothesis H2). We derive seven predictions from these two hypotheses (Fig. 2).

First is the idea that more mobile species should have larger scales of effect because they interact with environmental conditions during their daily or routine movements over a larger extent than do less mobile species (Fig. 3a, Hypothesis H1).

**Prediction 1** The scale of effect is larger for species with larger home ranges (or territories).

There is no empirical support for this relationship. Of the nine tests of this prediction (eight bird tests, one

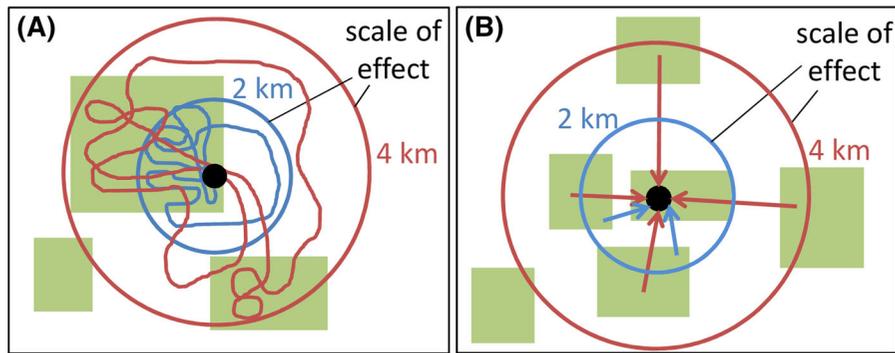
mammal test), none showed significant relationships. Six of the trends were non-significantly negative (the opposite of the prediction), one was non-significantly positive, and two did not report trend direction (Jackson and Fahrig 2015).

Second is the idea that species that can disperse further should have larger scales of effect because their local populations receive immigrants that have interacted with environmental conditions over a larger extent than do species that disperse shorter distances (Fig. 3b, Hypothesis H2).

**Prediction 2** The scale of effect increases with the mean (or median or maximum) dispersal distance.

This is well supported by simulation studies (Jackson and Fahrig 2012; Ricci et al. 2013), which further suggest that the dispersal distance is the main determinant of the scale of effect (of those considered). There are limited empirical data with which to evaluate this prediction, in part because dispersal distance estimates are rare. However, the one empirical study we are aware of that has tested this prediction in 22 bird species (Tittler 2008) did not find a relationship between dispersal distance and scales of effect.

In addition, we can imagine that the shape of the dispersal kernel for a given mean or median dispersal



**Fig. 3** The mobility of organisms is hypothesized to affect the scale of effect in two ways. **a** The distance that a species visits during its daily movement in its home range (red squiggle) is 4 km, which determines the scale of effect of foraging habitat amount (green) on abundance at a sample site (red circle); Home range size of another species is smaller, which reduces the extend of the foraging habitat visited (blue squiggle), thus reducing the scale of effect to 2 km (blue circle), Hypothesis H1

distance (i.e. the tail of the dispersal kernel) influences the scale of effect. However we do not have an intuitive idea about the expected direction of this influence on the scale of effect.

In addition to these two predictions, there are a number of proposed relationships between species traits and the scale of effect that depend on the assumption that the trait is related to species mobility (dispersal distance and/or home range size). We briefly describe the major predictions below.

**Prediction 3** The scale of effect is larger for larger-bodied species.

We predict that the scale of effect should be larger for larger-bodied species because large-bodied species tend to be more mobile than smaller-bodied species (Bowman et al. 2002; Bowman 2003; Brouwers and Newton 2009). Despite being the most studied of all relationships between species traits and scale of effect, there still remains only weak support for this prediction. One meta-analysis of 22 bird studies found a positive relationship between the scale of effect and body size within studies (Thornton and Fletcher 2014). However, a second meta-analysis of data from across a wide range of animal taxa found a positive relationship between body size and scale of effect for only three of the 19 cross-species comparisons (Jackson and Fahrig 2015, updated in Table S1). Of the remaining 16 relationships, one was significantly U shaped and 15 were non-significant.

and Prediction 1. **b** The distance from which immigrants can reach the central sample site (red arrows) is 4 km, which determines the scale of effect of habitat amount (green) on abundance at the sample site (red circle); Dispersal distance of another species is smaller, which reduces the distance from which immigrants can arrive to the site (blue arrows), thus reducing the scale of effect to 2 km (blue circle), Hypothesis H2 and Prediction 2. (Color figure online)

**Prediction 4** The scale of effect is larger for flying species, and even more so for those able to fly farther.

Species with functional wings and winged species with lower wing-loading (i.e. lower ratio of weight to wing area), and/or with higher aspect ratio (i.e. longer wings for a given width) should be able to move farther (Bowlin and Wikelski 2008), and so should show larger scales of effect. However, there is no support for this prediction; all studies of these relationships have reported non-significant results (Tittler 2008; Kallio 2014; Jackson and Fahrig 2015).

**Prediction 5** The scale of effect is larger for species at a higher trophic level.

We expect larger scales of effect for species at higher trophic levels because these species generally have greater mobility than species at lower trophic levels (at least within some taxonomic groups; Jetz et al. 2004). Jackson and Fahrig (2015) tested this prediction for four taxonomic groups (birds, invertebrates, bats, and ground mammals). None of the taxa showed larger scales of effect for species at higher trophic levels.

**Prediction 6** The scale of effect is larger/smaller for migratory species than non-migratory species.

There are reasons to predict opposing relationships between migration status and scale of effect. First, the scale of effect may be larger for migrant species,

because they are generally more mobile than resident species (Paradis et al. 1998). However, one could also formulate the opposite prediction: that the scale of effect is larger for resident species, because residents often spend winter exploring beyond the breeding territory of the previous breeding season, and may thus interact with the surrounding landscape over a larger extent than do migratory species. There is little support for either prediction. Of four tests of the relationship between migratory status and scale of effect (Jackson and Fahrig 2015), one test supported larger scales of effect in migrant birds, consistent with the first prediction, whereas no significant relationship was found in the other three cases.

**Prediction 7** The scale of effect is larger/smaller for specialists than for generalists.

The predicted relationship between scale of effect and specialization depends on whether you expect habitat specialists to disperse farther than generalists, or the opposite. We expect a larger scale of effect with greater habitat specialization for species groups with a positive correlation between habitat specialization and dispersal distance (e.g. temperate breeding birds; Martin 2015). However, a number of invertebrate studies suggest the opposite habitat specialization-mobility relationship: that habitat generalists have better dispersal abilities than habitat specialists (Bonte et al. 2003; Entling et al. 2011; Sekar 2012; Carnicer et al. 2013; Dapporto and Dennis 2013; Stevens et al. 2014; Dahirel et al. 2015). For such species, we expect specialists to have smaller scales of effect. There is little empirical support for either prediction; the only support is from Chaplin-Kramer et al. (2013), who found smaller scales of effect for habitat specialist arthropods than for habitat generalist arthropods, which is consistent with our prediction for invertebrates.

#### Demography-related predictions

We propose the hypothesis that species traits related to demography (e.g. reproductive rate, density) influence the scale of effect. This is because these traits may affect the importance of local demographic processes relative to dispersal processes on the biological response. We hypothesize that the scale of effect increases when the relative importance of local demography decreases compared to dispersal

(Hypothesis H3). We present two predictions derived from this hypothesis: one related to population density and the other related to reproductive rate. These predictions are valid only under the assumption that populations with higher densities and higher reproductive rates are more likely to be close to carrying capacity than populations with lower densities and reproductive rates. Other life history traits (e.g. mortality, generation time, longevity, age at first reproduction) that are strongly correlated with population density or reproductive rate should also exhibit similar associations with scale of effect.

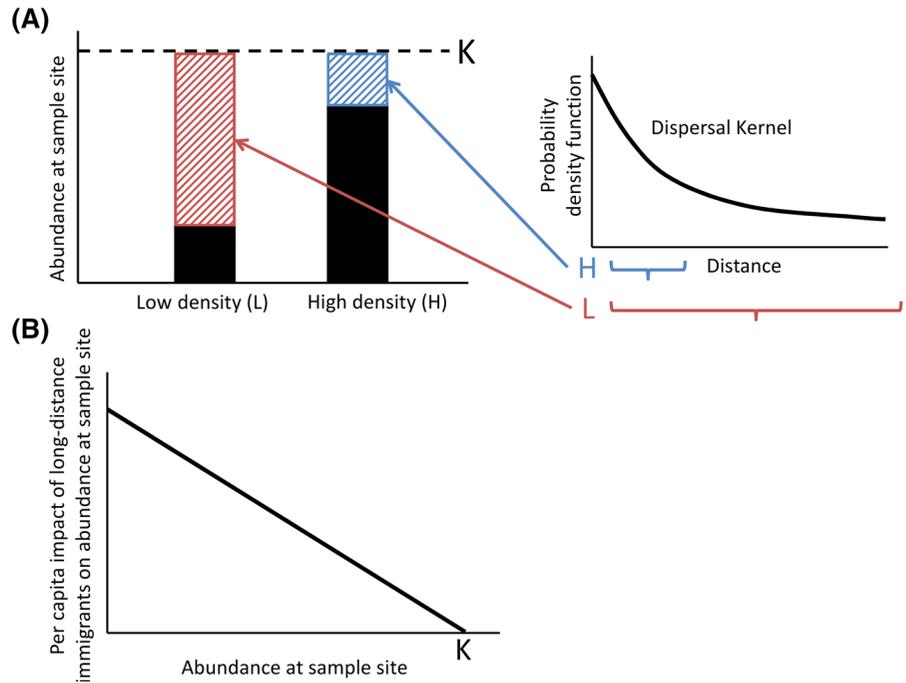
**Prediction 8** The scale of effect is smaller for higher-density populations than for lower-density populations.

We predict that, all else being equal, the scale of effect should be smaller for populations with higher densities. This negative relationship between population density and scale of effect was observed in a simulation study (Jackson and Fahrig 2012) in which carrying capacity was kept constant, indicating that populations at higher densities were closer to their carrying capacity. We suggest two explanations for this relationship. One explanation is that for high-density populations, the carrying capacity is quickly met by dispersers from the immediate surroundings, so longer-distance dispersers do not immigrate, and thus have little influence on population dynamics, resulting in a smaller scale of effect (Fig. 4). Another explanation is that when population growth is density-dependent, the demographic contribution of immigrants to high-density populations will be proportionally low compared to that of low-density populations. Therefore, the size of the focal population will be only weakly influenced by individuals arriving from long distances. In contrast, populations that are far from carrying capacity are likely to be especially sensitive to long distance dispersal. For example, Johst et al. (2002) show that slowly growing populations need to disperse longer distances to persist.

**Prediction 9** The scale of effect is smaller for species with a higher reproductive rate.

This prediction follows the same logic as described above for population density. A species with a higher reproductive rate should have a larger scale of effect because species with higher reproductive rates are likely to be closer to carrying capacity than are species

**Fig. 4** The scale of effect decreases with population density (Prediction 8). **a** For a species at high density (H), abundance at a site (e.g. the sample site) is usually near site capacity (K). Available capacity is quickly saturated by dispersers from the immediate surroundings (small scale of effect). In contrast, for a species at low density (L) abundance at the focal site is usually low, allowing immigrants from across the dispersal distance gradient to contribute to the population. **b** The impact of rare, long-distance immigration on abundance decreases as the abundance approaches the site capacity



with a lower reproductive rate. This prediction is supported by the simulation study discussed above (Jackson and Fahrig 2012) and by one empirical study (Kallio 2014) that found that the scale of effect for 13 carabid beetle species was negatively related to reproductive rate. On the other hand, Jackson and Fahrig (2015) did not find support for this prediction in their meta-analysis.

Because population growth rate may be negatively correlated with dispersal distance (e.g. Baguette and Schtickzelle 2006), we must be cautious about making causal inferences based on an observed relationship between either of these factors and scale of effect. For example, in two simulation studies, larger dispersal distances lowered overall population density due to greater exposure to non-habitat, and thus greater rates of dispersal mortality (Jackson and Fahrig 2012, 2014). This suggests that an apparent negative relationship between growth rate (or density) and scale of effect could in part be driven by dispersal distance, rather than by the direct effect of growth rate (or density).

In summary, although species traits are often considered the drivers of scale of effect (especially mobility traits), we show that there is actually little empirical evidence to support these predictions. This

may suggest that the scale of effect is driven by factors unrelated to species traits. We discuss these factors in the following sections.

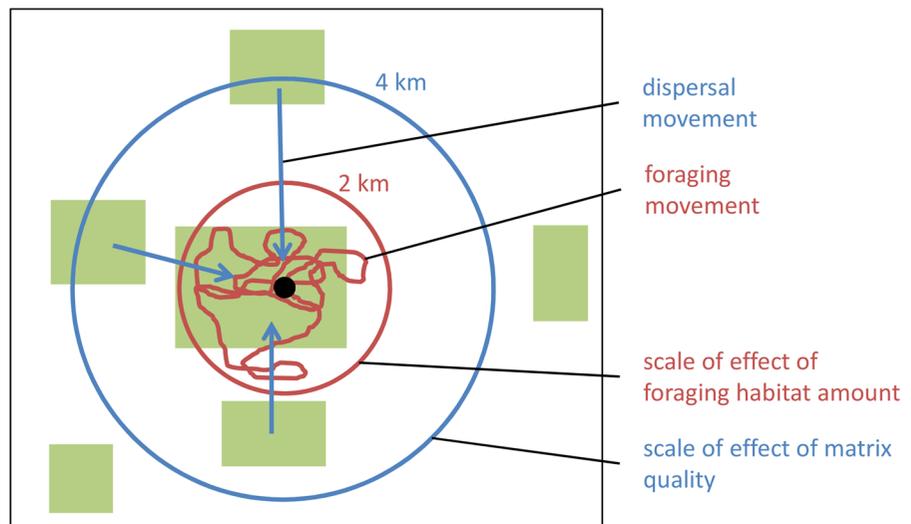
### Relationships between landscape variables and the scale of effect

Empirical studies suggest that the scale of effect of the landscape on a biological response can depend on which landscape variable is measured (e.g. Fuhlendorf et al. 2002; Duren et al. 2011; Coffey and Fahrig 2012; Patenaude et al. 2015). A landscape variable is defined by both what environmental condition is measured (e.g. forest) and how it is measured (e.g. proportional forest cover, number of forest patches).

**Prediction 10** The scale of effect is smaller for landscape variables that most strongly influence breeding and/or foraging success than for landscape variables that most strongly influence dispersal success.

This prediction is based on the idea that the scale of effect can depend on both the scale of interaction with environmental conditions during daily movements (Hypothesis H1; Fig. 3a) and during dispersal

**Fig. 5** Effect of the scale of movement process on the scale of effect. **a** The scale of effect of foraging habitat amount on abundance (*red circle*) depends on the distance over which individuals forage (*red squiggle*), e.g. 2 km. **b** The scale of effect of matrix quality on abundance (*blue circle*) depends on the distance from which dispersing individuals can reach the sample site (*blue arrows*), e.g. 4 km (Prediction 10). (Color figure online)



(Hypothesis H2; Fig. 3b). Landscape variables that most strongly affect breeding and/or foraging success (e.g. nesting site availability, foraging habitat) should have smaller scales of effect because breeding and foraging success mainly depend on interactions between individuals and the environment within their home range (i.e. during daily movements; Fig. 5). Landscape variables that most strongly affect dispersal success (e.g. matrix quality) should have a larger scale of effect because dispersal success mainly depends on interaction of individuals and the environment within the dispersal distance (Fig. 5).

To our knowledge no one has tested whether scales of effect for different landscape variables match independent estimates of space use associated with breeding, foraging, or dispersal (e.g. territory size, home range size, dispersal distance). However, if this prediction is true, we expect the scale of effect of habitat fragmentation to be smaller than the scale of effect of habitat amount. Habitat amount should most strongly influence dispersal success, because high habitat amount should reduce dispersal mortality and then increase dispersal success. In contrast habitat fragmentation, i.e. how broken apart habitat is, for a given habitat amount, should mainly influence foraging and breeding resource availability. This is because fragmentation determines the habitat patch size, and thus the relative amounts of core and edge habitat within a species home range. This prediction is supported by an individual-based simulation model, which found habitat fragmentation affected population abundance,

presence/absence, and allelic richness at a smaller scale than habitat amount (Jackson and Fahrig 2014). However, there is no clear empirical support for this prediction: of 26 comparisons from five studies, the scale of effect was larger for fragmentation than for habitat amount in nine cases, was the same for habitat amount and fragmentation in seven cases, and was smaller for fragmentation than for habitat amount in 10 cases (Ethier and Fahrig 2011; Feagan 2011; Smith et al. 2011; Flick et al. 2012; Ordóñez-Gómez et al. 2015).

**Prediction 11** The scale of effect is smaller for landscape variables that most strongly influence the biological response of a less-mobile life stage than for landscape variables that most strongly affect a more-mobile life stage.

This prediction is based on the idea that different environmental conditions are important at different life stages and different life stages of a species interact with the landscape over very different spatial extents (because life stages differ in mobility). This prediction may be particularly relevant for species that undergo metamorphosis (e.g. anurans, invertebrates). For instance, the spatial extent of the environment encountered by a caterpillar is much smaller than the extent encountered by a butterfly. In this case, either the life stage that is most strongly affected by the landscape variable in question may drive the scale of effect or, if the landscape variable is equally important at both life stages, support may be found for two

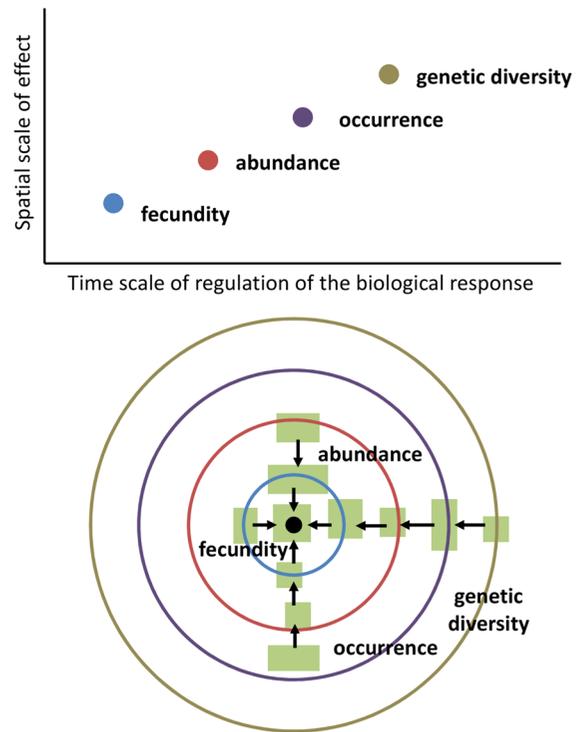
distinct scales of effect. To our knowledge, this prediction has never been tested.

### Relationships between the biological responses and the scale of effect

The scale at which the landscape affects species may be influenced by the biological response being measured. Many biological responses can be measured in focal site studies including occurrence, abundance, home range size, genetic diversity, demographic rates, or multi-species metrics such as species richness. We hypothesize that the spatial scale of effect is larger for biological responses that are influenced by forces acting over longer time scales than for biological responses influenced by forces acting over shorter time scales (Hypothesis H4). This is because we expect that influences over longer time scales come from longer distances.

**Prediction 12** The spatial scale of effect depends on the biological response, increasing according to this order: fecundity, abundance, occurrence, genetic diversity.

This prediction (Fig. 6) is based on the link between the spatial and temporal scales at which the landscape affects different biological responses for a given species or population. For example, population fecundity is influenced by resource availability within a population's breeding habitat during the breeding season; thus, the landscape likely influences fecundity over a short time span and a small spatial extent. In contrast, abundance at a focal site is typically influenced by the cumulative effects of the landscape on both local processes (births and deaths) and larger-scale, longer-term processes, including immigration and emigration. Occurrence, which is controlled by extinction and colonisation events, would generally depend on even longer time spans and larger spatial scales. This prediction was supported by a simulation study (Jackson and Fahrig 2014), which found larger scales of effect when going from measures of abundance to occurrence to genetic diversity. An empirical study by Cushman and McGarigal (2004) showed a small increase in the importance of landscape structure at large scales when predicting forest bird occurrence in comparison with predicting abundance. Extrapolating from this, we also predict that multi-species



**Fig. 6** The type of biological response variable affects the scale of effect (Prediction 12). For example, fecundity at the sample site is affected by resource availability within foraging distance of a breeding individual during a short time (the breeding season), resulting in a small scale of effect. In contrast, genetic diversity at the sample site is influenced by movements over many generations, resulting in a much larger scale of effect

responses based on combined occurrence information (e.g. species richness) should show larger scales of effect than multi-species responses based on combined abundance information.

### Indirect influences on the scale of effect

For our previous predictions, the core assumption was that the scale of effect of a landscape variable on a biological response depends on the scale at which the species (or species group) directly interacts with the landscape. For example, Prediction 1 is based on the idea that the scale of effect should depend on the spatial extent within which the species moves and interacts with its environment. However, the scale of effect of a landscape variable on a biological response may instead indirectly depend on the scale at which the landscape variable affects some other abiotic (e.g.

water quality) or biotic factor (e.g. predator density) that in turn has a strong influence on the biological response (Hypothesis H5). It is important to know whether the effect of a landscape variable is direct or indirect because we are looking for the processes that drive the scale of effect. If the landscape context directly affects a population, then we can (potentially) use the traits of that species to predict the appropriate scale of effect based on the scale at which the population interacts with the landscape. However, if the effect of the landscape is indirect (e.g. effects on water quality or predation), the scale of effect should be more closely associated with other factors (e.g. watershed size or predator mobility).

**Prediction 13** When (1) the direct effect of a landscape variable on a given biological response is weak, (2) a single factor (abiotic or biotic) strongly influences the response, and (3) the landscape variable strongly affects this factor, the scale of effect of the landscape variable on the given biological response will be the scale of effect of that landscape variable on the abiotic or biotic factor.

A factor that indirectly shapes the scale of effect can be abiotic. For example, water quality is an abiotic factor expected to have a strong effect on the response of aquatic or semi-aquatic organisms, and thus the scale of water movement may determine the scale of effect of the landscape on these organisms. Landscape attributes of a catchment affect physical and chemical attributes of a stream (e.g. Sliva and Williams 2001; Sponseller et al. 2001; Roy et al. 2003), supporting the suggestion that landscape attributes influence local water quality at the scale of water transport to the sample location. Some studies have found stronger catchment-scale effects of the landscape on stream biota than local (e.g. riparian buffer) effects, which is consistent with the idea that the scale of movement of water to the sample location drives the scale of effect (Roth et al. 1996; Walters et al. 2009).

Alternatively, the indirect factor may be biotic. For example, if a landscape variable strongly influences a predator species, and that predator strongly affects a prey species, then the apparent effect of that landscape variable on the prey population should occur at the scale of its effect on the predator population. To our knowledge this has not been directly studied. However, Manzer and Hannon (2005) found both a strong, negative effect of corvid density on sharp-tailed

grouse nesting success, and that the scale of effect of crop cover on grouse nesting success was the same as the scale of effect of crop cover on corvid density, which is consistent with our hypothesis.

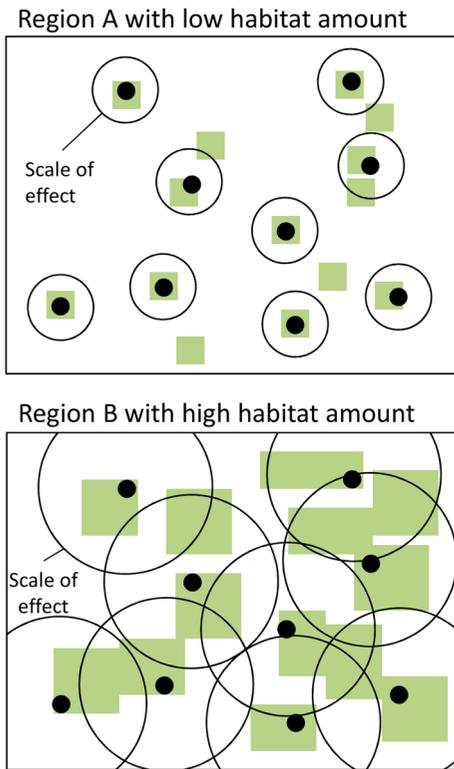
### Variation of the scale of effect with regional context

**Prediction 14** The scale of effect depends on the regional context because there exists variation in species traits, landscape variables, and indirect factors among regions that influence the scale of effect.

Variation in species traits and environmental characteristics across regions can contribute to intraspecific variation in scales of effect found in Thornton and Fletcher (2014) and Jackson and Fahrig (2015). A first corollary of this is that the scale of effect in one study region should not necessarily be extrapolated to another region, even for the same species. A second corollary of this is that if the regional context changes with time, then the scale of effect should also change with time to adapt to the new regional context. The importance of regional influence on scale of effect depends on how common scale-relevant regional differences are.

There is ample evidence for inter-regional variation in the traits that are thought to influence the scale of effect. This includes climate-mediated intraspecific variation in traits related to species mobility, such as body size (e.g. Chown and Klok 2003; Du et al. 2005; Cvetković et al. 2009; Boast et al. 2013; Munoz et al. 2014; Zeng and Zhu 2014), home range (e.g. van Beest et al. 2011; Boast et al. 2013), flight endurance (Ducatez et al. 2013), emigration rate and movement distance (Delattre et al. 2013), and in traits related to population density, such as life span (e.g. Morrison et al. 2004; Munch and Salinas 2009; DeFaveri et al. 2014) and reproductive rate (e.g. Du et al. 2005).

Regional variation in traits can also be mediated by differences in the landscape itself, and how landscape alters the realized dispersal distance. For instance, low matrix quality, road density or hilly topography can reduce the realized dispersal distance. Habitat amount and fragmentation can also affect mobility (Delattre et al. 2013). Dispersal distances may be longer in regions with greater habitat cover and/or greater aggregation of habitat because successful movement is favoured when habitat is abundant, in part due to reduced risk of dispersal mortality. This greater



**Fig. 7** The scale of effect on a given species can vary between regions (Prediction 14). *Region B* has higher overall habitat cover than *Region A*. Connectivity is therefore higher in *Region B*, leading to higher dispersal distances, which leads to a larger scale of effect in *Region B*. Habitat amount is only one example of the factors that contribute to the variability of the scale of effect between regions. Other factors such as matrix quality, topography or habitat fragmentation could also affect the scale of effect

dispersal distance should result in larger scales of effect (Fig. 7). In support of this expectation, Ricci et al. (2013) found in a simulation study that habitat aggregation increased the scale of effect. Conversely, if mortality in non-habitat is low, the scale of effect may be larger in regions with lower habitat cover because individuals may have to disperse farther to find the first available habitat.

We are not aware of any empirical studies that explicitly test for regional variation in the scale of effect. However, regional variability is one possible explanation for the wide variation in scales of effect for bird species of the same body size found in one meta-analysis (Thornton and Fletcher 2014), and for the lack of evidence for relationships between species traits and the scale of effect in another meta-analysis (Jackson and Fahrig 2015).

### Factors that can lead to misidentification of the scale of effect

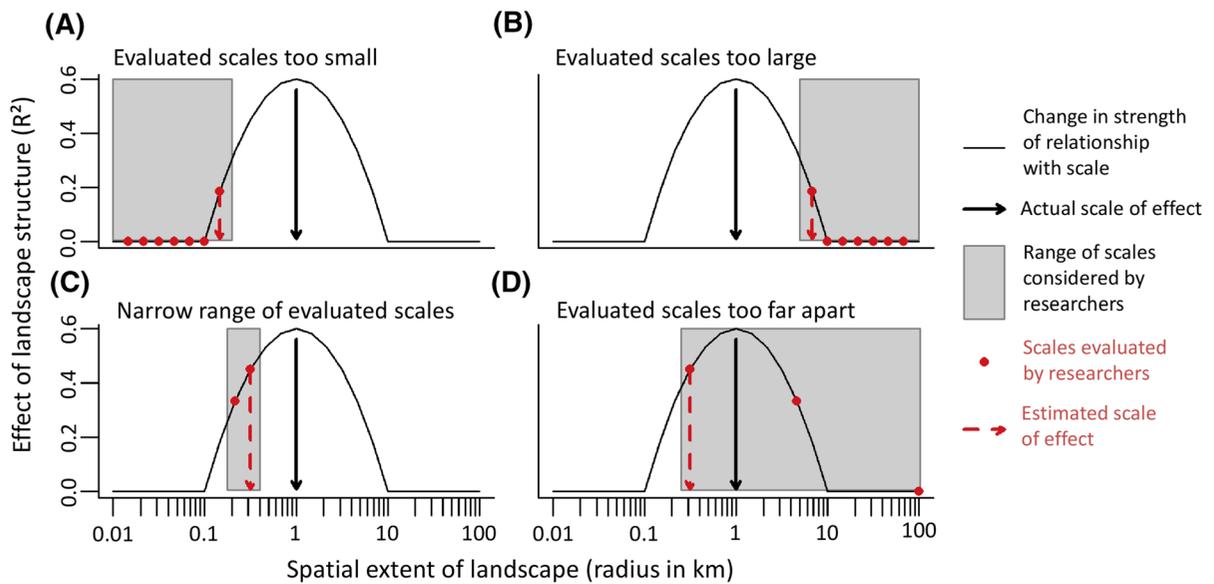
In the previous sections we showed that while there is a wide range of factors that can in principle predict the scale of effect, there is currently little evidence to support any of these. However, there are several factors that can influence the accuracy or precision with which the estimated scale of effect matches the actual scale of effect: (1) range and number of scales included in the analysis, (2) between-scales variability in landscape variable values, (3) collinearity among landscape variables, (4) correlation of a landscape variable's values among scales, (5) data resolution (spatial and thematic), and (6) type of statistical model. In this section, we discuss these factors, and suggest guidelines for study designs that can minimize the impact of these factors on the estimated scale of effect.

#### Range and number of scales included in the analysis

The scale of effect cannot be accurately estimated if the actual scale of effect is not included in the range of evaluated scales. This can occur if the landscape scales considered in the multi-scale analysis are (a) all smaller than the actual scale, (b) all larger than the actual scale, (c) too narrow in range to include the actual scale, or (d) too far apart within that range of scales (Fig. 8). This seems to be a common problem in many studies; a recent meta-analysis (Jackson and Fahrig 2015) found that most studies were unlikely to include the actual scale of effect.

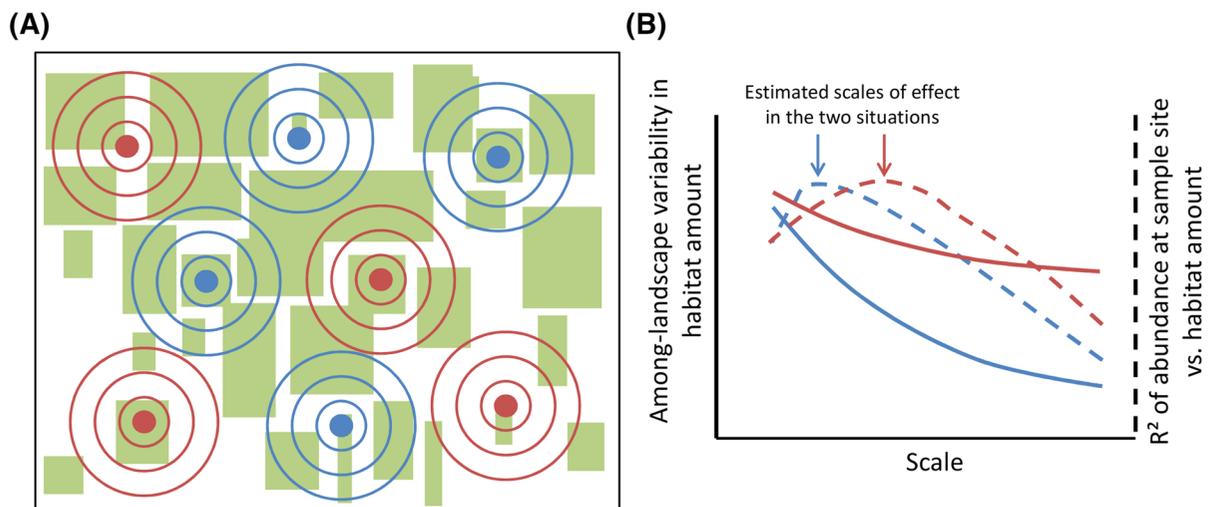
#### Between-scales variability in landscape variable values

The range and variance in the values of a landscape variable for a given set of landscapes usually decrease with increasing spatial extent of the landscapes (e.g. Wiens 1989; Pasher et al. 2013). This is because, as the spatial extent of individual landscapes increases and approaches the spatial extent of the entire sampled region, values of a given landscape variable for each individual landscape will approach the regional mean value. All else being equal, this could lead to underestimation of the scale of effect because decreased range and variance in landscape variable



**Fig. 8** Illustration of ways in which the estimated scale of effect can be different from the actual scale of effect, even when the influence of landscape structure is evaluated at multiple spatial extents. If landscape scales evaluated are **a** too small, **b** too large, **c** too narrow, or **d** too far apart, the estimated scale of

effect (indicated by *dotted arrow*) can be different from the actual scale of effect (indicated by *continuous arrow*). Modified with permission from Jackson and Fahrig (2015). © 2014 John Wiley & Sons Ltd



**Fig. 9** A given selection of sample sites (**a**, blue dots) can lead to under-estimation of the scale of effect. Among-landscape variance in habitat amount decreases with increasing scale (**b**, continuous blue line), until all local landscapes are similar to the 'average' landscape for the region. The probability of detecting an effect of habitat amount decreases with decreasing among-landscape variance in habitat amount, leading to an under-

values at larger scales reduces the estimated strength of large-scale landscape effects on the biological response (Fig. 9). This decreased variance with scale

estimation of the scale of effect (**b**, blue arrow). It is possible to control for declining variance with scale, by selecting sample sites (**a**, red dots) which minimize the decline in variance with scale (**b**, continuous red line), and allow detection of an estimated scale of effect (**b**, red arrow), closer to the true scale of effect. (Color figure online)

is expected to be exacerbated when sampling from landscapes whose spatial extents geographically overlap at larger scales (e.g., Region B in Fig. 7).

## Collinearity among landscape variables

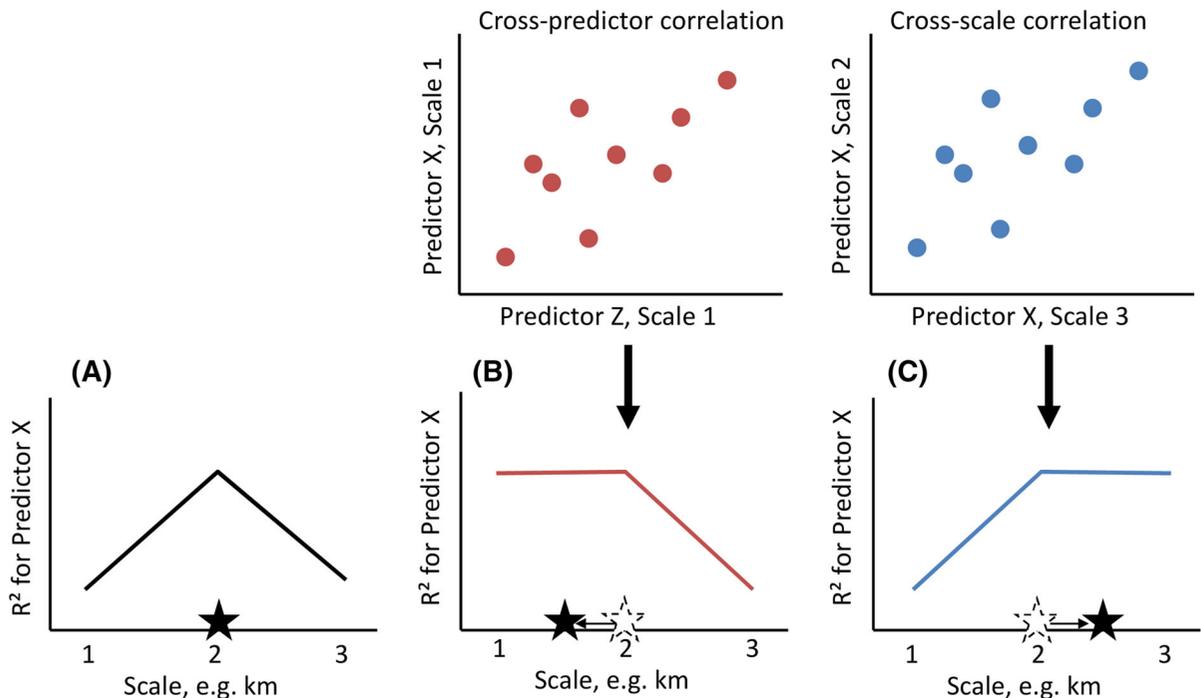
Because the multi-scale analysis approach is correlative rather than causal, the scale of effect of a given landscape variable could be driven by some other correlated landscape variable(s). Collinearity among landscape variables can affect the estimated direction and strength of the relationship between a given landscape variable and a biological response (e.g. Graham 2003; Smith et al. 2009; Eigenbrod et al. 2011). This can in turn influence estimated scales of effect if collinearity spuriously increases or decreases the effect size of a given landscape variable at different scales. In an extreme case, where two landscape variables are correlated and one of the variables has a much stronger effect on the biological response than the other variable, the apparent scale of effect of the weaker variable will be the scale of effect of the stronger variable (Fig. 10a, b). As long as the correlated variable actually has an effect on the response, it can affect the scale of effect irrespective of whether it is included in the analysis.

## Correlation of a landscape variable's values among scales

Correlations among measures of a particular landscape variable at different scales can also influence the estimated scale of effect (Battin and Lawler 2006). Strong correlations in a landscape variable across scales will result in similar effect sizes across scales (Fig. 10c). In this case, it may be impossible to estimate an actual scale of effect (Fig. 10a). But if strong correlation across scales is combined with decreased variance in landscape variables at large scales (discussed above in “Between-scales variability in landscape variable values” section), this may increase the chance of selecting a small scale of effect, regardless of the true value.

## Data resolution (spatial and thematic)

The accuracy and precision with which landscape variables are measured influence the accuracy and precision with which the scale of effect is estimated.



**Fig. 10** The apparent scale of effect of a given landscape variable (*star*) is influenced by its correlations with other landscape variables and by between-scale correlations. **a** In the absence of correlations, the ‘true’ scale of effect of predictor X on the response (e.g. abundance at samples sites) is 2 km.

**b** Predictors X and Z are correlated at the scale of effect of Z (here, 1 km), so the apparent scale of effect of X is shifted down. **c** Predictor X at its scale of effect (i.e. 2 km) is correlated to itself at 3 km, so its apparent scale of effect is shifted up

Hence it is important to pay attention to the spatial and thematic resolution of landscape data used to estimate the scale of effect. Spatial resolution refers to the pixel size or minimum identifiable unit of measurement. Thematic resolution refers to the number of different land cover categories used to describe a landscape. For example, a landscape in which all forest is classed as a single cover type has lower thematic resolution than a landscape in which coniferous, deciduous, and mixed forests are mapped as separate categories.

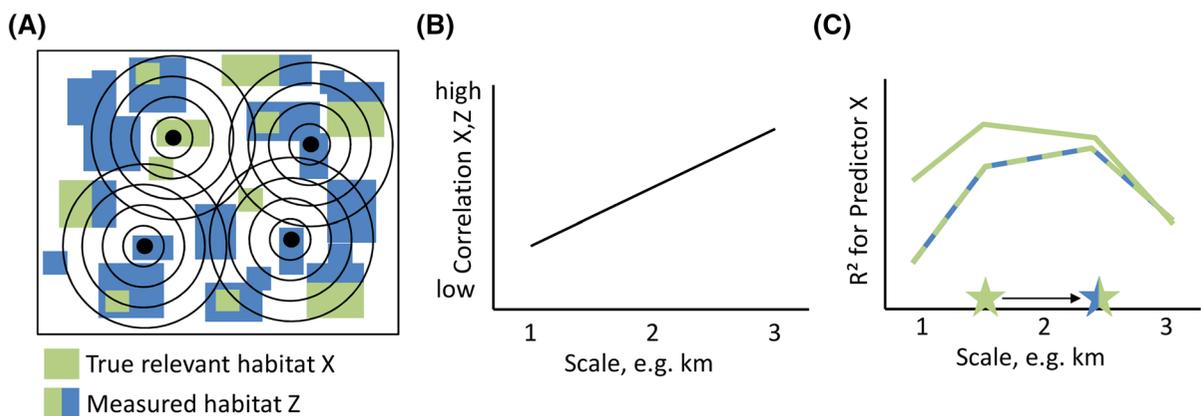
We predict that the estimated scale of effect will shift towards larger scales when the spatial resolution of the data is coarser. A pixel represents only the most abundant landscape variable value within a given area, thus it can under- or over-estimate the variable value within that pixel. At the smallest scales, containing only one or a few pixels, the resulting measurement error can be large. At larger scales (including more pixels), overestimation in some pixels will tend to balance underestimation in others, reducing this measurement error. Thus, greater measurement error at smaller scales when resolution is low will result in weaker relationships between the landscape variable and biological response at smaller scales than at larger scales. This should shift support toward larger estimated scales of effect. This prediction has been supported by simulation (Lechner et al. 2012) and empirical (Mendenhall et al. 2011) studies, which

found that finer data resolution reduced the estimated scale of effect, likely in response to improved model fit.

Similarly to spatial resolution, finer thematic resolution allows landscape variables to be more accurately and precisely measured for a given species. This should lead to stronger relationships between the landscape variable and biological response which, in turn, should lead to more accurate estimates of the scale of effect. In particular, we predict an overestimation of the scale of effect if the thematic resolution is too coarse (Fig. 11). The justification for this prediction is the same as for spatial resolution: low thematic resolution will disproportionately decrease accuracy of landscape variable measurement at small scales relative to large scales, thereby increasing the chance of incorrectly estimating a large scale of effect. To our knowledge, there is no empirical test of this prediction.

#### Type of statistical model and best model criteria

A few studies suggest that the statistical model and criterion used to determine the scale of effect may influence the estimated scale of effect (Martin and Fahrig 2012; Ricci et al. 2013). The statistical model may affect the estimated scale of effect because some statistical models better represent the shape of the species response than others. For example, if a



**Fig. 11** The apparent scale of effect (*star*) of a given landscape variable depends on its correlation with a landscape variable that has a functional role for the species (e.g. a habitat). **a** Here the true habitat is the green one, (e.g. a specific type of forest with a specific type of tree). But the resolution of our data only allows to map a coarser category in *green + blue* (e.g. the whole forest cover). The *blue* category is not functionally important for the

species. **b** If the habitat in green is randomly distributed within the coarser land use category, we could expect that the correlation between the habitat and the coarser category increases with the scale. So the coarse category became a better estimate of the true habitat at larger scale. **c** This could shift the estimated scale of effect toward a larger scale (e.g. 2.5 km instead of 1.5 km). (Color figure online)

biological response at its actual scale of effect is non-linear, but a linear model is used, the apparent scale of effect will likely be misidentified as a scale where the relationship is linear. The criterion used to select the scale of effect (e.g.  $R^2$ , AIC, regression coefficient) may also affect the apparent scale of effect, because different criteria measure different aspects of the statistical model fit. For example, if a regression model at a given scale produces a large regression coefficient but its estimate is imprecise (i.e. a small model  $R^2$ ), this scale may be selected as the scale of effect when using the regression coefficient as the criterion, but not when using  $R^2$ . A better understanding of the influence of model type and criterion would need further research.

#### Recommendations to avoid misidentification of the scale of effect

There are several things that can be done at different points in a multi-scale study (from sample site selection to data analysis) to reduce the chance of misidentifying the scale of effect.

First, the selected set of sample sites should minimize (1) the decline in landscape variable variance with increased scale and (2) correlations between variables. As an example of how this could be done, Pasher et al. (2013) developed an algorithm that optimizes landscape site selection by searching over the landscape parameter surface within a region and selecting sample sites in a way that optimizes a given set of criteria, such as the minimizing correlations among landscape variables.

The appropriate range of scales will depend on the study context, but should be chosen to ensure that the evaluated range of scales is likely to include the actual scale of effect. Simulation modeling suggests that the set of considered scales at which landscape metrics are measured should range from a value smaller than the species' home range up to more than 4–9 times the species' median dispersal distance when relating landscape to abundance data (Jackson and Fahrig 2012). In addition, more than a few scales should be tested within this range (Fig. 8d). We also recommend using the highest quality data available, i.e. with the smallest spatial resolution, and ensuring that there is detailed enough thematic resolution to measure the landscape variable that is relevant to the biological response of interest.

Metrics used to select the scale of effect (e.g.  $R^2$ ) may produce similar values at multiple scales; thus without information concerning the variation among scales, selection of a single scale with the highest  $R^2$  may provide the false impression that analysis of this scale is much better than others. Studies should report scale-sensitivity of a landscape variable, or the extent to which the relationship between a landscape variable and a biological response changes with scale. For instance studies could report the range of scales where the strength of the relationship is similar to the one at the scale of effect.

#### Conclusions

We present for the first time a comprehensive summary of the predictions regarding the possible factors that govern scales of effect. Although there are many predictions (Fig. 2), there currently exists little evidence to support any of these predictions. For most predictions, little to no research has ever been carried out to test them. Out of the 14 predictions, five have been evaluated by simulations (predictions 2, 8, 9, 12, 14), nine have been tested empirically, at least in part, with five showing some support (predictions 3, 6, 9, 12, 13) and four showing no support (predictions 1, 2, 4, 5), and five have never been tested empirically (predictions 7, 8, 10, 11, 14). For those predictions that have been studied (e.g., the body size prediction), this lack of evidence appears, at least in part, to result from the misspecification of scales of effect in empirical studies, which obscures any relationship that may exist between species traits and actual scales of effect (Jackson and Fahrig 2015). It may also be difficult to detect an effect of a single factor on the scale of effect if a large number of different factors influence the scale of effect simultaneously. Finally across-study comparisons of the relationship between the scale of effect and the factors thought to determine the scale of effect may produce ambiguous or inconsistent results when important differences exist among studies. For example, the estimated scale of effect for a given species or group may vary among studies if different landscape variables were measured, if the studies were carried out in different regions, or if distinct statistical models or selection criteria were used to identify the scale of effect. Ideally studies should control

important factors affecting the scale of effect before testing any of the 14 predictions.

The study of the spatial scale at which landscapes shape biological outcomes is in its infancy. For this reason, it is too early to make recommendations for conservation or management, and multi-scale analysis (e.g., Fig. 1) is currently the best way to ensure that landscape-species relationships are analyzed at the most biologically relevant scale. Nevertheless, a framework for predicting scales of effect a priori remains possible and desirable, but will require a database of studies that estimate the scale of effect from multi-scale analyses across a broad range of species and landscapes. In addition, better-controlled multi-scale studies of the scale of effect will be necessary to facilitate valid comparisons among studies. Simulations will also likely play an important role in evaluating whether the predictions proposed in this paper are plausible, helping to build a set of validated predictions that can be used by both researchers and conservation planners. The best case scenario is that the set of factors that determine the scale of effect is small and measurable, such that a simple set of guidelines can be devised for identifying the scale of effect. However, even if the forces that influence the scale of effect are complex, we can develop general rules which may significantly narrow the range of scales to consider in any particular case. Whether the factors influencing scale of effect are simple or complex, better understanding of those factors will contribute significantly to our understanding of how landscape context shapes biological responses.

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