Landscape Ecology

The consequences of interactions between dispersal distance and resolution of habitat clustering for dispersal success
--Manuscript Draft--

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Abstract:	Habitat clustering results from processes of habitat loss and fragmentation, which operate at different resolutions and with different intensities e.g. forest clear-cutting or thinning. Individual movements also vary at different spatial scales according to landscape structure and species dispersal strategies. Disentangling the relative impact of habitat loss and fragmentation on the long-term survival of species requires understanding how clustering at one resolution interacts with the amount of habitat, dispersal distance and clustering at other resolutions, to affect dispersal success. We addressed this problem by quantifying the magnitude of these interactions and how they were affected by the intensity of habitat removal. Individual-based simulations were conducted on artificial fractal landscapes where the intensity of habitat removal and the amount of clustering were varied independently at two nested resolutions, while the total amount of habitat in the landscape was controlled for. We show that the way the amount of habitat, the dispersal distance and the amount of clustering affect dispersal success depends on the resolution at which habitat clustering occurs, the intensity at which habitat is removed, and the strength of habitat selection. Our findings highlight: a) the importance of explicitly considering scale-dependent biological responses to landscape change; and b) the need to identify the appropriate scale at which to manage fragmentation, thus avoiding mismatches between the scale of ecological processes and the scale of management.
Response to Reviewers:	Responses to Reviewers' Comments Editor Dear authors, Thank you for submitting a revised version of your manuscript LAND-D-12-03315R1 "The consequences of interactions between scale of movement and scale of habitat

clustering for dispersal success." The two reviewers provide a somewhat contrasting evaluation of your manuscript. Reviewer 1 found the comments well accommodated and has only a few minor suggestions. Reviewer 2 again provided an unusually detailed review of you manuscript. The reviewer appreciates the substantial improvements in the manuscript and provides many constructive comments and suggestions; however, the main criticism of this reviewer still persists and must be addressed.

I appreciate your willingness to send me a summary of your results that finally allowed me to test my hypothesis on the influence of landscape structure, captured by O11(r), on your model output (i.e., the number of steps). Please look at attachments to download the file LAND-D-12-03315R1_Data_towi2.xls. My preliminary analysis showed that a single summary statistic, such as the OGG(r) is indeed able to capture the interactions between different factors for a given species profile (i.e., defined by the parameter dd and biased vs. unbiased random walk). As a consequence, the way you present your results must be substantially changed. This is in line with the evaluation of reviewer 2 that made it clear that the attempt present your results based on the parameters of the landscape generator were not very successful. I provide more detail in my additional comments below. You may also contact me directly if you have additional questions.

Based on the report of reviewer 2 and my own analysis I want to encourage again major revision of this manuscript. If you should decide to revise your manuscript, your revisions should address the specific points made by the reviewers and myself. You should also send a cover letter, indicating the changes you have made in the manuscript including a point-by-point response to the reviewer comments. If you disagree with a point, please explain why.

Thank you for considering Landscape Ecology for the publication of your work.

Yours sincerely

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Additional comments by the editor

-The results for simulation with the same species profile based on the 135 types of landscapes (destruction type x p x D1 x D2) show that the number of steps (=y) can be well predicted by a power law $y(O11) = a*O11^b$ for an appropriate critical spatial scale rcrit at which O11 is measured.

The power law is very similar to a function $y(O11) = (c/(O11-b) -1$ which resembles exactly the functional form of the solution for a random landscape with proportion h of habitat: $y(h) = (1/h) -1$ as I showed you in my first decision letter.

Thus, in non-random landscapes you have to replace the proportion h of habitat with an "effective" or "effectively perceived" proportion of habitat at a critical scale rcrit [captured by O11(rcrit)]. As expected, the critical scale rcrit increases with value of the parameter dd. Interestingly, it seems also relatively independent on the type of movement (i.e., unbiased vs. habitat biased). This scale represents the dominant scale at which interactions between movement and landscape structure occur. This is an exciting result: whatever complex landscape generation rules you use, you can describe its effect on the animal movement by knowing the second-order properties of the landscape at the critical scale! You can also directly observe the impact of the type of movement (i.e., unbiased vs. habitat biased) on the distance moved.

The landscape structure, as measured by O11(rcrit), is thus the key to the main underlying mechanism that drives your results, and an appropriate analysis and interpretation of your data need to be based on this. Reviewer 2 made it clear that the

attempts to understand the results based on the parameters of the landscape generator were not very successful. Once you determined the critical scale for a given dispersal characteristic, you can much easier discus the consequences of certain landscape manipulations (i.e., changes in the parameters of your landscape generator) because you only need to look how it changes O11(rcrit).

Response: Following the Editor's comments, we have changed the way we present the results. We have abandoned the generalized linear models fitted using the values of the parameters of the landscape generator (p, a , D1 and D2). Therefore, we have decided not to show the coefficients of those models and have removed (former) figures 6, 7 and 8 from the manuscript. We now present the results using simple scatter and bar plots (Figures 3 and 4) showing the output variable from the simulations (number of steps) against different values of habitat amount and values of clustering at the fine and coarse resolution (in a full factorial design of the other variables). Furthermore, we have incorporated the results of the analysis done used the O-ring statistic. First, for different landscape types and dispersal strategies, we have calculated the O-ring statistic, O11(r), for different values of r. Then, for each dispersal distance and dispersal strategy, we have calculated the critical scale at which the O-ring has the strongest correlation with the number of steps by constructing linear regression models between O11(r), calculated for different values of scale r, and the number of steps. We used the value of the R2 to select the best model and identify the critical scale, as described in Wiegand et al. (1999). The value of the O-ring statistic calculated at the particular critical scale has then been used as explanatory variable in a power law model to predict the number of steps, for a particular combination of dispersal distance and dispersal strategy. We have also explored how the landscape generator parameters affected the value of the O-ring and interpreted these effects in terms of the impacts of landscape structure on dispersal success. As a result of introducing the O-ring, which provides a detailed description of the simulation landscapes, we have removed the analysis of the simulation landscapes using the proportion of habitat surrounding an individual's location (and therefore removed former Figure 3).

-I was somewhat surprised that you constructed for each of the 10000 replicates an own landscape. This completely misbalances the different sources of stochasticity. The first important source is stochasticity in the movement track within the same landscape. The second source of variability is stochasticity in the landscape maps with the same parameters, i.e., destruction type, p, D1, and D2. To account for the first source of variability you need to release say 1000 animals in the same landscape and calculate the mean number of steps. This must be repeated one time for the 135 types of landscape (i.e., destruction type x p x D1 x D2) and can be used to update the attached file LAND-D-12-03315R1_Data_towi2.xls. I expect that the relationship between the O11 and the number of steps will even improve because then all simulation were done in the same landscape. One the other hand, the good fit I obtained in all cases indicates (even if the O11 was not that of the actual landscape replicate used) that each landscape treatment leaves a unique signal at the O11 and that the O11 may vary little among replicate landscapes. Therefore it may not be necessary to generate many landscape replicates.

Response: We have now separated the different sources of stochasticity (among individuals and among landscapes) by releasing 100 individuals in each landscape type (135 landscape types), for each combination of dispersal distance and dispersal strategy. We have then replicated each landscape type 100 times, so that the total number of replicates has not changed from the previous version of the manuscript (i.e., 10,000).

Reviewer #1: Review LAND-D-12-03315R1
The authors made numerous changes that significantly increase the quality of the paper.
All concerns raised in my previous review have been well addressed.

minor comments

-Lines 126-130 are brackets at the right place in the text?

Response: The position of the brackets has been corrected.

-Line 228: the authors refer to equation 3 (not eq. 4)

Response: The reference has been corrected.

Lines 238-250: The proportion of individuals that "died" (line 239) could also be an interesting measure to consider.

Response: We now include the proportion of individuals that successfully dispersed (i.e., settled) in Appendix S1. From this information the proportion of individuals that died can then be easily calculated (i.e., proportion of individuals that died = 1 - proportion of individuals that successfully dispersed).

Reviewer #2:
The authors have made great progress in terms of readability, focussing on the important points, particularly in the introduction, which now reads really interesting. Also the discussion section has improved significantly.

To my opinion, there are, however, still quite some parts in the methods section that could be improved, being shortened while still being more precise. Moreover, after having spent various hours again on the manuscript (now I feel I understand most of the results), I think there are also some bad errors particularly in the results sections, wrongly describing results figures. (for both, see the list below).

Even if the manuscript has improved also with respect to this issue, my major criticism is still that to my opinion the authors still did not manage to sufficiently explain why such a complex methodology for landscape creation and presentation of results (that requires a great deal of the reader to understand) is necessary for the major findings. And also, what these findings are explicitly. Even if I have been working in a very similar field of ecology, also with similar methods and even if I like that kind of modelling approaches, I still have trouble to say what I can learn from this study for 'real world ecology'. Major reasons for this weakness are still that:
a) Specific complex results are hardly comparable to real life situations or explainable in a way that would allow a transfer into real situations (which would make them findings that the reader can remember, a clear picture, a take home message). Examples:

-i) For the "cool result" of l. 408-409 not one reference can be found (and isnt this result kind of clear, looking at the landscape pictures?) And/Or could this result be quatified to some point, so it is easier to judge its relevance?

Response: We have modified the entire paragraph, which now includes several additional references to relevant work. The interaction between the two resolutions of clustering is now captured (and quantified) by the value of the O-ring statistic, as explained in the results, the discussion and the Appendix S2.

-ii) The results described l.370-375: the reasoning (and the refernce for it) is based on a very simple fact (fragmentation is bad for dispersal success). I think that all the rest of the paragraph actually cannot be stated if the size of the animal is not considered (dd in the model).

Response: We now explain more clearly that the reason behind the interaction between the amount of habitat and the resolution at which habitat clustering occurs is because fragmentation negatively affects dispersal success - using references, as it is not a novel result. We also mention, at the beginning of the paragraph, the values of dispersal distance for which the interaction occurs.

-iii) Result of l. 397: the resoning is either trivial (high dispersal distance leads to high probability of leaving a patch, with a reference) or it is also true for small scale clustering (probability of leaving a patch increases with decreasing patch size), and not only for coarse scale clustering (what the explanation shoud be specifically about).

Response: We thank you the reviewer for this comment. However we think that the reasoning for the interaction between the impact of the dispersal distance and the resolution of habitat clustering (i.e., high dispersal distance leads to high probability of leaving a patch) is worth mentioning. However, based on the results obtained, we have now clarified that the above explanation only applies to the impact of coarse resolution clustering. For the impact of fine resolution clustering we proposed a different explanation.

-iv) The reasoning of the result "movement is more strongly affected by coarse scale clustering" with frogs and squirrels is also not convincing (for a frog a 1ha scale fragmentation might be a coarser scale than a 3ha scale is for a squirrel).

Response: We now use the caribou (Rangifer tarandus caribou) as example of species affected more by coarse-resolution than fine-resolution clustering, and provide a reference for this example.

-b) It is still really hard to distinguish between the different landscape parameters. To my opinion (looking at the figures in Appendix 1) changing a also affects D1 and D2 (particularly if D1 clustering is high), so that it is hard to tell and to understand how the effect of D1 or D2 differs with changing a (if there was a way to calculate the D1 and D2 of the final landscapes, I think that these would strongly differ between different a, even if the same D1 and D2 were used for landscape generation).
A fact that proves this difficulty, obviously even for the authors, is their use of an a-related processes to explain a result that is about changing D1 and D2 (l. 387-391). Also the fact that results figures are wrongly described (l. 307- 315) reveal the complexity to properly describe these complex and interacting landscape parameters.

Response: We have now considerably improved the explanation of how the landscape generator parameters influence the properties of our simulation landscapes, by exploring in the Results the impact of changing the landscape generator parameters on the value of the O-ring. The analysis clearly revealed that changing a does not change D1 and D2, as the three parameters are varied independently in our landscape simulation framework. However the analysis also showed that a, D1 and D2 affect the degree of habitat clustering of the landscapes, as measured by the value of the O-ring. We have also clarified that we did not use the a-related processes of the example cited by the reviewer to explain a result that was about changing D1 and D2. Rather, we used the a-related processes of the cited example to support the finding that "the interaction between the amount of habitat and the resolution at which habitat clustering occurs depends on the process of habitat removal". We have also removed from the manuscript the results wrongly described that the reviewer mentioned.

Some efforts have been made to overcome this criticism since the last review. Providing figure 4 is a good start! This could, however, be much futher improved (see suggestions for figure 4 and figures 5-8 below).
Also other landscape measures are now given (that could make the landscape complexity better understandable and easier to grasp) but these measures are not discussed in relation to results of dispersal success.

Other more specific comments:

Methods:

-I wonder if a dd of 0.5 grid cells make sense? To better imagine the meaning of the results I had thought of a cell being ca. 10x10meters (is this what the authors also imagine?). I think that it might not make sense to investigate the dispersal success of an animal with a dispersal distance of 5 meters with a landscape grid of 10 m resolution. In general it would help the reader if the authors stated how they interpret cell size and what animals could for example be represented by the different scenarios.

Response: We agree with the reviewer that a value of 0.5 does not make biological sense. We have now eliminated the value of 0.5 from the values simulated and decided to use 1 as the minimum value of dispersal distance in the simulations.

-The paragraph l. 198-207 is too long and still confusing. Why not just say that 'to add some stochasiticity, animals were not only to veer from the starting point by dd, but by a distance drawn from a truncated exponential distribution with median of dd, a maximum of 50, and beta being determined to guarantee an integral of 1 (wasnt that the reason?)

Response: We have shortened and clarified the paragraph.

-I don't understand why the authors need time t for. Only for interpretation of d, dd and da as a risk or dispersal success? Then this should be stated (only) in the paragraph l. 243-252

Response: We have moved explanation of the time t to the paragraph mentioned by the reviewer.

-l. 232 why not say 'animals must have covered the eucledian distance d from the starting point' ('moved the full distance d' is confusing because they have actually moved much longer distance until they covered d)

Response: We have modified the sentence according to the reviewer's comments.

-l. 237-242: confusing: did they move another d from where they stopped the first walk? Or start again from starting point? How often did they retry? 50 movement steps before dying - or does that mean da ?- then this should please be explained clearly.

Response: We have clarified the sentence.

-l. 242 why use some explanation about depleting resources (are there resources? do animals eat? do animals die? no, but the explanations sound as if). If 'maximum nuber of movement steps' is the 50 steps before 'dying', then this has already been explained 3 lines earlier. Why not just say instead of both long and confusing explanations. 'We set a maximum of 50 steps (which can be interpreted as depletion of all resources and subsequent death of the individual)' which is much shorter and makes clear what part of the information is model world and wich is the interpretation of the model rule.

Response: We have modified the sentence according to the reviewer's comments.

-Where do animals start their dispersal events? From any random cell?

Response: The information was already included in the first sentence of the paragraph describing an example simulation run.

-Still (see last review, same question), I would like to know how often that happened that animals do not manage at first try? At second try? At third try? (how often do they try?) How does this depend on lsc properties?

Response: We now include the proportion of individuals which successfully dispersed, out of the 10000 replicates, in Appendix S1.

-The final variable that is used as response variable in statistical models is what the authors call 'movement steps'. This is confusing to me because I consider da to be the movement steps actually executed. As they describe the variable it is rather a relative distance (da/dd). In this context I am confused about the y-axes of the plots (in fig 4 and 5 - doas a da/dd of 30 make sense? or are this real steps? however, for example fig 6,7,8 y-axes make more sense for the ratio da/dd)

Response: We have decided to keep the wording 'number of steps', rather than changing it to 'relative distance', as suggested by the reviewer, to avoid confusion with the 'dispersal distance' dd. However, we refer to the movement step actually executed using the term 'cell-to-cell moves' throughout the manuscript, to distinguish it from the response variable used in the statistical model. We clarified in the figure captions the meaning of the variable displayed on the y axis of figures 4 and 5 (now figures 3 and 4).

-Or do the y axes in fig 6,7,8 show the log(da/dd) which is supposively used as response variable for the statistical models? If so, have the authors performed a back-transformation to be able to interpret the results as number of steps or relative distance (da/dd)?

Response: We have removed from the manuscript the glms originally used to present the results (Please see response above in response to the Editor's comments). As a consequence, we do to not show the coefficients of those models anymore and have removed figures 6, 7, and 8 from the manuscript.

-Residual plots in appendix indicate strong increase of variance with increasing value / predicted value. Which could be accounted for using poisson errors (the normal for a glm with log-link for count data) - but it is said that teh authors used normal error assumption and checked for this in residual plots. This is to my opinion not justified by the residual plots! Because I am confused about your response variable 'number of steps' (how it is called) or the relative distance, the ratio da/dd (how it is described), I am not sure if a log-link is appropriate.

Response: Residuals plots have been removed from the manuscript, as a consequence of changing the way of presenting the results.

Results:

-Paragraph l. 306-319: As I understand the figure 3 the first three statements in this paragraph are just the contrary of what figure 3 shows:
For example the first statement: 'for blocky the proportion of habitat surrounding an individual's location declined more when coarse scale clustering was low than when fine-resoultion clusering was low'. The figure shows the contrary (for large dispersal distance, where the effect is stated to be strongest, the sub figure on the top right corner): for coarse scale clustering being low, the 3 columns (as a block on the right side) show no difference with fine scale clustering, but for fine scale clustering being low, the three light gray columns show a large difference with different coarse scale clustering.
Same with the next statements (310-313), at small dd, where the effect is said to be highest.
The next statement (331-315) is that both fine and coarse have an influence. However with high dd only coarse has an effect, for small dd only fine has an effect.

Response: The whole paragraph has been removed, as a consequence of changing the way of presenting the results.

-l. 324 the effect described is not obviously shown by the figure. SE clearly overlap - so would the CI (even overlap more). In the end of this paragraph the authors state that a certain effect is much weaker (6C habitat biased) - however, here I see a much clearer effect between high fine and low fine (at least no overlapping SE).
Did the authors test for significance of the different model coefficients by deleting them from the model and doing likelihood ratio tests? (see my question already in the last review), or is the strenght of effects only evaluated by the SE?

Response: The whole paragraph has been modified, as a consequence of changing the way of presenting the results. The figures to which the paragraph was referring (and therefore the SE) have been removed.

-l. 420-422 figures 4A,C and E do not show that dd has an effect (like stated here by the authors), because they also differ with respect to a. Here a full factorial design in figure 4 would help to disentangle the two effects (see below).

Response: Figures 3 (former Figure 4) now shows a full factorial experimental design that distinguishes between the effect of a and dd.

Figures:

-Fig 2. I suggest to use the same gray scale for the coarse scaled landscape picutres. Then the reader could directly see a clear difference between differnet a (all values

close to the extremes or close to the mean).

Response: We have decided not to modify Figure 2 because we believe that by showing the coarse-scaled landscape maps using the same gray scale the reader might not be able to see the specific patterns of habitat (low degree vs. high degree of clustering), which is a critical piece of information of the figure (y axis).

-Fig 4 - So far Figure 4 is only used to show that dispersal success goes down with decreasing p and that high dd decreases dispesal success only for blocky and mixed. Are all these complex figures needed for these statements? This does not mean that I think this figure shold be deleted, I particularly like it because it transports a much clearer process understanding than for example fig. 5-8.
For example, the fact that in perforation habitat-biased animals are less affected by p than unbiased (compared with all blocky or mixed) appears to me as the most interesting and most obvious result from this figure (also makes sense to some point: biased animals move along habitat, so they end up finding habitat more easily once they are out of the dd-circle - it is intersting how this is affected by landscape properties in the context of different dd!!). This result is however discussed nowhere in the ms. However, obviously the main reason why this difference (between the effect of p on biased or unbiased) is so strong in E (compared to A and C) is not perforation alone but the smaller dd in subplot E. I wonder what subfigures A,C,E can be used for, because the vary in a and in dd, so they can not explain the effect of any of the effects. Why not show only dd=7.5 to explain the effect of a, or the other way round to explain how dd affects results?
Another issue about figure 4 is that it actually demonstrates that D1 and D2 have very little effect on the results, no?! Again, the relative effect of a, D1 and D2 could be better assessed if A, C and E had the same dd(=7.5?).
To conlclude, to my opinion having figures like 4 A,C and E, for a=0.1 a=1 and a=20 and dd=1.5, dd=7.7 and dd=17.5 (altogether 9 subplots) could maybe even replace to some extent Figures 4 B,D and F as well as the complicated figures 5,6,7 and 8.

Response: We have modified Figure 4 (now Figure 3) according to the reviewer's comments (Please see response above).

-Figure 5 for example is only used for the statement that clustering increased dispersal success, which can be nicely shown in a figure 4 - like figure. Moreover, in figure 5, again a and dd are changed together so that the reader cannot see which effect caused any differences.

Response: We have modified Figure 5 (now Figure 4) according to the reviewer's comments, and now present a full factorial design. We now clarify that we have used this figure for showing one of the most important results of the paper, that is 'the impact of habitat clustering at one resolution on dispersal success depends on the degree of habitat clustering at another resolution'. This result can not be clearly seen in Figure 4 (now Figure 3).

-Are figures showing confidence intervalls (l. 354 stating this for figure 8) or SE (l. 575 figure caption of figure 8).

Response: We have removed Figure 8 from the manuscript.

-The landscape figures in the appendix (S.1.1 etc): Why are the two coarse-gridded landscape pictures besides each other not exactly the same (they are the same with respesct to their statistical properties, no?), if so the authors could also only show one landscape, and the two (fine-gridded) sub-figures below then show the how different fine scale clustering look like in the same coarse-gridded landscape (see my similar criticism in the last review). this would illustrate better (while being simpler) how fine scale clustering works.

Response: The two coarse-gridded landscape maps besides each other are not exactly the same because the fractal algorithm that generates them is stochastic (i.e., it works by using a random number generator that generates different numbers every time runs). However, the degree of clustering of the two coarse-gridded landscape maps is the same, because the maps have the same statistical properties (i.e., same

D1), as the reviewer correctly pointed out. We have decided not to change the figures in Appendix S1 (now Appendix S2) to show the stochastic nature of the fractal algorithm.

Wording:

-l. 163 replace 'each cells' with 'all cells'.

Response: done.

-l. 198 better enter ... distance (dd, a model parameter) which... for clarity
Response: the paragraph has been slightly modified and the reviewer's suggestion incorporated (line 202).

-l. 211 and 222 better add for clarity: ... particular turning angel (i.e. by moving to cell i), in ...

Response: done.

-l. 374 how can an interaction be 'of the amount of habitat with low degrees of clustering' - interaction is between two varaibles not between one variable and low values of another variable.

Response: the sentence has been removed as a consequence of changing the presentation of the results.

-l. 425 misses the word "occurs"

Response: the paragraph has been removed.

-l. 502: (20082008)

 Response: corrected.

The consequences of interactions between dispersal distance and resolution of habitat clustering for dispersal success

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Abstract

Habitat clustering results from processes of habitat loss and fragmentation, which operate at different resolutions and with different intensities e.g. forest clear-cutting or thinning.Individual movements also vary at different spatial scales according to landscape structure and species dispersal strategies.Disentangling the relative impact of habitat loss and fragmentation on the long-term survival of species requires understanding how clustering at one resolution interacts with the amount of habitat,dispersal distance and clustering at other resolutions, to affect dispersal success. We addressed this problemby quantifying the magnitude of these interactions and how they were affected by the intensity of habitat removal. Individual-based simulations were conducted on artificial fractal landscapes where the intensity of habitat removal and the amount of clustering were varied independently at two nested resolutions,while the total amount of habitat in the landscape was controlled for. We show that the way the amount of habitat, the dispersal distanceand the amount of clustering affect dispersal success depends on the resolution at which habitat clustering occurs, the intensity at which habitat is removed, and the strength of habitat selection. Our findings highlight: a) the importance of explicitly considering scale-dependent biological responses to landscape change; and b)the need to identify theappropriate scale at which to manage fragmentation, thusavoiding mismatches between the scale of ecological processes and the scale of management.

Key words:landscape change,intensity of habitat removal, scale of fragmentation, scale of management, life-history characteristics, scale mismatch, fractal landscapes, individual-based model.

Introduction

Animal movement plays a key role in many ecological processes, such as foraging (Stephens and Krebs 1986), home range establishment (Borger et al. 2008), dispersal (Bowler and Benton 2005) and migration (Dingle 1996). Habitat loss and fragmentation,which refer to the 'removal' and 'breaking apart' of habitat respectively(Fahrig 2003),can disrupt the capacity of individuals to move among habitat patches(With and King 1999a),and therefore represent major threats to the persistence of populations (Flather and Bevers 2002).Movements occur at a range of spatial and temporal scales because they are undertaken for different biological reasons (e.g. foraging or reproduction) (Stenseth and Lidicker 1992),and because they provide different payoffs to individuals (e.g. reduced inter-specific competition)(Hiebeler 2004). Habitat fragmentation, which determines the clustering of habitat,can also occur at different scales (Lindenmayer and Fisher 2006). While the impact of the amount and clustering of habitaton species movement has been well studied (Gustafson and Gardner 1996; Pearson et al. 1996; With and King 1999b), there is a limited understanding of how the scale at which habitat clustering occurs, the amount of habitat, and the scale of movement interact to affect dispersal success.

The scale at which habitat clustering occurs refers to the *resolution* (i.e. grain) of the habitat pattern, which is a direct consequence of natural and anthropogenic disturbance processes that occur with different resolutions(Lord and Norton 1990). For example, the dieback ofisolated trees and forestry practices, such as selective logging, usually generates habitat patterns with a fineresolution, while large-scale fires, insect outbreaks andland-cover change driven by land use (e.g. pasture and cropping) tend to create habitat patterns with a coarser resolution (Broadbent et al. 2008; Fearnside 2005; Mori 2011).Different resolutions of habitat clustering can occur simultaneously, and in combination with different processes of habitat removal (Franklin et al. 1997). For example, in forestry landscapes, logging units of

3

different sizes combined with harvesting practices that remove different amounts of

70 vegetation in a single removal event (e.g. selective logging or clear cutting) can create a

mosaic of unevenly dense vegetation patches of different sizes (Gustafson 2007). The process

of habitat removal and habitat clustering at different resolutions combine to affect the success

of species dispersal (Doak et al. 1992). Tenhumberg et al. (2001)found that one resolution of

75 clustering can interact with another resolution of clustering to affect dispersal. A critical

issuethenis how different resolutions of habitat clustering and processes of habitat

removalinteractto affect species dispersal.

The resolution of habitat clustering can have important consequences for species

moving different distances during dispersal,i.e.the movement away from a natal/breeding site

80 (Clobert et al. 2001). While some species, such as beetles, can move no more than few

meters, others species, such as carnivores or ungulates, can move several kilometres(Crist et

al. 1992; Fryxell et al. 2008; Revilla et al. 2004). Numerous studies have shown that the

impact of one resolution of habitat clustering on species dispersal, depends on the dispersal

distance(Buchi and Vuilleumier 2012; Hiebeler 2004; Johst et al. 2002).However, species

85 moving different dispersal distances are affected by habitat clusteringat different resolutions.

For instance, while species moving short dispersal distances (e.g.a beetle) are affected by the

spatial configuration of fine-grained habitat patches, species moving large dispersal distances

(e.g. caribou) are more affected by the spatial arrangement of coarse-grained land cover types

(Johnson et al. 2002; McIntyre and Wiens 1999). In addition, movement responses to habitat

90 clustering may depend on whether movements are biased towards specific directions

(e.g.habitat) (Farnsworth and Beecham 1999). This is an important problem in landscape

ecology because the fitness consequences of large dispersal distancesare different from the

fitness consequences of small dispersal distances(Johnson et al. 2009),with potential

repercussions for the evolution of dispersal (Travis 2001).

95   The resolution at which habitat clustering occurs can also affect howthe amount of

habitat influences species movement.Pearson et al. (1996)demonstrated that, as the amount of

habitat in a landscape decreases, fine-resolutionclustering has a greater impact on

connectivitythan coarse-resolutionclustering, even for species dispersing over distances larger

than the resolution of clustering. This is an important issue, since the effect of the amount of

100   habitat on movements may change according to the resolution of the habitat pattern. For

example, the threshold in the relationship between the amount of forest cover and the

selection of breeding territory by a forest-dependent avian species was found to varyamong

the scale of a nest site, the territory scale and the landscape scale (Suorsa et al. 2005). Pearson

et al. (1996)provide useful insights into whether the interaction between the amount of habitat

105   and the resolution at which habitat clusteringoccurs affectsspecies moving different dispersal

distances. However, they did not control for the degree of clustering, and therefore were

unable to separate the independent effect of the amount of habitat from that of the clustering

of habitat.

In this paper, we addressed three questions: (1) how does the resolutionat which

110   habitat clusteringoccurs interact with habitat amount to affect dispersal success; (2) how does

the resolution at which habitat clustering occurs interact with the distance moved during

dispersal to affect dispersal success;and (3) does the degree of habitat clusteringat one

resolutioninteract with the degree of habitatclustering at another resolution to affect dispersal

success?We addressed these questions by applying a spatially-explicit simulation approach,

115   whereby individuals with different dispersal strategies move on binary landscapes, where the

amount of habitat, theintensity of habitat removal and the degree of clustering at two

resolutions were controlledindependently.Weused a second order spatial statistic, the O-ring

statistic(Wiegand et al. 1999), to predict the impact of changes in landscape structure on

dispersal success and then explored how the value of the O-ring varied with changes

120   inlandscape structure. We show that the resolutionat which habitat clustering occurs interacts

with the amount of habitat,the dispersal distance,and the degree of clustering at

otherresolutions to affect dispersal success. We also show that these interactions depend on

the intensity of habitat removal and the dispersal strategy.

Methods

125   Our approach consisted of two main components. First, we constructed a

hierarchically-structured landscape where the *intensity*of the process of habitat removal (i.e.

the amount of habitat removed in a single removal event)and the clustering of habitat at two

different nested resolutions werecontrolled independently from the total amount of habitat in

the landscape. We then developed an individual-based model ofdispersal of species that adopt

130   different dispersal strategies, and simulated dispersal of individuals on the hierarchically-

structured landscapes.We calculated the O-ring statistic (Wiegand et al. 1999) and used it to

quantify the impact of changes in landscape structure ondispersal success, by fitting a power-

law model to simulation data. Finally, we explored how the value of the O-ring statistic

depended on the landscape generator parameters.

135   *Landscape construction*

Landscapes were constructed using a hierarchical approach, based on a two-level

framework. At the top level, we controlled the intensity with which habitat was removed and

the degree of coarse-resolution clustering, while at the bottom level we controlled the degree

of fine-resolution clustering. To generate patterns of habitat clustering with different

140   resolutions, fractal maps were nested within each other. Fractal landscapes are grid-based

maps extensively used in percolation theory studies to assess the impact of landscape

structure on organism spatial dynamics (With 2002). The degree of habitat clustering was

represented by the fractal dimension (*D*), which in fractal landscapes is bounded between 2 to

6

3(Palmer 1992). High values of *D* generate landscapes with low habitat clustering and low values of *D* generate landscapes with high habitat clustering. Landscapes with low habitat clustering are more fragmented than landscapes with high habitat clustering. Fractal landscapes were created using the midpoint displacement algorithm (Saupe 1988).

Initially, we created a fractal map, whose fractal dimension (*D1*) represented the degree of coarse-resolution habitat clustering, and which formed the upper-level of the landscape. We transformed the normally-distributed raw values derived from the fractal algorithm, into proportions, using a rank-based Beta transformation (Gupta and Nadarajah 2004):

$$p_i = B(a,b)w_i^{1-a}(1-w_i)^{1-b}, a>0, b>0, 0<w<1 \tag{1}$$

where p_i represents the proportion of habitat in map cell i, $B(a,b)$ is the beta function

$\int_0^1 z^{a-1}(1-z)^{b-1}dz$, with a and b the two shape parameters, and w_i the quantile of the raw value for map cell i. Equation(1) scales the range of quantiles of the raw values (w_1, w_2, w_3...w_i) between 0 and 1. At this level, each cell had a certain proportion of habitat, and the degree of clustering influenced the likelihood that adjacent cells would have similar proportions of habitat. We then assumed that the average proportion of habitat in the landscape, p, was equal to μ, where μ was the mean of the Beta distribution, which was equal to $a/(a+b)$. The value of the parameter b was calculated based on p, for different values of the parameter a. Varying the parameter a allowed us to control whether the proportions of habitat in all cells were close to the mean proportion of habitat in the landscape ($a = 20$), uniformly distributed between 0 and 1 ($a = 1$), or clustered around 1 and 0 ($a = 0.1$)(Figure 1), while keeping the amount of habitat in the landscape (p) constant.

165   Different values of the parameter *a* represented processes of habitat loss that remove

different amounts of habitat from each cell of the landscape's upper level (Figure 1). Low

values of *a* represent processes of habitat removal of high intensity, such as clear-cutting,

which remove all habitat in a cell. This removal process creates landscapes where large blocks

of habitat are interspersed with large gaps of non-habitat (i.e. 'Blocky' processes) (Figure 2A

170   and 2D). High values of *a* represent processes of habitat removal of low intensity, such as

thinning, which remove small amounts of habitat (i.e. single trees). This removal process

results in 'perforated' landscapes where gaps of non-habitat are smaller compared to a

'Blocky' process (Figure 2C and 2F). Intermediate values of *a* represent processes of habitat

removal of medium intensity, such as the ones retaining vegetation at harvest (Franklin et al.

175   1997). In this case, landscapes are transformed by a heterogeneous mix of perforation and

blocky processes (i.e. 'Mixed' processes) (Figure 2B and 2E).

        Next, we used the fractal algorithm to nest a fractal map within each cell of the upper-

level maps. Lower-level maps had all the same fractal dimension (*D2*), which represented the

degree of fine-resolution habitat clustering. At this level, habitat was distributed as a binary

180   map. A value of 1 (habitat) or 0 (non-habitat) was assigned to each lower-level cell, so that

the proportion of each lower-level map that was habitat equalled the p_i value of the cell in the

upper-level map. The surface made up by these lower-level maps combined represented the

binary landscape on which individuals moved. We constructed landscapes of 289 by 289 cells

by creating upper- and lower-level maps of 17 by 17 cells. To represent the processes of

185   habitat removal of different intensities, landscapes with different degrees of clustering at

different resolutions were created by varying independently the fractal dimension of the

upper- and lower-level maps. These are shown graphically in Figure 2.

Dispersal model

8

We simulated dispersal of individualsasa first-order, correlated random walk(Kareiva

190   and Shigesada 1983). First-order correlated random walk models assume that the direction of

each move depends on the location and direction of the last move (Kareiva and Shigesada

1983).Furthermore, first-order correlated random walk models can be extended to incorporate

mechanisms for the response of movements to landscape patterns (Gardner and Gustafson

2004).

195   Every time step, an individual tooka movement step, which consisted in moving

anEuclidean distance, *d*. We assumed that individuals had a higher probability of taking small

steps than large steps (e.g. Revilla and Wiegand 2008). Therefore, the value of *d*was chosen

at random from a truncated exponential distribution, $f(d) = \dfrac{\beta e^{-\beta d}}{1 - e^{-\beta d_{max}}}$ (Vogel et al. 2009),

with rate parameter *β*, median equal to *dd*(a model parameter), and maximum dispersal

200   distance d_{max} equal to 50 cells. We calculated the parameter *β* for different values of *dd*, by

setting the 50th percentile equal to *dd*.

Individuals covered the distance*d*by taking cell-to-cell moves between adjacent cells.

An individual could move into one of the eight cells surrounding its current location. The

probability, P_i, of moving to cell, *i*, was

$$P_i = \frac{\phi_i w_i I(i, j)}{\sum_{k=1}^{8} \phi_k w_k I(k, j)} \tag{2}$$

205   where *Φ$_i$*is the probability of taking a particular turning angle (i.e. by moving to cell *i*) in the

absence of land-cover preference, $w_j$is the habitat preference parameter for land cover

type*j*(i.e. habitat and non-habitat) and *I(i,j)* is an indicator function which is 1 if cell *i* is

habitat and 0 otherwise. The denominator of equation (2) acts as a normalizing constant and

ensures the probabilities, P_i, add to one.

210   Dispersing individuals of several taxa often adopt movement behaviour where the directions of successive movement steps are correlated and the movement path tends to approach a straight line (Van Dyck and Baguette 2005). In order to introduce a directional bias caused by the persistence of moving in the same direction of the last move, we assumed that turning angles, θ_i, between successive moves followed a truncated normal distribution,

215   ranging between -180 and +180, with mean zero and variance σ^2_{turn}. The probability, Φ_i, to take a particular turning angle by moving to cell i, in the absence of any habitat selection and given the direction of the previous move, was expressed as a function of σ^2_{turn} such that

$$\phi_i = \int\limits_{\theta=\theta_i-22.5}^{\theta=\theta_i+22.5} f(\theta,\sigma^2_{turn})d\theta \qquad (3)$$

where θ_i is the turning angle to cell i relative to the previous movement direction and $f(\theta,\sigma^2_{turn})$ the normal probability density function, with mean zero and variance, σ^2_{turn},

220   equal to one, i.e. $\theta \sim N(0,\sigma^2_{turn})$. The turning angles to move to the centres of the eight neighbourhood cells could only take the discrete values of 0°, 45°, 90°, 135°, 180° (-180°), -135°, -90° and -45°. Therefore, equation (3) calculates Φ_i as the integral of the turning angle probability density function 22.5° either side of the discrete angle for a move to the centre of each cell, with the distribution truncated at 180°.

225   The starting position of an individual was initialized at a randomly chosen habitat cell in the landscape. Dispersing animals could not settle until they had covered the Euclidean distance d from the starting point and they had found a habitat cell. Therefore, the actual distance d_a, moved through cell-to-cell moves, depended on the spatial distribution of the habitat. By forcing individuals to move the distance d, we assumed that dispersal distance was

230   an evolutionary trait that species had evolved in response to forces affecting individual

fitness, such as density-dependent dynamics (Rousset and Gandon 2002). If individuals did

not find habitat after they had moved the distance d, theymovedanother whole distance

d,starting from the cell where they stopped. Individuals could not move more than 50 steps

(which can be interpreted as depletion of all resources and subsequent death of the

235   individual). Therefore, individuals continued to take cell-to-cell movements until they

hadcovered the whole distance d, they hadfound habitat orthey hadmoved 50 steps.

As searching for habitat has an associated risk of mortality per step taken, the number

of steps can be viewed as a measure of dispersal success (Doak et al. 1992). We assumed that

individuals take a fixed amount of time, t, to move a movement step. The higher the number

240   of steps an individual has to move, the higher the risk of mortality, and the lower the

dispersal success is likely to be. Therefore, we used the number of movement steps as a

measure of dispersal success. We assumed that,in a time step, individuals incurred a risk of

mortality which depended on the distance d. Individuals dispersing large distances may have

a higher risk of mortality than individuals dispersing shorter distances, as a consequence,for

245   example, of moving faster or spending more time in the matrix (Andreassen and Ims 1998;

Baker and Rao 2004). The number of movement steps was calculated by dividing the actual

distance moved$d_a$by the dispersal distance$d$. In doing so, we assumed that the risk mortality

was the same for species moving large and small dispersal distances, asspecies moving large

dispersal distances also evolve mechanisms to reduce mortality(Hebblewhite and Merrill

250   2009). The edge of the grid-based landscape was modelled as a *torus*, with the bottom row

adjoining the top row and the right-most column adjoining the left-most column.

Simulation design

Simulations were conducted in a factorial experimental design, in which the amountof

habitat, the intensity of the process of habitat removal, the degree of fine- and coarse-

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255 resolutionhabitat clustering and the dispersal distancewere varied. We created landscapes

with relatively lowamounts of habitat ($p = 0.05, 0.1$, 0.2, 0.3 and 0.4) because fragmentation

is generally not important for dispersal success when the proportion of habitat in the

landscape is greater than 30-40 % (King and With 2002). For each amount of habitat, we

simulated three processes of habitat removal ('Blocky', 'Mixed' and 'Perforation'), three

260 values of the degree of fine- and coarse-resolutionhabitat clustering($D1$= 2.1, 2.5, 2.9, $D2$=

2.1, 2.5, 2.9), and five values of dispersal distance, which were selected to encompass the

range of resolutions of habitat clustering (dd = 1,2,3,7 and 17 cells).

For eachof the 675 unique combinations of factors (135 landscape types $\times$ 5 dispersal

distances),we simulated the dispersal of 100independent individualswhich had no preference

265 for land cover type when dispersing (i.e.*unbiased strategy*), and 100 independent individuals

which preferentially moved through habitat (i.e.*habitat-biased strategy*). The habitat

preference parametersfor habitat and for non-habitat wereboth set to 1, in the case of an

unbiased strategy; and to 50 and 1,in the case of a habitat-biased strategy. At the end of each

simulation,the number of dispersal steps taken was recorded. Each combination of landscape

270 type and dispersal distance was replicated 100 times, resulting in a total of

6,750,000simulation runsfor each dispersal strategy. We also recorded the proportion of

individuals who successfully located habitat out of the total number of replicates. The model

was implemented in the R programming language for statistical computing (R Development

Core Team 2012).

275 *Model fitting*

To quantify the effect of landscape structure on the number of steps taken, we used

the O-ring statistic, which has been widely used to quantitatively capture the impact of

changes in landscape structure on the spatial dynamics of plant and animal species

(Bruggeman et al. 2010; Wiegand et al. 2007; Wiegand et al. 1999). The O-ring measures the probability that a habitat cell is located at a distance r from another habitat cell, thus providing a measure of the degree of habitat clustering. By being measured over different distances r, the O-ring is also able to isolate the *scale* of habitat clustering (i.e. the distance at which the probability to find two habitat cells away from each other is larger than the probability for a random map)(Wiegand and Moloney 2004; Wiegand et al. 1999).

For each landscape type, we first calculated the O-ring, for values of r ranging from 1 to 140 cells.Then, for each value of *dd*and dispersal strategy, we constructed linear regression models between the average number of steps and the value of the O-ring for different r. The value of r of the model with the best fit (calculated using the R^2)represented the critical scale r_{crit} at which the landscape structure interacts with an organism movements(Wiegand et al. 1999).Then, for each value of *dd*and dispersal strategy, we fitted the following power-law model, which was found to successfully predict the impact of landscape structure on dispersal distances (Wiegand et al. 1999):

$$y = cO_{11}(r_{crit})^p$$

(4)

where$y$ is the average number of steps taken, $O_{11}(r_{crit})$ is the value of the O-ring calculated at the critical scaler_{crit}, $c$is a scaling constant and $p$is the exponent.Goodness of model fit was assessed using the R^2value.

To better understand the effect of landscape structure on the number of steps taken, and consequently on dispersal success, we explored how the amount of habitat (p), the intensity of the process of habitat removal (a), the degree of habitat clustering at the coarse resolution (*D1*) and the degree of habitat clustering at the fine resolution (*D2*) affected the value of the O-ring statistic. As we used the O-ring to predict the number of steps, we could

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interpret the effect of the landscape generatorparameterson the O-ring as the effect of landscape structure on dispersal success.

Results

Almost all the individuals, out of the total number of replicates, found habitat within 50 dispersal steps (see Appendix S1 in supplementary electronic material).

Interaction between resolution of clustering and habitat amount

As the amount of habitat increased, the number of steps decreased (Figure 3). However, the impact of the amount of habitat depended on the degree of habitat clustering at different resolutions. In the case of a 'Blocky' process of habitat removal, the amount of habitat had a greater impact on the number of steps when clustering occurred at the coarse resolution than when it occurred at the fine resolution (white point-up and point-down triangles, Figures 3B and 3C). The effect was stronger when the amount of habitat was low than when it was high, and when the dispersal distance was large than when it was small. A similar result was found for a 'Mixed' process of habitat removal (Figures 3E and 3F). When habitat removal was the consequence of a 'Perforation' process, the amount of habitat had a greater impact on the number of steps when clustering occurred at the fine resolution than when it occurred at the coarse resolution (white squares and point-down triangles, Figure 3G). However, that was true for lower than higher amounts of habitat and for smaller than larger dispersal distances.For individuals with a habitat-biased dispersal strategy, the effect of the resolution at which habitat clustering occurred on the impact of the amount of habitat on the number of steps was much weaker.

Interaction between resolution of clustering and dispersal distance

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As the dispersal distance increased, the number of steps required to find habitat increasedfor a 'Blocky' and 'Mixed' process of habitat removal (Figures 3A-3F). In the case

325 of a 'Perforation' process, as the dispersal distance increased, the number of steps required to find habitat slightly decreased (Figures 3G-3I). The effect of the dispersal distance on the number of steps was more pronounced when the amount of habitat was low then when it was high. In addition, the effect of the dispersal distance depended on the resolutionat which habitat clusteringoccurred. For a 'Blocky' process of habitat removal, the impact of the

330 dispersal distance on the number of steps was greater when clustering occurred at the coarse resolutionthan when it occurred at the fine resolution(Figures 3A-3C). A similar result was found for a 'Mixed' process of habitat removal (Figures 3D-3F). For a 'Perforation' process of habitat removal, the impact of the dispersal distance on the number of steps was greater when clustering occurred at the fine resolutionthan when it occurred at the coarse resolution

335 (Figures 3G-3I). For individuals with a habitat-biased dispersal strategy,the interaction between the resolutionat which habitat clustering occurred and the dispersal distance was smaller compared to individuals with an unbiased dispersal strategy.

Interaction between different resolutions of clustering

Habitat clustering at bothresolutions decreased the number of steps, thus increasing
340 dispersal success (Figure 4). The effect of clustering at different resolutionsdepended on the process of habitat removal and it was more pronouncedwhen the amount of habitat in the landscape was low than it was high. Interestingly, the impact of the degree of clustering at one resolution depended on the degree of clustering at the other resolution. In the case of a 'Mixed' process of habitat removal, and for a small dispersal distance,the impact of fine-

345 resolution habitat clustering on the number of steps was greater when the degree of coarse-resolution clustering was low than when it was high (Figure 4D).The interaction between

different resolutions of habitat clustering was smaller in the case of an unbiased than habitat-biased strategy.

Effect of landscape structure on the value of the O-ring

350   The value of the O-ring measured at the appropriate critical scalesuccessfully predicted the number of steps moved(Table 1; see also Appendix S2). As the distance $r$at which the O-ring was measured increased, the degree of habitat clustering of the simulation landscape, as measured by the $O_{11}(r)$, decreased (Appendix S3). The value of the $O_{11}(r)$also depended on the landscape generator parameters. The $O_{11}(r)$was lower when the amount of

355   habitat (p) was low than when it was high. However, the effect of the amount of habitat on the $O_{11}(r)$ was greater when clustering occurred at the coarse ($D1$) than fine resolution ($D2$), for a 'Blocky' process, and vice versa for a 'Perforation' process. The $O_{11}(r)$ also was lower when the degree of clustering at the fine and coarse resolution ($D1$ and $D2$) was low than it was high. However, for a 'Mixed' process, the effect of low degree of clustering at the fine

360   resolution ($D2$) on the $O_{11}(r)$ was stronger when clustering at the coarse resolution ($D1$) was low. Calculation of the O-ring statistic further showed that the landscape generator parametersdid not affect the *scale* of habitat clustering (sensu Wiegand et al. 1999).

Discussion

Our study provides new insights into the impact of habitat fragmentation at different

365   scales on species dispersal (Doak et al. 1992; Pearson et al. 1996). We demonstrate, for the first time, that a species' dispersal success is dependent on theresolutionat which habitat clustering occursand its interaction with the amount of habitat,its dispersal distance,and the degree of habitat clustering at other resolutions. This is of critical importance in the context of the impact of habitat loss and fragmentation on the movement and persistence of species

370   (Flather and Bevers 2002; With and King 1999b); highlighting that the impact of the amount

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of habitat, the dispersal distance and the degrees of habitat fragmentation depends on the resolution at which habitat fragmentation occurs. We have shown that these interactions also depend on the intensity with which habitat is removed from the landscape, and anindividual's dispersal strategy. Our findings have important implications for the use of habitat thresholds across spatial scales, conservation of species that adopt different scales of movement as part of their life histories, and the interaction between management actions at different scales.

Under processes of habitat loss of high intensity, such as forest clear-cutting, coarse-resolution clustering determines the rate of decline in dispersal success with loss of habitat, for species with a large dispersal distance. On the other hand, under processes of habitat loss of low intensity, such as forest thinning, fine-resolution clustering determines the rate of decline in dispersal success with loss of habitat,for species with a short dispersal distance.As habitat is lost, dispersal success is lower when habitat is fragmented than when it is more clumped(Andrén 1994; Fahrig 1997; With and King 1999a). However, we have demonstrated that the interacting effect of the amount of habitat and habitat fragmentation on dispersal success depends on the resolution at which habitat fragmentation occurs. This is captured by the $O_{11}(r)$, whose decline, as habitat is lost, depends on the resolutions at which habitat clustering occurs. It is important to note that the interaction between the amount of habitat and the resolution of habitat clustering strongly depends on a species' dispersal distance, which determines whether an individual can perceive habitat heterogeneity at a particular resolution (McIntyre and Wiens 1999).

The interaction between the amount of habitat and the resolution at which habitat clustering occurs depends on the process of habitat removal. Empirical studies suggest that under processes of habitat removal of different intensities, clustering of habitat at different resolutions has different consequences for animal movements. For example, Chan-McLeod

395 and Moy (2007)observed that the red-legged frog (*Rana aurora*) movements were mainly

affected by the size of small forest patches (<1 ha) in landscapes where habitat removal was

the result of low intensity disturbance processes, such as selective logging. On the other hand,

Moreau et al. (2012)showed that,in landscapes dominated by clear-cutting forestry practices,

the movements of woodland caribou(*Rangifertarandus caribou*) were affected by habitat

400 fragmentation within the home range (~ 500 ha). This suggests that when habitat is lost as a

consequences of high intensity processes, the movements of highly mobile species might be

more affected by clustering of habitat at a coarse than at a finer resolution.

We also found that the dispersal distance interacts with the degree of clustering at

different resolutions in non-intuitive ways. Under processesof habitat lossof high intensity,

405 coarse-resolution clustering determines the rate of decline in dispersal success with

increasing dispersal distance. This is because when organisms cover a distance, per

movement step taken, smaller than the resolution of habitat clustering, the dispersal success

of individuals who randomly select cover types decreases as the dispersal distance increases,

becauselarge dispersal distances increase the chances of leaving a patch (With and King

410 1999a). On the other hand, we found that under processes of habitat loss of low intensity,

fine-resolution clustering tends to increase the rate of dispersal success with increasing

dispersal distance.Increasing the dispersal distance increases the probability of finding a

patch when organisms cover a distance, per movement step taken, larger than the resolution

of habitat clustering. A similar positive effectof dispersal distance on dispersal success has

415 been reported by previousstudies (Buchi and Vuilleumier 2012; Hiebeler 2004).

Under a process of habitat removal of medium intensity ('Mixed'), the rate of decline

in dispersal success with reduced fine-resolution clustering depends on the amount of coarse-

resolution clustering. This finding suggests that different resolutions of habitat fragmentation

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may have a synergistic impact on dispersal success; that is their impactsmay be greater than the sum of the impact of habitat fragmentation at each resolution. The interactive effect of different resolutions of habitat clustering on dispersal success is well captured by the O-ring statistic. Previous authors have suggested an interacting effect of habitat fragmentation at different resolutions on species movement(Frey et al. 2012; Tenhumberg et al. 2001). However, this is the first study to show a cross-scale interactionin the context of habitat clustering occurring at different resolutions. Our finding is important for conservation of species in fragmented landscapes because the interaction between different resolutions of habitat fragmentation may reduce individual fitness(Cornell and Donovan 2010; Williams and Kremen 2007), thuspotentially affecting the long-term persistence of species in human-dominated landscapes.

All the interactions quantified here are weaker when dispersal direction is strongly biased towards habitat. This result is not unexpected because individuals can always locate habitat around them and therefore need fewer steps to successfully disperse than in the case of an unbiased strategy, as suggested by the higher proportion of successful dispersers with a habitat-biased than unbiased dispersal strategy (Appendix S1). This finding isconsistent with Gardner and Gustafson (2004), who investigated the impact of clustering at one resolution only. Habitat selection, however, might also have negative consequences for population dynamics in human-modified landscapes, such as increased density-dependent mortality (Tyre et al. 1999), or reduced individual fitness in selected habitat,as a consequence of natural or anthropogenic perturbations (i.e. ecological *traps*) (Schlaepfer et al. 2002). Our findings suggest that the resolution at which clustering occurs may have a greater impact on species that conduct passive dispersal, such as wind-dispersed plants, than on species that perform active search, such as many animals, whose dispersal is often driven by visual or memory cues (Nathan and Muller-Landau 2000; Zollner and Lima 1997).

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Limitations and future research

445   In our simulations, we used binary landscapes and assumed that the matrix does not impede animal movements, although it is inhospitable to settlement. Although this is a common approach often used in models of dispersal (Doak et al. 1992; King and With 2002; With and King 1999a), we recognize that the effect of the matrix on movements can be highly heterogeneous, with different land cover types having different impacts on movement

450   (Ricketts 2001; Wiegand et al. 2005). Nevertheless, it has been shown that the effect of matrix heterogeneity on dispersal success and population size is usually much weaker than the effect of the amount and spatial arrangement of habitat(Wiegand et al. 2005).This is why we do not expect our results to be significantly affected by a binary representation of habitat.

      Another caveat is thatindividualswith a habitat-biased movement strategy were less

455   affected by the resolution at which habitat clustering occurred compared to individuals who selectedhabitat type at random. However, organisms can exhibit a range of intensities in the bias with which they choose movement direction (Farnsworth and Beecham 1999). While the assumption of strong habitat selection is not likely to affect the robustness of our results, it highlights that our conclusions are only applicable to cases of species that either select any

460   cover type at random (e.g. plants, Nathan and Muller-Landau 2000),or have a strong tendency to preferentially select habitat(e.g. mammalian carnivores, Revilla et al. 2004). As the intensity of an individual's bias to move towards habitat declines, the impact of the resolution at which habitat clustering occurs on species movement should increase. This is an important considerationfor species whose movement decisions do not strongly depend on

465   patterns of habitat distribution.

      Also in our model, we allowed individuals to adopt one dispersal distance per simulation, and therefore assumed that species only move at one *scale* (i.e., the distance

moved in a time step *t*) (Fauchald and Tveraa 2003). However, individuals of many species

exhibit different movement behaviour states (or *modes*) (e.g. foraging vs. dispersal or

470   migration), which are conducted at different scales and adopted in response to physiological

and environmental stimuli (Fryxell et al. 2008). Our results may have important implications

for the impact of landscape change on small-scale animal movements (e.g. foraging)

(Andreassen and Ims 1998). The overall responseto habitat clustering for individuals who

adopt different scales of movement will depend on how different resolutions of clustering

475   affect different movement modes(Forester et al. 2007; Johnson et al. 2002). Further

development of our model could include investigating how the resolutionat which habitat

clustering occurs affects the fitness and persistence of species that adopt different scales of

movement as part of their life histories.

Conservation and management implications

480   Management of habitat fragmentation necessitates a multi-scale

approach(Lindenmayer et al. 2008). However, a critical step to manage fragmentation at

multiple scales is to match the scale of management with the scale of the ecological process

(Cumming et al. 2006; Saunders and Briggs 2002). Our findings demonstrate that the relative

importance of managing fragmentation at each scale depends on the amount of habitat, a

485   species'dispersal distances, and theinteraction between the intensity of fragmentation at

different scales. For instance, management approaches based on habitat-amount thresholds,

which are already known to be landscape and species-specific (Radford and Bennett 2004;

Rhodes et al. 2008), should not be applied across scales (Lindenmayer and Luck 2005),

because, as shown here, the relationship between the amount of habitat and species dispersal

490   success is dependent on the resolution at which habitat clustering occurs. Explicit recognition

of the scale at which management of fragmentation should occur would also be important for

species that adopt different scales of movement, such as marine organisms with a dispersive

larval stage (White and Costello 2011). Finally, management of scale-dependent

fragmentation should also consider the interaction between different scales of fragmentation,

495   as suggested by Rundlof et al. (2008), who demonstrated that organic farming management

practices aimed at reducing fragmentation at the scale of the individual farm and at the scale

of multiple farms, have a synergistic interactive effect on the abundance on farmland

biodiversity.

Acknowledgments

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Table 1. Summary of the dispersal strategy, dispersal distance, critical scale, coefficient values and R^2 of the power-law models.

Model	Strategy	dd	Critical scale	Coefficients		R^2
				c	p	
1	Unbiased	1	2	4.483	-1.189	0.802
2	Unbiased	2	14	3.521	-0.834	0.862
3	Unbiased	3	29	3.194	-0.811	0.873
4	Unbiased	7	45	2.965	-0.827	0.894
5	Unbiased	17	70	2.154	-0.842	0.940
6	Habitat-biased	1	2	2.596	-0.533	0.708
7	Habitat-biased	2	29	2.104	-0.494	0.821
8	Habitat-biased	3	39	2.076	-0.538	0.857
9	Habitat-biased	7	65	2.005	-0.609	0.952
10	Habitat-biased	17	90	1.619	-0.650	0.952

520

Figure 1.Probability densities of habitat proportions for different values of the shape parameter *a*of the Beta function, representing Blocky (*a* = 0.1), Mixed (*a* = 1) and Perforation (*a* = 20) processes of habitat removal. Landscapes are shown with constant amount of habitat (*p* = 0.5).
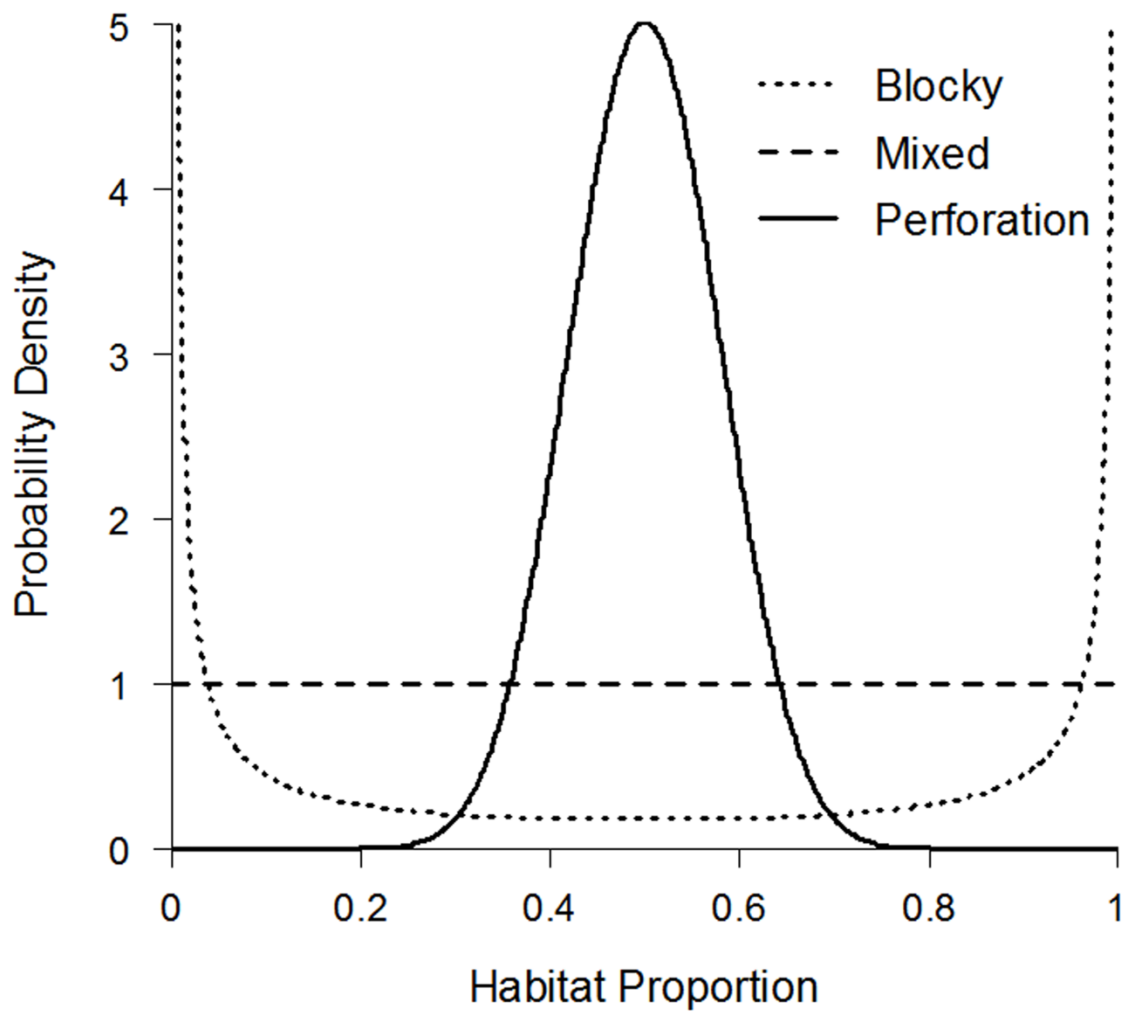
Figure 2. Examples of the landscapemaps used in the simulations.The columns A, D; B, E and C, F show different processes of habitat removal; the rows A, B, C and D, E, F show different degrees of clustering at different resolutions. At the coarser resolution, habitat is distributed as different proportions of habitat, while at the finer resolution habitat is binary. Landscapes are shown with constant amount of habitat (*p* = 0.4).

Figure 3.Mean number of steps (*N* = 10000 replicates) as a function of the amount of habitat(*p*) and the dispersal distance (*dd*),for different degrees of coarse-(*D1*) and fine-resolution (*D2*) habitat clustering, processes of habitat removal (*a*) and dispersal strategies (Unbiased and habitat-biased). The variable displayed on the y axis (No. of steps) is the average of the movement steps, which have been calculated by dividing the actual distance moved d_a by the dispersal distance *dd*. The terms "Low" and "High" indicate the degree of habitat clustering; "Coarse" and "Fine" refer to the resolutionof habitat clustering.

Figure 4.Mean number of steps(*N* = 10000 replicates)± 1 SE,as a function of the degree of coarse-(*D1*) and fine-resolution(*D2*) habitat clustering, for different dispersal distances (*dd*), processes of habitat removal (*a*) and dispersal strategies (Unbiased and habitat-biased). The variable displayed on the y axis (No. of steps) is the average of the movement steps,which have been calculated by dividing the actual distance moved d_a by the dispersal distance *dd*. The terms "Low" and "High" indicate the degree of habitat clustering; "Coarse" and "Fine" refer to the resolutionof habitat clustering. Results are shown for a constant amount of habitat (*p* = 0.1).
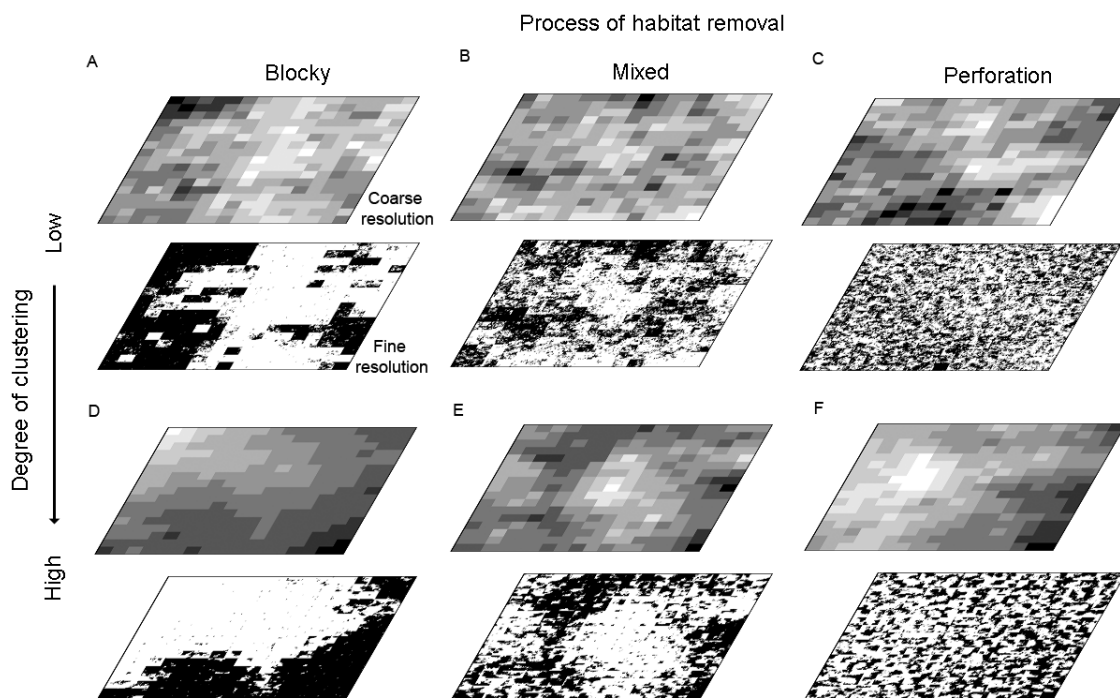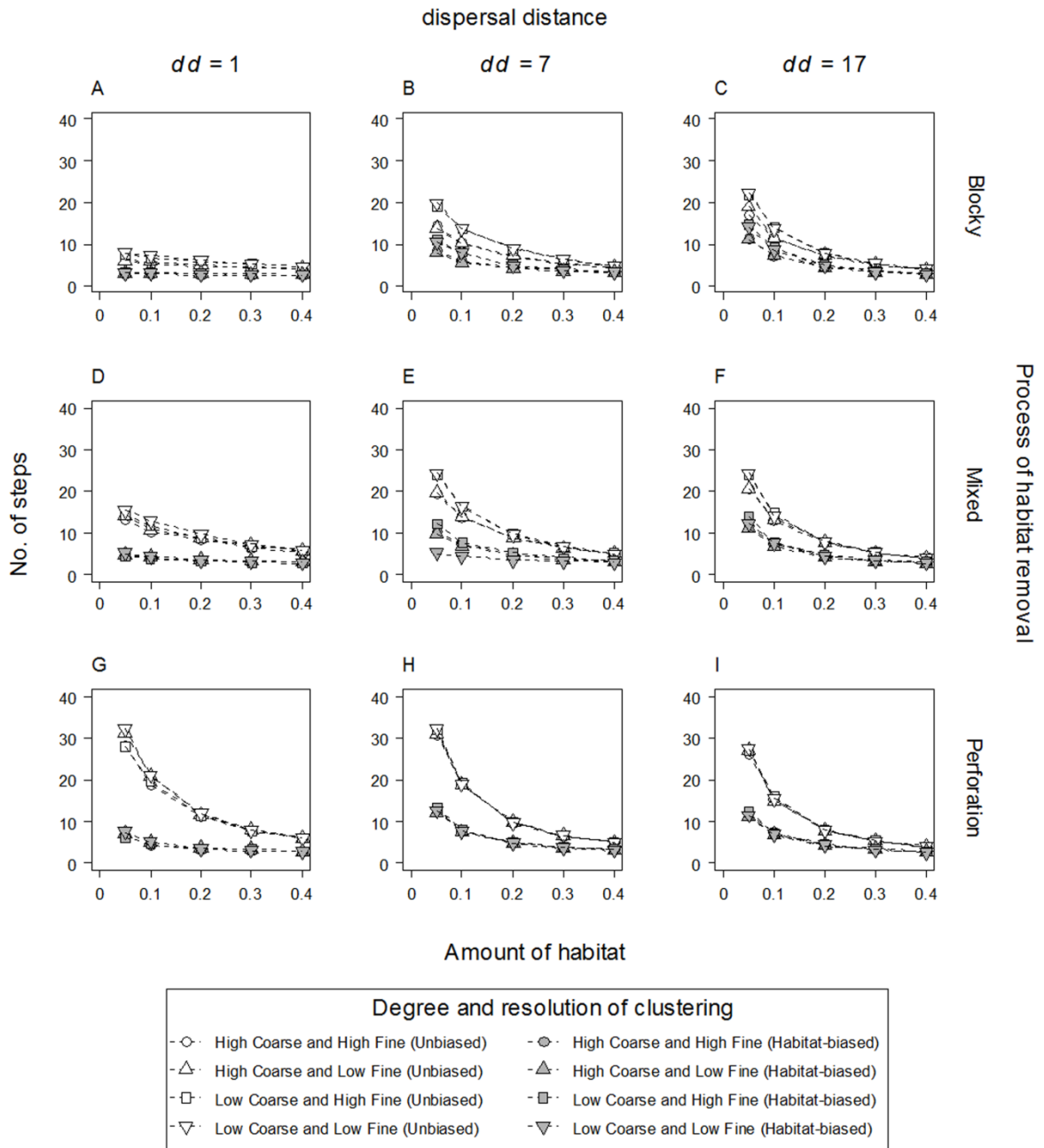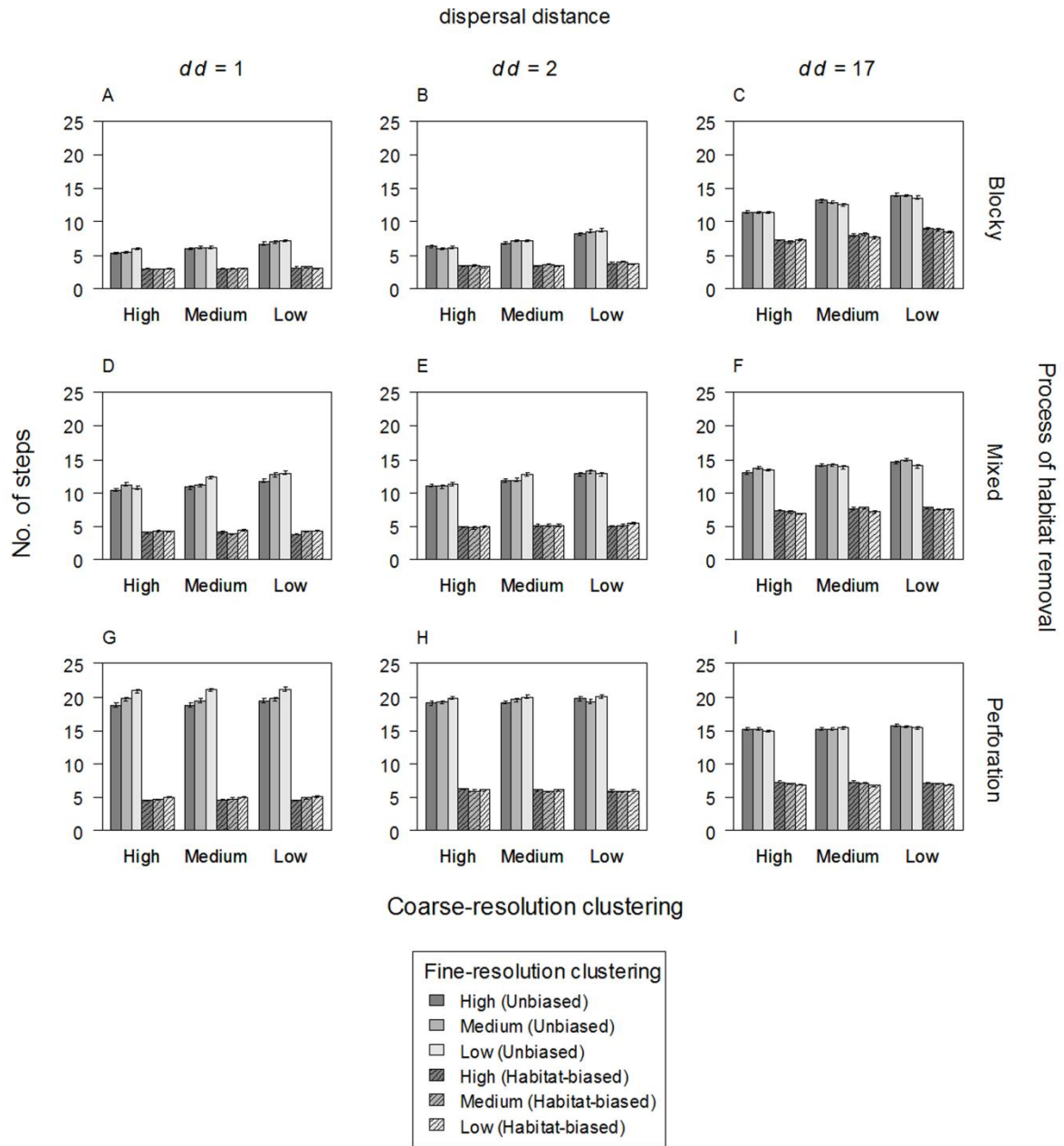
Figure

1

550

555

560   Figure 2

Process of habitat removal

A Blocky   B Mixed   C Perforation

D   E   F

Low   Coarse resolution

Fine resolution

High

Degree of clustering

565

570

26

Figure 3

dispersal distance

dd = 1   *dd* = 7   *dd* = 17

No. of steps

Amount of habitat

Process of habitat removal

Blocky

Mixed

Perforation

Degree and resolution of clustering

High Coarse and High Fine (Unbiased)   High Coarse and High Fine (Habitat-biased)
High Coarse and Low Fine (Unbiased)   High Coarse and Low Fine (Habitat-biased)
Low Coarse and High Fine (Unbiased)   Low Coarse and High Fine (Habitat-biased)
Low Coarse and Low Fine (Unbiased)   Low Coarse and Low Fine (Habitat-biased)

580

Figure

4

590

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