Forum

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Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal

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Although generations of researchers have studied the factors that limit the distributions of species, we still do not seem to understand this phenomenon comprehensively. Traditionally, species' ranges have been seen as the consequence of abiotic conditions and local adaptation to the environment. However, during the last years it has become more and more evident that biotic factors – such as intra- and interspecific interactions or the dispersal capacity of species – and even rapidly occurring evolutionary processes can strongly influence the range of a species and its potential to spread to new habitats. Relevant eco-evolutionary forces can be found at all hierarchical levels: from landscapes to communities via populations, individuals and genes.

We here use the metapopulation concept to develop a framework that allows us to synthesize this broad spectrum of different factors. Since species' ranges are the result of a dynamic equilibrium of colonization and local extinction events, the importance of dispersal is immediately clear. We highlight the complex interrelations and feedbacks between ecological and evolutionary forces that shape dispersal and result in non-trivial and partially counter-intuitive range dynamics. Our concept synthesizes current knowledge on range biology and the eco-evolutionary dynamics of dispersal.

Synthesis

What factors are responsible for the dynamics of species' ranges? Answering this question has never been more important than today, in the light of rapid environmental changes.

Surprisingly, the ecological and evolutionary dynamics of dispersal – which represent the driving forces behind range formation – have rarely been considered in this context. We here present a framework that closes this gap.

Dispersal evolution may be responsible for highly complex and non-trivial range dynamics. In order to understand these, and possibly provide projections of future range positions, it is crucial to take the ecological and evolutionary dynamics of dispersal into account.

Since the early beginnings of ecology as a natural science, unravelling the processes that determine the abundance and distribution of species on earth has been a classical research focus (Andrewartha and Birch 1954). Although more than half a century of intense research has passed since the pioneering days of quantitative biogeography we still have significant problems in explaining why some species occur in certain sites and others do not (Gaston 2009). We here aim to provide a new perspective on the formation of species' ranges by highlighting the importance of the evolutionary and ecological dynamics of dispersal. While we do not claim to present a comprehensive review of this immense field of research, we hope that our synthesis will spark new thoughts and thereby help to advance our understanding of this central question of ecology.

Beyond the abiotic paradigm

Traditionally, the ranges of species have been understood to result from abiotic factors, such as temperature, humidity or soil composition, for example, interacting with species' autecological requirements. This perspective has allowed scientists to develop modelling tools for the prediction of species distributions under specific climate change scenarios (Elith and Leathwick 2009). Yet, such an approach ignores multiple dimensions of the problem under investigation:

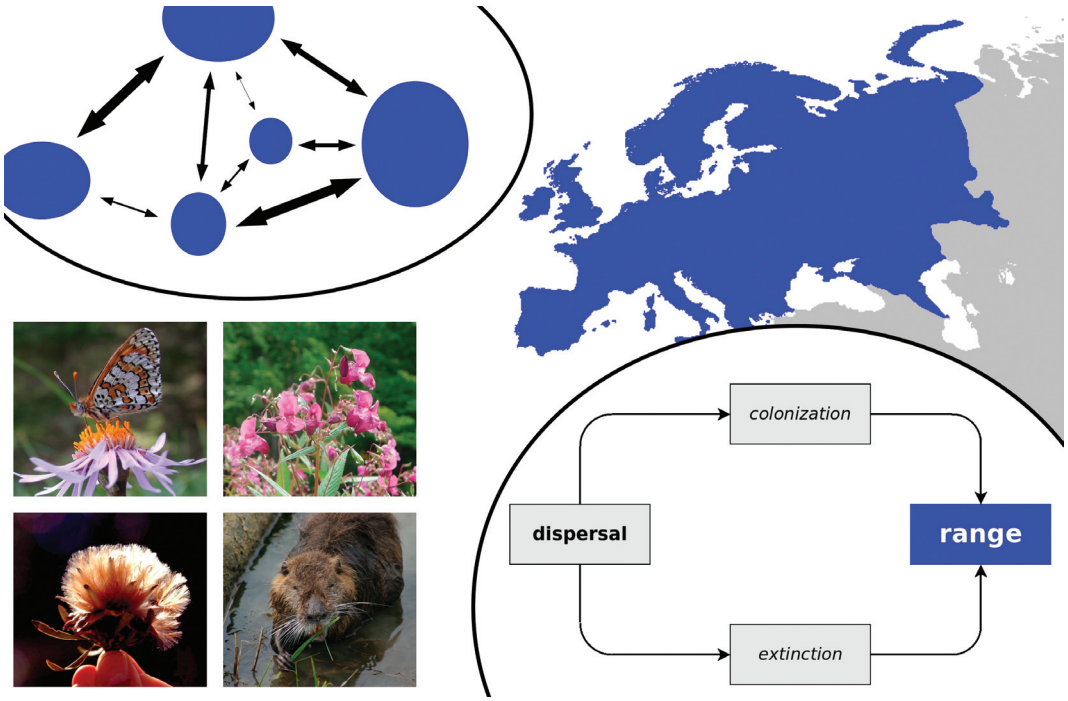

Figure 1. When investigating the distribution of species (as shown in the map for a hypothetical species distributed across Europe; occupied habitat in blue), trivial range borders occur e.g. along coastal lines, but also non-trivial range margins, here the eastern border towards potentially suitable habitat in grey. These stand in the focus of many scientific studies. As most species do not live in homogeneous habitat, but in more or less distinct patches of suitable habitat (blue patches in the upper left inset), dispersal between these is the key mechanism allowing for species' survival. By taking such a metapopulation perspective, colonizations and local extinctions of populations are the fundamental processes that determine the range of a species. It is dispersal, which allows for colonization and is an important factor influencing extinction risk (lower right inset). The two left pictures show well known examples for spatially structured populations: *Melitea cinxia* (Foto: Niclas Fritzén) and *Leucadendron rubrum* (Foto: Frank Schurr). The two right pictures show two species that have recently expanded their range: *Impatiens glandulifera* (Foto: Gerd Vogg) and *Myocastor coypus* (Foto: Emanuel Fronhofer).

evidence is rapidly accumulating that dispersal, biotic interactions and rapid evolutionary changes are at least as important as abiotic factors for determining the distribution of species (Pearson and Dawson 2003, Hampe 2004, Dormann 2007, Schloss et al. 2012, le Roux et al. 2012). Although some species distribution models (SDMs) have attempted to incorporate these factors (Zurell et al. 2012), Gaston (2009) goes as far as to generally state that "we still do not understand comprehensively the distribution of any single species on earth". This is especially worrying since, besides being used to advance our basic understanding of ecological processes, such models may be employed to derive conservation strategies or policies to mitigate the effects of global change. In this context erroneous predictions might have severe consequences both ecologically and economically.

Ranges are the consequence of colonizations and local extinctions

The formation of species' ranges has been studied from multiple perspectives – ecological, evolutionary, genetical or historical, to name just a few – and at multiple scales in the biological hierarchy – from genes to metacommunities (Gaston 2009, Geber 2011). We will here take a metapopulation approach (Fig. 1; Holt and Keitt 2000), as this level of complexity allows us to include abiotic landscape influences, such as habitat availability or fragmentation, and to take into account the effects of dispersal as well as biotic interactions. Although the metapopulation concept sensu stricto may not apply to all species (Baguette 2004, Driscoll et al. 2010, Fronhofer et al. 2012), many habitats are indeed fragmented and, as a consequence, populations of species in those habitats are spatially structured and form metapopulations sensu lato. And almost all species upon close inspection reveal substantial internal spatial structure in their ranges, even in seemingly continuous habitats. Fundamentally, the dynamics of such spatially structured populations (SSPs), i.e. occupancy or turnover, are defined by two processes: colonizations and local extinctions of habitat patches. These processes also define the dynamics of a species' range (Fig. 1): as long as in front of a range margin the number of colonization events exceed local extinctions, the range will expand. As soon as local extinctions equal colonizations, which may, for example, along a gradient in abiotic conditions, the range margin will achieve equilibrium (albeit one which may fluctuate because of stochastic processes). Of course, if local extinctions become more frequent than colonizations – as a consequence of changing climatic conditions, or human land use practices, for example – a species' range will shrink, possibly to the point of global extinction.

The eco-evolutionary dynamics of dispersal

The fact that species' range dynamics are the consequence of colonizations and local extinctions (Fig. 1) immediately clarifies the importance of dispersal: while population extinctions may be due to a range of phenomena – from deterministic successional patterns, intra-specific competition, Allee effects or predation, for example – colonizations are uniquely the consequence of dispersal, at least if we use this term in a broader sense. Of course, survival during the transition phase of dispersal and establishment success do affect colonization rates, too. However, for reasons of simplicity we assume these to be a part of the dispersal process, which can thus be seen as 'effective dispersal', considering only the interactions between migrants and their biotic and abiotic environment. Dispersal is also capable of modifying local extinction rates, on the one hand potentially increasing extinction risk of populations through emigration, but also, on the other, potentially preventing extinctions through immigration (e.g. the rescue effect; Gotelli 1991).

It is of utmost importance to take into account evolutionary dynamics, especially since dispersal has been shown to be heritable (Saastamoinen 2007) and, as a consequence, be subject to evolution (Bowler and Benton 2005, Ronce 2007, Clobert et al. 2012). As the feedback between ecology and evolution can occur extremely rapidly (Stockwell et al. 2003, Carroll et al. 2007), the strict discrimination between ecological and evolutionary time-scales traditionally assumed may be obsolete. In particular, we emphasize that range biology has to take into account the intertwined ecological and evolutionary dynamics of dispersal.

Dispersal evolution has been reviewed in detail elsewhere (Bowler and Benton 2005, Ronce 2007, Clobert et al. 2012) and we will not attempt a comprehensive review of this topic here. To summarize briefly, evolution favours dispersal in three broad circumstances: 1) in spatio-temporally variable environments (including both abiotic and biotic drivers), 2) under intense competition, especially kin competition, and 3) in order to avoid inbreeding. The former two apply both to asexual and sexual species, the third is unique to sexual species. These selective forces are balanced by a number of costs, which can be classified as energetic or material – e.g. building wings or accumulating fat reserves required to disperse, time – e.g. the transition phase, i.e. the period of movement along the landscape, may be long, risky – e.g. due to predation during dispersal – and opportunity costs – which emerge as a consequence of the loss of social rank, for example (Bonte et al. 2012), or due to the loss of local information (e.g. about locations or refuges or food sources), or simply the risk of leaving high-quality habitats and ending up in low-quality ones.

Range formation and the eco-evolutionary dynamics of dispersal

In order to clarify the complex interrelations between dispersal ecology and evolution and the formation of species' ranges we here propose to organize the most important eco-evolutionary forces acting on dispersal according to hierarchical levels. These forces are the result of internal and external conditions or limiting factors, mechanisms, processes and interactions. These may be broadly classified into abiotic (landscape) and biotic forces, where the latter can be subdivided into intraspecific (on the levels of genes, individuals or populations) and interspecific forces (community level). Please note that this categorization may sometimes be redundant and that some mechanisms or processes can be situated at multiple levels. We do not claim that our scheme is comprehensive, or that it might be better than other conceivable schemata. We only intend to highlight a range of major ecological and evolutionary forces involving the eco-evolutionary dynamics of dispersal, and relevant for a better understanding of range dynamics.

Our hierarchical classification is summarized in Table 1, which also contains a number of examples for each hierarchical level and the consequence of these forces for range formation. A graphical summary of this classification is provided in Fig. 2, which subdivides into eco-evolutionary forces affecting range formation. These forces could be abiotic (e.g. landscape properties, shown in brown) or biotic (e.g. competition, shown in green) nature. This figure outlines important interactions between these forces and dispersal that can influence species' range formation. The core of this scheme is identical to the inset in Fig. 1: when colonization and local extinction rates are equal, a stable range is formed. Dispersal affects both of these processes. Colonization and extinction, but also dispersal, are affected by the different eco-evolutionary forces emerging on all hierarchical levels through ecological (black arrows) and evolutionary (red arrows) interactions and feedbacks.

In this synthesis we will provide individual-based simulation examples that illustrate these forces and demonstrate that they can at times quite strongly influence range dynamics. The details of the simulation model we use to generate these examples are laid out in the appendix.

Abiotic conditions: the influence of the landscape

At the landscape level, the most straight forward explanation for stable species' ranges are abiotic dispersal barriers (habitats where dispersers either cannot move, or cannot survive), such as mountains or the edge between terrestrial and aquatic environments for air-breathing organisms. While these ecological effects may seem trivial, landscape structure and habitat composition (including the boundary constraints of absolute barriers to dispersal) will feed back on the evolution of dispersal and can potentially influence range limits (Fig. 2). Abiotic landscape properties – such as connectivity, habitat area, as well as spatial and temporal variance in habitat conditions – have received considerable attention in analyses of dispersal evolution. Although most work has been done on equilibrium metapopulations (Bowler and Benton 2005, Ronce 2007, Clobert et al. 2012) the connection between dispersal and colonization and, as a consequence, range border position is relatively straightforward (Fig. 1) and some predictions can be derived directly (Table 1).

The effect of the degree of habitat isolation on dispersal evolution, i.e. connectivity, has been intensely studied in

Table 1. Summary of important mechanisms for range formation with respect to the hierarchical level they act on, and selected references. Terms, which are included in the schematic summary (Fig. 2) are in bold.

Force	*Level*	*Eco-evolutionary force*	*References*
Abiotic	landscapes	**isolation** increases dispersal costs (energy, time, mortality during dispersal, etc.), decreases colonization probability and therefore favors lower **dispersal**	Virgos 2001, Poethke and Hovestadt 2002, Baguette et al. 2003, Leimu et al. 2010, Bonte et al. 2012
		increasing **area** leads to selection for lower **dispersal**	McPeek and Holt 1992, Gonzalez-Guzman and Mehlman 2001, Poethke and Hovestadt 2002
		spatial variance in patch size (quality) favors selection for reduced **dispersal**	Hastings 1983, Poethke et al. 2011
		temporal variance in patch size, quality or population density selects for high **dispersal** and increases **localextinction risk**	Lande 1998, Ronce et al. 2000, Cadet et al. 2003, Poethke et al. 2007, Kubisch et al. 2011
Biotic	intraspecific genes	**dispersal** reduces **local adaptation** through migration load (in sexual organisms)	Haldane 1956, Garcia-Ramos and Kirkpatrik 1997, Bridle and Vines 2007, Bolnick and Nosil 2007
		mutation surfing at expansion fronts can increase their frequency regardless of their fitness effect	Klopfstein et al. 2006, Travis et al. 2007, Hallatscheck et al. 2007, Excoffier and Rey 2008, Lehe et al. 2012
		local adaptation reduces **colonization** of new patches through lack of genetic diversity	Bradshaw 1984, Al-Hiyaly et al. 1993, Kawecki 2008
		local adaptation reduces **localextinction** risk	Jump and Peñuelas 2005
		recombination increases genetic diversity and thus adaptive evolution	Booy et al. 2000, Holt and Barfield 2011
	intraspecific individuals	*kin competition* favors increasing **dispersal** in marginal habitats during range expansion	Kubisch et al. 2013a
		information use (conditions in target patch) improves **local adaptation**	Kawecki and Ebert 2004
		information use (conditions in natal patch) reduces the increasing effect of **dispersal** on **local extinction risk**	Ruxton and Rohani 1998, Amarasekare 2004, Hovestadt and Poethke 2006, Kubisch et al. 2011
		trade-offs may lead to selection for abilities favouring colonization (e.g. dispersiveness, aggression) at the cost of growth rate or competitiveness during periods of range expansion	Duckworth et al. 2008, Burton et al. 2010, Fronhofer et al. 2011
		dispersal costs (flight apparatures, fat reserves, etc.) favor lower **dispersal**	Poethke and Hovestadt 2002, Bonte et al. 2012
	intraspecific populations	*competition* (negative **density dependence**) favors increased **dispersal**	Poethke and Hovestadt 2002, Holt and McPeek 1996
		Allee effects (positive **density dependence**) decrease **colonization probability** and increase **local extinction risk**	Keitt et al. 2001, Taylor and Hastings 2005, Cabral and Schurr 2010, Courchamp et al. 2010, Gastner et al. 2010, Vercken et al. 2011
		Allee effects (positive **density dependence**) lead to selection for reduced **dispersal** and favor density-dependent *(„pulsed")* migration	Travis and Dytham 2002, Johnson et al. 2006, Cabral and Schurr 2010, Kubisch et al. 2011
		spatial selection favors increasing **dispersal** in marginal habitats during range expansion	Phillips et al. 2010, Shine et al. 2011
	interspecific communities	interspecific **competition** decreases colonization probability	Case et al. 2005, Price and Kirkpatrick 2009, Jankowski et al. 2010, Kubisch et al. 2013b
		predator-prey/host-parasite interactions increase **local extinction risk**	Holt 1984, Hochberg and Ives 1999, Holt et al. 2009
		predators may release prey from migration load	Holt et al. 2011
		predator-prey/host-parasite interactions favor selection for higher **dispersal**	Prakash and De Roos 2002, Poethke et al. 2010, Chaianunporn and Hovestadt 2012
		mutualism may increase colonization probability due to vector-based dispersal (e.g. of seeds) or faciliated establishment	Howe 1986, Nara and Hogetsu 2004
		mutualism decreases colonization probability and selects for lower **dispersal**	Taylor 1992, Doebeli and Knowlton 1998, Killingback et al. 1999, Case et al. 2005, Mack 2012

equilibrium metapopulations. Such geographic isolation may result from increased distance between habitat patches or decreased permeability of the matrix (Zajitschek et al. 2012), which might be species-specific. Increased isolation is known to select for lower dispersal rates and thus leads to decreased colonization rates (Virgos 2001, Cody and Overton 1996, Gros et al. 2006). However, fragmentation at the same time can favour the evolution of long-distance dispersal, i.e. the emergence of fat-tailed dispersal kernels (Hovestadt et al. 2001). This prediction has been empirically shown for stream salamanders (Lowe 2009) and might lead to an increase in invasion speed as long as the costs of dispersal are not too high. If dispersal costs scale with the distance a disperser moves (e.g. because it is exposed to mortality agents during dispersal, or has to draw on a finite energy reserve as it moves), then these fat-tails could be largely truncated. Examples from island biogeography show that – following colonization of islands due to long-distance dispersers from the main land – rapid evolution towards low levels of dispersal can be observed (Cody and Overton 1996). The resulting small and isolated populations may consequently be subject to strong

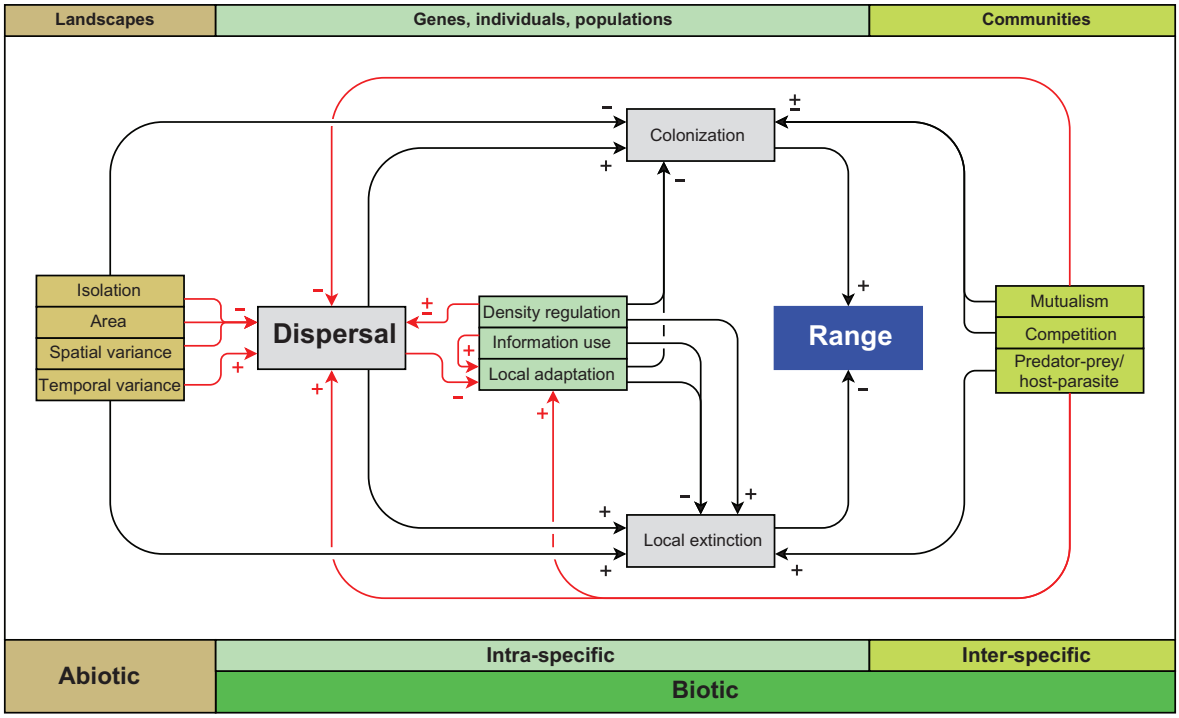

Figure 2. A schematic representation of the interrelations between colonization and local extinction in shaping the range of a species. We show internal and external conditions or limiting factors, mechanisms, processes and interactions that act on all relevant hierarchical levels (abiotic and biotic, intra- and interspecific), and directly affect colonization and local extinction, but also shape dispersal evolution. The complex interplay and feedback loops between the evolution of dispersal and all the different forces leads to non-trivial range dynamics. The algebraic sign at the end of an arrow denotes, whether an element has a positive or a negative influence on another element. Black arrows denote direct, ecological effects, whereas red arrows denote evolutionary impacts.

inbreeding depression or depleted genetic variation, both of which can increase the risk of population extinction (Frankham 2008). Thus, isolation at the landscape scale can lead to strong genetic consequences finally resulting in the extinction of local populations.

A second landscape factor which can influence dispersal evolution is habitat area. Increasing habitat area (for a given habitat quality) may reduce kin competition because more sites are available for individuals to move away from kin and the selective advantage of bet-hedging. (Ronce 2007). Larger habitat patches also exhibit less fluctuations in population size. This leads to selection for lower dispersal rates and thus reduces colonization (Fig. 2).

Although dispersal can be advantageous even in stable habitats due to interactions among kin (Hamilton and May 1977) spatio-temporal variation in population densities also selects for dispersal and increases colonization rates, even without kin competition (McPeek and Holt 1992, Cadet et al. 2003, Lowe 2009). For instance, in source–sink systems, increasing temporal variability in the source can make it adaptive for individuals to disperse into sinks (Holt 1987) which provides a pool of potential dispersers which can colonize other source habitats. However, it is important to keep in mind that spatial heterogeneity in patch size or quality on its own typically leads to selection against dispersal (Hastings 1983, Holt 1985, Poethke et al. 2011). It is therefore crucial to discriminate carefully between spatial and temporal variance in population or patch size and density.

In summary, the ecological and evolutionary forces emerging from the landscape structure, temporal variation, and biotic interactions are major determinants of dispersal potential and evolution. These factors are of pivotal importance for the establishment of species ranges.

Example 1. Invasions into a fragmentation gradient

One typical abiotic property of landscapes is its degree of fragmentation. Increasing fragmentation often leads to a simultaneous decrease in connectivity and patch size, an effect that is increasingly observed due to anthropogenic habitat conversions and global climate change (Magle et al. 2010, Hof et al. 2011). Both decreased patch size as well as increased isolation of remaining habitats increases the extinction risk of local populations. Thus, local extinction rates may increase severely as fragmentation increases. If fragmentation increases along a spatial gradient, this will necessarily limit the distribution of the species. Up to a certain degree of fragmentation colonizations may be frequent enough to allow range expansion, yet an equilibrium range will ultimately form where decreasing colonization rates do not balance increasing extinctions because suitable habitats are too sparse (Holt and Keitt 2000). Evolution of dispersal can substantially alter where this limit arises.

In this example we model a species' range along a fragmentation gradient, which is comprised of two changing landscape characteristics: spatially increasing habitat patch isolation (represented by increased dispersal mortality) and decreasing patch size (or quality, as reflected in local carrying

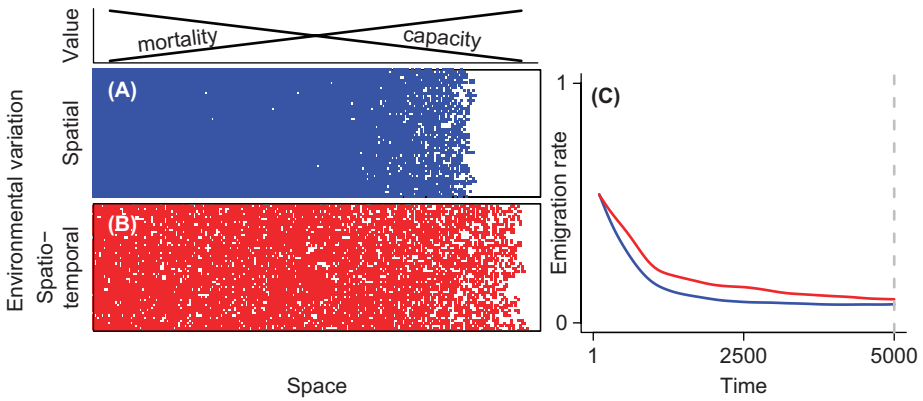

Figure 3. Simulation results for the landscape-level mechanisms. We compared dispersal evolution and invasion speed of a single species expanding into a fragmentation gradient, implemented through co-occurring gradients in dispersal mortality (i.e. patch connectedness) and habitat capacity (i.e. patch size), for scenarios with constant and variable environmental conditions (fluctuating growth rates). Although strong environmental stochasticity results in lower overall occupancy caused by increased extinction risk, under this scenario the range is extended deeper into areas with unfavorable conditions (B). The reason is that higher emigration rates are selected for, which allow for subsequent colonizations of habitat patches (C). The shown emigration rates are averaged over the marginal habitat patches (see Appendix 1 for details).

capacity; Appendix 1). We compare two different scenarios (Fig. 3): scenario A assumes spatial, but not temporal, variability in habitat conditions, which directly affects the growth rate of populations (caused e.g. by small-scale variability in temperature or resource quality). Scenario B superimposes temporal variation on this spatial gradient. A detailed model description for this and all following examples can be found in the Appendix 1.

We observe that in our example adding temporal environmental fluctuations strongly increases demographic extinction risk, which leads to an overall lower occupancy (compare Fig. 3A and B). Generally, one would predict that increasing local extinction risk should lead to range contraction. However, as extinctions also strongly select for increased dispersal rates due to bet-hedging (Fig. 3C), colonization rates are increased simultaneously. In this example, this evolutionary feedback even outweighs the effect of increased extinction rate and leads to range expansion, along with a scattering of unoccupied gaps within the range (Fig. 3). Note that in this example fragmentation affects patch size. Thus, near the margin of the range, patches are comparably small, which itself leads to higher evolutionarily stable dispersal rates, caused by increased demographic stochasticity and high kin competition. It may also be reasonable to assume equally large but less densely occurring patches. In that case results may differ, because less dispersal would be selected for at the margin.

Another factor that is worth briefly mentioning is that if there is spatial variation in patch size (influencing the strength of kin competition), or in local spatio-temporal variability (influencing the importance of bet-hedging), the evolutionarily stable rate of dispersal should vary across space. This should lead to a kind of 'migrational load' for dispersal itself, which will be asymmetrical across space. Patches where dispersal is selected to be low will not export many low-dispersal genes, compared to patches where dispersal is selected to be high. Marginal habitats where dispersal is selected for can thus help maintain a pool of genetic variation for dispersal in habitats where selection is pushing the population towards low dispersal. This could help facilitate responses by those populations to temporal shifts in environmental conditions.

This example clearly shows how important it is to include evolutionary feedback into models of range formation, as predicted patterns may change qualitatively. More specifically, our example suggests that increased risk of local extinction by expanded fluctuations in local conditions does not always imply the shrinking of a species' range. By selecting for increased dispersal into unoccupied patches and therefore enhancing colonization rates, these spatio-temporal environmental fluctuations counteract and even invert this effect.

Biotic forces: intra-specific interactions

The gene level

As we have described in the introduction, traditionally the presence or absence of species is often explained through adaptations to local abiotic conditions (Bridle and Vines 2007); hence, a range margin is thought to arise when local adaptation is insufficient to permit local persistence. Adaptation logically increases individual fitness – i.e. reproductive success or survival, for example – and thus often decreases the risk of local extinctions (leaving aside the possibility of 'evolutionary suicide'; Ferriere and Legendre 2013). If species have the potential to adapt to local conditions, and adaptation lowers local extinction rates, this will stabilize a species' range and potentially permit a species to occupy wider swathes of environmental gradients.

However, if local conditions change rapidly in space, e.g. in a temperature gradient along the slope of a mountain, and the relative fitnesses of alternative phenotypes varies spatially, dispersal between populations living in different locations can lead to an influx of locally maladapted genotypes into a marginal population. This is particularly likely if there is spatial variation in abundance or there are asymmetries in individual movement. If dispersal is asymmetric,

i.e. if it leads to a net gene flow from the densely populated range core to the sparsely populated range margin, this effect may lead to constrained species' ranges (Haldane 1956, Bolnick and Nosil 2007). To understand this effect it is important to distinguish between (asexual) species without genetic recombination and species with recombination. For reasons of simplicity we will in the following use the terms 'asexual' and 'sexual' (although recombination is not necessarily implied by sexuality, in general).

In the case of asexual species, the interaction between maladapted immigrants and locally well adapted residents of a marginal population is limited to competition for resources and other forms of density dependence. Even though no genetic exchange is possible, the maladapted individuals may still indirectly lower the fitness of the whole population through competitive interaction and thus hamper local adaptation (Holt and Gomulkiewicz 1997). However, if the species reproduces sexually, asymmetric gene flow from the range core to the margin may result in an increased migration load, where maladapted immigrants mate with better adapted residents and lower the fitnesses of the latter (Haldane 1956, Bridle and Vines 2007). This reproductive load results in increasing maladaptation of all individuals in a local population, which could be shown theoretically (Garcia-Ramos and Kirkpatrick 1997), as well as empirically (Bolnick et al. 2008).

Both scenarios – either competition, or competition combined with migration load – lower the fitness of local populations and may thus increase the risk of their extinction, which will lead to range contraction or at least constrain further expansion.

While the potential range forming mechanisms described above are negative consequences of dispersal for range expansion along gradients, dispersal may also have positive effects (Fig. 2). Gene flow through immigrants increases genetic variation in a population and, as a consequence, the evolutionary potential for adaptation (Gomulkiewicz et al. 1999, Kawecki 2008), which in turn may increase colonization rates. Vice versa, too low levels of dispersal may lead to a lack of genetic variation and make local adaptation to new conditions – e.g. in new habitat patches, or as a consequence of climatic changes – difficult, thereby decreasing colonization rates (Bradshaw 1984). A nice example has been provided by Al-Hiyaly et al. (1993), who showed that small populations of *Agrostis capillaris*, which were separated from larger ones in terms of gene flow, showed substantially lower adaptation to zinc contamination. This effect should be especially dramatic for species living in steep environmental gradients, in which local conditions change rapidly over space, as these environments select strongly against dispersal. Yet, in such steep gradients higher genetic variation is required to allow lineages to adapt to new habitat conditions. Theoretical models combining the above effects suggest that often intermediate rates of immigration maximize the likelihood of local adaptation (Gomulkiewicz et al. 1999); how this translates into altered extinction and colonization rates is an important challenge for future theoretical studies.

In addition to migration load there is another non-adaptive evolutionary phenomenon, which might strongly alter the dynamics of ranges. This so-called 'mutation surfing' describes that mutations, which occur close to the range margin during a period of expansion, might drift to higher frequencies due to interlinked chains of subsequent founder effects, without necessarily being associated with a higher fitness (Klopfstein et al. 2006, Travis et al. 2007, Lehe et al. 2012). Hallatschek et al. (2007) demonstrated this effect in an experimental approach with microbes. Slightly deleterious mutations can potentially surf to high densities during range expansion, and by clonal interference slow establishment of more favorable alleles, thus constraining further range expansion. Range expansions thus can create complex genetic patterns, which might affect range dynamics even in the absence of directed evolution (Excoffier and Ray 2008).

Example 2. Ploidy and recombination

The way in which genetic variation is organized (e.g. ploidy, rates of recombination) can have a strong influence on evolutionary dynamics. As we have noted above in the context of asymmetric gene flow, the genetic system – especially with respect to sexuality, ploidy, and recombination – is a very important factor influencing range expansion. However, this aspect is often overlooked in the literature. Although some authors have shown that these assumptions may heavily influence evolutionary trajectories (Parvinen and Metz 2008, Fronhofer et al. 2011), for reasons of simplicity many models simply assume asexual species with clonal reproduction (Bonte et al. 2010, Travis et al. 2010). An exception are models that assume a quantitative trait influenced by many loci, each of small effect (Holt et al. 2011). In this exemplary simulation we focus on processes occurring during phases of range expansion, i.e. before an equilibrium range limit has been reached, to demonstrate that genetic architecture can qualitatively influence range expansion.

Here we highlight the consequences of these contrasting genetic assumptions for organisms invading into gradients of local abiotic conditions (e.g. temperature), during the range expansion phase. The individuals in our simulations can be more or less adapted to local conditions (with highest juvenile survival probability in those areas, where local conditions perfectly match the genetically encoded optimum conditions). We simulated range expansion by introducing individuals initially well-adapted at one end of the landscape, and then letting them expand their range via the coevolution of dispersal and local adaptation with the buildup of genetic variation via mutation (see Appendix 1 for details). We compare scenarios in which organisms may adapt to local abiotic conditions for clonally (haploid; Fig. 4A, D) and sexually (diploid; Fig. 4B, E) reproducing species, each with two loci (one governing dispersal, the other adaptation to local environments); in the sexual species, there is free recombination. In addition, dispersal can evolve. As we have noted above, the steepness of an environmental abiotic gradient may be of relevance, therefore we test two different degrees of gradient steepness.

There is an interaction between gradient steepness and genetic architecture in determining the rate of invasion along the gradient. For the reasons presented above, our example shows that for clonally reproducing organisms increasing gradient steepness selects against high dispersal

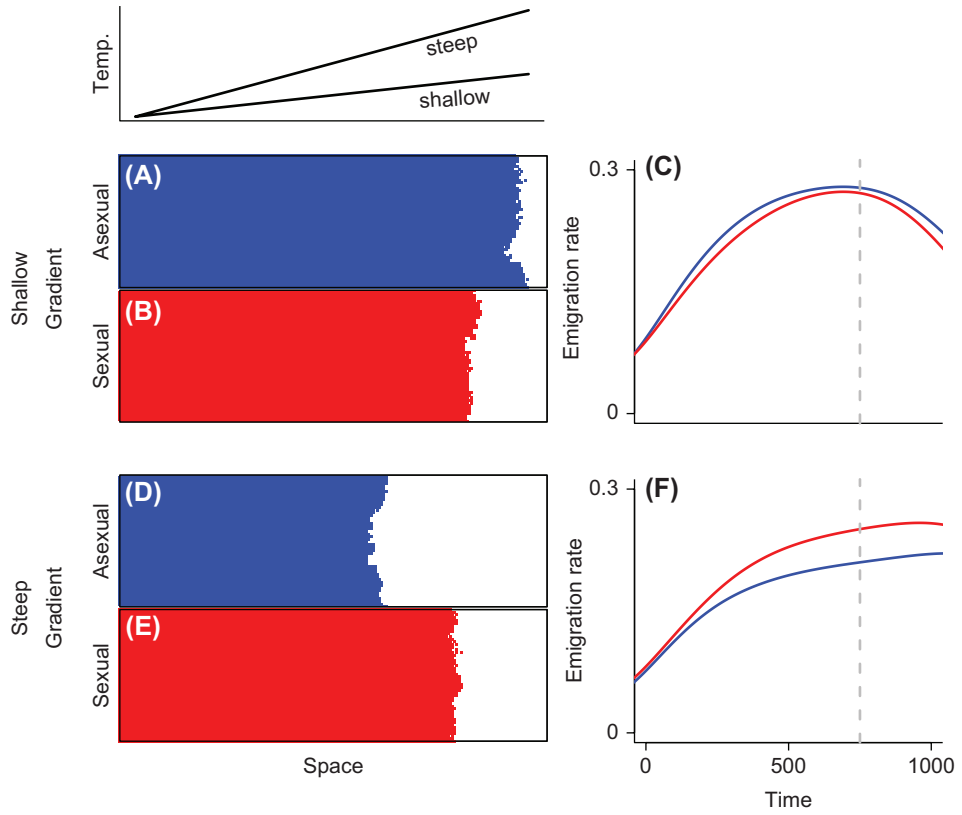

Figure 4. Dispersal evolution and range expansion for different modes of inheritance. We modeled invasions of asexual (blue) and sexual (red) populations into a temperature gradient (top panel). Offspring survival is based on adaptation to local temperature. The figure shows snapshots of the simulations (A, B, D, E) from generation 750, unoccupied habitat is shown in white. Note that in order to keep the scenarios comparable the mate finding Allee-effect for sexual organisms has been corrected for. In a shallow gradient (A–C), asexual populations evolve towards slightly higher emigration rates (C) and show a faster invasion than sexual populations (A). However, when the gradient is steep (D–E), strong selection for local adaptation drastically reduces genetic variability and thus adaptive potential in the asexual populations. Hence, dispersal is selected against and invasion progresses slower. However, sexual populations are rather unaffected by gradient steepness, as they can maintain genetic diversity at the level of individuals. These results show that the interactions emerging between the genetic system, dispersal evolution and landscape setting may drastically influence range expansion.

rates (Fig. 4A, D). This effect is caused by the steep gradient exerting strong selective pressures on the populations, which lead to high local adaptation and low genetic variability locally. Consequently, in shallow gradients invasion speed is higher for the clonal species. However, this phenomenon cannot be observed in sexual populations: steeper gradients do not necessarily slow down invasions (compare Fig. 4B and E). This happens because genetic variability can be high in diploid genotypes, without maladaptation appearing necessarily in the phenotypes. Gene flow in steep gradients can have a large effect on genetic variation. Similar effects have been observed by Holt and Barfield (2011): sexual reproduction increased genetic variance (and indeed the shape of the entire distribution of genotypic values), which in turn increased the potential for adaptive colonization. In some cases, haploid and diploid models can lead to similar results (Holt and Gomulkiewicz 1997), but our example provides one scenario where there is substantial differences between these modes of genetic architecture. Along the shallow gradient, the asexual species invades more rapidly (Fig. 4A–B), whereas along a steep gradient, the sexual species is the more rapid invader (Fig. 4D–E).

In their review on adaptive evolution of invasive species, Prentis et al. (2008) gathered evidence that higher degrees of ploidy of plants are correlated with faster range expansion. This effect might be – similar to our results – caused by a larger amount of genetic material, which could foster the speed of evolution. There is also evidence that hybridization of plants might increase their adaptive potential (Rieseberg et al. 2003). Changes of ploidy and hybridization could generate species which grow clonally, or sexually with recombination. The issue of how the details of genetic architecture influences range dynamics, and conversely how the structure of the range and dispersal evolution may influence the evolution of the genetic architecture itself, is largely unexplored. Holt and Barfield (2011; see also Yeaman and Whitlock 2011) demonstrate that genetic architecture (e.g. the number of loci contributing substantially to genetic variance in a trait) can itself evolve substantially under the combined influence of gene flow, mutation, and local adaptation in spatially structured populations. For instance, a species in which the genetic differences between populations are initially polygenic can evolve to one in which most genetic differences are focused in one to a few loci. These studies assumed fixed dispersal propensities.

It would be instructive to examine how the genetic architecture of dispersal itself might evolve. In summary, we have shown that eco-evolutionary forces resulting from ploidy and recombination may heavily influence and even invert predicted patterns of range dynamics through their interaction with dispersal evolution.

The individual level

So far we have ignored that animals have perceptual and cognitive capacities, which allow them to perceive their environment and then act upon that information. Information may be used during all three phases of dispersal (Fig. 2; Conradt et al. 2000, Enfjäll and Leimar 2009, Fronhofer et al. 2013). In general, information use for emigration, such as density-dependent emigration, should broadly influence the eco-evolutionary dynamics of dispersal. It may at times lead to less dispersal, i.e. reduced colonization rates and slower invasions, caused by a more efficient equalization of population densities, minimizing spatial variance in fitness and so reducing the advantages of individuals leaving their current habitat (Hovestadt et al. 2010). Yet, colonization rates might also be increased by density-dependent dispersal, because of 'pulsed' emigration events (Kubisch et al. 2011). Such pulsed emigration may be a consequence of relying on current population densities for emigration decisions, even when environmental conditions are fluctuating. In 'bad' years with low resource occurrence, population densities remain low and emigration is low, too. However, when resource availability is high, population densities increase drastically, thus leading to higher emigration. This is particularly likely if dispersal is driven in part by direct intraspecific interference. Consequently, when populations fluctuate dispersal and hence immigration into new patches occurs not at a constant rate, but in a pulsed manner, thus episodically increasing colonization rates. This could be a particularly important process to circumvent constraints on invasion arising from Allee effects (Keitt et al. 2001). Besides being dependent on population density (De Meester and Bonte 2010), dispersal rates and distances might also be a function of the sex ratio (Gros et al. 2008), relatedness (Sinervo and Clobert 2003, Bitume et al. 2013) or cues of local fitness in general (Ruxton and Rohani 1999), for instance as affected by the abundance and activity levels of predators. Temporal and spatial variation in any of these could thus generate parallel variation in dispersal rates.

Information may also be used for immigration decisions, i.e. habitat choice by dispersers deciding where to settle. Evidently, choosing one's habitat improves the match between phenotype and environment and thus increases local adaptation of populations and reduces extinction risk (Kawecki and Ebert 2004). However, habitat choice also reduces colonization of less suitable habitat and may thus lead to sharper range boundaries and more restricted ranges than random immigration (Armsworth and Roughgarden 2005). Adaptive habitat selection (Holt 1985) could substantially limit the geographical ranges occupied by a species, simply because individuals can avoid traversing unsuitable, risky habitats.

These thoughts assume that individuals utilize information accurately in making decisions. Another possibility is that informational cues which are useful in one environment (say the natal environment) may not be useful in another, or even maladaptive (say upon dispersal into sharply different habitats). There are many examples of predators and parasites (e.g. brood parasites such as cuckoos) which exploit the sensory capabilities of their prey and hosts, to the detriment of the latter. In such cases, dispersers which use the 'wrong' cues in making decisions should suffer reduced fitness, with consequences for both the evolution of dispersal and local adaptation. Conversely, those individuals which make adaptive 'mistakes' in dispersal might provide the pool of long-distance dispersers permitting a species to traverse dispersal barriers, and thus expand its range.

Another important issue at the individual level are life-history tradeoffs. Organisms may reduce landscape-specific dispersal costs by investing into their movement and survival abilities, such as a flight apparatus or fat reserves. These investments decrease dispersal costs with the consequences already discussed earlier. However, this investment usually trades off with other life history traits, such as competitive ability or fertility, leading to the well-known colonization-competition tradeoff. These life-history tradeoffs may become especially important during range expansions (Burton et al. 2010). For instance, at the leading edge of an invasion intraspecific density-dependence should be weak, so the adaptive advantage is tilted towards colonization ability. In general, life-history tradeoffs are known to have an important impact on dispersal evolution and may even lead to the emergence of distinct dispersal morphs (Fronhofer et al. 2011). In passively dispersing species, such as corals or trees, maternal investment, which reduces dispersal mortality of seeds, may lead to bimodal and heavily fat-tailed dispersal kernels (Fronhofer et al. unpubl.). Such kernels that lead to rare long distance dispersal events might strongly increase colonization, especially when habitat fragmentation is high (Boeye et al. 2013).

In addition to these simple life-history tradeoffs, more complex and multidimensional behavioral syndromes can be found that influence dispersal (Edelaar and Bolnick 2012). More dispersive individuals often also show characteristic combinations of other traits, such as increased aggressiveness and boldness or decreased sociability (Dingemanse et al. 2003, Duckworth 2008, Cote et al. 2010). These syndromes can potentially speed up range expansions, affect metapopulation dynamics and certainly also the formation of stable ranges after periods of expansion. However, their long-term consequences are largely unexplored and provide a wide field of research.

Example 3. Information use during immigration

As in our previous example we here focus on range expansion dynamics, i.e. a non-equilibrium situation. We model a species' invasion into an abiotic gradient, characterized by a decreasing amount of suitable habitat. In this landscape we compare dispersal evolution and invasion speed for scenarios with A) informed immigration and B) random dispersal. We show that in comparison to random dispersal, informed (and accurate, as assessed by expected fitness) dispersal leads to a strongly increased invasion speed because of higher dispersal rates during range expansion (Fig. 5). However, as dispersal is more efficient in equalizing

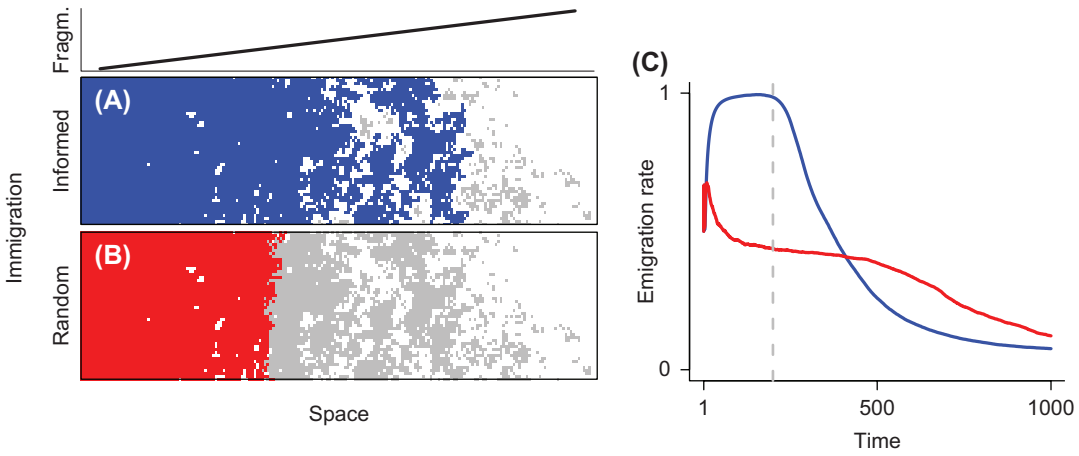

Figure 5. Simulation results for the behavioral/population-level mechanisms. We show the influence of informed immigration (i.e. habitat choice; blue, A) compared to random nearest-neighbor immigration (red, B) on the speed of invasion into a gradient of decreasing habitat suitability. Grey areas denote unoccupied, but suitable habitat patches, white space unsuitable habitat. It is evident that informed immigration allows for much higher emigration rates during invasion (C), as effective dispersal costs are reduced. However, after a stable range margin has emerged (where patch connectivity gets too low), habitat choice leads to less emigration at the margin than in the uninformed scenario.

population densities, leading to an ideal-free distribution (rather than say source–sink population dynamics) informed immigration also favors less emigration as a stable range is approached, i.e. reaches both ecological and evolutionary equilibrium. This sharpens range boundaries. Habitat selection can also increase habitat specialization and have a variety of other indirect effects on evolutionary processes, such as gene flow and drift (Holt 1987).

In summary, habitat choice and information use may be crucial for invasions in fragmented landscapes. Informed immigration in some circumstances increases invasion speed by reducing dispersal costs and thus selecting for higher dispersal rates, which increase colonization rates, while also the unwillingness of individuals to cross maladaptive spatial gaps can potentially constrain the ultimate limit reached by a species when it reaches its spatial equilibrium.

The population level

Often the effects of genetical or individual processes are expressed at the level of populations, as for instance kin competition and spatial selection driving invasions or cooperative behavior resulting in Allee effects (Table 1; Courchamp et al. 2010, Kubisch et al. 2013a). Evolution that affects sensitivity to Allee thresholds can alter extinction risks of colonizing populations (Kanarek et al. unpubl.). It is often difficult to discriminate between population- and individual-level forces. Nevertheless, some mechanisms, such as intra-specific competition, and Allee effects, can best be described at the population level.

Intraspecific competition and other causes of negative density-dependence are clearly among the main drivers of individual dispersal (Fig. 2). Increased competition for resources or mating partners that is spatially heterogeneous in its intensity will necessarily lead to selection of an increased dispersal tendency (Holt and McPeek 1996, Poethke and Hovestadt 2002, Nowicki and Vrabec 2011). Additionally, the type of density regulation (e.g. scramble vs contest competition) can have strong consequences on metapopulation dynamics and thus range formation. When over-compensatory dynamics are assumed, the extinction probability of local populations increases due to increasingly chaotic population dynamics. High dispersal, which is selectively advantageous under such conditions, synchronizes population dynamics and may thus result in metapopulation extinction (Münkemüller and Johst 2007).

Yet, density-dependence may not always imply a negative relationship between individual fitness and population size, as it does for intraspecific competition. An often overlooked population-level mechanism with far reaching consequences for population dynamics and ranges are the class of Allee effects (reviewed by Courchamp et al. 2010). By reducing colonization rates and increasing local extinction risk (Kanarek et al. 2013), Allee effects will reduce invasion speed and range size, particularly in patchy environments with gaps between suitable habitat (Keitt et al. 2001). In combination with delayed population growth, strong Allee effects may result in 'pulsed' migration, leading to cyclic invasion dynamics (Johnson et al. 2006) or sporadic invasion waves (Keitt et al. 2001). However, as mentioned above, these effects also make informed dispersal highly adaptive, resulting in wider ranges across gradients in fragmented landscapes (Kubisch et al. 2011).

In empirical range expansion studies, dispersal rates increasing during the expansion have been documented (Shine et al. 2011). This dispersal increase can be traced back to several evolutionary forces. One is termed 'spatial selection' (Phillips et al. 2010, Shine et al. 2011), which is an ecological filtering effect that arises automatically when there is colonization into a new area. Those individuals from marginal populations which are most dispersive will automatically be differentially likely to be found in the propagule that newly colonizes previously empty habitat patches. As these colonists reproduce in these sparsely populated patches and their offspring disperse, the effect

increases over multiple generations, given that dispersiveness is heritable (see also Travis et al. 2009).

The second evolutionary force responsible for increased dispersal rates during invasions is kin competition (Kubisch et al. 2013a). As populations of a species undergo massive founder effects during invasions, their relatedness increases and so the benefit for emigration increases, caused by an increase in indirect fitness gains, particularly if local populations have a low carrying capacity (Hamilton and May 1977). Depending on the landscape, either spatial selection or kin competition will be the key processes leading to increased colonization abilities of species during transient phases of invasion.

Invasion can be enhanced not just because individuals are more dispersive, but because more of them are available to be dispersed. A third evolutionary force which can increase invasion is thus adaptation. A species introduced into a homogeneous environment may initially be maladapted to it, so have low intrinsic growth rates and carrying capacities. As it adapts, its local growth rates and abundance can increase. This in turn provides a greater pool of individuals who can colonize new areas, so there should be an acceleration of invasion due to improved adaptation (Holt et al. 2005).

The processes described in this section have only been relatively recently identified. There are many open questions which warrant further investigation. For instance, there is expected to be an interplay between the evolution of dispersal, the evolution of local adaptation, and the evolution of phenotypic plasticity (Scheiner et al. 2012). All these processes could influence colonization–extinction dynamics along gradients and thus both the transient dynamics and ultimate stable range limits of a species.

Biotic forces: inter-specific interactions and the community level

Up to now we have exclusively considered single-species studies and ignored all possible inter-specific interactions. This level of complexity is rarely studied in the context of species distributions or dispersal evolution and is the least understood (but see Travis et al. 2005, Holt and Barfield 2009, Jankowski et al. 2010, Cabral and Kreft 2012). Yet, these interactions are of great relevance for the position of range borders (Fig. 2; Kissling et al. 2012, Kubisch et al. 2013b). Except for abiotic dispersal barriers, and leaving such counterexamples aside, competitive interactions between species provide the most straightforward explanation for restricted distributions of species. It has been shown that inter-specific range borders based on competition between species for shared resources (and thus a decrease in colonization probability for both interaction partners) produce stable range limits over ecological time scales (Case et al. 2005, Kubisch et al. 2013b). It has also been shown that such interspecific range limits based on competition may be evolutionarily stable (Price and Kirkpatrick 2009).

But in some circumstances, competition can actually facilitate range expansion. Consider for instance a species which has a limited range along a gradient, because gene flow from an abundant central population hampers adaptive evolution in a marginal population. If a competing species now colonizes the central population, suppresses numbers there, and does not itself spread along the gradient, this could weaken the inhibitory effects of gene flow, permitting adaptation in the marginal population and further spread along the gradient.

The ranges of species can be influenced by additional inter-specific interactions, such as predator–prey or host–parasite interactions. Specialist predators and pathogens are likely to have ranges which are constrained by any limits on the distributions of their own required prey or hosts. Yet even specialist predators might increase extinction risk of sparsely populated marginal prey populations through spillover from adjacent habitats (Holt and Barfield 2009), limiting the range of their required prey, and thus of themselves. This mechanism is also applicable to parasitoids, given high attack and dispersal rates (Hochberg and Ives 1999). Predators might also (somewhat surprisingly) induce range expansion of prey species, either by predator-induced dispersal enhancing colonization into empty patches (Weisser et al. 1999, Prakash and De Roos 2002, Poethke et al. 2010, Chaianunporn and Hovestadt 2012), or by decreasing prey population density in the prey's range core and thereby releasing the prey from asymmetric gene-flow and the resulting migration load (Holt et al. 2011; see above section about gene-level eco-evolutionary forces). Specialist predators persisting with their prey can often generate unstable dynamics, leading to the kind of spatiotemporal variation in fitness which promotes the evolution of dispersal. Generalist predators can reduce local population size, and even lead to strong local density-dependence. This makes it more likely that related individuals will compete, thus potentially bringing into play kin selection as a driver of dispersal. Predation could thus indirectly modulate dispersal evolution and range dynamics in a variety of ways.

In the above section on population-level eco-evolutionary forces we have pointed out that over-compensatory population dynamics in combination with high dispersal might lead to metapopulation extinction (Münkemüller and Johst 2007). This scenario becomes even more complex, when interactions with predator–prey dynamics are considered, as a high prey depletion rate can reduce the variation of population sizes and thus counteract the extinction of metapopulations (Sinha and Parthasarathy 1996). This highlights again that interactions across all hierarchical levels need to be considered to obtain a comprehensive view on eco-evolutionary forces affecting range formation. These ideas need further theoretical exploration, and have yet to be evaluated closely in empirical studies of range limits.

Besides these negative interactions, mutualism may also influence range dynamics. Consider a species involved in an obligate mutualistic interaction with another species. If individuals of one of both species immigrate into new habitat patches, this bears the risk of not finding the mutualistic partner species there. Thus, the probability of successful colonization is decreased, which can lead to selection for lower dispersal rates (Case et al. 2005, Leonardo and Mondor 2006, Chaianunporn and Hovestadt 2012). In a recent study, Mack (2012) investigated the joint evolution of mutualism and dispersal distance in metapopulations. The author indeed found a strong correlation between high degrees of mutualism and low dispersal distances. Conversely, there are

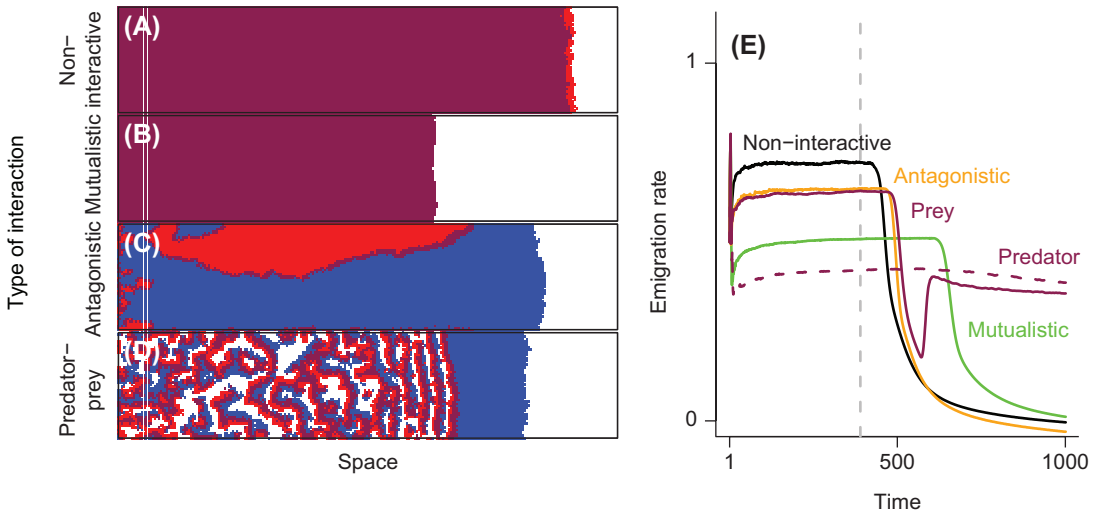

Figure 6. Influence of several types of species' interactions on invasion speed and dispersal evolution. We simulated the expansion of two interacting species into an empty (unoccupied) landscape. Patches with one of the two species are plotted in red, resp. blue, patches with both species co-occurring are shown in violet. For the predator–prey scenario the prey populations are plotted in blue, predators' in red. For mean emigration rates (E) the black line indicates non-interactive, the orange line antagonistic, the green line mutualistic, the solid violet line prey and the dashed violet line predator populations. Results show that all investigated types of interactions lead to the evolution of lower dispersal rates and as a consequence to a decreased speed of range expansion, compared to the non-interactive control scenario. The effect is strongest for the mutualistic scenario (B). However, it is especially surprising that neither antagonistic (C), nor predator–prey interactions (D) induce higher dispersal in comparison to the non-interactive scenario (A).

some species which for long-distance dispersal rely entirely upon highly mobile animals, and mutualism enhances dispersal. Skellam (1951) in his classic work on invasion argued that dispersal by birds (e.g. the Eurasian jay) was required to explain the rate of increase of the range of the English oak across the United Kingdom, after the end of the last Ice Age. In most of these cases, the mutualism is not highly specialized. Facultative mutualisms can boost local population sizes, and thereby indirectly enhance colonization success, by increasing the pool of individuals available for dispersal.

The phenomena described above show that the impacts of biotic interactions on dispersal evolution and thus range dynamics are manifold and not comprehensively understood, yet. We can nevertheless be sure that their contribution to range formation is important as all species have to interact with others. This topic is certainly in need of an increased research effort.

Example 4. Inter-specific interactions

Here we use individual-based simulations to investigate dispersal evolution and invasion speed of two species expanding into empty, but homogeneously suitable habitat. The species are A) non-interactive, B) mutualistic, C) symmetrically antagonistic or D) predator and prey. For a detailed model description see Appendix 1.

We find that a mutualistic interaction (Fig. 6B) results in a slower expansion speed caused by lower dispersal rates evolving during expansion (green line in Fig. 6E), as predicted above. This is caused by a decreased colonization probability in absence of the mutualistic partner for both species.

Similarly, antagonistic (competitive) interactions slow down the invasions, though to a lower degree, and lead to the emergence of spatial segregation (Fig. 6C). The latter results in lower dispersal rates than for non-interacting species (orange and black lines, respectively, in Fig. 6E). This is a consequence of the important costs of dispersal at the inter-specific range boundaries, since dispersal leads to immigrating into habitat already occupied by the other species.

In a fourth scenario we investigate the influence of predator–prey interactions on range dynamics. Our specific assumptions about predation (Appendix 1) include a saturating functional response for the predator, which can generate sustained predator–prey oscillations in productive environments. Although we would have expected a faster range expansion of prey due to predator-induced dispersal, in our example we actually find a decrease in invasion speed (Fig. 6E). What we also find are complex spatial dynamics, with seemingly chaotic distributions of prey and predator in the range core, a homogeneous distribution of prey alone at the range front and a certain area of periodic waves in between (Fig. 6D). These findings are very similar to those of Sherratt (2001). It seems as if this specific spatial structure is the reason for the prey populations' slower range advance compared to the non-interactive scenario. In the areas behind the range margin, where the predator is absent, we find a strong decline of prey emigration rates from the prey's towards the predator's range limit (not shown). Thus, high dispersal of marginal prey populations rapidly declines after settlement. This obviously strong selection for lower dispersal after first colonization does not allow for a strong increase of prey dispersal during range expansion. This phenomenon also leads to the sudden decrease and following increase in prey dispersal, which is shown in Fig. 6E. As soon as the prey populations have reached the end of the simulated landscape, the high dispersal phenotypes disappear and the individuals with low dispersal propensities from the area behind remain. Later, the

whole landscape will be occupied by prey and predators, showing the complex spatial patterns from inside the range core, which increase prey emigration due to predator-induced dispersal. We suggest that examining the interplay of coupled predator–prey evolution along gradients allowing dispersal evolution, local adaptation, and coevolution of each species to each other, would be a valuable direction for future work.

In summary, we could show that also inter-specific interactions influence dispersal evolution and, as a consequence, both range border formation and invasion speed. This additional level of complexity may lead to new phenomena such as emerging range boundaries and alter invasion dynamics. The outcomes are clearly non-trivial and may be counter-intuitive as in our predator–prey simulation.

Conclusions

Currently, range biology suffers from a too narrow focus on ecological and often uniquely abiotic factors for explaining species' distributions. As outlined in the introduction, this approach ignores multiple dimensions of the problem under study and especially one of the most fundamental forces in biology: evolution.

We here try to outline a possible way forward by integrating range biology and the eco-evolutionary dynamics of dispersal. Dispersal evolution has been extensively studied both theoretically and empirically (Clobert et al. 2012) but largely decoupled from the issue of range dynamics. These findings are of central relevance for explaining species' distributions as all ranges are the consequence of past invasions, which are directly determined by a species' dispersal ability across a spatially varying templet of environmental conditions and biotic interactions. In order to explain how the interactions between ecological and evolutionary forces influence a species' distribution, we propose a hierarchical concept, which is outlined in Fig. 2 and Table 1 and summarizes our thoughts. Our concept includes abiotic as well as biotic eco-evolutionary forces and organizes them hierarchically from genes via individuals and populations to communities and landscapes. While we do not claim that this approach is comprehensive, we are confident that the integration of range biology and dispersal evolution provides a novel view on current problems and might help to deal with unanswered questions.

While it is generally accepted that species' stable range limits emerge as a consequence of colonizations and local extinctions being equally frequent, it is less well appreciated that both colonization and extinction rates are not only a function of space, but also a function of time, since dispersal itself evolves. Furthermore, as dispersal is influenced by the eco-evolutionary forces summarized in our concept, colonization and extinction rates are in turn shaped by these forces. Resulting range dynamics are highly non-trivial and partially counter-intuitive, as can be seen in the simulations we performed as illustrations for this synthesis. Especially the numerous interactions and feedbacks between different eco-evolutionary forces, like e.g. density regulation, predator-prey interactions and dispersal evolution, are important drivers of range dynamics and in urgent need of further research.

We would like to encourage researchers working on basic and applied aspects of range biology as well as managers and conservationists to keep this crucial aspect in mind: species' ranges are shaped by both ecological and evolutionary dynamics. Failing to integrate this into models of species' distributions may lead to erroneous results and predictions. As effective conservation measures are badly needed, especially in the context of ongoing global climate change, the importance of taking these aspects into account cannot be overestimated. Furthermore, thorough knowledge of the focal species' dominant intraspecific processes, as well as potential interspecific interactions and prevailing abiotic (landscape) conditions are necessary prerequisites.

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Appendix 1

Model description

For the illustrative simulations in the main text we use an individual-based model of a spatially structured population, which has been successfully used by ourselves and others in previous studies (Travis et al. 1999, Poethke and Hovestadt 2002, Fronhofer et al. 2012). This model is most appropriate for arthropods with non-overlapping generations, but we suggest that the qualitative patterns it reveals pertain much more broadly. To simulate range dynamics and dispersal evolution we have modified the model in several ways, which are described below.

The simulated landscape consists of 200×50 habitat patches arranged on a rectangular grid, i.e. a total of 10 000 patches. Local populations are composed of discrete individuals, which are characterized by one gene (l_d), encoding their density-independent emigration probability (and in one example below, a second gene determining local adaptation).

Local population dynamics

Local population dynamics follow the density-dependent growth model for discrete generations formulated by Beverton and Holt (1957). For simplicity, we assume clonal reproduction. As many insects exhibit strongly fluctuating growth rates we assume that the average fertility of individuals ($\Lambda_{x,y,t}$) is drawn for each patch x,y and generation t from a lognormal distribution with mean λ and standard deviation σ (standardly $\sigma = 0.5$). Each individual gives birth to a number of offspring drawn from a Poisson distribution with mean ($\Lambda_{x,y,t}$) Due to density-dependent competition offspring survive with probability s calculated as:

$$s = \frac{1}{1+\frac{\lambda-1}{K}} N_{x,y,t}$$

Here, $N_{x,y,t}$ denotes population size N in patch x,y and generation t. K denotes the carrying capacity for density-dependent growth (unless otherwise stated, we assume $K = 100$).

Dispersal

Following reproduction, offspring may disperse with a probability given by their dispersal gene (l_d). If an individual chooses to disperse it may die with a certain probability μ (standardly $\mu = 0.3$). This term includes all costs associated with dispersal (Bonte et al. 2012). If the disperser is successful, it immigrates randomly into any of the eight surrounding habitat patches, i.e. we assume nearest-neighbor dispersal. We implemented reflecting boundary conditions in the x-direction and wrapped the world to a tube in the y-direction.

Genetics

Offspring inherit their genes from their parents. However, every inherited gene l_d may mutate with probability $m = 10^{-4}$. In case of a mutation, a Gaussian distributed random number with mean 0 and standard deviation 0.2 is added

to the allele's value. At the beginning of simulations, dispersal alleles of every individual are initialized as random numbers from a uniform distribution between 0 and 1.

Example 1. Invasions into fragmentation gradients

Here we investigate the effect of spatio-temporal stochasticity in environmental conditions on dispersal evolution and range formation. Therefore we modeled a fragmentation gradient, which is based on two assumptions: i) where habitat is more fragmented, single patches concurrently are smaller and ii) their connectedness decreases. This can be implemented by decreasing the carrying capacity of patches (K_x) from $K_1 = 150$ to $K_{200} = 0$ and increasing dispersal mortality (μ_x) from $\mu_1 = 0$ to $\mu_{200} = 1$. We compared two simulation runs with either only spatial variation in growth rates (i.e. patch-specific growth rates drawn from a lognormal distribution with mean σ only once at the initialization) or spatio-temporal variation (i.e. patch-specific growth rates drawn every time step, as in any other scenario). In both cases, the degree of environmental fluctuations (σ) was set to 1.5.

Simulations over 5000 generations were repeated 100 times and marginal emigration rate was averaged for both scenarios.

Example 2. Ploidy and recombination

To account for the interplay between adaptation to local conditions and dispersal evolution for this scenario we implemented a spatial gradient in an abiotic environmental characteristic τ_x (e.g. temperature). The slope of this gradient is either shallow (i.e. a change of the value of τ_x of 5 units along the x-dimension) or steep (i.e. a change of 10 units along the *x*-dimension). Individuals therefore carry not only a gene encoding emigration probability, but also a second gene coding for their adaptation to local conditions (l_a). The mismatch between this genetically encoded optimum τ_{opt} ($\tau_{opt} = l_a$ for clonal reproduction) and the environmental conditions in a focal patch (τ_x) is used to determine the survival probability of offspring during development. Hence, the calculation of offspring survival probability s has been extended to include mortality selection:

$$s = exp\left(-\frac{1}{2}\left(\frac{\tau_{opt} - \tau_x}{\eta}\right)\right)\frac{1}{1+\frac{\lambda-1}{K}N_{x,y,t}}$$

In this equation, η denotes niche width of the individuals ($\eta = 0.5$ for all simulations; for a detailed analysis of the effects of niche width see Kubisch et al. 2013b). Hence, we assume a Gaussian shape for the relationship between adaptation-dependent offspring survival and habitat trait mismatch.

Additionally, we test for the influence of sexual reproduction. In this case, individuals carry two alleles at the dispersal locus and two alleles at another, unlinked locus coding for thermal preference (where dispersal probability *d* and τ_{opt} are calculated as the arithmetic means of the two respective corresponding alleles) and are also characterized by their sex. During reproduction, females randomly choose a male in their patch. To exclude Allee effects, which are per default included in sexual scenarios, we allow both females and males to reproduce parthenogenetically, if they arrive in an empty patch without mating partners. If they do, the sex of the offspring is randomly chosen. They do not reproduce parthenogenetically, if individuals of the other sex are present.

Simulations were initialized with a forerun period of 2000 generations to allow for local adaptation of populations. During that time the range of the species was limited to the area between $x = 1$ and $x = 50$, with reflecting boundary conditions in *x*-direction. Afterwards, range expansion was allowed for 1000 generations. We calculated emigration rates only for habitat patches located within the five columns (in *y*-direction), which lay immediately behind the range margin (defined by the outmost occupied patch). The simulation was repeated 100 times, and the resulting emigration rates were averaged.

Example 3. Information use for immigration

Here we focused on the use of information for immigration decisions of individuals. We implemented a gradient in habitat suitability. Habitat patches can either be suitable for reproduction (i.e. patch-specific growth rate $\lambda_{x,y} = 2$) or unsuitable (i.e. $\lambda_{x,y} = 0$). For the generation of a fractal landscape we made use of the spectral synthesis algorithm provided by Chipperfield et al. (2011; Hurst exponent set to 0) and multiplied this landscape with a linear spatial gradient ranging from 0 to 1, similar to the approach of Travis and Dytham (2004). To discretize the landscape, we defined all patches with a value of less than 0.45 as unsuitable and all others as suitable for reproduction. The two scenarios we compare include random immigration (nearest-neighbor dispersal as described above) and habitat choice. For the latter the individuals are able to assess the expected number of offspring in each of the neighbouring patches (i.e. they have complete knowledge of immigrant population density there) and choose that patch for immigration, in which they expect maximal reproduction. If offspring expectation is equal in several patches, one is chosen at random. In order to avoid artefacts resulting from the sequence of choice, dispersing individuals were chosen in a random sequence throughout the whole spatially structured population. In other words, each individual had an equal probability of being the first chosen to potentially disperse; the next individual was chosen at random from the remainder to disperse (but note that its decision might be influenced by what the first disperser did); and so forth, until all individuals have been given an opportunity to disperse.

Simulations were carried out over 1000 generations, emigration rate was calculated as for the gene-level simulation. Again, it was averaged over 100 replicates.

Example 4. Inter-specific interactions

In this example we compare the influence of mutualistic, antagonistic, and predator–prey interactions of species on dispersal evolution and invasion speed into empty landscapes. In the case of the non-interactive scenario we assume that both species have a carrying capacity of $K = 200$ and do not interact in any way.

To implement a strong mutualistic interaction between the two species we assume that local populations of both species achieve their highest carrying capacity ($K_{max} = 200$) when both

species occur in equal numbers in a given habitat patch. Additionally we assume that a local population, which is composed of individuals from one species only, has a carrying capacity of zero. To achieve this, before reproduction we calculate the proportion p of each species in the local community as:

$$p_i = \frac{N_{x,y,i}}{\sum_{j=1,2} N_{x,y,i}}$$

In the above equation, i denotes the species in focus. We further multiply carrying capacity K ($K = 400$) with the smaller of the two proportions which gives the effective capacity for each species.

For the antagonistic scenario we assume that interspecific competition is stronger than intraspecific competition. Therefore we make the effective carrying capacity K_i for each species dependent on its proportion in the local community, whereas the other species has a proportionally higher influence. This means, we calculate K_i for species 1 as:

$$K_1 = K \frac{N_1}{N_1 + \alpha N_2}$$

Thus, the factor α describes the impact of one species on the other ($\alpha = 2$ for all simulations). K is set to 200.

In our predator–prey scenario we implemented population growth for the prey species as described above. However, we assume that predators can only reproduce by consuming prey. The overall number of prey items consumed depends on the predator's searching efficiency and on the population sizes of both species, and follows a type II functional response (Holling 1959):

$$P = N_{pred} \frac{aN_{prey}}{1 + aN_{prey}}$$

In this equation, P denotes the number of consumed prey items, a denotes the searching efficiency of the predator ($a = 0.2$). After dispersal, P prey individuals die from predation. Every predator afterwards gives birth to a number of offspring, which is drawn from a Poisson distribution with mean $(\frac{P}{N_{pred}} b)$, where b denotes the assimilation efficiency ($b = 3$). Thus, the amount of consumed prey is allocated evenly to all predators in one habitat patch.

For the above described scenarios during initialization of simulations we introduce 100 individuals of each species into all habitat patches at $x = 1$. The simulations were run for 1000 generations afterwards, with calculation of emigration rates for 100 replicates as above described.