Effect of dispersal at range edges on the structure of species ranges

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Range edges are of particular interest to ecology because they hold key insights into the limits of the realized niche and associated population dynamics. A recent feature of Oikos summarized the state of the art on range edge ecology. While the typical question is what causes range edges, another important question is how range edges influence the distribution of abundances across a species geographic range when dispersal is present. We used a single species population dynamics model on a coupled-lattice to determine the effects of dispersal on peripheral populations as compared to populations at the core of the range. In the absence of resource gradients, the reduced neighborhood and thus lower connectivity or higher isolation among populations at the range edge alone led to significantly lower population sizes in the periphery of the range than in the core. Lower population sizes mean higher extinction risks and lower adaptability at the range edge, which could inhibit or slow range expansions, and thus effectively stabilize range edges. The strength of this effect depended on the potential population growth rate and the maximum dispersal distance. Lower potential population growth rates led to a stronger effect of dispersal resulting in a higher difference in population sizes between the two areas. The differential effect of dispersal on population sizes at the core and periphery of the range in the absence of resource gradients implies that traditional, habitat-based distribution models could result in misleading conclusions about the habitat quality in the periphery. Lower population sizes at the periphery are also relevant to conservation, because habitat removal not only eliminates populations but also creates new edges. Populations bordering these new edges may experience declines, due to their increased isolation.

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Range edges hold a special place in the study of the distribution and abundance of species, which is at the core of ecology (Andrewartha and Birch 1954, 1984, Krebs 1972). Designating the transition between occupied and unoccupied habitat, range edges are a key for understanding the processes that determine the ecological and evolutionary fate of a species (Holt and Keitt 2005). In a recent feature of Oikos, several authors explored the state of the knowledge on range edge ecology (Case et al. 2005, Fortin et al. 2005, Guo et al. 2005, Holt and Keitt 2005, Holt et al. 2005, Parmesan et al. 2005). These authors reviewed important processes influencing the patterns and dynamics of range edges, with the central questions being: what causes range edges, how are they maintained, and which processes control range edge dynamics? Explanations were primarily based on gradients from center to range edge in the factors controlling population dynamics (environ-

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mental conditions and species interactions), and evolutionary factors concerning the adaptation to conditions in the range edges.

We investigated a process that fits well into the single species theoretical frame work of Holt et al. (2005), but was explored neither by them nor by Guo et al. (2005) – the two papers dealing with single species processes. We turned the original question of what causes range edges around and asked: How do range edges affect the abundance patterns within the range? The idea was that populations at range edges have fewer neighbors and thus a lower connectivity or higher isolation, resulting in lower immigration rates than at the range core.

Under the assumption that new species necessarily evolve in a relatively small area, every species starts out having range edges. As species adapt to the conditions in the range edges, a key question is, what keeps them from spreading further (Kirkpatrick and Barton 1997, Gaston 2003)? Initially, they will spread to all areas they can reach and that have good enough conditions to support above zero growth but will not colonize areas in which birth plus immigration is smaller than death plus emigration. Over time, though, species should adapt to conditions at the range edge, develop higher birth and/or lower death rates under these marginal conditions and colonize adjacent habitats unless they represent a "hard" physiological border such as water for terrestrial species. If populations in the periphery were systematically disadvantaged by isolation, range edges themselves could inhibit spread by furthering extinction events and suppressing adaptations and thus help perpetuating themselves.

Metapopulation models have investigated the effects of dispersal and isolation on population persistence in much detail, but with a focus on extinctions and recolonizations of populations rather than on shifts in population sizes over the range (Hanski 1999). Our approach differs from classical metapopulation models in its explicit treatment of space and its investigation of abundance, not incidence. Extinctions (and also low genetic variability) are secondary consequences of low population size and are dependent on characteristics of individual species and situations. Therefore, the investigation of abundance more directly addresses the question of the effect of range edges on range structure than the investigation of incidence.

The effects of dispersal have also been extensively investigated in the reaction–diffusion literature (Okubo and Levin 2001). Under passive diffusion, a gradient in population densities from core to periphery is virtually implicit in these types of models (R. Holt, pers. comm.). However, the focus of this literature is quite different from our research questions. It is mainly concerned with population dynamics under diffusion and minimum patch sizes, typically of spreading populations. While approaching our question with partial differential

equations would undoubtedly also be possible, we are not aware that it has been addressed explicitly in this literature. In addition, we found our simulation approach to be more intuitive and accessible to ecologists than a set of partial differential equations would have been.

Our main goal was to determine whether the relative isolation of populations at the periphery of a species distribution could lead to lower abundances than at the core of a range when dispersal is present. We did not make the typical assumptions about range structures, such as better habitat or higher carrying capacities at the center of a range than in the periphery, but kept average carrying capacities equal at the center and the periphery. This approach allowed an assessment of the effect of dispersal on population sizes at the edge of a range without confounding gradients in environmental conditions.

Methods

We investigated the effects of dispersal on peripheral populations using a 30×30 coupled lattice containing 900 individual populations (Fig. 1). We simulated habitat quality through carrying capacity (K), analogous to Hanski (2001) using patch size to represent habitat quality in metapopulation models. Following Wiegand et al.'s (1999) insight that the reduction of habitat quality into the dichotomous categories "suitable" and "unsuitable" hampers the understanding of demographic processes, we sampled the K-values from a continuous normal distribution with mean 0 and standard deviation 1. However, we used the absolute of the randomly drawn values, in effect folding the negative part of the distribution onto the positive side. Brown et al. (1995) and McGill and Collins (2003) noted that species ranges
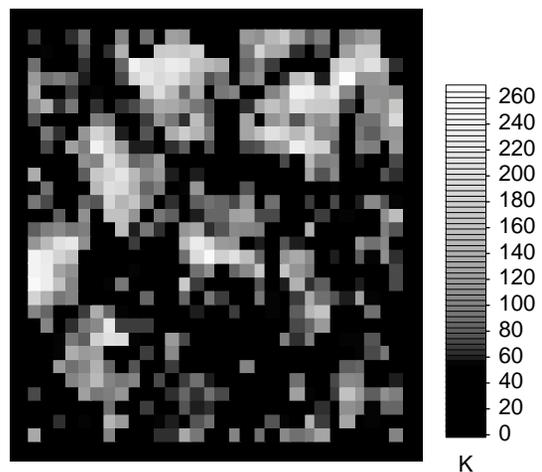

Fig. 1. Randomly generated 30×30 grid of carrying capacities (K), which are used in the logistic growth formulas of the 900 populations – one in each grid cell. The K-values are autocorrelated with a spherical decay function up to a range of eight cells.

typically have relatively few locations with very high abundances and many with low abundances, which is also true for the resultant sample distribution of the K-values.

It is well documented that environmental conditions are autocorrelated in space (Legendre and Fortin 1989). Therefore, we introduced spatial autocorrelation in the distribution of K-values using the S-PLUS function rfsim (Kaluzny et al. 1996: 117–119). This function uses a standard method for generating random variables with a known covariance structure (Cholesky decomposition). In our case the covariance is defined by the locations (x and y) and a distance-based covariance function (Ripley 1981). We used the spherical model as a covariance function of distance (Legendre and Legendre 1998: 730), which we assigned a maximum range of eight cells. The random vector of K-values is multiplied with the Cholesky decomposition of this matrix. The resulting distribution of K-values over the 30×30 matrix is spatially positively autocorrelated up to a distance of eight cells with similarities among neighbors decaying with distance according to a spherical function. We also included a test run on an uncorrelated random landscape as a null model for comparison.

Note that our method of generating landscapes did not include a bias for higher K-values at the center of the range than in the periphery. Thus, the initial external factors were similar for peripheral and central populations, which we confirmed in a t-test on the respective K-values.

Each population was governed by the basic processes of birth, death, immigration and emigration. Birth and death rates were combined in a potential population growth rate R (Begon and Mortimer 1986), which is one when no growth occurs. The formula for population change in each time step (ΔN) was based on the logistic growth formula in Begon and Mortimer (1986), which adjusts the potential population growth rate R by a density-dependent term:

$$\Delta N = N_t \times (R/(1 + (R-1) \times N_t/K) - 1) + I - E$$

where N_t = population size at time t, R = potential population growth rate (birth minus death rate not adjusted for density-dependent effects), K = carrying capacity (maximum number of individuals supported at the location before the realized growth rate falls to 1), I = immigration (number of individuals entering the population), and E = emigration (number of individuals leaving the population).

All cells in the model were habitable, within the limits on reproduction given by carrying capacities. However, carrying capacities were not absolute caps on the population sizes. Rather, they were the point at which the realized population growth rate crossed from positive growth (at population sizes below K) to negative growth (at population sizes larger than K).

A fixed proportion of each population emigrated in each time step (E). This proportion was distributed to neighboring cells in reverse relationship to their distance – the further the distance between populations the lower their exchange of migrants. We implemented this dispersal pattern by replacing the distances among cells with a weight calculated as 1/distance[2] (Fig. 2). Then, we added up all weights for each population and standardized them so that they added up to the proportion of the population to be dispersed. In addition, we truncated this dispersal scheme at different distances for a series of experiments simulating different dispersal patterns.
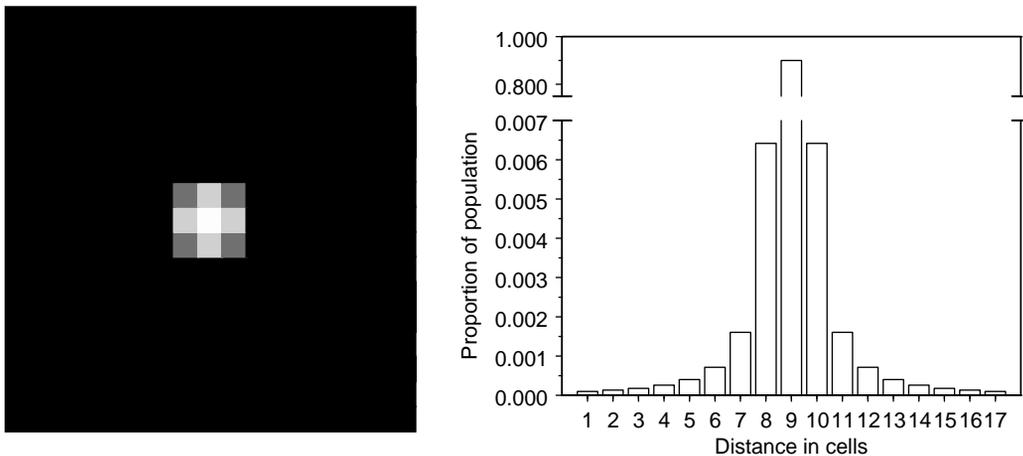

Fig. 2. Graphical representation of the dispersal kernel of a single population in the center of the two graphs. In the left graph the lighter the shade of a cell, the higher the percentage of the dispersers from the center going into that cell. The right graph shows a cross section through the left graph. The center cell retained 90% of the population while 10% dispersed to neighboring cells. The proportion of dispersers decreased with 1/distance[2]. The maximum dispersal distance was eight cells in each direction from the center cell.

In the default model dispersers leaving the range perished. Letting all dispersers distribute equally in all directions, be it into better or inferior habitat, or even outside of the range, where they perish immediately, is a neutral approach that most closely fits the dispersal of plants. Sentient animals are more likely to make better choices. Therefore, we evaluated an alternative dispersal scheme in which all dispersers stay in the range, thus eliminating the direct loss of individuals through leaving the range and moving into inhospitable habitat. In this alternative scheme, the dispersers that would have left the range in the default dispersal scheme were redistributed to neighboring populations within the range according to the same distance weighted function used in the regular dispersal. This alternative scheme is at the other end of the spectrum than the default scheme, and represents an animal that is perfectly able to avoid habitat with a K of zero. However, we used the default scheme in most experiments because it led to clearer results and thus allowed a better depiction of the sensitivities of the model.

The number of immigrants for a given population in a time step was simply the sum of all emigrants coming from other populations. Note that this approach is deterministic and allows fractions of individuals. While dispersing individuals in a stochastic way would be more realistic, it would average out to the same result given enough runs, and thus was omitted for the sake of simplicity. Also note that no mortality was associated with dispersal within the range. While this simplification is unrealistic, systematic mortality would have been equivalent to higher local mortality and a lower dispersal rate (or a different shape in the dispersal function), which are parameter variations covered in the tests below.

For a comparison between range core and periphery we had to define members of the two areas. We a priori chose the outer two rows of cells as periphery ($n = 224$) and a central 16×16 block of cells as core ($n = 256$). Other designs would have been possible, but we found this to be a good compromise between maximizing the sample size in each category and maximizing the distance between the two groups for clear effects.

We needed to find a dependent variable that would capture the relative effect of dispersal on population sizes in the periphery compared to the core. Simply taking the difference between the average population sizes in core and periphery would have expressed the absolute population sizes as well as the difference in the two places. A percentage difference in population size between the two places was the more meaningful measure (from here on called "percent difference"), calculated as:

$$100 \times (N_c - N_p)/N_p$$

where N_c = average central population size and N_p = average peripheral population size.

We tested the sensitivity of the modeling results to the potential population growth rate R and different structures of the model. We varied the R-values to simulate a range of different organisms and to determine the sensitivity of the observed effects to different combinations of these two population dynamics parameters. The values of R covered in the simulation encompass the range of maximum possible R-values (1.32–5.23) for passeriform and piciform birds in Saether and Bakke (2000). These maxima were derived from fecundity values that assumed both absence of adult or juvenile mortality and onset of reproduction within the first time step after birth. We also varied the proportion of each population dispersing in each time step to simulate different levels of dispersal activity. Finally, we varied the maximum distance of dispersal from 1–20 cells to simulate different dispersal strategies. A maximum dispersal distance of one means that dispersal is only allowed to the four next neighbors, while a maximum dispersal distance of 20 covers two thirds of the range width, which should reasonably cover the existing dispersal distances among animals.

We omitted some complications in the model that may have influenced the results but were beyond the scope of this study. Such complications include a directional bias in dispersal towards good habitat, differential mortality associated with movement through different quality habitats, and different dispersal strategies (e.g. density-dependent dispersal, Johst and Brandl 1997, Travis et al. 1999).

Simulations were run up to 600 time steps or until populations changed by less than 0.01. The analyses varying the model parameters reproductive rate R and the proportion of dispersal were based on a single typical random landscape shown in Fig. 1, because the duration of the calculations prohibited the repetition on 100 landscapes. In addition, the confidence intervals on the basic approaches run on 100 landscapes were very tight (Table 1), indicating that the variability in the results added by randomness in landscapes was small. To avoid biases in the selection of this typical landscape we randomly pulled a landscape out of the 100 generated landscapes until one was identified that was within 1 standard deviation of the average value from the 100 landscapes for summary statistics on the difference between core and margin population sizes under default parameter settings. Selecting a landscape that lay within 1 SD of all landscapes was a reasonable way to avoid the random selection of an atypical outlier. All simulations and statistics were programmed in S-PLUS 6.2 (Anon. 2003, use of this product does not imply endorsement).

Table 1. Difference in average population size between populations in the core (n =256) and periphery (n =224) of a range over 100 randomly generated landscapes. The average carrying capacities of each population in the two areas were not significantly different (p >0.05). The overall average population size was 48.89 in the default and 62.07 in the alternative approach. Underlying the difference were 10% dispersal per population per time step and a potential population growth rate (R) of 1.05. Confidence intervals are based on a 95% probability and the % difference is the percentage core populations (N_c) are larger than populations in the periphery (N_p): $100 \times (N_c - N_p)/N_p$. In the default dispersal scheme, dispersers moved in all directions equally and perished upon leaving the range. In the alternative dispersal scheme, dispersers moved exclusively within the range, simulating "reflective" borders and intelligent dispersers.

Approach	Population size			
	Difference	Lower limit CI	Upper limit CI	% difference
Default	28.02	26.04	30.00	86.59
Alternative	11.27	9.62	12.92	20.73
Carrying capacity (K)	−3.10	−3.61	2.99	–

Results

All experimental setups and parameter value combinations led to a significantly lower average population size at the periphery of the range than the core (Table 1). This difference was observed in the absence of a difference in average carrying capacities between core and periphery ($t = -0.187$, df =99, p-value =0.853). However, the relative difference in population sizes between the two range positions depended upon the structure of the model and the selected parameters for potential population growth rate (R), proportion of dispersal, and maximum dispersal distance.

Under the default values of 10% dispersal per time step and an R-value of 1.05, core populations were on average 86.6% (95% CI: 80.5–92.7%) larger than peripheral populations. Higher rates of dispersal led to larger differences between the average population sizes of the two areas (Fig. 3) but did not change the relationship between these differences and R-values. Smaller R-values led to larger differences in population sizes, with a sharp increase in differences for R-values smaller than 2. In other words, species that were unable to at least double their population size under ideal conditions within one time step experienced strong decreases in population sizes at the margins of their ranges. These decreases quickly intensified with further declines in potential growth rates from two on down. In contrast, species that could at least potentially double their population size within one time step experienced a fairly small but still observable and consistent disadvantage in peripheral populations when dispersal was present. When R was larger than two, its value did not have a strong influence on the difference in average population size between core and periphery. This percentage difference then mostly depended on the percent of dispersers in the population, being around 10% lower for 10% dispersal and 20% lower for 40% dispersal (Fig. 3).

The maximum dispersal distance showed a non-monotonic relationship to the difference in population sizes between core and periphery with a single global maximum (Fig. 4). The maximum difference was reached at a maximal dispersal distance of 11 cells. However, the differences were fairly similar among dispersal distances from 7 to 20 cells and only dropped sharply with dispersal distances below six cells. The gap between populations classified as peripheral and core in the experimental setup was also six cells, so that dispersal distances below six cells prevented a direct exchange of individuals between the two areas. As before, larger R-values led to smaller differences between core and peripheral populations, and, in this case, also to a weaker influence of dispersal distance.

The observed effect – reduced population sizes in the periphery – was not only due to loss of individuals that left the range and perished. The alternative dispersal scheme, in which individuals dispersed exclusively into the range, also led to reduced population sizes in the
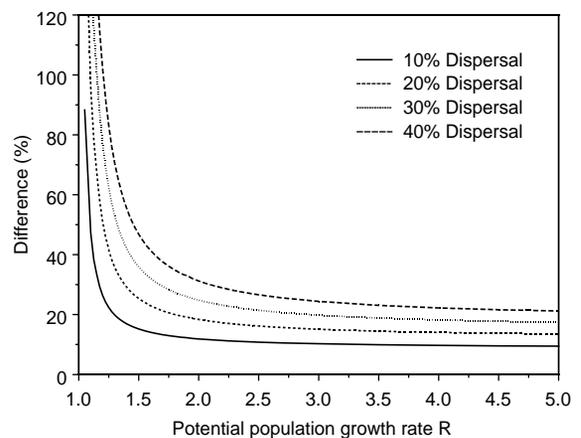

Fig. 3. Connection between potential population growth rate (R), percent dispersal, and the disadvantage populations in the periphery of a range experience from dispersal. Difference is the average percentage by which populations in the core (n =256) of a simulated landscape were larger than populations in the periphery (n =224), in the absence of differences in the average carrying capacities in the two areas. Dispersal is the percent of individuals leaving a population in each time step. The potential population growth rate is the factor a population can maximally grow by before adjustment to density-dependence in a logistic growth equation.
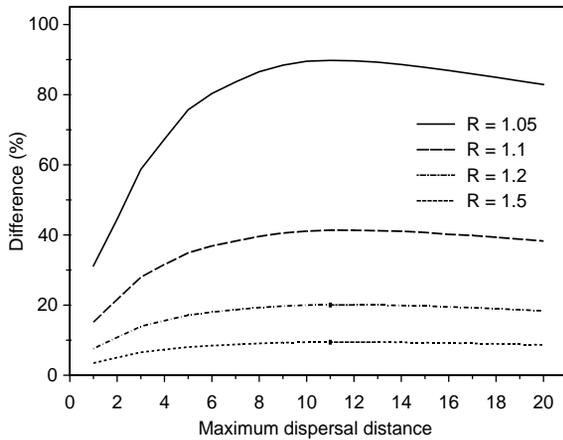
Fig. 4. Influence of maximum dispersal distance (measured in cells) on the disadvantage populations in the periphery of a range experience from dispersal. Difference is the average percentage by which populations in the core (n =256) of a simulated landscape were larger than populations in the periphery (n =224), in the absence of differences in the average carrying capacities in the two areas. The model was run with 10% dispersal per population per time step and four different potential population growth rates (R).

periphery. With the standard parameter values of R = 1.05 and 10% dispersal, core populations were on average 20.73% larger than peripheral populations (95% CI: 17.70–23.77%) under the alternative dispersal scheme.

Discussion

Isolated populations are more likely to experience a net loss of individuals to dispersal than well-connected populations because dispersers are more likely to find themselves in unfavorable habitats or perish due to longer or more difficult dispersal events. In the simulation model presented here, all populations followed the same rules with carrying capacities (K-values) randomly sampled from the same distribution and identical growth and dispersal rates. However, due to their location, peripheral populations had a reduced neighborhood and thus were less well connected than populations at the core of the range. As a consequence, peripheral populations were on average smaller than core populations in absence of any systematic gradients in habitat quality, reproductive rates or other factors that could have influenced population sizes and provided an alternative explanation for the observed difference.

Lower population sizes in the periphery may have several consequences for population dynamics in the range edge and thus for the range edge itself. The model presented here did not include extinctions because fractions of individuals were allowed and all K-values were ≥0. Had extinctions been part of the model, the lower population size would have led to a higher

likelihood of extinction (Holt et al. 2005) and the peripheral populations would have been even more isolated. The introduction of an Allee effect would have further amplified this consequence of lower population sizes. Therefore, the demonstrated effect of lower population sizes in the periphery due to dispersal could be intensified in synergism with extinctions and Allee effect, leading to more isolation and even lower population sizes in the periphery. In addition, lower population sizes bring a reduced genetic variability and thus a reduced adaptability to range edge conditions (Holt et al. 2005). All these factors work together to inhibit range expansion and promote range contraction. Under the assumption that species typically tend to extend their range through adaptations (Kirkpatrick and Barton 1997), factors inhibiting such expansion could lead to a higher than expected stability of range edges.

The effect of lower population sizes due to isolation and dispersal need not be limited to range edges. The same model used for range edges here would be similarly valid for populations bordering unoccupied areas within the distribution or existing in highly fragmented areas. In these cases, scale and resistance of the landscape to the organism become important issues. If the unoccupied gap in the range is small relative to the dispersal distance of the species and does not represent a barrier to dispersal, populations bordering the gap will not be impacted. However, if the unsuitable gap in the range is large enough or has a high enough resistance to dispersal, it could act in a similar manner as the range edges in the model presented here and thus lead to reduced population sizes along the border of the gap. Thus the often observed peak and tail pattern in range structures (Brown et al. 1995), which is used as starting point in some important macroecological theories and models (McGill and Collins 2003, Guo et al. 2005), could partly be caused or at least amplified by the spatial arrangement of habitats, the dispersal behavior of the species and the resistance of the landscape to the species, and not solely by gradients in habitat suitability or competition.

The relation between dispersal distance and distances in the range is also important (Fig. 4). Very short dispersal distances at a spatial extent similar to distances between populations result in low effects of dispersal on population size structure within the range. Such short dispersal distances approach the situation of no dispersal, when all populations merely reflect the local carrying capacity. As dispersal distance increases, the lowering effects of dispersal on the size of relatively isolated populations in the range edge increase up to the point were a maximum effect is reached. The consequent decrease in effect with increase in dispersal distance owes to a direct exchange of individuals between core and periphery, which leads to an equalization in population sizes. Thus, the largest effect of isolation on population

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sizes can be expected in species with a medium dispersal distance that is large enough to reach well into unoccupied areas but not large enough to break the isolation effectively.

Another parameter important to the magnitude in the difference of population sizes was the potential population growth rate R (Fig. 3). The lower the R-value, the more local populations were influenced by dispersal. A high R-value, in contrast, meant that local recruitment was strong and dispersers had but a small influence on population sizes. Thus, species with a low potential of population growth under ideal conditions are expected to suffer more dire consequences from isolation and fragmentation. In addition, their populations in the periphery are expected to be relatively weak, inhibiting range expansion and furthering range contraction. Examples for species with a low potential for population growth are large mammals and long-lived bird species. However, even species with high R-values showed 10–20% larger core populations (depending on the percent of dispersal).

The determination of R-values from empirical data is problematic. Realized R-values are necessarily close to 1 – otherwise, the population would be expanding or contracting rapidly. However, potential R-values used in the growth equation require knowledge on how fast a population could grow under ideal circumstances. A maximum is given through maximum fecundity. For example, a bird that is only able to lay a clutch of 2 eggs cannot have an R larger than 2. However, it could have a much smaller R when effective population size, proportion of juveniles, natural mortality under ideal conditions and similar factors are considered. Therefore, R-values are likely lower than clutch sizes may suggest and effects of dispersal on peripheral populations may be considerable.

A part of the observed effect was due to the dispersal scenario selected. The death of all individuals that left the range in the default approach contributed substantially to the lower population sizes in the periphery. In the alternative scenario, individuals were not allowed to leave the range and perish, but dispersed exclusively into the range, causing the difference in average population size between periphery and core to drop from 86.6% to 20.7%. Dispersal out of the range did not only cause loss to peripheral populations but also lowered the average population size of all populations from 62 to 49 individuals. This decline contributed to the larger difference in the default approach because population size went directly into the denominator of the calculation of the percentages. However, the remaining effect in the alternative dispersal scenario underscores that it is more difficult for the relatively isolated peripheral populations to use immigration to replenish individuals lost to emigration than it is for the populations at the core of the range. This effect is independent of the direct loss of individuals leaving the range.

These two extreme scenarios cover most dispersal strategies, from plants that have no control over habitat selection during passive dispersal to intelligent animals, which exclusively disperse into habitats with a carrying capacity >0. Most animals are likely to be found somewhere in between these two extremes. The more capable a species is in selecting habitat during dispersal, the weaker the effect of dispersal on population sizes in the periphery or in fragmented habitats is expected to be.

Some other aspects of our model structure may have influenced the quantitative outcome of our simulations. We had to reduce the variety of dispersal and population dynamics scenarios to a simple but realistic and fairly general approach. For example, our modeling of density-dependence in growth rate is but one popularly used model of reality. Other existing density-dependence representations may have changed our results. Holt (1985) showed that different dispersal and density-dependence scenarios in a two patch linked system could lead to different total population sizes over the whole range and thus could also lead to different strengths of range edge effects as shown in our simulations. For example, stronger density-dependence would not allow sinks to maintain population sizes much above carrying capacity. However, in our model the average difference between core and peripheral populations is most pronounced in such sink populations, which are well fed by immigration in the core but not in the periphery. Thus, the observed average difference between core and peripheral populations would likely diminish under stronger density-dependence. More importantly, adding density-dependence to dispersal would have had the potential to change the outcome of our simulation. The most extreme case would have been balanced dispersal, where dispersal is so dependent on local density that immigration and emigration is identical for each population and no change in relative density results from dispersal. In such a scenario, obviously, edge and core populations would both simply reach carrying capacity and no difference would be found. With a less dramatic introduction of density-dependence in dispersal, we would expect a decrease in the observed difference in average population size between core and peripheral populations.

The most direct and strongest explanations for range structure and range edges are undoubtedly a species' niche and interspecific interactions (Holt and Keitt 2005). The effect of dispersal on range structure studied here is neither to be seen as competing with these processes nor as an alternative process; rather, it augments existing insights by describing an important effect that is independent of suitability gradient or interspecific interactions. Future work needs to confirm

the theoretically predicted effect of dispersal on range edge populations using empirical data.

The results presented here have implications for the modeling of the geospatial distributions of species. The population sizes in the periphery were lower than in the core in the absence of systematic difference in habitat quality. Traditional distribution models, based on habitat associations but not spatial information, would not be able to interpret this situation correctly. Based on the lower population sizes, they would associate the habitat conditions in the periphery with a lower value than they actually have, distorting the actual resource preferences of the analyzed species. Or, alternatively, if the model was based on sample locations mostly from the core of the range, the population sizes or probability of occurrence would be over-predicted at the periphery of range. A spatially explicit model may remedy such a bias.

Lower population sizes in the periphery imply additional stress on the populations and individuals located there. However, when the range becomes fragmented at a sensitive spatial scale, similar stresses can occur within the range. The processes demonstrated here thus reemphasize the importance of connectivity for the survival of a species. In particular, additional habitat fragmentation in the periphery could lead to increased population extinction and thus to range contraction. The new periphery after range contraction would then again experience population decreases because of new isolation. An important lesson for conservation from this study is that habitat conversion not only decreases the total population by the equivalent of lost carrying capacity but also by jeopardizing populations at the newly formed edge. These effects are particularly important in species with low R-values and medium dispersal distances.

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