Evolving Perspectives on Monopolization and Priority Effects

Luc De Meester,[1,*] Joost Vanoverbeke,[1,3] Laurens J. Kilsdonk,[1] and Mark C. Urban[2]

[1]Universiteit Leuven, Laboratory of Aquatic Ecology and Evolutionary Biology, Charles Deberiotstraat 32, 3000 Leuven, Belgium

[2]University of Connecticut, Department of Ecology and Evolutionary Biology, 75 North Eagleville Road, Storrs, CT 06269 USA

[3]Institute for Nature and Forest Research, Kliniekstraat 25, 1070 Brussels, Belgium

*Correspondence: Luc.DeMeester@bio.kuleuven.be (L. De Meester).

Biologists are often confronted with high levels of unexplained variation when studying the processes that determine genetic and species diversity. Here, we argue that eco-evolutionary interactions might often have an important role during colonization and have longstanding effects on populations and communities. Adaptation following colonization can produce a strong positive feedback loop that promotes priority effects and context-dependent trajectories of population or species assembly. We establish how monopolization, and more generally evolution-mediated priority effects, influence ecological patterns at multiple scales of space, time, and biological organization. We then highlight the underappreciated implications for our understanding of population and landscape genetics, adaptive evolution, community diversity, biogeography, and conservation biology. We indicate multiple future directions for research, including extending theory beyond competition.

Trends

Eco-evolutionary priority effects during colonization could explain the highly context-dependent patterns of genetic and species diversity observed in nature.

We highlight one such eco-evolutionary priority effect, the monopolization effect, whereby the first colonist to a new patch adapts to local conditions and thereby gains an advantage over later immigrants. This evolution-mediated priority effect suggests explanations for both context-dependent intraspecific population genetics and interspecific community assembly.

Monopolization effects can determine biological patterns not only at biogeographical scales, but also at the finer scales that characterize metapopulations and metacommunities.

Recent advancements are extending this approach beyond competitive interactions to understand more generally how trait evolution affecting any type of interaction might alter population and community assembly dynamics.

Explaining Context Dependency in Nature

Biologists often cannot explain a substantial proportion of the variation in genetic and species composition in space and time. Natural biological patterns demonstrate high context dependency, provoking strong critiques of our capacity to make accurate predictions [1–3]. Although neutral theory explains some patterns, it performs poorly elsewhere, and becomes problematic when organisms differ substantially in niche [4,5]. Here, we argue that adaptive evolution can divert populations and communities along alternative trajectories depending on colonization history and thereby provide an underappreciated perspective on context dependency in biology.

Ecological, Genetic, and Eco-Evolutionary Priority Effects

Biology focuses on how species and genes are distributed in heterogeneous environments. This research usually assumes that arrival order does not matter, and species and genotypes assort across environments according to their fitness [6,7]. However, arrival order often influences ecological or genetic dynamics through priority effects [8–11]. **Ecological** and **genetic priority effects** (see Glossary) are common when species or genotypes have similar fitness, and neutral processes dominate (e.g., **founder effects** and high-density blocking in population genetics [10,11]). Priority effects often occur when the first colonist obtains a numerical advantage over subsequent competitors (Figure 1B). These numerical priority effects depend on the time lag before other immigrants arrive, resident population growth rate, and local carrying capacity. Ecological and genetic priority effects usually are considered separately. Yet, ecological and evolutionary dynamics often interact [12–14]. One potentially important eco-evolutionary feedback occurs when the first colonists adapt to local conditions and gain an additional advantage over later immigrants [15–17] (Figure 1C,D). This evolution-mediated priority effect is called 'monopolization' and was originally developed to explain intraspecific patterns of genetic differentiation (**population monopolization** [15]). The concept was later broadened to describe community assembly among competing species (**community monopolization** [16–18]). Under monopolization, adaptation augments transient numerical priority effects by accelerating the initial rate of increase of the colonist and promotes its long-term dominance by equalizing or elevating its fitness relative to later-arriving immigrants (Figure 1D,E). Although the term 'monopolization' suggests competitive dominance, evolution can alter ecological and evolutionary dynamics even if monopolization is transient (Figure 1 C,D), as can standard priority effects [9]. Thus, monopolization is equivalent to priority effects via niche pre-emption, *sensu* Fukami [9], but refers to priority effects mediated by genetic adaptation. The degree to which monopolization occurs depends on a race between the local adaptation of early colonists and immigration of pre-adapted genotypes or species [19,20]. We differentiate three levels of monopolization (Figure 1C–E). For transient monopolization (Figure 1C), a pre-adapted immigrant arrives before the resident evolves similar fitness. Given that the initial adaptation alters immigrant population or

community dynamics, it qualifies as an evolution-mediated priority effect even if it disappears once better-adapted immigrants establish. If the resident evolves a fitness equivalent to the pre-adapted immigrant, the resident and immigrants drift neutrally from initial abundances (Figure 1D). This monopolization effect is transient mathematically, but both the numerical advantage and co-occurrence of the resident with immigrants could persist for long timescales in practice. If the resident evolves a fitness advantage over immigrants (Figure 1E), then monopolization qualitatively shifts dynamics and the initial priority effect becomes stable and potentially permanent.

Monopolization across Time and Space

Monopolization can occur across spatial and temporal scales ranging from long-term adaptive radiations on isolated islands to the smaller spatiotemporal scales of metapopulations and metacommunities (Box 1). On isolated patches, such as oceanic islands, the first colonists encounter abundant ecological opportunity in the form of open niches. Over time, the resident population might not only adapt its particular niche, but also radiate into multiple forms or species to fill other available niches [19,21,22]. Most evolutionary biology focuses on the mechanisms underlying adaptive radiation [23,24] rather than its ecological consequences. However, adaptive radiations can alter the establishment of immigrants via monopolization [19,25,26]. When pre-adapted species arrive, their niche is already filled by adapted residents, lowering their establishment success and population growth rate [20].

At finer spatial scales, speciation is unlikely, and weaker monopolization effects might be expected. Yet, substantial intraspecific trait divergence can occur on fine spatial scales, and this trait divergence could alter local dynamics through monopolization. Gene flow is often orders of magnitude lower than dispersal owing to mechanisms such as strong selection or selection against migrants, and this reduced gene flow can allow microgeographic adaptation [27]. There are probably only a few generations before immigrant arrivals can theoretically generate a selective advantage for the first colonists and promote their long-term dominance [17]. Hence, monopolization also might be important at the finer spatial scales that characterize neighboring patches in metapopulations and metacommunities [19,20].

To Monopolize or Not?

Monopolization effects are promoted by species and landscape properties that enhance ecological opportunity, time lags between arrival of immigrants, population growth and evolutionary rates, and mechanisms that reduce establishment success of immigrants in resident populations or communities. Each component can interact with, complement, and offset other components.

Traits Promoting Monopolization

Intraspecific and interspecific variation in dispersal ability and arrival times will allow early-arriving genotypes and species to take advantage of ecological opportunities and adapt before other immigrants arrive. Population and community monopolization will also be enhanced by traits that confer rapid population growth and high niche breadth or plasticity facilitating colonization of new environments. Monopolization is enhanced by high evolutionary rates, which are aided by short generation times and standing genetic variation. Monopolization can also depend on the evolutionary history of colonists [28]. Reproductive mode affects population growth and evolutionary rates in opposite directions. Asexual species grow quickly by not producing males, but sexual recombination generates more genetic variation. Facultative sexual species might be the best monopolizers because they grow quickly through asexuality and adapt quickly through recombination.

We predict that small passive dispersers will monopolize habitats because their vectors transport them far distances, and short generation times allow for rapid population growth and adaptation. Whereas large active dispersers also disperse well, they often have low population growth and evolutionary rates. Bacteria [29], zooplankton [30,31], and ballooning spiders [32] are some of the taxonomic groups expected to monopolize communities (Box 1). Monopolizers are also likely to have traits that limit immigrant establishment or population increase. For example, they might pre-empt habitats, monopolize resources via high population growth, or have features that reduce population fluctuations (e.g., overlapping generations or seed banks [15]).

Landscapes Promoting Monopolization

Spatial isolation creates ecological opportunity and increases time lags between arrival of immigrants (Box 1). Processes that create new habitats (e.g., island formation or forest tree falls) or extirpate populations promote ecological opportunity. Environments should differ, but not so much that colonists cannot establish successfully. Human disturbances, such as habitat degradation, climate change, eutrophication, and habitat fragmentation, might promote monopolization.

Characteristics of regional genetic and species pools can affect monopolization. Low regional metapopulation abundances will favor population monopolization by increasing ecological opportunity and time lags between immigrants, assuming strong competition and sufficient adaptive capacity. Similarly, low regional species abundances and diversity should promote community monopolization by limiting the regional pool of pre-adapted immigrants [33].

Enemies of Monopolization

Monopolization effects could be reduced where residents become the target of the adaptation of other species. Parasites and pathogens, in particular, often rapidly adapt to resident host genotypes [34]. Enemies

can reduce local population sizes, thereby increasing the scope for immigration. Inbreeding depression following colonization also lowers fitness or resistance against enemies and could promote outbred immigrants over residents [35] or outbreeding between immigrant and resident conspecifics. Whereas the negative effect of co-adapting parasites on monopolization can become permanent because parasites continue to adapt to prevailing host genotypes, inbreeding depression might erode when the new immigrants introduce genetic variation. Thereafter, population monopolization can decrease additional immigration.

Novel Insights from Population Monopolization

Monopolization suggests predictions that provide novel insights into unexplained patterns in population and landscape genetics, community and metacommunity ecology, biogeography, phylogeography, and conservation biology.

Reduced Genetic Connectivity

Following population monopolization, fewer genotypes will establish than expected from dispersal rates, promoting strong genetic differentiation even at fine spatial scales. By promoting high genetic differentiation at fine scales, monopolization reduces the slope and increases the intercept of patterns of isolation by distance. One consequence is that landscape genetics studies might incorrectly infer strong landscape dispersal barriers, whereas genetic breaks in fact reflect monopolization. Monopolization can reinforce initial adaptive differences among neighboring populations and, thus, promote microgeographic adaptation at surprisingly fine spatial scales [15,27,36,37].

Reduced Covariation of Neutral and Adaptive Responses

Monopolization can produce divergent patterns of neutral genetic and adaptive trait differentiation [38–40] akin to those generally observed in nature [41,42]. With monopolization, neutral genetic differentiation can largely reflect colonization history, whereas adaptive trait differentiation reflects selection gradients. In sexual populations, recombination can spread beneficial alleles from immigrants through a resident population via selective sweeps. These genes fuel further adaptation of residents to local conditions, which could facilitate subsequent monopolization.

Steep Phylogeographic Breaks

Many phylogeographic genetic patterns indicate sharp boundaries, especially along natural boundaries, such as large rivers and mountains. Although many of these dispersal barriers are incomplete, sharp boundaries remain after thousands of years (e.g., phylogeographic patterns in the postglacial recolonization of Europe [43]). Even a minor dispersal barrier might generate the isolation necessary to generate monopolization, which would strengthen isolation as adaptive evolution proceeds. Phylogeographic patterns under this scenario would reflect colonization patterns fixed by monopolization. Thus, monopolization potentially

provides an explanation for steep phylogeographic breaks without invoking hybrid inferiority and reinforcement [44] and for complex phylogeographic patterns in widely dispersed microorganisms [45].

Novel Insights from Community Monopolization

Apparent Neutrality

Monopolization can fix the stochastic effects of initial colonization and create mismatches between pre-adapted organisms and their environments. Thus, monopolization can make patterns appear more neutral and enhance the spatial or unexplained variation in community composition [3,16]. We call this effect 'apparent neutrality' because distribution patterns appear random, although the mechanism involves non-neutral evolution of local niche differences. Hence, monopolization effects could explain why more neutral patterns are observed than expected from the non-neutral ecologies of constituent species (e.g., [46]).

Beta Diversity

With pure niche-based species sorting, community composition should become similar among ecologically similar environments. However, evolution-mediated monopolization can reduce links between environments and species composition. Among patches with the same environment, divergent communities can develop along unique trajectories and generate higher community dissimilarity and beta diversity (see Figure S1 in the supplemental information online). Among patches with different environments, community similarity should be higher relative to pure niche sorting because some species monopolize multiple environments, displacing otherwise pre-adapted species and consequently reducing overall (gamma) and beta diversity.

Biogeography

Community monopolization might contribute to range boundaries among ecologically similar species owing to colonization and evolutionary history instead of initial niche differences [47]. Monopolization can also contribute to lower species and genetic diversity at higher latitudes [48] if the first colonizers of newly ice-free landmasses after the ice ages decreased the establishment of other species.

Conservation Biology

Monopolization effects can provide novel insights into restoration ecology, impacts of altered connectivity, and climate change impacts. For instance, under monopolization, the initial dynamics of recolonization upon habitat restoration would determine the trajectory of community assembly and ultimate success of the restoration. Also, adaptation to new climates might occur rapidly following extirpation of species at range boundaries. By contrast, ranges might retract under climate change if a competitor monopolizes the habitat intersecting two ranges [49].

Empirical Tests of Monopolization

Although theory suggests that monopolization should occur frequently [16,17,19,20], strong empirical tests are rare because monopolization effects are still underappreciated and difficult to detect unambiguously. The limited research to date mostly focuses on adaptive radiations at large spatiotemporal scales where the signals are stronger (e.g., [32,50,51]) or on experiments with short-lived organisms [29]. Empirical explorations in nature are particularly rare at the fine spatial scales where trait changes are less pronounced. Experimental approaches can provide proof of principle of monopolization. Most experiments so far have only provided partial tests, showing that differently adapted populations can produce different patterns of community assembly in old-field plants [52], pond zooplankton [30,31], and salamanders [53]. Given the importance of evolutionary rates in monopolization, we need experiments that quantify how rapidly adaptation can affect immigrant establishment. In one example, bacteria adapted *in situ* and reduced the establishment success of later-arriving strains over only a few days [29]. In another example, a genetically variable population of *Daphnia* water fleas that was hatched from a dormant egg bank altered community assembly after divergent selection over just a few months [31]. Future experiments should test the capacity of small numbers of colonists to adapt rapidly and thereby influence establishment success of immigrants. We predict that monopolization will often depend on standing genetic variation rather than *de novo* mutations.

In nature, population monopolization is expected to weaken the slope of the relation between interpatch (β) genetic diversity and geographic distance compared with neutral dynamics, and the intercept is expected to be higher due to strong genetic differences at short distances among similar habitats [40]. For community monopolization, the relation between interpatch (β) species diversity and ecological distance is expected to be weaker than under purely niche-based dynamics because evolution prolongs founder events so that natural patterns are more reflective of colonization history. Field observations consistent with monopolization include evidence for microgeographic adaptation [27], sharp and stable phylogeographic boundaries without clear dispersal barriers [43], and divergent community compositions between similar habitats [54].

Moving beyond pattern analysis, studies need to demonstrate local genetic adaptation and its influence on priority effect via manipulative experiments. Field experiments can quantify the establishment success of new invaders [55,56] at different points during resident adaptation. Resurrection ecology, which reconstructs ecological and evolutionary dynamics from layered dormant egg banks [57–60], provides unique opportunities to document both the local adaptation of residents and the dynamics of colonization of additional genotypes and species over time. However, the power of this approach will depend on how precisely past environments can be reconstructed. Whereas these tests by themselves do not provide definitive proof, the resulting patterns can be compared across organisms and landscapes to establish

whether patterns consistent with monopolization occur more in species-poor areas, isolated situations, and in sexual compared with asexual species. The best tests of monopolization in nature require monitoring the full sequence of colonization, adaptation, and population and community assembly via long-term time-series on population abundances and neutral and adaptive trait changes in multiple new or perturbed habitats. No field studies have yet achieved this level of testing.

Broadening the Scope

Community monopolization was originally defined for competitive interactions. The next frontier is to explore how the evolution of early colonists alters species interactions of any type, just as ecological priority effects can operate through any interaction type [61,62]. These more general **evolution-mediated priority effects** can either impede or facilitate future immigrants. For example, imagine a prey and predator pair that colonizes a patch. The prey might adapt defenses against the predator [63] or the predator might adapt to specialize upon a resident prey species. In either case, the adaptation of early colonists can alter the invasion success of other prey species via changes in predator numbers or prey preference. A potential prey species might also adapt defenses against a local predator and become more vulnerable to alternative predator species due to tradeoffs, which would promote the establishment of these predators. Adaptation of parasites to initial host populations or species could either inhibit or facilitate the establishment of alternative host genotypes and species depending on the reservoir function of the first host [64]. Early arrival and adaptation by a facultative mutualist to the environment could facilitate colonization by additional mutualists. Similarly, coadaptation of a plant and its mycorrhizal mutualists might increase the fitness and, thus, population size of both partners to such an extent that it facilitates establishment success of herbivores and, indirectly, top predators. This area is almost entirely unexplored and, thus, is likely to reveal novel insights.

Concluding Remarks and Future Directions

The study of evolution-mediated priority effects offers to unlock a deeper and more synthetic understanding of ecological and evolutionary patterns by decoding how evolution interacts with colonization history to divert populations and communities onto alternative trajectories. Monopolization spans not only levels of biological organization from genes to communities, but also spatial scales from fine-scaled landscapes to global biogeography.

By shifting to a view informed by monopolization, we can begin to value multiple underappreciated facets of eco-evolutionary interactions. Monopolization stresses the importance of the short, but important, time period during early colonization of new habitats, where seemingly transient eco-evolutionary dynamics can result in permanent changes to the structure and function of populations and communities. Thus, what would commonly be dismissed as a transient nonequilibrium becomes the new equilibrium through adaptive

evolution. Moreover, monopolization emphasizes the role of historical context, often neglected in favor of more deterministic processes. Especially in the context of rapid environmental changes caused by restoration efforts, climate change, and urbanization, in-depth consideration of initial eco-evolutionary dynamics following disturbances might be crucial for predicting biological responses. This perspective emphasizes the dominant role that ecological constraints can have in determining the power of evolution (Box 2). Through these perspectives, evolution-mediated priority effects shed new light on widely accepted concepts, such as character displacement and niche conservatism, provide novel explanations for large-scale patterns, such as range sizes and phylogeography, and suggest important considerations for conservation biology. Monopolization generates a host of further novel questions, which offer to generate novel insights for years to come (see Outstanding Questions). For instance, evolution-mediated priority effects can produce regime shifts with respect to local genetic adaptation (Box 3), are relevant beyond competitive interactions, and could reveal new insights into the assembly dynamics of mutualisms and trophic interactions. The work on monopolization and the more general evolution-mediated priority effects is still in its infancy. Many opportunities exist for novel theory, proof-of-principle experiments and long-term field studies. We expect that many new insights will emerge once the importance of eco-evolutionary interactions during colonization and exposure to novel environments is given sufficient attention.

Outstanding Questions

Ecological and Evolutionary

Does population monopolization facilitate community monopolization?

Can monopolization lead to the evolution of apparent neutrality?

What other species interactions result in evolution-mediated priority effects, and can we derive general rules that predict their impacts?

To what extent do monopolization effects 'cascade' through the food web? Monopolization effects might be common in lower trophic levels given higher evolutionary rates, yet, given keystone effects, monopolization effects might also cascade towards lower trophic levels.

Does monopolization affect ecosystem functioning and ecosystem services in a predictable manner?

Are niche differences among species a cause or consequence of large phylogeographic and biogeographic patterns? Does the answer depend on the degree to which the world is saturated with species?

To what degree can monopolization effects affect range boundaries?

To what degree are genetic constraints in fact ecological constraints (Box 1)?

To what extent do patterns consistent with character displacement reflect monopolization, where evolution following ecological release prevents the establishment of a competitor?

What are the consequences of dispersal evolution for evolution-mediated priority effects? Is there selection for dispersal rates that promote monopolization?

Conservation Biology

What are the implications of monopolization for nature restoration? Does the potential monopolization by nontarget species suggest the need to introduce target species? What are the optimal genetic composition, variability, and timing of target species during introductions?

What are the implications of monopolization for invasion biology? Do invasive species succeed when enemies co-adapt to residents and thereby counteract monopolization?

What are the implications of monopolization for responses to global change? Does monopolization alter the risks and benefits of assisted migration and gene flow?

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Figure 1. Fitness Differences, Adaptation, and the Time Interval between Arrivals of Genotypes or Species Determine the Opportunity for Monopolization Effects. Different genotypes or species are indicated as circles and triangles in the left column. The match between the colors of the colonists and the habitat indicates their relative fitness (i.e., green has higher fitness in the green habitat than blue). We show a single patch at three points in time. In the middle column, we show numbers of descendants of colonists and immigrants (genotypes or species) through time, with colonization and immigration events indicated by

arrows. Line color indicates phenotype. The gray line indicates the baseline growth rate of the maladapted blue colonist for comparison. In the right column, we display the fitness of colonists (solid line) relative to the green pre-adapted immigrant (hatched line) for scenarios (A–E). Note that, for the case of sexual or hybridizing species, we reserve the right column to depict the frequencies of neutral loci. We assume no evolution in (A) and (B) and evolution in the rest of the scenarios. In (A), the green triangle increases and outcompetes the maladapted blue genotype or species despite arriving later (clonal or species sorting). In (B), the green circles establish before the green triangle arrives, and this numerical dominance lasts for potentially long periods via neutral genetic or community dynamics. In (C–E), we assume three levels of monopolization for species or asexual clones that differ in niche. In (C), the blue colonist adapts to the green habitat, which accelerates its rate of increase relative to a nonevolving colonist (gray line). It reduces the growth rate of the pre-adapted green immigrant and, thus, imposes a monopolization effect, but this effect is transient because, ultimately, the higher fitness of the later immigrant will allow it to dominate. In (D), the initial colonist evolves faster than in (C) and reaches a fitness equal to the pre-adapted immigrant. From then on, neutral numerical dynamics dominate. In (E), the initial colonist evolves to become better adapted than the immigrant and, thus, dominates both through numerical and fitness advantages. Monopolization can also occur with sexual populations or hybridizing species (F,G). However, in this case, the resulting pattern may be gene dependent, and we depict this in simplified graphs in (F,G); actual patterns will be more complicated and depend on a variety of factors, such as the genetic architecture of traits under selection. Genes conferring a fitness advantage from immigrating pre-adapted genotype or species might spread through the resident population (indicated by inner shapes at the third time point) and, in doing so, facilitate evolution. Partly because of this, neutral loci might show strong monopolization effects and, thus, reflect colonization history. Whether adaptive genes can spread depends on whether the resident population had sufficient standing genetic variation to achieve adaptation equivalent to the level of adaptation that could be achieved through the genes carried by immigrants.

Box 1. Monopolization at Different Spatial Scales and Levels of Biological Organization

The likelihood of monopolization depends on the balance between rates of adaptation and rates of immigration. Therefore, monopolization depends on landscape connectivity and spatial scales on the one hand and on species traits related to dispersal and local adaptation (reproduction mode, standing genetic variation, generation time) on the other hand. Figure I illustrates how the time lag between the first and second immigrant in a habitat depends both on spatial scale and dispersal ability. For different taxa, this translates into differences in the slope of the positive relation between the likelihood of monopolization (facilitated by time lag) and spatial scale (Figure I). For a given landscape, this translates into different

probabilities of monopolization for different organism groups (Figure II). We use specific taxonomic groups as examples, but any group could fit into this scheme. These examples are inspired by studies on species sorting versus evolution-mediated priority effects and adaptive radiation for bacteria [29], zooplankton [31,65], spiders [32], land birds [24], and sea birds [66].

Figure I. The Time of Arrival of the Second Immigrant in a Patch Increases with Spatial Scale, but the Slope of this Relation Differs among Taxa, Depending on Dispersal Traits and Regional Abundance.

Figure II. Differences Shown in Figure I Translate in Differences in the Likelihood of Monopolization with Increasing Spatial Scale in Different Taxa. The graph visualizes the likelihood of monopolization to occur for five different organism groups that differ in generation time, reproductive mode, and dispersal rates. The landscape icons visualize different spatial scales from neighboring habitats to the continental scale.

Box 2. The Ecological Dimension of Genetic Constraints

Genetic constraints, reflecting the lack of genetic variation or strong genetic correlations, are often not absolute [67,68], but rather result in a slowing down of evolution. Genetic constraints are most likely to prevent evolution and its effects on population or community assembly where pre-adapted species are plentiful or immigration rates are high. However, in more isolated or species-poor settings, time might prove sufficient to overcome genetic constraints and allow evolution-mediated priority effects. Thus, the degree to which genetic constraints prevent evolution depends on ecological context and, more specifically, on the time period of ecological release [69]. Therefore, genetic constraints translate into one of the factors that modulate the race between adaptation and immigration, which determines population or community assembly trajectories. This dependence on species richness and immigration rates explains why we observe adaptive radiation on islands and following mass extinctions. It also explains why so many examples of strikingly rapid evolution occur in experimental settings or following abrupt environmental change [70], whereas we see long-term niche conservatism in nature [71]. As an example, niche conservatism in climate niches is sometimes so strong that paleoecologists can use past community compositions as proxies to reconstruct past climates [72].

The eco-genetic constraints as outlined here also bear a cautionary tale: one should be prudent in extrapolating rapid evolutionary dynamics observed in the laboratory to field situations where species pre-adapted to many different environmental conditions are the rule rather than the exception. In a species-rich world, the ecological dimension of genetic constraints can reduce the impact of evolutionary compared with ecological dynamics. One key exception is given by the eco-evolutionary dynamics during the initial phases of colonization of a habitat, precisely because, during these initial phases, evolution is promoted through ecological release.

Box 3. Monopolization and Regime Shifts

A regime shift can occur when a system abruptly changes between two divergent alternative stable equilibria [73]. For instance, shallow lakes sometimes undergo a shift between phytoplankton-dominated 'green-water' phases and macrophyte-dominated 'clear-water' phases [74]. Here, we suggest an evolutionary regime shift between maladapted and adapted states that can occur via population monopolization.

We assume a new population in a landscape with patches characterized by different environments and low connectivity (Figure I). In a nonadapted population, gene flow is proportional to connectivity and might be low enough to prevent genetic load and allow for local adaptation [75]. Through adaptation and subsequent monopolization, gene flow (i.e., effective dispersal) will decrease substantially (point 1 on Figure I) relative to connectivity as measured by dispersal because maladapted immigrants will not establish. If connectivity increases, the population is likely to remain locally adapted contrary to expectations based on connectivity alone because realized gene flow remains low owing to monopolization.

However, at a sufficiently high connectivity, maladapted genes might nevertheless establish and prevent further monopolization. The population will abruptly shift to the maladapted state (point 2, Figure I), characterized by high gene flow. To return the system back to an adapted state requires a major decrease in connectivity because of hysteresis. Hysteresis occurs when state transitions depend both on a parameter such as connectivity and the current state of the system. In the current example, hysteresis occurs because gene flow depends on monopolization, and whether monopolization occurs depends on connectivity. Once connectivity is decreased sufficiently, the system can shift back to the adapted state.

Predictions are that population monopolization can occur more commonly than expected based on landscape connectivity in the absence of evolution, and that rapid shifts between adapted and maladapted states can occur with small changes in connectivity. This is highly relevant in relation to impacts such as habitat fragmentation, exotic species and climate change, which all have the potential to change landscape connectivity.

Figure I. Regime Shifts of Realized Gene Flow in Relation to Interpopulation Connectivity. The solid lines are the stable states of the system. The dashed lines with arrows indicate state transitions occurring when a bifurcation point is reached. Point (1) indicates where a population can adapt at a given rate of gene flow relative to the migration–selection balance and in the absence of monopolization effects. Point (2) indicates when increasing gene flow overcomes the monopolization effect and leads to maladaptation.

Glossary

Community monopolization: an evolution-mediated priority effect whereby the arrival order of species and their evolution influences competitive dynamics and structure.
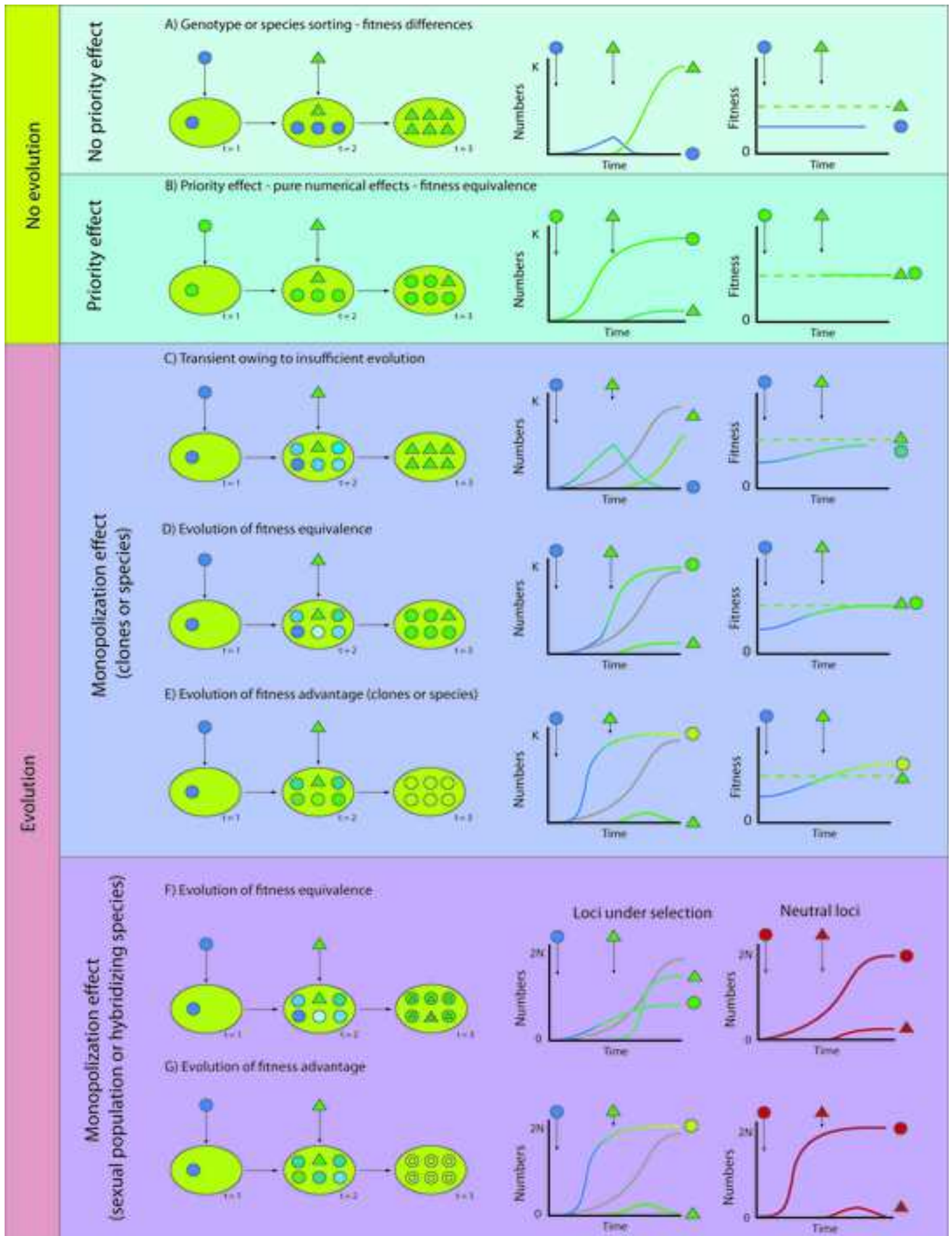
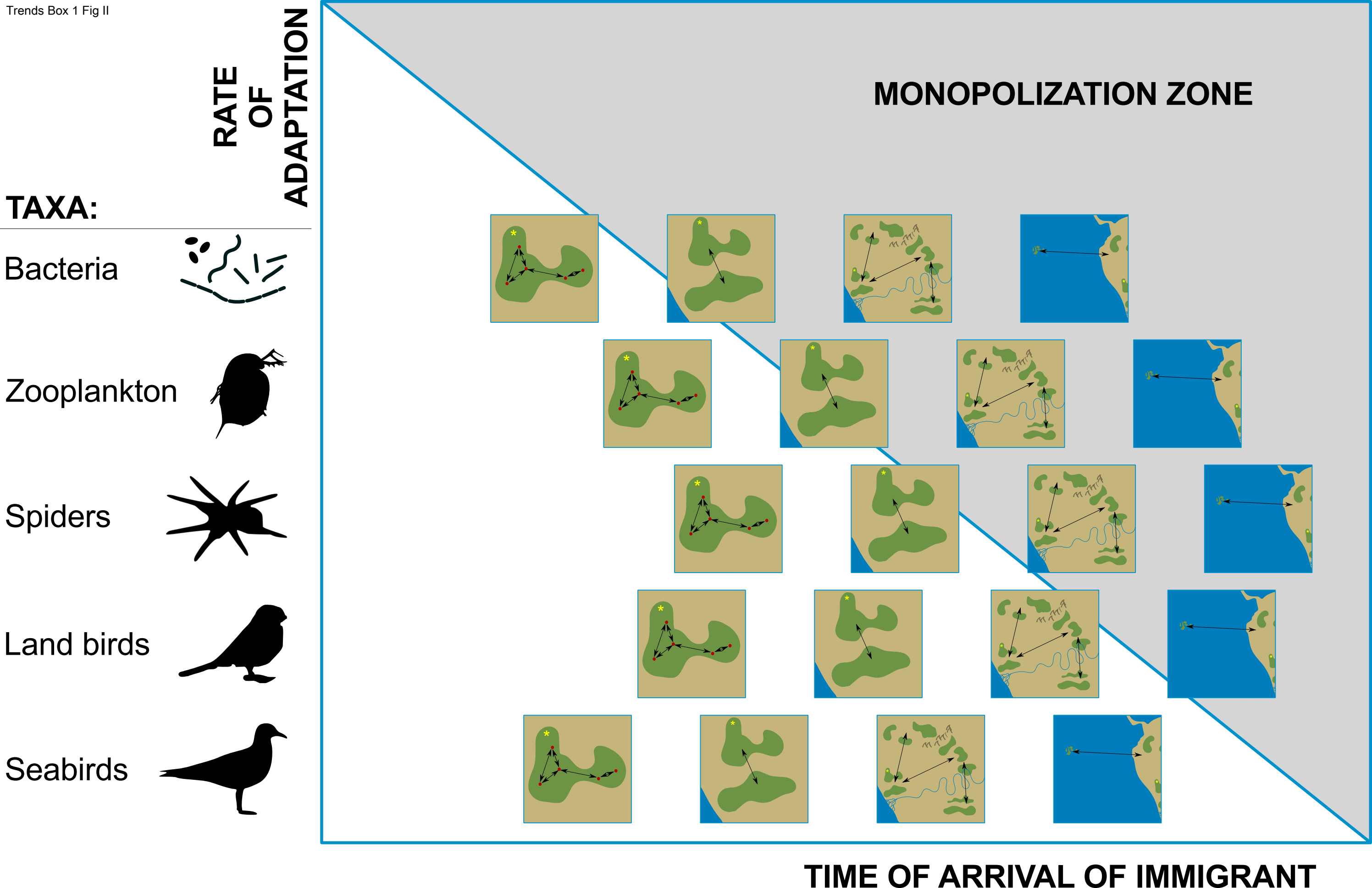**Ecological priority effect**: the arrival order of species influences community dynamics and structure.

Evolution-mediated priority effect: the arrival order of genetic lineages or species and their evolution influences population genetic or community dynamics. This broad term encompasses monopolization but also includes other species interactions, such as predation, parasitism, and mutualism.

Founder effects: genetic priority effects following random sampling of a small group of colonizers from a regional gene pool.

Genetic priority effect: an evolutionary priority effect whereby the arrival order of genotypes influences population genetic structure**.**

Population monopolization: an evolution-mediated priority effect whereby the arrival order of lineages and their evolution influences population genetic structure.
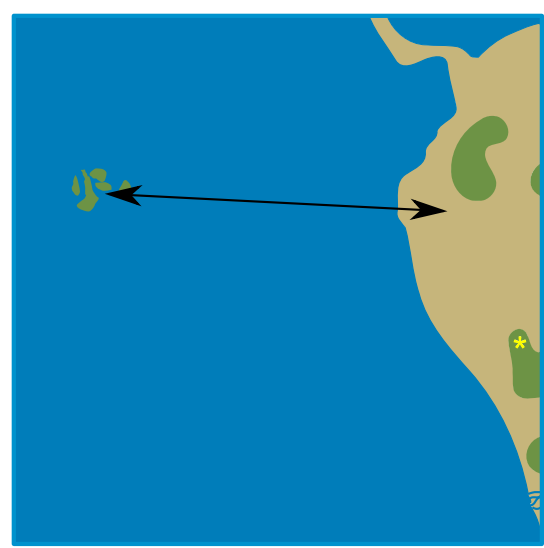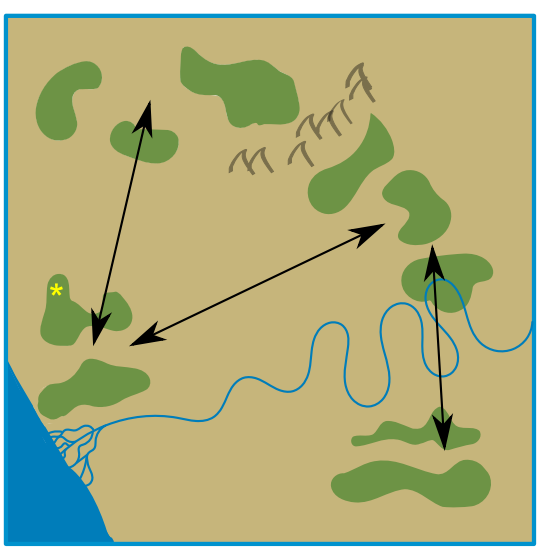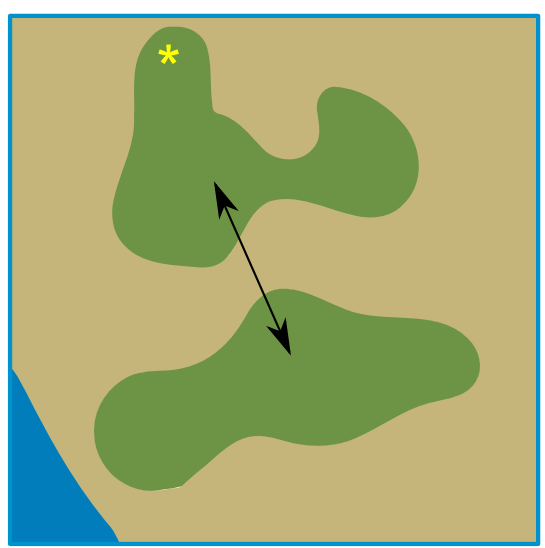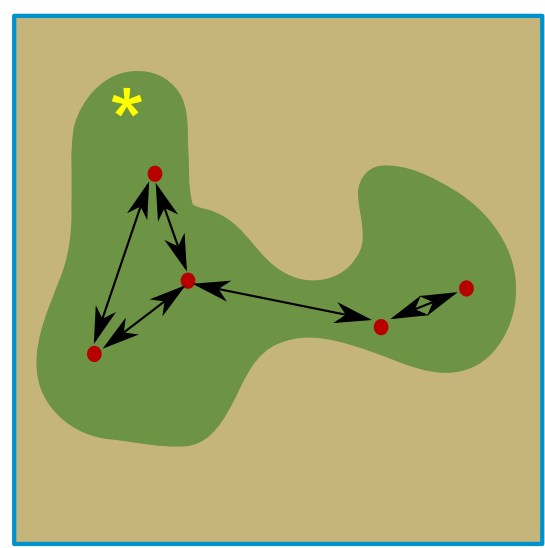
Trends Box 1 Fig II

RATE OF ADAPTATION

MONOPOLIZATION ZONE

TAXA:

Bacteria

Zooplankton

Spiders

Land birds

Seabirds

TIME OF ARRIVAL OF IMMIGRANT

TIME OF ARRIVAL of second immigrant

Slow disperser

Fast disperser

SPACE (four different spatial scales)