

Habitat structure mediates spatial segregation and therefore coexistence

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Abstract Understanding the mechanisms driving diversity in nature is an important and ongoing challenge in our changing world. To efficiently protect ecosystem diversity it is crucial to explain why and how species coexist. Over the last decades models explaining species coexistence have increased in complexity but usually don't incorporate a detailed spatial context. However, spatial structure has been shown to affect species coexistence and habitat deterioration is one of the biggest threats to biodiversity. We therefore explore a spatially explicit two-species model and assess the effects of habitat

structure on species coexistence using a wide diversity of fractal landscapes. Each species is specialized in a particular habitat type. We find that landscape structure has a major influence on the stability and constitution of a two species system and may be sufficient to explain the coexistence of two species. Well connected and highly structured habitat configurations allow spatial segregation of both species and this decreases local interspecific competition; in our model this is the most important process stabilizing coexistence.

Keywords Coexistence · Competition · Habitat structure · Habitat fragmentation · Habitat loss · Spatial segregation · Storage effect · Dispersal

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Introduction

For more than half a century the question of what processes allow coexistence of competing species has been central in ecology. Early work by Lotka (1932) and Volterra (1926) provided the foundations of this field by demonstrating that two species can only coexist if intraspecific competition is stronger than interspecific competition. Coexistence among competing species is, however, a common phenomenon (Gravel et al. 2011). This discrepancy between theory and reality can be explained by the simplifying assumptions in the basic Lotka-Volterra equations,

such as an environment that is spatially homogeneous and temporally stable, with interactions occurring globally. Already in 1933 Nicholson stated that the environment has an important influence on the ‘balance’ between species after competition. More recently, the importance of spatial complexity for species co-existence is slowly becoming fully appreciated (Chesson 2000; Snyder and Chesson 2004). Particularly, when resources are heterogeneously distributed, a “spatial storage effect” can take place, concentrating intraspecific competition relative to interspecific competition (Amarasekare 2003), resulting in a reduced spatial overlap of metapopulations (Murrell et al. 2002; Snyder and Chesson 2003; Hanski 2007). The inclusion of a spatial component and local interactions will in consequence alter predictions based on non-spatial models (Pacala and Tilman 1994; Neuhauser and Pacala 1999) and is therefore essential to understand metacommunity dynamics (Holyoak et al. 2005) and biodiversity patterns in general (Jeltsch et al. 2013). Although models explaining species coexistence have increased in complexity over the last decades, they usually don’t incorporate detailed spatial properties and are thus not designed to explore the spatial parameter space allowing coexistence.

Spatial habitat structure is in its simplest form determined by two parameters, habitat availability and its level of clumping (i.e. the opposite of the level of fragmentation). It is known lowering either of these parameters can decrease the stability of species coexistence through the reduction of metapopulation sizes and the alteration of species interactions (Ewers and Didham 2006). Quite counter intuitively, the effects of habitat fragmentation per se (when ignoring the effects of habitat loss) on biodiversity are often positive [see Hanski (1995) and Fahrig (2003) for a review as well as Yaacobi et al. (2007), Bonin et al. (2011)] and partially attributed to the fact that weaker competitors can refuge in empty habitat fragments (Levin 1974) and/or that equally competitive species become spatially segregated (Hanski 2007). In order to test the impact of spatial structure on how two species interact and coexist, we developed a model simulating two competing habitat specialist along a variety of fractal landscapes consisting of two types of suitable habitat. A two specialist species system represents one of the simplest forms of competition and, following niche-theory, allows potential coexistence (Chesson

2000). We manipulate the competitive balance in the system by varying the proportions and spatial structure of two suitable habitat types which are favoured by either specialist. Furthermore, we test different dispersiveness levels over several simulations since higher dispersal distances are expected to destabilize coexistence (Débarre and Lenormand 2011). We hypothesize that when habitat availability and habitat clumping are high, coexistence will be most stable—although species in a weak competitive position might benefit from fragmentation.

The model

A version of this section following the Overview, Design concepts, Details (ODD) protocol has been added to the supplementary material (Grimm et al. 2006, 2010). An overview of the parameter values used can be found in Table 1.

Landscape

We generated fractal landscapes on a square lattice using the diamond-square algorithm (Miller 1986) with dimensions of 64×64 grid cells. In earlier work these theoretical landscapes usually only consist of unsuitable and suitable habitat (McInerney et al. 2007). Like Wiegand et al. (1999) we increased complexity by splitting the suitable habitat into two types, edge and core habitat, with the former typically surrounding the latter (see core–edge configuration in Fig. 1). Each species is specialised in one of those two suitable habitat types (i.e. higher reproductive output), but apart from this both species are identical. The spatial structure of habitat patches is determined by the parameters P , H and P_{core} . P controls the total proportion of available suitable habitat (edge + core) and H stands for the spatial autocorrelation, which determines the degree of clumping of the suitable habitat patches (i.e. the opposite of the level of fragmentation). The third parameter P_{core} denotes the proportion of suitable habitat that is of the core type, $1 - P_{\text{core}}$ would thus result in the proportion of suitable habitat of the edge type. The diamond-square algorithm creates a continuous 3D landscape with varying altitude. We simplified the altitude in this landscape into three discrete classes where the lowest altitudes become unsuitable habitat, the intermediate

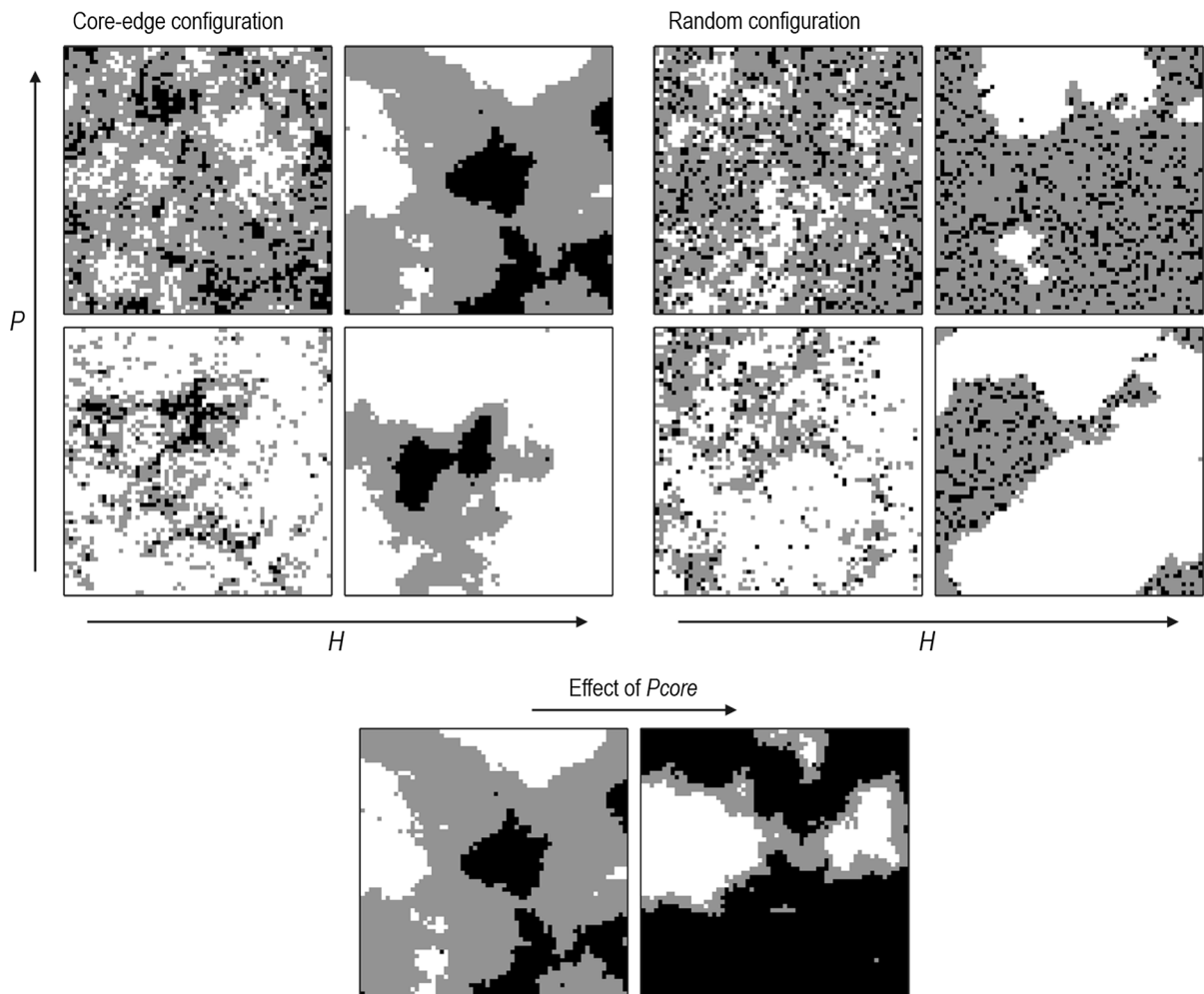


Fig. 1 Illustration of the effects of the three landscape structure parameters. Colour code: *white* unsuitable habitat, *grey* edge habitat, *black* core habitat. Both edge and core habitats are suitable to the model species

altitudes become edge habitat and highest altitudes become core habitat. Therefore, core habitat is typically, but not always, surrounded by edge habitat. We investigated population dynamics in landscapes where P , H and P_{core} systematically varied between their minimal (0.2 for P , 0 for H and P_{core}) and maximal value (1). Parameter values were changed in equidistant steps of 0.1, except for P_{core} in the random configuration which was changed in steps of 0.025 between 0.4 and 0.6. This led up to ± 1000 possible combinations of P , H and P_{core} which all were tested. Each parameter combination was replicated 20 times in independently generated landscapes. The three spatial parameters are independent of each other and can result in unintuitive landscape structures. For

example, when both habitat clumping (H) and availability (P) are low but P_{core} is high, it is possible to have a highly fragmented landscape with lots of edges but little “edge” habitat; instead, “core” habitat will directly border to unsuitable habitat, thus forming the “edge” of a habitat patch. However, in the majority of spatial parameter combinations core habitat is surrounded by edge habitat resembling fragmented landscapes with patches under influence of edge effects. This could for instance represent a system where an insect herbivore is confronted with host plants sensitive to edge effects having clumped distributions in the centre of an area of suitable habitat, and more stress tolerant host plant species inhabiting edges; or plants confronted with buffered

Table 1 Overview of all parameters and variables

Parameters	Explanation	Value/ range
$\lambda_{\text{preferred}}$	The growth rate in preferred habitat	2.5
$\lambda_{\text{unpreferred}}$	The growth rate in unpreferred habitat	1.5
σ	The standard deviation of the Gaussian dispersal kernel	0.5, 1 or 2
P	The total proportion of suitable habitat (core + edge type)	0.2–1
H	The Hurst exponent denoting habitat clumpedness	0–1
P_{core}	The proportion of core type habitat within the suitable habitat	0–1
N^*	The population equilibrium density (per patch)	2
Measured variables		
Nt	The summed local density of both species (per patch)	0–n/a
Global coexistence	How even both species abundances are on a global level, it is maximal when the two species abundances are equal and minimal when one species is extinct.	0–100 %
Local co-occurrence	The proportion of occupied patches that is occupied by the two species	0–100 %

Note that σ has a value of 1 in all simulations except those where the effect of dispersiveness was explicitly tested. The maximum value for N_t is not applicable since in theory there is none

soils surrounded by more micro-climatologically variable soils. In the first example, insect herbivores might either specialize on the plant species in the core or edge of the habitat, in the second case, plants could specialize to a buffered core- or unstable edge habitat.

In order to test the impact of this specific habitat structure generated by the diamond-square algorithm, we also generated a more scattered landscape with core and edge habitat randomly distributed within the suitable habitat patches (see random configuration in Fig. 1). In this case it no longer makes intuitive sense to refer to core and edge habitat, but we keep doing so for reasons of consistency.

The model species

We initialized the landscape with one thousand individuals of each of two specialist species. We only

used two species to keep our model as simple as possible. No overlapping generations occur since adults die after reproduction. The reproductive output of individuals is sensitive to the type of suitable habitat they find themselves in. Also, the number of offspring produced is influenced by the total number of individuals (from both species) within a patch (i.e., grid cell). The fact that individuals from both species contribute equally to the perceived local density makes intra-specific competition particularly strong since local density is the only driver of competition in our model. Offspring disperse a certain distance drawn from a predefined kernel (see below) and survive if they settle in a patch of suitable habitat. Reproduction was modelled as an asexual process. Within-population dynamics are based on well-understood density dependent demographic processes (Hassell and Comins 1976). The mean number of offspring μ which each individual will produce in its local patch is calculated as follows:

$$\mu = \lambda(1 + aNt)^{-1}$$

with

$$a = (\lambda - 1)/N^*$$

Here, λ specifies the net reproductive rate which is different for the two species, N^* is the population equilibrium density for a single patch and is a constant set to 2, Nt is the summed local density of both species at time t ; if Nt is higher than N^* the mean number of offspring (μ) will decrease below 1 due to competition and the local population will shrink. The actual number of offspring is drawn from a Poisson distribution with mean μ (Travis and Dytham 2002; Kubisch et al. 2011). In our models individuals have a net reproductive rate (λ) of 1.5 if they find themselves in a patch of their non-preferred habitat type and 2.5 if the patch is of their preferred habitat type. These relatively low parameter values were chosen for reasons of speeding up computational power and because we found by sensitivity analyses that they did not impact the qualitative model outcome.

Dispersal

In order to focus on the effect of competitive abilities generating coexistence, and not factors related to asymmetric dispersal, all individuals share the same

dispersal kernel from which their individual dispersal distance is sampled. The shape of this kernel is defined by the parameter δ which determines the standard deviation of a two dimensional Gaussian distribution with mean zero (Bonte et al. 2010). We use δ as a measure for dispersiveness since high δ values lead to wide kernels with approximately 32 % of the population moving beyond distance δ (principal characteristic of a Gaussian distribution). We explore the effect of different δ values in several simulation runs; the standard value is 1 and results in an average dispersal distance of 1.3 grid cells (for more details see Boeye et al. 2013).

Quantifying population dynamics and coexistence

After 1000 generations we measure three population statistics. The first one is a measure of coexistence at the global scale, i.e. co-occurrence under equilibrium conditions at the landscape level. This value is calculated by dividing the number of individuals of the rarest species at the last time step by the number of individuals of the most abundant species and multiplying this number by 100. The global coexistence is at its maximum (100 %) when on a global scale both species are equally abundant whereas a value of 0 % indicates the total exclusion of one species.

The second value is the percentage of inhabited grid cells occupied by individuals of both species (i.e. the local co-occurrence) and is a measure of the rate of interspecific competition at the final time step. By combining these two values we are capable of inferring whether, and to what extent, species coexist and interact on a local and global scale for each landscape structure. The third value represents the habitat fidelity; it is a measure of how true individuals of a species are to their preferred habitat type and is calculated by dividing the number of individuals in the preferred habitat type by the total number of individuals from that species. The habitat fidelity results are summarised in Fig. S1 in the Supplementary material.

In order to partition the variance explained by landscape parameters P , H and P_{core} and their interactions we performed logistic regression on the population size of one species relative to the total population size based on 20 replicates within each parameter combination. The three variables were modelled as random effects to determine the percentage of explained variation.

The size of the landscape has a positive effect on the success of the weakest species in any type of habitat structure. It also increases the range of parameter combinations in which two species share a significant amount of patches. Increasing the length of simulations from 1000 to 2000 generations had no significant effect on the results, although some additional extinctions occurred in scenarios where one species was rare. However, we chose not to further increase the length of the simulation since the assumption of temporal stability then becomes increasingly unrealistic. Changing the reproductive output of both species had no qualitative effect on the results as long as the average reproductive output of both species in the two suitable habitat types was equal.

Results

The impact of landscape structure: habitat availability (P), -clumping (H) and -distribution (P_{core})

The outcome of competition is principally determined by the relative proportions of core and edge habitat (P_{core}), which alone explained 44 % of the variation and another 39 % in interactions with the total proportion of habitat P (15 %), its clumpedness H (16 %) and the three way interaction with these two (8 %). When we focus on the sole effect of P_{core} we notice that global coexistence gets higher as P_{core} values approach 0.5 (Fig. 2a); this results from a gradual shift in dominance from the edge-specialist to the core-specialist as we increase P_{core} . When we do include the effects of P and H we notice that the parameter space of global coexistence becomes smaller and less predictable in landscapes where little habitat is available and clumping is low (P and H are low) compared to when both are high (Fig. 3). Thus, although P_{core} is the main factor mediating global co-occurrence, P and H determine the exact outcome of competition (see Figs. 3–5) and local level co-occurrence (see Figs. 4b and 5b, Animation 1 in Supplementary material). Furthermore, the impact of both parameters is highly interactive and has a major effect on local community structure (see Fig. S1 in Supplementary material). For instance, when both habitat availability and clumping are low, conditions are so poor that stable coexistence is only possible on a

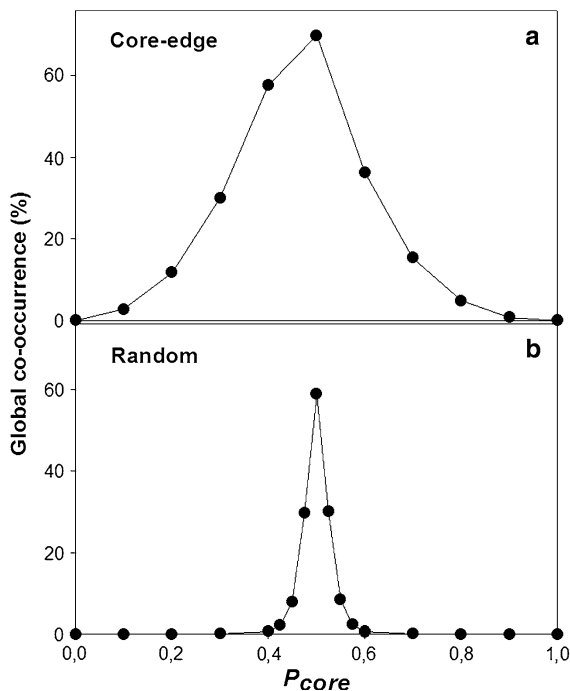


Fig. 2 The separate effect of P_{core} on the proportion of generalists when other parameter dimensions are averaged out for both the core–edge and random habitat configuration. Of all spatial parameters P_{core} has by far the strongest influence on the outcome of competition. The separate effects of P and H are negligible; however the interactions with P_{core} can be highly significant (Figs. 3–5)

global level when both species don't interact locally due to spatial isolation. Only when more suitable habitat becomes available and when it is more clumped together stable local coexistence becomes possible (see Figs. 4, 5).

When little habitat is available and clumping is low, the parameter space, in which coexistence is possible, shifts to low P_{core} values (core–edge in Fig. 3a; Fig. S1 in Supplementary material). This means that core-specialists tend to benefit from these conditions relative to edge-specialists since they can coexist when their preferred habitat type is scarce. In contrast, when habitat availability and clumping are high, the outcome of competition becomes very predictable in that both coexist according to the proportion, of their preferred habitat (core–edge in Fig. 3i). The predictability of the outcome of competition can be explained by the fact that when more suitable habitat becomes available and when it is more clumped together, continuous areas of either the core or edge type

become available and the two species tend to monopolize the areas where they have the competitive advantage. When habitat availability and clumping are sufficiently high the spatial distribution of species thus tends to equalize the spatial distribution of both habitat types. Furthermore, this process of spatial segregation stabilizes coexistence, since interspecific competition is excluded from the centres of monopolized areas and only occurs near borders. Therefore, in the core–edge configuration, the proportion of local co-occurrence increases steadily when both habitat availability and clumping are low, but remains constant once the combined effects of habitat availability and clumping allow continuous areas of one habitat type (see Fig. 4a). This can only be explained by a process reducing interspecific competition, since total population size and thus global density increases with habitat availability (data not shown).

The effect of a random habitat distribution within the patches

When both habitat types are distributed randomly within the suitable habitat, P_{core} becomes the only determinant of the global outcome of competition individually explaining 92 % of the variance. Moreover, the range of P_{core} values allowing global coexistence becomes much smaller (see base model in Fig. 2b), there is thus a more rapid shift in dominance. While in the more spatially structured core–edge habitat configuration global and local coexistence is prevalent within P_{core} values of 0.1–0.8 (regardless of P and H values), this is now only the case in the narrow range of 0.4–0.6 (see base model in Fig. 2a, b; Animation 1 in Supplementary material). If we repeat our statistical analysis in this narrow range of P_{core} values other parameters also become significant; P_{core} then only explains 29 % of the variance individually and the interaction with P becomes equally important (31 %). Weaker explaining variables of significance are P individually (8 %), the interaction between P_{core} and H (9 %) and the three way interaction between P_{core} , P and H (10 %).

When both species coexist within a landscape where both habitat types are distributed randomly within the suitable habitat, the proportion of local co-occurrence can increase up to a maximum of 41 %, relative to 28 % in the core–edge habitat configuration when $P = 1$ (see Animation 1 in Supplementary

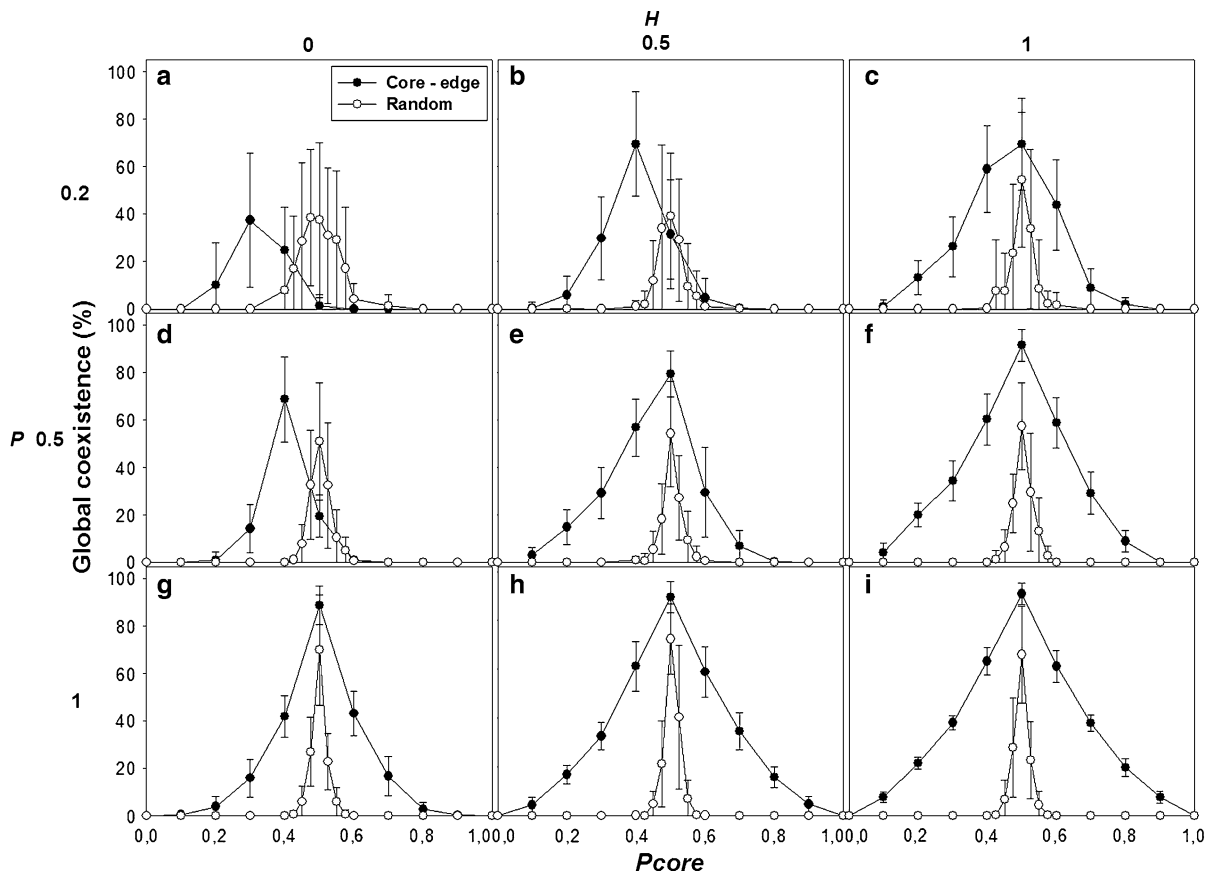


Fig. 3 The global co-occurrence over P_{core} for different combinations of P and H , in the core-edge- (full circles) and random habitat configuration (empty circles). The extent of global co-occurrence becomes larger and more predictable as P and H , allowing coexistence in a wider parameter space of

P_{core} . However, in the random-habitat configuration the shift in dominance as P_{core} increases always occurs very swift, resulting in a small parameter space where global co-occurrence is possible. The error bars denote the standard deviation based on 20 replicates

material). This means that interspecific competition is much more prevalent in the random landscape structure after 1000 generations. The impact of habitat availability and clumping on the persistence of both species was different compared to the more spatially structured core-edge habitat scenario: predictability of the exact level of global coexistence remains low for all combinations of P and H and the benefit core-specialist seem to have from low P and H conditions in the core-edge configuration is absent (Fig. 3a).

The effect of dispersiveness

Dispersiveness has a negative effect on species coexistence. Higher dispersal distances increase the prevalence of interspecific competition and narrows the range of P_{core} values in which both species can

coexist on a global (Fig. 6a, c) and local level (Fig. 6b, d). In a core edge structure higher dispersal distances ($\delta = 2$) result in less local co-occurrence for either low or high values of P_{core} , however, for intermediate values of P_{core} the local co-occurrence increases (Fig. 6b). In a random configuration the results are less distinct yet qualitatively similar, although higher dispersal distances don't increase the maximal local co-occurrence (Fig. 6c, d).

Discussion

We aimed to gain insight into the influence of spatial structure on the interactions and coexistence of two species. Our findings can be summarized in four main points:

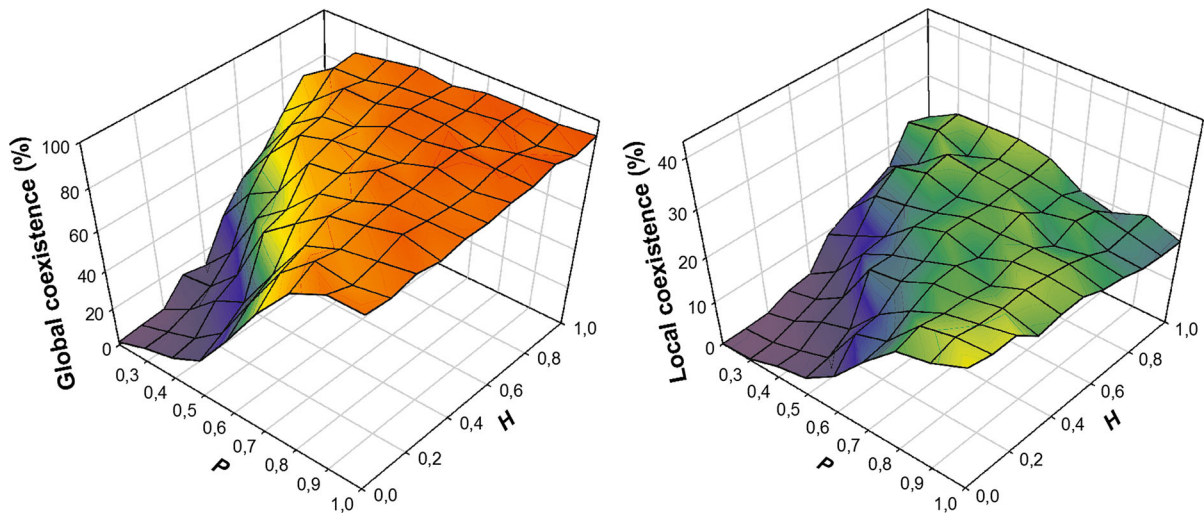


Fig. 4 A representation of population dynamics after 1000 generations in the scenario with a core–edge habitat configuration. The extent of global co-occurrence for 99 combinations of P and H is represented in the graph to the left. In the right graph the percentage of local co-occurrence is depicted for the same parameter space. For both graphs the proportion of core habitat is 0.5. The prevalence of local co-occurrence strongly

increases when P and H approach a value of 0.6 but remains rather constant above this value (± 25 % local co-occurrence). This is due to spatial segregation of both species within one-species aggregations. Note that in this scenario the H value has an influence on both the fragmentation of the suitable habitat itself as on the core habitat within

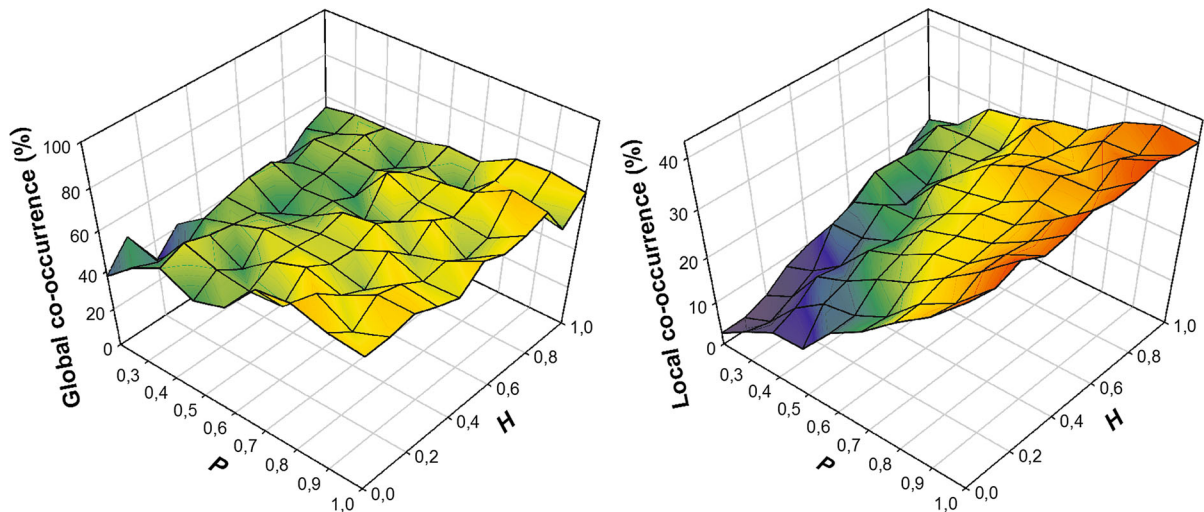


Fig. 5 As Fig. 4 but for the scenario with a random configuration of suitable habitat. The extent of local co-occurrence increases with P and to a minor extent with H to reach values up to 40 %. Note that in this scenario H only has an influence on the

fragmentation of the suitable habitat and not on the distribution of the two habitat types within. This means that when P is 1 there is no effect of H

- Certain landscape configurations allow spatial segregation of both species resulting in a stabilization of coexistence through the avoidance of inter-specific competition.
- Shorter dispersal distances also promote spatial segregation and consequently coexistence.
- The main determinant of the outcome of competition is the relative proportion of the two preferred

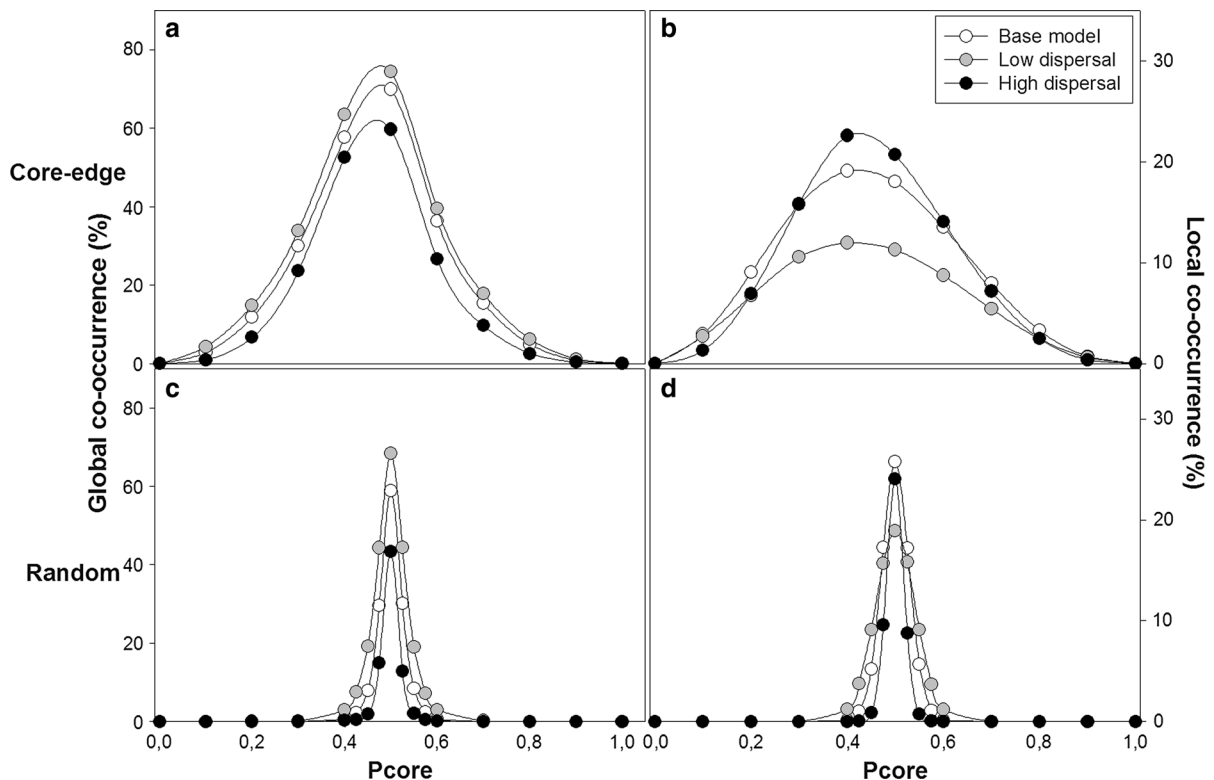


Fig. 6 The effect of dispersiveness on the global (a, c) and local (b, d) coexistence over P_{core} . Both values are averaged over all combinations of P and H . Dispersal distances are either low ($\delta = 0.5$), normal ($\delta = 1$) or high ($\delta = 2$). Dispersal distances

have a negative effect on the P_{core} -parameter space in which global coexistence occurs (a, c). The maximal local co-occurrence increases with dispersiveness in the core-edge configuration (b) but not in the random configuration (d)

habitat types (P_{core}). For example, if 75 % of the suitable habitat is of the core type then the core specialist will dominate regardless of habitat configuration. However, on a lower level habitat availability and clumping will influence the exact outcome of competition.

- The effect of habitat deterioration (i.e. high fragmentation and habitat loss) was ambiguous. In most scenarios it decreased coexistence but under specific conditions it could work beneficial.

The effects of both habitat availability and clumping over different habitat distributions (i.e. values of P_{core})

Logically, the outcome of competition is primarily determined by the abundance of the two suitable habitat types (P_{core}); overall, species become dominant when their preferred habitat is most abundant.

However, for a wide range of P_{core} values coexistence can be either stable or unstable depending on the amount of habitat availability (P), habitat clumping (H) and the exact spatial distribution of habitat types (i.e. in a core-edge or random fashion). In simulations with the core-edge configuration we find that in cases of a fully filled landscape (P and $H = 1$) the proportions of both species are equal to the proportions of their preferred habitat type. Furthermore, when there is severe habitat loss and fragmentation, core-specialists seem to profit compared to edge-specialists. This is a rather unexpected result but was clarified by ad hoc tests in which we quantified the proportion of core habitat in all occupied patches after competition. This proportion is expected to be equal to the global proportion of core habitat (P_{core}) but was much higher under low P and H conditions (Boeye et al. unpub. results). Furthermore, when we look at the habitat fidelity of the edge specialist in these conditions this fidelity is lower in the core-edge configuration

compared to the random configuration although in all other situations the opposite is true (Fig. S1(a) in Supplementary material). This means that the core–edge configuration in low P and H conditions forces edge specialist to live in core habitat which gives them a competitive disadvantage towards the core specialist. They are forced there because under these circumstances the suitable habitat is very fragmented and many fragments are too small to maintain a local population. These small, uninhabitable fragments mainly consist of edge habitat; consequently in the larger habitat fragments, that do allow a local population to survive, the core habitat is overrepresented. In nature this would relate to a situation where edge-specialists suffer more from fragmentation because the only fragments large enough to sustain a population, are high quality relicts where core-specialists thrive. In addition to this, the dispersal mortality disadvantage that is inherently connected to the edge habitat lying on the outside of patches reaches its highest significance in these highly deteriorated landscapes. In a recent review Driscoll et al. (2013) emphasize the importance of edge habitat surrounding remnant vegetation for species conservation. When we distributed both habitat types randomly, core habitat was no longer overrepresented in large habitat fragments and the effect disappeared. Therefore, this difference is entirely driven by the configuration of the landscape (core–edge or random) rather than by the habitat composition, since P , H and P_{core} did not differ among the scenarios.

Reduced competition by spatial segregation

Competition typically results in the local exclusion of the weaker competitor and thus destabilizes local coexistence. The inherent spatial nature of competition implies an important role of the environmental structure. When this structure allows competitors to become spatially segregated, local interspecific competition will be avoided and coexistence stabilised (Hanski 2007; Snyder 2008). Such an intraspecific aggregation stabilises competitive interactions (Remer and Heard 1998; Amarasekare 2003) and increases species diversity at the landscape scale (Wassmuth et al. (2009)). Nevertheless there has been debate about the importance of spatial segregation and under what conditions the process can stabilize coexistence (Murrell et al. 2001; Murrell et al. 2002; Chesson and Neuhauser 2002;

Rejmanek 2002). Our results allow us to compare a landscape configuration that does not allow stable spatial segregation, the random configuration, with one that can allow this, the core–edge configuration. These results indicate that there is a large range of spatial parameter values in which coexistence is only possible when the landscape is structured so that spatial segregation becomes possible; this is clearly visualized in Fig. 2 and Animation 1 (Supplementary material). Furthermore we found that spatial segregation is only possible if both species can claim continuous areas of habitat that are large enough, relative to the dispersal distance, so that competitors can be excluded from the centre of these areas. This requires high habitat availability and clumping (i.e. high P and H) which allows high fidelity towards the preferred habitat type (Fig. S1 in Supplementary material). Do note that in our model segregations results from local exclusions and short distance dispersal rather than aggregation behaviour. Moreover, once an area has been monopolised the local species will benefit from a priority effect over invaders.

When habitat types are distributed randomly species no longer form stable intraspecific aggregations, since there are no more homogeneous areas of one habitat type, from which they can exclude each other.

The effect of dispersiveness

Reduced dispersal distances ($\delta = 0.5$) decreased local co-occurrence and allowed populations to become spatially segregated thereby promoting global coexistence. Increasing dispersal distances ($\delta = 2$) had the opposite effect because more dispersive individuals tend to end up further from their natal patch and therefore have a higher chance of competing with heterospecific individuals. In addition to enlarging the dispersal distance we also tested a scenario where dispersal resulted in a random repositioning of individuals on the landscape (results not shown). In this scenario global coexistence became much rarer in the core–edge configuration, with results comparable to those from the random configuration with the standard dispersal distance. In the random configuration the maximal local co-occurrence did not increase with dispersiveness. This is due to the fact that there is very little intraspecific aggregation in this habitat structure and the chance to co-occur with a heterospecific individual is thus not affected by the dispersal distance.

There is a large body of evidence demonstrating the importance of dispersal scale relative to the scale of landscape heterogeneity on the stability of coexistence, with the relationship between spatial segregation and dispersal distance not necessarily being linear (Débarre and Lenormand (2011)). Both Snyder and Chesson (2003) and Zhang et al. (2006) concluded from theoretical models that lower dispersal distances can enhance the effects of spatial variance thereby facilitating spatial segregation of species and eventually promoting coexistence. However, in general, the prevalence and outcome of interspecific competition reflects dispersal ability and patch composition as much as the intrinsic competitive abilities of species themselves (Bowers and Dooley (1991)). While previous theoretical work often envisaged dispersal-competition trade-offs, our results are in accordance with previous findings and predictions. This is explained by higher dispersal distances destabilizing coexistence, such that dispersive populations are less likely to become spatially segregated. This, subsequently, increases the global level of intraspecific competition.

Conclusions

We have demonstrated that habitat structure is an important driver of the outcome of a two-species competition model. We found that the parameter space allowing coexistence is much wider when the landscape is distributed in a core–edge habitat configuration compared to when both habitat types are distributed randomly. This highlights the importance of spatial segregation by local competitive exclusion as a process stabilising coexistence. Although spatial segregation is not a novel phenomenon, we here elucidate the mechanism behind this process by linking coexistence—explicitly the landscape’s structure and dispersal.

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References

- Driscoll D a, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol Evol* 28:605–613
- Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecol Lett* 6:1109–1122
- Boeye J, Travis JMJ, Stoks R, Bonte D (2013) More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance. *Evol Appl* 6:353–364
- Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* 92:1503–1512
- Bonte D, Hovestadt T, Poethke H-J (2010) Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos* 119:560–566
- Bowers MA, Dooley JL (1991) Landscape composition and the intensity and outcome of two-species competition. *Oikos* 60:180–186
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Chesson P, Neuhauser C (2002) Intraspecific aggregation and species coexistence—comment from Chesson and Neuhauser. *Trends Ecol Evol* 17:529–530
- Débarre F, Lenormand T (2011) Distance-limited dispersal promotes coexistence at habitat boundaries: reconsidering the competitive exclusion principle. *Ecol Lett* 14:260–266
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515
- Gravel D, Guichard F, Hochberg ME (2011) Species coexistence in a variable world. *Ecol Lett* 14:828–839
- Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jorgensen C, Mooij WM, Müller B, Pe’er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rügner N, Strand E, Souissi S, Stillman RA, Vabo R, Visser U, DeAngelis DL (2006) A standard protocol for describing individual-based and agent-based models. *Ecol Modell* 198:115–126
- Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF (2010) The ODD protocol: a review and first update. *Ecol Modell* 221:2760–2768
- Hanski I (1995) Effect of landscape pattern on competitive interactions. In: Hansson L, Fahrig L, Merriam G (eds) *Mosaic landscapes and ecological processes*. Chapman and Hall, London, pp 203–224
- Hanski I (2007) Spatial patterns of coexistence of competing species in patchy habitat. *Theor Ecol* 1:29–43
- Hassell MP, Comins HN (1976) Discrete time models for two-species competition. *Theor Popul Biol* 9:202–221
- Holyoak M, Leibold MA, Holt RD (2005) *Metacommunities spatial dynamics and ecological communities*. The University of Chicago Press, Chicago
- Jeltsch F, Bonte D, Pe’er G, Reineking B, Leimgruber P, Balchenhol N, Schröder B, Buchmann CM, Mueller T, Blaum N, Zurell D, Böhning-Gaese K, Wiegand T, Eccard JA, Hofer H, Reeg J, Eggers U, Bauer S (2013) Integrating movement ecology with biodiversity research—exploring new avenues to address spatiotemporal biodiversity dynamics. *Mov Ecol* 1:6
- Kubisch A, Poethke H-J, Hovestadt T (2011) Density-dependent dispersal and the formation of range borders. *Ecography (Cop)* 34:1002–1008
- Levin SA (1974) Dispersion and population interactions. *Am Nat* 108:207–228

- Lotka AJ (1932) The growth of mixed populations: two species competing for a common food supply. *J Washington Acad Sci* 22:461–469
- McInerny G, Travis JMJ, Dytham C (2007) Range shifting on a fragmented landscape. *Ecol Inform* 2:1–8
- Miller GSP (1986) The definition and rendering of terrain maps. *ACM SIGGRAPH Comput Graph* 20:39–48
- Murrell DJ, Purves DW, Law R (2001) Uniting pattern and process in plant ecology. *Trends Ecol Evol* 16:529–530
- Murrell D, Purves D, Law R (2002) Intraspecific aggregation and species coexistence—response from Murrell, Purves and Law. *Trends Ecol Evol* 17:211
- Neuhauser C, Pacala SW (1999) An explicitly spatial version of the Lotka-Volterra model with interspecific competition. *Ann Appl Probab* 9:1226–1259
- Nicholson AJ (1933) The balance of animal populations. *J Anim Ecol* 2:132–178
- Pacala SW, Tilman D (1994) Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am Nat* 143:222–257
- Rejmanek M (2002) Intraspecific aggregation and species coexistence. *Trends Ecol Evol* 17:209–210
- Remer LC, Heard SB (1998) Local movement and edge effects on competition and coexistence in ephemeral-patch models. *Am Nat* 152:896–904
- Snyder RE (2008) When does environmental variation most influence species coexistence? *Theor Ecol* 1:129–139
- Snyder RE, Chesson P (2003) Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecol Lett* 6:301–309
- Snyder RE, Chesson P (2004) How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *Am Nat* 164:633–650
- Travis JMJ, Dytham C (2002) Dispersal evolution during invasions. *Evol Ecol* 4:1119–1129
- Volterra V (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem R Accad Naz dei Lincei* 6:31–113
- Wassmuth BE, Stoll P, Tschardt T, Thies C (2009) Spatial aggregation facilitates coexistence and diversity of wild plant species in field margins. *Perspect Plant Ecol Evol Syst* 11:127–135
- Wiegand T, Moloney KA, Naves J, Knauer F (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *Am Nat* 154:605–627
- Yaacobi G, Ziv Y, Rosenzweig ML (2007) Habitat fragmentation may not matter to species diversity. *Proc R Soc B* 274:2409–2412
- Zhang F, Li Z, Hui C (2006) Spatiotemporal dynamics and distribution patterns of cyclic competition in metapopulation. *Ecol Modell* 193:721–735