eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

OXFORD

Adaptive colonization across a parasitism–mutualism gradient

Alexandre Mestre[1], Roger K. Butlin[2,3], Joaquín Hortal[4,5,6], Marina Rafajlović[2,7,8]

[1]Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Paterna, Spain
[2]Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden
[3]Ecology and Evolutionary Biology, School of Bioscience, The University of Sheffield, Sheffield, United Kingdom
[4]Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain
[5]cE3c—Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal
[6]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, GO, Brazil
[7]Centre for Marine Evolutionary Biology, University of Gothenburg, Gothenburg, Sweden
[8]Gothenburg Global Biodiversity Centre, University of Gothenburg, Gothenburg, Sweden

Corresponding authors: Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Catedrático José Martínez 2, Paterna 46980, Spain. Email: alexandre.mestre@uv.es; Department of Marine Science, University of Gothenburg, Box 461, Gothenburg 405 30, Sweden. Email: marina.rafajlovic@marine.gu.se

Abstract

Adaptive colonization is a process wherein a colonizing population exhibits an adaptive change in response to a novel environment, which may be critical to its establishment. To date, theoretical models of adaptive colonization have been based on single-species introductions. However, given their pervasiveness, symbionts will frequently be co-introduced with their hosts to novel areas. We present an individual-based model to investigate adaptive colonization by hosts and their symbionts across a parasite–mutualist continuum. The host must adapt in order to establish itself in the novel habitat, and the symbiont must adapt to track evolutionary change in the host. First, we classify the qualitative shifts in the outcome that can potentially be driven by non-neutral effects of the symbiont–host interaction into three main types: parasite-driven co-extinction, parasite release, and mutualistic facilitation. Second, we provide a detailed description of a specific example for each type of shift. Third, we disentangle how the interplay between symbiont transmissibility, host migration, and selection strength determines: (a) which type of shift is more likely to occur and (b) the size of the interaction effects necessary to produce it. Overall, we demonstrate the crucial role of host and symbiont dispersal scales in shaping the impacts of parasitism and mutualism on adaptive colonization.

Keywords: dispersal, evolutionary rescue, eco-evolutionary dynamics, host–symbiont interactions, local adaptation, sink population

Lay Summary

Global change is forcing many species to shift their ranges. Colonizing new areas often requires adaptation to novel environmental conditions. Without adaptation, a colonizing population may only be temporarily sustained, thanks to migration. However, although immigrants are poorly adapted to the new habitat, they provide a source of genetic variation that might help the population to adapt to local conditions and persist. Theoretical models have been used to explore this "adaptive colonization" process, but without accounting for the role of symbionts, not withstanding the fact that practically all plant and animal species host symbionts on or inside their bodies. When colonizing new areas, host species also introduce their symbionts. Symbionts range from beneficial mutualists through simple passengers to harmful parasites, so some may help and some may hinder colonization. Furthermore, colonizing symbionts may also experience new selective pressures that would be likely to influence the colonization process. Here we bring together two fields in evolutionary biology—colonization of novel habitats and host–symbiont interactions—to address an important issue for understanding the response of populations to global change: How does the interaction between a colonizing host population and its co-introduced symbionts influence their respective abilities to adapt to new conditions? To do this, we developed a simulation that follows the eco-evolutionary dynamics of a host and its symbiont after being introduced into an empty island with external environmental conditions that differ from those in their source habitats. We considered different types of impact of the symbiont on the host, from strongly negative to strongly positive. Our results show that sometimes neither of the species can establish a population on the island, sometimes both do, and sometimes only the host succeeds. The outcome depends on the dispersal rates of both partners, on the interaction type and strength, and on their need for local adaptation.

Introduction

Evolution plays a fundamental role in the colonization of novel habitats (Lavigne et al., 2019). The need for adaptation to a new environment may compromise the establishment of a viable population. If this evolutionary hurdle is overcome, there is "adaptive colonization" (Gomulkiewicz et al., 2010), a concept inspired by models of source–sink dynamics governed by local adaptation and migration (e.g., Holt & Gomulkiewicz, 1997). Indeed, the

canonical model of adaptive colonization is a black-hole sink from which emigration is negligible (Lavigne et al., 2019). Within this initially empty sink, immigration creates the opportunity for adaptive colonization to occur because a maladapted population is maintained by demographic rescue (Hanski, 1998; Kanarek et al., 2015). However, despite its role in replenishing the local population and increasing local genetic variation, immigration tends to limit local adaptation by decreasing the mean fitness of the local population ("migration load"; Lenormand, 2002). A maladapted population sustained by immigration will decline if migration becomes disrupted. The isolated population will face extinction unless adaptive evolutionary change restores its positive growth in a process called evolutionary rescue (Bell, 2017; Carlson et al., 2014; Gomulkiewicz & Holt, 1995). The general criterion for successful adaptive colonization is when the population is self-sustaining even in the absence of immigration (i.e., the sink becomes a source), a state that might be reached by adaptation in the presence of moderate gene flow (Kawecki, 2008) or by evolutionary rescue after a maladapted population becomes isolated (Lavigne et al., 2019).

Theoretical studies of adaptive colonization have investigated how a variety of factors influence the establishment success of a single species, including immigration and mutation rates, the genetic architecture underlying phenotypic expression, the degree of maladaptation of immigrant phenotypes, and Allee effects, among others (Gomulkiewicz et al., 2010; Kanarek et al., 2013; Lavigne et al., 2019). Evolutionary rescue theory has incorporated biotic interactions in a variety of ways (Klausmeier et al., 2020; Searle & Christie, 2021). In particular, evolutionary rescue has been applied to the colonization of a novel host by a pathogen (Gandon et al., 2013), the evolution of a "naive" host in response to a novel pathogen (Christie & Searle, 2018; DiRenzo et al., 2018; Golas, 2021), success in the establishment of a novel mutualism (Dinges et al., 2022), the effects of a novel pathogen on evolutionary rescue of a host metapopulation (Jiao et al., 2020), and the influence of positive interactions in evolutionary rescue (Goldberg & Friedman, 2021; Henriques & Osmond, 2020). Moreover, Jones and Gomulkiewicz (2012) revealed how interactions with resident species (including predator–prey, mutualistic, and competitive relationships) shape the establishment success of an introduced species. However, no theoretical framework has been developed to investigate adaptive colonization involving two intimately associated species, such as obligate symbionts and their hosts, where both species reach a novel habitat together, and both require adaptation to establish.

Symbionts (organisms that use the body of their hosts as a living place) represent a substantial fraction of biodiversity, including mutualists, commensals, and parasites (Larsen et al., 2017). Virtually all metazoan species harbor their own particular biota of associated symbionts (Drew et al., 2021). Symbionts' niche and dispersal dynamics can be strongly tailored to their hosts, with potential implications for their colonization processes (Mestre et al., 2020). First, the dynamics of symbiont–host interactions are prone to be driven by coevolution, where host bodies may play a crucial role in modulating the micro-environment of their symbionts (Clayton et al., 2015). Second, symbionts' dispersal dynamics can depend critically on specific events of the host life cycle, such as reproduction in vertically transmitted symbionts, and often operate at multiple scales, showing strong dependencies on host dispersal capacity (e.g., Mestre et al., 2019). In fact, many symbionts can travel passively while carried by their hosts, facilitating co-introduction to novel areas. Finally, symbiont–host interactions cover a continuous gradient of interaction types and strengths (from parasitic to mutualistic) that vary among and within species, including context-dependent transitions among types (Drew et al., 2021; Skelton et al., 2016). Therefore, the development of adaptive colonization models that incorporate the particularities of symbiont–host associations is critical for a thorough understanding of the colonization of novel habitats.

We present an individual-based model designed to investigate the dynamics of adaptive colonization involving a host and its coevolving symbiont. The model simulates eco-evolutionary dynamics following co-introduction into an empty island. Hosts have a trait that evolves in response to the island environment (e.g., vertebrate body size evolution in islands; Benítez-López et al., 2021; Diniz-Filho et al., 2021). Symbionts have a trait that evolves in response to this host trait (e.g., feather-louse body size evolution; Villa et al., 2019). The island receives migrants (hosts harboring symbionts) from large coadapted source populations. We test for adaptive colonization by both species, varying migration regime, symbiont transmissibility, selection strength, and the nature of the interaction, from strongly negative to strongly positive effects of the symbiont on host fitness. Using commensalism as the baseline, we show that our model recreates patterns agreeing with previous studies of adaptive colonization/evolutionary rescue for a single species. Then, we demonstrate how mutualistic and parasitic effects shape the adaptive colonization process, crucially depending on the dispersal rates of both associates, the strength of selective pressures, and the size of the effects.

Materials and methods
Model description

We model the evolution of a population of hosts and their symbionts during colonization of an initially empty island from a very large mainland. The environmental conditions on the mainland differ from those on the island, so that adaptation is required for successful colonization. The mainland is assumed to be in mutation–selection equilibrium, under stabilizing selection for the adaptive trait in both the host and the symbiont. The assumption that the mainland is very large allows us to neglect the effect of drift on the mainland. Under these assumptions, the mainland population does not need to be simulated explicitly.

Model variables and parameters are described in Supplementary Tables S1 and S2. The model is largely motivated by obligate, vertically transmitted ectosymbionts associated with birds, which complete all their life stages on the body of their hosts (see Supplementary Appendix S1). However, our model is general, essentially requiring just that a trait value of a host influences both the fitness of the host in a new environment and the fitness of symbionts. Parameter settings are loosely based on the life histories of a louse–pigeon association (e.g., Villa et al., 2019; Supplementary Table S2). We assume that both host and symbiont populations are diploid and dioecious. The carrying capacity of the insular population of hosts is denoted by $K \in \{500, 1000, 2000\}$, which is constant over time. Symbionts are able to survive only while on a host, and each host is assumed to be a potential habitat for a local population of symbionts, which we call an infrapopulation (following Poulin, 2007). To each local population of symbionts inhabiting a host, we assign a carrying capacity k_L (the subscript L refers to "local"). We assume that k_L is constant over time, and equal for all hosts.

Hosts have a quantitative trait under environmental selection, with $\theta = 0$ being the optimal phenotype on the island, and $\theta_M \in \{-5, -7\}$ the optimum on the mainland. Symbionts respond to the island environment indirectly, through a trait-mediated

interaction with the host: symbionts inhabiting a given host experience stabilizing selection on a quantitative trait with its optimal phenotype determined by the value of the host trait. In the pigeon–louse example, both symbiont and host traits are body size. The selection strength in both species is determined by the width of stabilizing selection, $V_s \in \{2,5,20\}$ (smaller V_s signifies stronger selection).

In each species, the trait under selection is assumed to be underlain by $L = 32$ bi-allelic loci that recombine freely (see Supplementary Appendix S2). The recombination rate between any pair of loci per generation, per gamete is 0.5. The alleles at these loci contribute additively to the phenotype. For simplicity, we assume that the effect size of each allele is either $a = |\theta - \theta_M|/L = 0.15625$ or $-a$, so that the possible phenotypic range exceeds the range bounded by the two optima. Furthermore, because standing genetic variation is often considered as the predominant source of rapid adaptation (e.g., Bitter et al., 2019; Lai et al., 2019; Sheng et al., 2015), we neglect new mutations and, instead, assume that the mainland (along with recombination) is the only source of genetic variation for the host and symbiont populations on the island. We ensured that standing genetic variation is high enough to facilitate adaptive evolution in our simulations (Supplementary Figure S1).

Life cycles are modeled as follows (see Figure 1 and Supplementary Appendix S2). Symbionts are assumed to have non-overlapping generations and vertical transmission from both host parents (i.e., assuming a biparental care system and negligible adult social transmission dynamics in hosts). The reproductive cycle of symbionts has a monthly frequency (one time step) and consists of symbiont sexual reproduction by random mating locally within each host. After reproduction, all adult symbionts die, whereas their offspring become adults entering the next generation. Vertical transmission (from a host to its offspring) occurs at the frequency of host reproductive events (yearly, every 12 time steps). New symbionts arrive on the island via hosts that carry them while migrating from the mainland. Finally, the entire infrapopulation of symbionts inhabiting a given host is assumed to die when the host dies. Hosts are assumed to have overlapping generations, with one reproductive event per year and 4-year life span on average. The order of events between two host reproductive seasons (or between the start of the simulation and the end of the first host reproductive season) is as follows: (a) immigration of hosts from the mainland, (b) random mating followed by reproduction and fecundity selection, and (c) death of adult hosts.

The number of gametes produced by each symbiont depends on the local population density of symbionts (within a given host), the phenotype of the symbiont, and the phenotype of its host. Gamete production by a host depends on the population density of hosts, the phenotype of the host, and the density of the symbiont population inhabiting the host. A detailed description of fitness equations for both host and symbiont (adapted from Bridle et al., 2019 and Polechová & Barton, 2015) is available in Supplementary Appendix S2.

Simulations

The temporal range of simulations covered 1,100 years, divided into two periods (Supplementary Figure S3a). Each simulation started with a 1,000-year period during which the island received migrants. This period is followed by 100 years without migration. Different combinations of symbiont transmissibility (high vs.

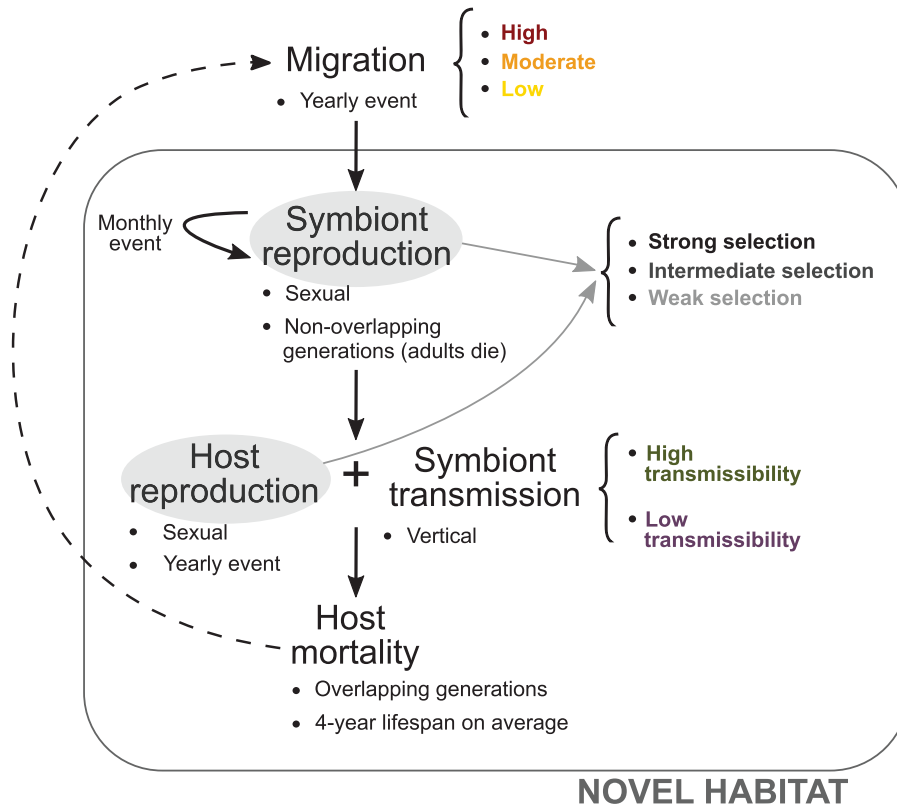**Figure 1.** Schematic description of the adaptive colonization model that simulates the eco-evolutionary dynamics of a symbiont–host association attempting to colonize an island. The island represents a novel habitat that is a black-hole sink (with no emigration) and receives maladapted immigrants from source populations. The dashed arrow has the purpose of connecting separate rounds of life cycles.
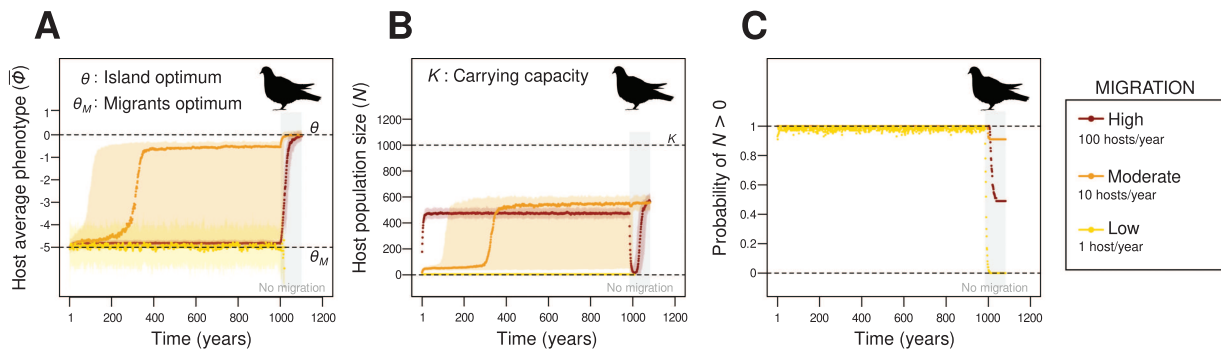
Figure 2. Effects of migration rate on temporal eco-evolutionary dynamics of an incipient host population attempting to colonize an island and subject to commensalism originated from the source: (A) Average phenotype of individuals inhabiting the island over time; (B) number of individuals inhabiting the island over time; and (C) fraction of replicates with at least one individual inhabiting the island at time t. The analyses are based on 100 replicates. For each year, replicates with no hosts (i.e., with $N = 0$) were disregarded in (A) and (B) (the fractions of replicates with $N > 0$ are shown in C); dots are the median values and shadows are 5 and 95 percentiles. Parameter setting: $\theta_M - \theta = -5$, $K = 1,000$, commensalism ($\lambda = 0$), intermediate selection ($V_S = 5$), and high transmissibility ($\rho_M = 1$ and $\gamma = 0.2$). For detailed explanations of the model variables and parameters, see Supplementary Tables S1 and S2 and Supplementary Appendix S2.

low), host migration rate (low, moderate, and high), and selection strength (weak, intermediate, and strong) were simulated across a range of interaction strengths (λ) from strong parasitic to strong mutualistic effects ($-0.003 \leq \lambda \leq 0.003$ at intervals of 0.0005). We performed 100 simulations per parameter combination. For detailed explanations of the model variables and selected parameter values, see Supplementary Tables S1 and S2, and Supplementary Appendix S2.

The model was implemented with a C++ code built *ad hoc* (available at https://github.com/almestre/hosydy) based on object-oriented programming techniques that allowed us to track individuals and populations of both hosts and symbionts. Interactions were managed through "slot map" data structures adopted from the field of game design; genetic information was stored in bits and managed through bitwise operations (details in Supplementary Appendix S3).

Data analysis

Following Lavigne et al. (2019), we assume that a population that persisted throughout the 100 years simulated in the absence of migration is a *successfully established population*. We used three metrics specifically designed to measure the effects of interaction strength on the adaptive colonization process in both hosts and symbionts (Supplementary Figure S3). Time to adapt is the time passed (in years) from the beginning of the simulation until the average phenotype of the island population is halfway to the island optimum [$(\theta_M - \theta)/2$], calculated from median values across replicates (Supplementary Figure S3a). The loss ratio is the fraction of the island population lost during the isolation period before the point when the population starts experiencing a positive population growth due to evolutionary rescue. The loss ratio is obtained exclusively from successful replicates (those with population size higher than zero at the end of the simulation) and median values across replicates (Supplementary Figure S3b). Finally, the relative persistence size is the cumulative population size over the isolation period divided by the cumulative population size expected if the population was always at the carrying capacity. This metric is calculated for each replicate (Supplementary Figure S3c). It indicates how effectively a population occupies the potentially available habitats/resources on the island during the isolation period. In the case of symbionts, because their global carrying capacity varies over time depending on host population size ($k_{G,T} = k_L N_T$), the relative persistence

size is a measure of effectiveness in occupying available hosts at high densities. Therefore, it also reveals the effectiveness of non-neutral symbionts in transferring their benefits or costs to the isolated host population.

Results

Adaptive colonization involving a symbiont and its host has three possible outcomes: both persist, host only persists, and neither persists. Considering a baseline case for a commensalism (Figure 2; see also Supplementary Appendix S4 and Supplementary Figure S4), wherein host dynamics are unaffected by the symbiont, intermediate rates of host migration favor host adaptation during the migration period (Figure 2A, orange line), and persistence after migration disruption (Figure 2C, orange line). By contrast, high migration rates maintain a maladapted population of hosts (Figure 2A, red line) that experiences a strong bottleneck during the isolation period (Figure 2B, red line), thus challenging the persistence of both associates (Figure 2C, red line). When migration is too low, host adaptation and persistence are highly unlikely (Figure 2, yellow line). Alternative parameterizations show qualitatively similar patterns, although quantitative differences occur in the migration rate required for adaptation and the conditions allowing for successful colonization (details in Supplementary Appendix S4 and Supplementary Figures S6–S13). These results are consistent with former models of source–sink dynamics (Supplementary Appendix S5).

Focusing on symbiont dispersal among hosts, high transmissibility situations represent extreme cases where practically all hosts harbor symbionts during the simulations (Supplementary Figure S4g), and therefore, host and symbiont share either coexistence or co-extinction. By contrast, low transmissibility hinders the prevalence and persistence of symbionts (Supplementary Figure S4h and k), making it more likely that the host ends up persisting alone at the end of the simulation (e.g., Supplementary Figure S4i and k, red lines).

The effects of the interaction strength on adaptive colonization

Taking commensalism as the reference neutral situation described above, non-neutral interactions (either parasitic or mutualistic) are potential drivers of three main types of shift

in the outcomes of adaptive colonization (Figure 3): (i) parasitism drives the extinction of both associates; (ii) parasitism drives the extinction of the symbiont, releasing the host from parasitic effects; and (iii) mutualism enhances long-term persistence of one or both associates. Below, we explore an example of each type of shift and provide a brief summary of how these shifts are shaped by dispersal (i.e., both host migration and symbiont transmissibility) and interaction strength. A more comprehensive description of results including alternative parameterizations and focusing on process-specific effects is available in Supplementary Information (Supplementary Figures S14–S31), presenting time to adapt across a λ gradient (Supplementary Appendix S6), evolutionary rescue across a λ gradient (Supplementary Appendix S7), and establishment across a λ gradient (Supplementary Appendix S8).

Parasite-driven co-extinction

Parasite-driven co-extinction occurs when parasites keep the island population of the host below a population-size level that allows local adaptation. Figure 4 illustrates a case of a highly transmissible parasite ($\lambda < 0$) precluding adaptive colonization of both associates, where they would persist under commensalism ($\lambda = 0$, all else equal). Neither associate is able to achieve adaptation to the island, while migration is present (Figure 4A and B, blue lines), and both fail to establish a persistent population once migration is disrupted, resulting in co-extinction (Figure 4C and D, blue lines). Without parasitic effects, both associates reach high levels of adaptation to the island conditions during the migration period (Figure 4A and B, brown lines), so that populations thrive and overcome the isolation period without bottlenecks (Figure 4C and D, blue lines). Relatively low levels of parasitic effects can be sufficient to preclude adaptation when migration is present (Figure 4E and F). Parasitism provokes an identical drop in persistence probability in both species (Figure 4G and H, black line). Overall, this demonstrates that parasitism is the underlying cause of co-extinction in this representative example with $\lambda = -0.0015$ (Figure 4A–D), as well as for stronger parasitism (Figure 4E–H).

However, for weaker parasitism (i.e., $0 > \lambda > -0.0015$), we observed a positive probability that both the host and the symbiont populations persist (Figure 4G and H, black). As the parasitism approaches the critical value above which persistence is highly unlikely (and not achieved in any of the 100 runs we performed), the loss ratio increases slightly (Figure 4G and H, green). This indicates that stronger parasitism (but not too strong) may allow population persistence but at a cost of producing a more severe population decline after disrupting migration and prior to rescue. The high values of relative persistence size across the λ-gradient observed in the symbiont (Figure 4H, red line) mean that symbionts successfully established thriving infrapopulations in most of the hosts over the isolation period, thereby effectively transferring parasitic costs to the isolated host population. The initial increase in the relative persistence size with increasing parasitic effects is explained by the loss of a dilution effect that is present under commensalism, wherein frequent reproduction in a thriving population of well-adapted hosts increases the proportion of newborn hosts free of symbionts or carrying smaller symbiont infrapopulations. This produces a somewhat smaller average infrapopulation size compared to a parasitized host population mainly sustained by maladapted migrants with very low reproduction rates (Supplementary Figure S5a and c, orange lines). Therefore, the symbiont relative persistence size increases when parasitism is stronger due to the negative impact of parasitism on host reproduction.

Parasite release

Parasite release occurs when parasitism reduces symbiont vertical transmission below the threshold necessary to allow the parasite to coadapt to the evolving host, causing the extinction of the island population of the parasite. In contrast with the previous case, weakening selection strength and sharply constraining symbiont dispersal, we obtain a parasite release where parasitic effects exclusively disfavor adaptive colonization of the symbiont, provoking its extinction without affecting the host (Figure 5). Under commensalism, both associates achieve a
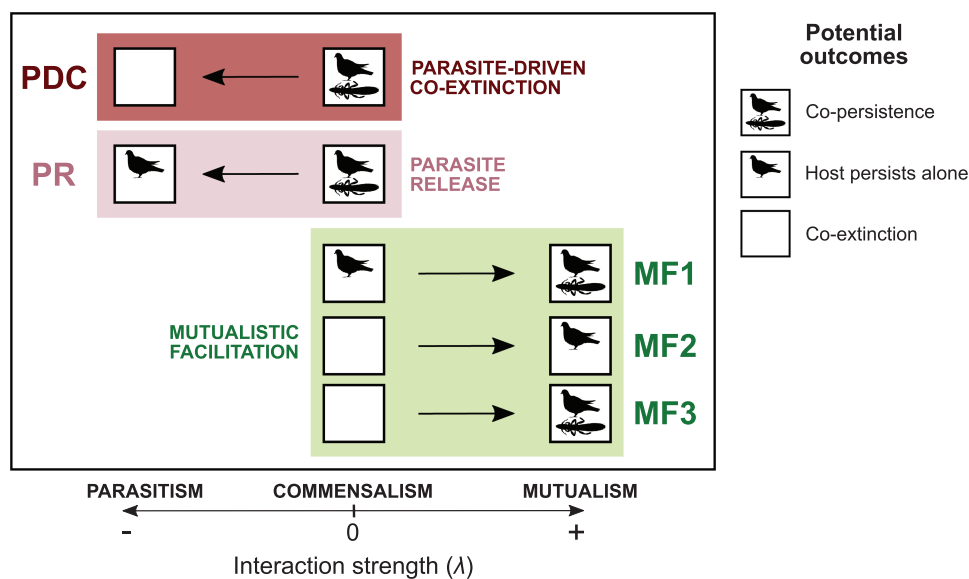

Figure 3. Types of shift in the outcomes of adaptive colonization involving a host and its symbiont that can potentially be driven by non-neutral effects of the symbiont–host interaction. Parasite-driven co-extinction occurs when parasitism drives the extinction of both associates. Parasite release refers to a parasitism that drives the extinction of the symbiont, releasing the host from parasitic effects. Mutualistic facilitation occurs when mutualism enhances long-term persistence of either one or both associates.

substantial degree of local adaptation and population growth within the first 200 years of simulation (Figure 5A–D, brown lines). With sufficiently strong parasitic effects (i.e., $\lambda = -0.0025$), parasitism precludes coadaptation of symbionts to the evolving host population (Figure 5A and B, blue lines), thus preventing migrant symbionts from effectively colonizing the growing fraction of

newborn hosts undergoing adaptation (notice the prevalence decline in Figure 5D coinciding with the thriving of adapted hosts in Figure 5C, blue lines). Time to adapt, loss ratio and persistence metrics of hosts remain unaffected by parasitism (Figure 5E and G). Conversely, parasitism hinders adaptation of symbionts during the migration period (Figure 5F), produces a severe decline in
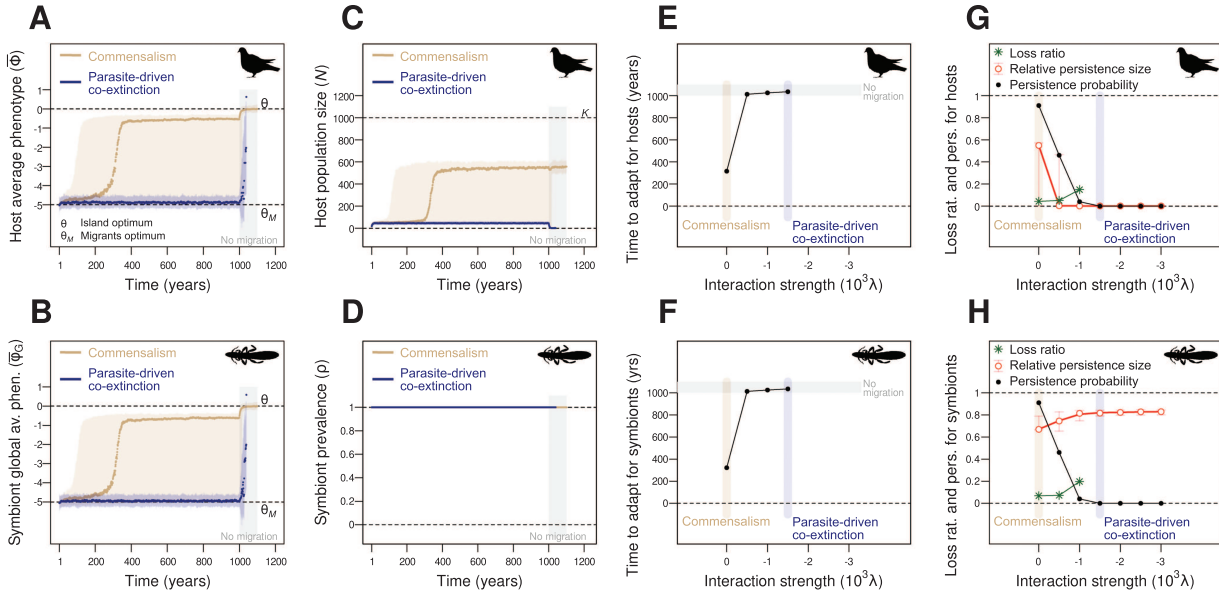

Figure 4. Example of parasite-driven co-extinction (blue lines) showing the effects of parasitism ($\lambda = -0.0015$) on temporal dynamics of a host (A, C) and a high transmissibility symbiont (B, D). Light brown lines show the results of a baseline case with $\lambda = 0$ (all else being the same). For each year, replicates with no hosts (i.e., $N = 0$) were disregarded; dots are the median values and shadows are 5 and 95 percentiles. The remaining panels show the impact of varying interaction strength (all other parameters being the same as in A–D) on the adaptive colonization metrics (see Figure 1) for hosts (E, G) and symbionts (F, H). Note that the strength of the parasitism increases toward the right on the x-axis (and this corresponds to decreasing λ). Parameter setting: $\theta_M - \theta = -5$, $K = 1,000$, intermediate selection ($V_s = 5$), high transmissibility ($\rho_M = 1$ and $\gamma = 0.2$), and moderate migration ($M = 10$). For detailed explanations of the model variables and parameters, see Supplementary Tables S1 and S2 and Supplementary Appendix S2.
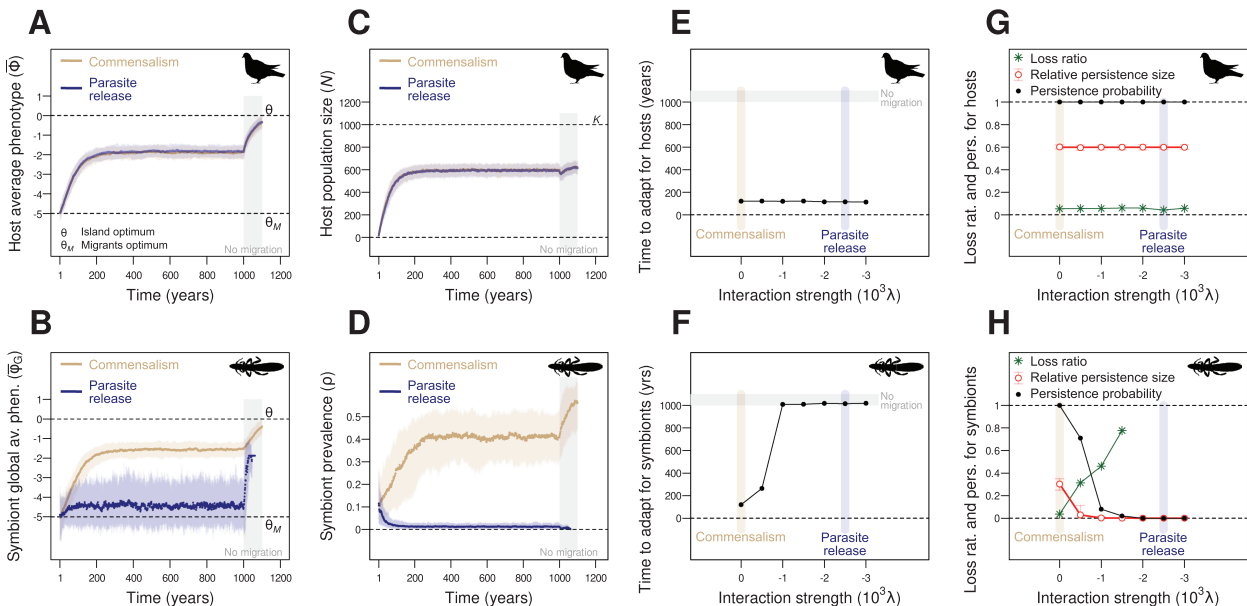

Figure 5. Example of parasite release (blue lines) showing the effects of parasitism ($\lambda = -0.0025$) on temporal dynamics of a host (A, C) and a low transmissibility symbiont (B, D). Light brown lines show the results of a baseline case with $\lambda = 0$ (all else being the same). For each year, replicates with no hosts (i.e., $N = 0$) were disregarded; dots are the median values and shadows are 5 and 95 percentiles. The remaining panels show the impact of varying interaction strength (all other parameters being the same as in A–D) on the adaptive colonization metrics (see Figure 1) for hosts (E, G) and symbionts (F, H). Note that the strength of the parasitism increases toward the right on the x-axis (and this corresponds to decreasing λ). Parameter setting: $\theta_M - \theta = -5$, $K = 1,000$, weak selection ($V_s = 20$), low transmissibility ($\rho_M = 0.1$ and $\gamma = 0.02$), and moderate migration ($M = 10$). For detailed explanations of the model variables and parameters, see Supplementary Tables S1 and S2 and Supplementary Appendix S2.

population size during the isolation period previous to the rescue (Figure 5H, green line), and a decrease in both persistence metrics (red and black lines). Under the same conditions but with stronger selection, symbiont persistence is unlikely even under commensalism (Supplementary Figure S23p), so that parasitic effects become irrelevant in producing a qualitative shift in the outcome.

Mutualistic facilitation

Mutualistic facilitation occurs when a mutualism increases the likelihood of adaptive colonization in one or both associates. Figure 6 shows a case of mutualistic facilitation where strong mutualism ensures long-term persistence in both associates that, otherwise, would face co-extinction (case MF3 in Figure 3). Conditions vary from the previous cases in that selective pressures are stronger so that adaptive colonization under commensalism is highly unlikely irrespective of host migration or symbiont transmissibility (Supplementary Figure S25m–p). Under such adverse conditions, strong mutualistic effects ($\lambda = 0.0025$), combined with high levels of dispersal in both hosts and symbionts, foster adaptation (Figure 6A–F), reduce population loss experienced during the isolation phase (Figure 6G and H, green lines), and increase persistence probability (black lines). Again, the high values of relative persistence size observed in the symbiont (Figure 6H, red line) are indicative of a highly effective transfer of benefits of the interaction to the isolated host population during the isolation period; the slight decrease in relative persistence size as interaction increases from 0.0015 to 0.002 is a signal of mutualistic effects boosting host reproduction which produces a dilution effect in the symbiont infrapopulations (see a similar effect in Figure 4H, red line).

Persistence patterns across a parasitism–mutualism gradient

The interaction between transmissibility, migration, and selection strength determines which type of shift in the outcome might occur (among those represented in Figure 3), and also the size of the interaction effects (λ) necessary to produce a shift (Figure 7).

Under high transmissibility (Figure 7, vertical green bar), we expect a more effective transfer of the interaction effects from symbionts to hosts, leading to larger impacts of parasitism and mutualism on hosts where both associates will tend to respond together, either via parasitism-driven co-extinction (e.g., Figure 4) or mutualism-driven co-persistence (e.g., Figure 6). Parasite-driven co-extinction (Figure 7, PDC) is expected when selection is weak to intermediate. With intermediate selection, weaker parasitism is enough to cause co-extinction. Mutualism-driven co-persistence (Figure 7, MF3) is expected when selection is intermediate to strong. When selection is strong, only strong mutualism can facilitate co-persistence. Furthermore, the higher the host migration rates, the more likely it is that mutualistic-driven co-persistence occurs. Similarly, with higher host migration rates, mutualistic-driven co-persistence is attained with weaker mutualistic effects (Supplementary Figure S25m and n). Lastly, when selection is not too strong but low migration rates hinder host adaptation, mutualism can also facilitate co-persistence (Supplementary Figure S23m and n, yellow lines).

Low transmissibility (Figure 7, vertical purple bar) may make the symbiont population vulnerable and reduce its impact on the host. In these circumstances, parasitism is likely to drive the loss of the symbiont (e.g., Figure 5), mutualism can facilitate its persistence (e.g., Supplementary Figure S23p), and the impacts of the interaction on the host persistence patterns tend to be moderate (e.g., Supplementary Figure S23o) or negligible (e.g., Supplementary Figure S24o). When selection is weak, weak parasitic effects are sufficient to produce parasite release (Figure 7, PR). If selection is intermediate, then the symbiont cannot persist under commensalism though mutualism might prevent its extinction (Figure 7, MF1), critically depending on host migration (Supplementary Figure S23p). When migration is
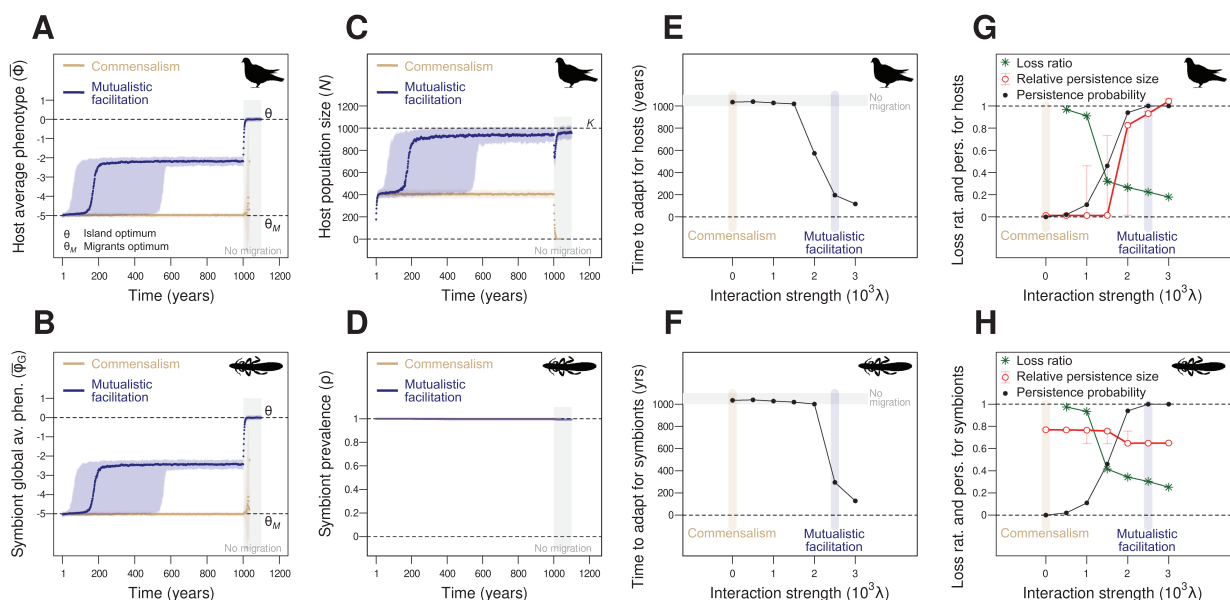

Figure 6. Example of mutualistic facilitation (blue lines) showing the effects of mutualism ($\lambda = 0.0025$) on temporal dynamics of a host (A, C) and a symbiont (B, D), both having high dispersal abilities but being subject to strong selective pressures. Light brown lines show the results of a baseline case with $\lambda = 0$ (all else being the same). For each year, replicates with no hosts (i.e., $N = 0$) were disregarded; dots are the median values, and shadows are 5 and 95 percentiles. The remaining panels show the impact of varying interaction strength (all other parameters being the same as in A–D) on the adaptive colonization metrics (see Figure 1) for hosts (E, G) and symbionts (F, H). Parameter setting: $\theta_M - \theta = -5$, $K = 1,000$, strong selection ($V_s = 2$), high transmissibility ($\rho_M = 1$ and $\gamma = 0.2$), high migration ($M = 100$). For detailed explanations of the model variables and parameters, see Supplementary Tables S1 and S2, and Supplementary Appendix S2.
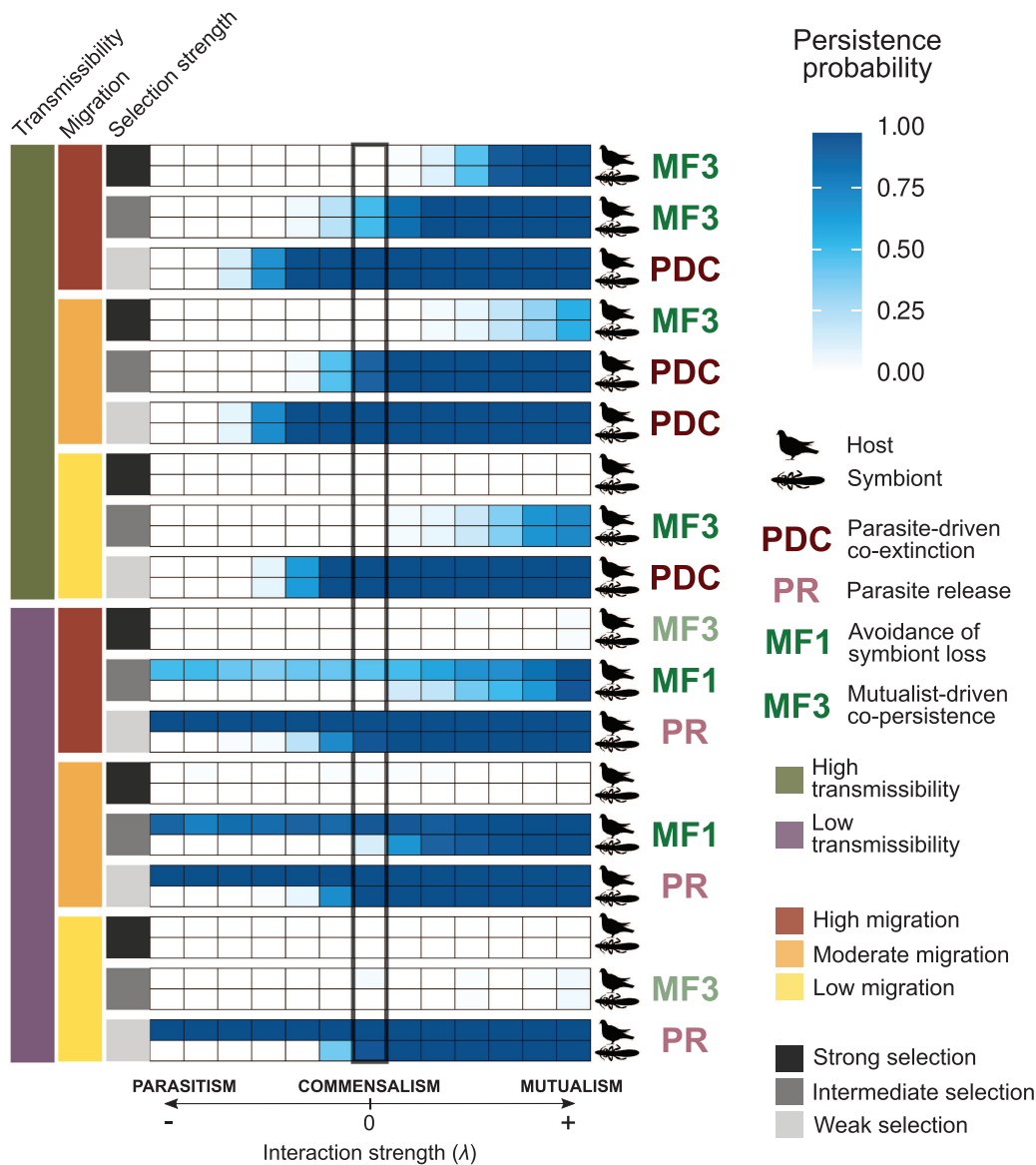
Figure 7. Effects of the interaction between symbiont transmissibility, host migration, and selection strength on persistence patterns across a parasitism–mutualism gradient in a symbiont–host association subject to adaptive colonization. PC is parasite-driven co-extinction, PR is parasite release, MF1 is mutualistic facilitation allowing persistence of the symbiont, and MF3 is mutualistic facilitation allowing the persistence of both associates (see Figure 3).

moderate, a weak mutualism is enough to avoid the symbiont loss (Supplementary Figure S23p, orange line). This is because moderate migration allows host adaptation prior to isolation (Figure 2, orange lines), during which weak mutualistic effects can facilitate access of symbionts to the evolving host population (Supplementary Figure S32q and w, orange line) through coadaptation (Supplementary Figure S33l and p, orange line). When migration is too high, host adaptation is only possible during the isolation period at a cost of experiencing a severe bottleneck (Figure 2, red lines), so that a strong mutualism is necessary to alleviate the bottleneck (Supplementary Figure S23c and d, red lines) and avoid symbiont loss (Supplementary Figure S23p, red line). When migration is too low, host adaptation is not possible (Figure 2, yellow lines) and co-extinction is practically guaranteed (Supplementary Figure S23p, yellow line). Finally, strong selection makes adaptive colonization of a low-transmission symbiont and its host highly unlikely irrespective of the existence of mutualistic effects (Supplementary Figure S25o and p).

In our simulations, we found no evidence for a mutualistic symbiont favoring adaptive colonization of its host but being lost during the colonization process (i.e., Figure 3, MF2).

Discussion

Biotic interactions can be either facilitators or disruptors of adaptive colonization (Goldberg & Friedman, 2021; Jones & Gomulkiewicz, 2012). We present here a model specifically designed to investigate joint adaptive colonization by a symbiont–host association. In agreement with single-species source–sink models of local adaptation (Akerman & Bürger, 2014; Bridle et al., 2010; Gomulkiewicz et al., 1999), our model shows that immigration can be critical for the persistence of sexual species subject to strong density dependence, and rapid adaptation underpinned by standing genetic variation. For instance, sexual reproduction amplifies the maladaptive effects of high migration rates (Brady et al., 2019; see Supplementary Appendix S5 for more details). Our results go beyond these earlier

single-species studies by demonstrating how symbionts carried from the source can modulate the adaptive dynamics of hosts. Mutualistic interactions will tend to broaden the range of migration regimes that allow for successful establishment, thereby making migration less critical for adaptive colonization. Moreover, our model suggests that mutualistic effects might reduce heterozygosity, especially in symbionts (Supplementary Figure S34), thus agreeing with other coevolutionary models that predict polymorphism erosion driven by mutualism (Nuismer, 2017). By contrast, parasitized hosts will be more dependent on a specific, optimal migration rate for success, or will even fail to establish regardless of the migration regime if the parasitism is strong enough. Notably, we illustrate a novel mechanism whereby low transmission of the symbiont combined with rapid host evolution in response to the novel environment results in an adapted host population free of parasites. Overall, we identified three qualitatively different outcomes that capture the most biologically significant situations that a symbiont–host association might face when jointly colonizing a novel habitat: parasite-driven co-extinction, parasite release, and mutualistic facilitation.

Empirical evidence indicates that introduced species are less parasitized than their relatives in their native ranges (Torchin et al., 2003). A potential explanation is that the invasion process filters symbiont–host interactions, removing both partners where host damage is high (Lymbery et al., 2014). We provide an eco-evolutionary mechanism whereby a species co-introduced with a highly transmissible parasite is unable to establish itself in a novel habitat just because the parasite precludes local adaptation. Interestingly, the dynamics are nonlinear such that even a small increase in parasitic effects can cause a dramatic drop in host persistence (e.g., Figure 4G). The relevance of the host evolutionary constraint in driving co-extinction is demonstrated by the fact that weakening selection strength allows establishment under stronger parasitic effects (compare Supplementary Figures S23m and S24m).

Another explanation for the lower parasite richness observed in introduced species is a loss of parasites during the colonization process (Roy et al., 2011). Individual-based model simulations have demonstrated that invasive hosts can lose their parasites in the invasion vanguard due to stochasticity affecting low-density frontal populations, especially in the case of density-dependent transmission rates (Phillips et al., 2010). We show that low-transmission parasites are likely to become lost during an adaptive colonization process, even under density-independent transmission. If rapid host adaptation occurs (e.g., Supplementary Figure S4d, orange line), low-transmission symbionts may face an evolutionary barrier, such that they become unable to colonize adapted hosts due to both dispersal limitation and maladaptation (Supplementary Figure S4h, orange line). Alternatively, if host adaptation is hindered due to high host migration (e.g., Supplementary Figure S4d, red line), low transmission symbionts are at a high risk of stochastic extinction during a host population bottleneck when host migration is disrupted (Supplementary Figure S4h, red line). Such disruption might result from the appearance of novel geographical barriers (e.g., due to human activity altering landscapes), or declines of source populations, for example, driven by climate change or habitat destruction, major proximate causes of vertebrate population losses (Ceballos et al., 2017). Parasitism increases the probability of symbiont loss by aggravating the bottleneck through its impacts on host dynamics. We found situations wherein a poorly transmissible symbiont that persists well under neutral or positive interactions becomes extinct with only a small parasitic effect (Figure 5).

Previous theoretical studies of the role of interspecies mutualisms on the ability of species to adapt to new environments do not apply to mutualistic symbionts (Goldberg & Friedman, 2021; Jones & Gomulkiewicz, 2012). In particular, their approaches disregard the strong dependencies of the symbiont's population structure and dispersal dynamics on hosts. Using a more realistic model that captures the particularities of symbiont–host interactions, we demonstrate that mutualistic effects prevent a vertically transmitted symbiont from being lost during an evolutionary rescue event, even if the symbiont has limited dispersal capacity (Supplementary Figure S23p). Furthermore, we portray scenarios of extremely harsh conditions driven by strong selective pressures, where a strong mutualism facilitates establishment, provided that both associates display high enough dispersal rates (Figure 6). Our results provide theoretical support for the role of mutualistic symbionts in expanding the abiotic niche of their hosts, acting as mitigators of adverse conditions faced during the colonization of highly unsuitable habitats (Mestre et al., 2020).

In summary, our findings suggest that, depending on their respective dispersal capacities and the interaction strength, the need for local adaptation can create evolutionary challenges for either or both associates, with potential implications for their establishment success. Unlike previous approaches exclusively focused on parasites and pathogens (e.g., Searle & Christie, 2021), the modeling framework presented here adopts a "mutualist–parasite continuum" view of symbiont–host interactions (Drew et al., 2021; Skelton et al., 2016), which, we believe, will contribute to a better integration of the full diversity of symbiont lifestyles into studies of colonization and range expansion. The framework can be extended to other biological contexts, including horizontally transmitted symbionts with free-living stages (e.g., Mestre et al., 2015), host metapopulations (Jiao et al., 2020), or interactions between symbionts, such as competition (Mideo, 2009). Thus, we envisage this work will open new avenues to achieve a better understanding of the colonization of novel habitats by co-introduced symbiont–host partnerships.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

This manuscript presents theoretical research. The C++ code of the model is available at https://github.com/almestre/hosydy.

Author contributions

All authors participated in the design and development of the theoretical framework and analyses. A.M. wrote the model code, performed the analyses, and wrote the first draft. All authors contributed to the final draft.

Funding

Acknowledgments

References

Akerman, A., & Bürger, R. (2014). The consequences of dominance and gene flow for local adaptation and differentiation at two linked loci. *Theoretical Population Biology*, 94(100), 42–62. https://doi.org/10.1016/j.tpb.2014.04.001

Bell, G. (2017). Evolutionary rescue. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 605–627. https://doi.org/10.1146/annurev-ecolsys-110316-023011

Benítez-López, A., Santini, L., Gallego-Zamorano, J., Milá, B., Walkden, P., Huijbregts, M. A. J., & Tobias, J. A. (2021). The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. *Nature Ecology & Evolution*, 5(6), 768–786. https://doi.org/10.1038/s41559-021-01426-y

Bitter, M. C., Kapsenberg, L., Gattuso, J. -P., & Pfister, C. A. (2019). Standing genetic variation fuels rapid adaptation to ocean acidification. *Nature Communications*, 10, 5821.

Brady, S. P., Bolnick, D. I., Angert, A. L., Gonzalez, A., Barrett, R. D. H., Crispo, E., Derry, A. M., Eckert, C. G., Fraser, D. J., Fussmann, G. F., Guichard, F., Lamy, T., McAdam, A. G., Newman, A. E. M., Paccard, A., Rolshausen, G., Simons, A. M., & Hendry, A. P. (2019). Causes of maladaptation. *Evolutionary Applications*, 12(7), 1229–1242. https://doi.org/10.1111/eva.12844

Bridle, J. R., Kawata, M., & Butlin, R. K. (2019). Local adaptation stops where ecological gradients steepen or are interrupted. *Evolutionary Applications*, 12(7), 1449–1462. https://doi.org/10.1111/eva.12789

Bridle, J. R., Polechova, J., Kawata, M., & Butlin, R. K. (2010). Why is adaptation prevented at ecological margins? New insights from individual-based simulations. *Ecology Letters*, 13(4), 485–494. https://doi.org/10.1111/j.1461-0248.2010.01442.x

Carlson, S. M., Cunningham, C. J., & Westley, P. A. (2014). Evolutionary rescue in a changing world. *Trends in Ecology and Evolution*, 29(9), 521–530. https://doi.org/10.1016/j.tree.2014.06.005

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Christie, M. R., & Searle, C. L. (2018). Evolutionary rescue in a host–pathogen system results in coexistence not clearance. *Evolutionary Applications*, 11(5), 681–693. https://doi.org/10.1111/eva.12568

Clayton, D.H., Bush, S.E. & Johnson, K.P. (2015) *Coevolution of life on hosts. Integrating ecology and history*. The University of Chicago Press.

Dinges, Z. M., Phillips, R. K., Lively, C. M., & Bashey, F. (2022). Post-association barrier to host switching maintained despite strong selection in a novel mutualism. *Ecology and Evolution*, 12(6), e9011. https://doi.org/10.1002/ece3.9011

Diniz-Filho, J. A. F., Santos, A. M. C., Barreto, E., Naves, F., Santos, W., Souza, K. S., Santos-Silva, R., Dobrovolski, R., Soares, T. N., Tidon, R., Spigoloni, Z. A., Rangel, T. F., Raia, P., Hortal, J., & Jardim, L. (2021). Quantitative genetics of extreme insular dwarfing: The case of red deer on Jersey. *Journal of Biogeography*, 48, 1720–1730.

DiRenzo, G. V., Zipkin, E. F., Grant, E. H. C., Royle, J. A., Longo, A. V., Zamudio, K. R., & Lips, K. R. (2018). Eco-evolutionary rescue promotes host–pathogen coexistence. *Ecological Applications*, 28(8), 1948–1962. https://doi.org/10.1002/eap.1792

Drew, G. C., Stevens, E. J., & King, K. C. (2021). Microbial evolution and transitions along the parasite–mutualist continuum. *Nature Reviews Microbiology*, 19(10), 623–638. https://doi.org/10.1038/s41579-021-00550-7

Gandon, S., Hochberg, M. E., Holt, R. D., & Day, T. (2013). What limits the evolutionary emergence of pathogens? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 368(1610), 20120086. https://doi.org/10.1098/rstb.2012.0086

Golas, B. D., Goodell, B., & Webb, C. T. (2021). Host adaptation to novel pathogen introduction: predicting conditions that promote evolutionary rescue. *Ecology Letters*, 24(10), 2238–2255. https://doi.org/10.1111/ele.13845

Goldberg, Y., & Friedman, J. (2021). Positive interactions within and between populations decrease the likelihood of evolutionary rescue. *PLoS Computational Biology*, 17(2), e1008732. https://doi.org/10.1371/journal.pcbi.1008732

Gomulkiewicz, R., & Holt, R. D. (1995). When does evolution by natural selection prevent extinction? *Evolution*, 49(1), 201–207. https://doi.org/10.1111/j.1558-5646.1995.tb05971.x

Gomulkiewicz, R., Holt, R. D., & Barfield, M. (1999). The effects of density dependence and immigration on local adaptation in a black-hole sink environment. *Theoretical Population Biology*, 55(3), 283–296. https://doi.org/10.1006/tpbi.1998.1405

Gomulkiewicz, R., Holt, R. D., Barfield, M., & Nuismer, S. L. (2010). Genetics, adaptation, and invasion in harsh environments. *Evolutionary Applications*, 3, 97–108.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41–49. https://doi.org/10.1038/23876

Henriques, G. J. B., & Osmond, M. M. (2020). Cooperation can promote rescue or lead to evolutionary suicide during environmental change. *Evolution*, 74(7), 1255–1273. https://doi.org/10.1111/evo.14028

Holt, R. D., & Gomulkiewicz, R. (1997). How does immigration influence local adaptation? A reexamination of a familiar paradigm. *The American Naturalist*, 149(3), 563–572. https://doi.org/10.1086/286005

Jiao, J., Gilchrist, M. A., & Fefferman, N. H. (2020). The impact of host metapopulation structure on short-term evolutionary rescue in the face of a novel pathogenic threat. *Global Ecology and Conservation*, 23, e01174.

Jones, E. I., & Gomulkiewicz, R. (2012). Rapid evolution, and the establishment of introduced species. *The American Naturalist*, 179(2), E28–E36. https://doi.org/10.1086/663678

Kanarek, A. R., Webb, C. T., Barfield, M., & Holt, R. D. (2013). Allee effects, aggregation, and invasion success. *Theoretical Ecology*, 6(2), 153–164. https://doi.org/10.1007/s12080-012-0167-z

Kanarek, A. R., Webb, C. T., Barfield, M., & Holt, R. D. (2015). Overcoming Allee effects through evolutionary, genetic, and demographic rescue. *Journal of Biological Dynamics*, 9, 15–33. https://doi.org/10.1080/17513758.2014.978399

Kawecki, T. J. (2008). Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics*, 39(1), 321–342. https://doi.org/10.1146/annurev.ecolsys.38.091206.095622

Klausmeier, C. A., Osmond, M. M., Kremer, C. T., & Litchman, L. (2020). Ecological limits to evolutionary rescue. *Philosophical Transactions of the Royal Society B*, 375, 20190453.

Lai, Y. -T., Yeung, C. K. L., Omland, K. E., Pang, E. -L., Hao, Y., Liao, B. -Y., Cao, H. -F., Zhang, B. -W., Yeh, C. -F., Hung, C. -M., Hung, H. -Y., Yang, M. -Y., Liang, W., Hsu, Y. -C., Yao, C. -T., Dong, L., Lin, K., & Li, S. -H. (2019). Standing genetic variation as the predominant source for adaptation of a songbird. *Proceedings of the National Academy of Sciences of the United States of America*, 116(6), 2152–2157. https://doi.org/10.1073/pnas.1813597116

Larsen, B. B., Miller, E. C., Rhodes, M. K., & Wiens, J. J. (2017). Inordinate fondness multiplied and redistributed: the number of species on earth and the new pie of life. *The Quarterly Review of Biology*, 92(3), 229–265. https://doi.org/10.1086/693564

Lavigne, F., Martin, G., Anciaux, Y., Papaïx, J., & Roques, L. (2019). When sinks become sources: adaptive colonization in asexuals. *Evolution*, 74, 29–42.

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*, 17(4), 183–189. https://doi.org/10.1016/s0169-5347(02)02497-7

Lymbery, A. J., Morine, M., Kanani, H. G., Beatty, S. J., & Morgan, D. L. (2014). Co-invaders: The effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife*, 3(2), 171–177. https://doi.org/10.1016/j.ijppaw.2014.04.002

Mestre, A., Castillo-Escrivà, A., Rueda, J., Monrós, J. S., & Mesquita-Joanes, F. (2015). Experimental spillover of an exotic ectosymbiont on an European native crayfish: The importance of having a chance. *Hydrobiologia*, 755(1), 225–237. https://doi.org/10.1007/s10750-015-2236-y

Mestre, A., Poulin, R., Holt, R. D., Barfield, M., Clamp, J. C., Fernandez-Leborans, G., & Mesquita-Joanes, F. (2019). The interplay of nested biotic interactions and the abiotic environment regulates populations of a hypersymbiont. *The Journal of Animal Ecology*, 88(12), 1998–2010. https://doi.org/10.1111/1365-2656.13091

Mestre, A., Poulin, R., & Hortal, J. (2020). A niche perspective on the range expansion of symbionts. *Biological Reviews of the Cambridge Philosophical Society*, 95(2), 491–516. https://doi.org/10.1111/brv.12574

Mideo, N. (2009). Parasite adaptations to within-host competition. *Trends in Parasitology*, 25(6), 261–268. https://doi.org/10.1016/j.pt.2009.03.001

Nuismer, S. (2017). *Introduction to coevolutionary theory*. W. H. Freeman and Company.

Phillips, B. L., Kelehear, C., Pizzatto, L., Brown, G. P., Barton, D., & Shine, R. (2010). Parasites and pathogens lag behind their host during periods of host range advance. *Ecology*, 91(3), 872–881. https://doi.org/10.1890/09-0530.1

Polechová, J., & Barton, N. H. (2015). Limits to adaptation along environmental gradients. *Proceedings of the National Academy of Sciences of the United States of America*, 112(20), 6401–6406. https://doi.org/10.1073/pnas.1421515112

Poulin, R. (2007). *Evolutionary ecology of parasites*. 2nd ed. Princeton University Press.

Roy, H. E., Handley, L. -J. L., Schönrogge, K., Poland, R. L., & Purse, B. V. (2011). Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? *BioControl*, 56, 451–468.

Searle, C. L., & Christie, M. R. (2021). Evolutionary rescue in host–pathogen systems. *Evolution*, 75, 2948–2958.

Sheng, Z., Pettersson, M. E., Honaker, C. F., Siegel, P. B., & Carlborg, O. (2015). Standing genetic variation as a major contributor to adaptation in the Virginia chicken lines selection experiment. *Genome Biology*, 16, 219. https://doi.org/10.1186/s13059-015-0785-z

Skelton, J., Doak, S., Leonard, M., Creed, R. P., & Brown, B. L. (2016). The rules for symbiont community assembly change along a mutualism–parasitism continuum. *Journal of Animal Ecology*, 85(3), 843–853. https://doi.org/10.1111/1365-2656.12498

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J., & Kuris, A. M. (2003). Introduced species and their missing parasites. *Nature*, 421(6923), 628–630. https://doi.org/10.1038/nature01346

Villa, S. M., Altuna, J. C., Ruff, J. S., Beach, A. B., Mulvey, L. I., Poole, E. J., Campbell, H. E., Johnson, K. P., Shapiro, M. D., Bush, S. E., & Clayton, D. H. (2019). Rapid experimental evolution of reproductive isolation from a single natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 13440–13445.