

How maladaptation can structure biodiversity: eco-evolutionary island biogeography

Timothy E. Farkas^{1*}, Andrew P. Hendry², Patrik Nosil¹, and Andrew P. Beckerman¹

¹ Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

² Redpath Museum, Biology, McGill University, Montreal, H3A 2K6, Canada

Current research on eco-evolutionary dynamics is mainly concerned with understanding the role of rapid (or ‘contemporary’) evolution in structuring ecological patterns. We argue that the current eco-evolutionary research program, which focuses largely on natural selection, should be expanded to more explicitly consider other evolutionary processes such as gene flow. Because multiple evolutionary processes interact to generate quantitative variation in the degree of local maladaptation, we focus on how studying the ecological effects of maladaptation will lead to a more comprehensive view of how evolution can influence ecology. We explore how maladaptation can influence ecology through the lens of island biogeography theory, which yields some novel predictions, such as patch isolation increasing species richness.

Evolution and biodiversity: past research and a new direction

The idea that evolution generates biodiversity through speciation [1,2] has been well recognized for over a century. More recently, ecologists and evolutionary biologists are learning how rapid (or ‘contemporary’) evolution can influence a variety of ecological processes over short timescales [3,4], and thus might be an important driver of biodiversity without causing speciation [5–10]. The past two decades have seen an accumulation of research supporting this idea, both in the field of community genetics (see [Glossary](#)) [11,12] and more recently in the field of eco-evolutionary dynamics, the latter focusing explicitly on how rapid evolution can influence populations, communities, and ecosystems on contemporary timescales [13–16].

Much current research in eco-evolutionary dynamics focuses on scenarios where natural selection causes local adaptation to divergent habitats ([Figure 1A](#)) and thereby generates divergent ecological dynamics. This approach generally invokes local adaptation as an almost inevitable consequence of divergent ecological pressures, and thereby

underemphasizes an important and fundamental aspect of evolutionary ecology. Namely, the degree of local adaptation varies on a continuum from highly adapted to poorly adapted, with some degree of maladaptation being common in nature [17].

On the one hand, simply recognizing the existence of maladaptation is trivial because local adaptation can rarely if ever be perfect [18]. On the other hand, quantifying the degree of maladaptation – that is, the location of a population along an adaptation continuum – is decidedly non-trivial because it can vary substantially through time or across space and is expected to have a diversity of consequences. Quantitatively, adaptation and maladaptation can be measured in percentages or proportions and are converse quantities ($1 - \text{adaptation} = \text{maladaptation}$). Therefore, a population that is 100% locally adapted (achieving maximum possible fitness) is 0% maladapted, and vice versa. This formulation works very generally in theory, although in practice requires attention to nuances, such as the use of traits versus fitness to define maladaptation, and whether

Glossary

Community genetics: a field of study investigating the influence of genetic variation within species on the ecology of communities and ecosystems.

Connectivity: measure of predicted immigration to a habitat patch from surrounding patches, calculated using distances between patches, dispersal ability of the focal organism, and population sizes (see also Isolation).

Eco-evolutionary dynamics: related to community genetics, a field of study investigating interactions between ecology and evolution on contemporary timescales.

Founder effects: a stochastic process by which the genetic makeup of a population in a newly colonized habitat differs from that of the source population (see also Genetic drift).

Gene flow: movement of alleles between populations via dispersal/migration, yielding modified allele frequency in recipient populations.

Genetic drift: stochastic changes in allele frequency owing to finite population size.

Inbreeding: increased population homozygosity due to mating among close relatives.

Isolation: the inverse of connectivity, although traditionally with respect only to distance between island and mainland.

Linkage disequilibrium: non-random association of alleles at multiple genomic loci

(Mal)adaptation: a continuously variable spectrum of local adaptation, from very poorly adapted to very well adapted.

Metacommunity: a group of local communities linked by dispersal.

Metapopulation: a group of local populations linked by dispersal.

Pleiotropy: when variants (alleles) of a single gene influence multiple phenotypic traits.

Corresponding author: Farkas, T.E. (timothy.farkas@gmail.com).

Keywords: maladaptation; biodiversity; eco-evolutionary dynamics; island biogeography; species interactions; gene flow.

*Current address: Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA.

0169-5347/

© 2015 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2015.01.002>

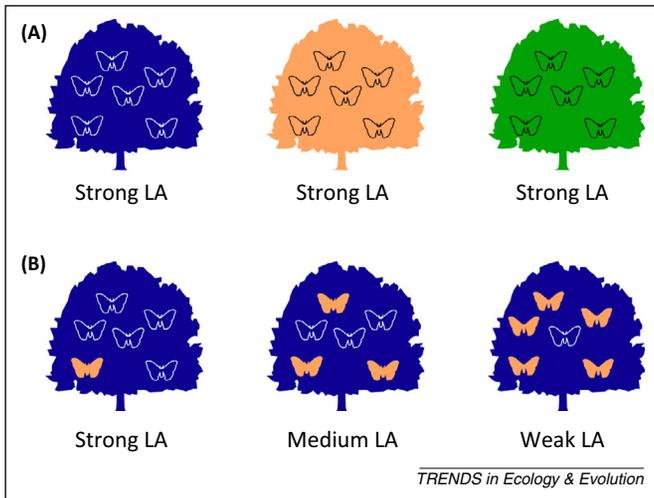


Figure 1. Divergent local adaptation versus degrees of (mal)adaptation. Different-colored trees represent divergent habitat types and therefore different selective environments. Moths represent an evolutionarily dynamic species, with color-matching to habitats representing local adaptation (LA). (A) Local adaptation to divergent habitats results in phenotypically divergent populations that each exhibit 100% local adaptation (0% maladaptation). (B) Evolutionary processes lead to variation in the degree of local adaptation, and hence to phenotypically divergent populations, but habitats all have the same type (i.e., there is no divergent selection).

maladaptation should be considered in an absolute or relative sense [18].

Our main thesis is that the degree of maladaptation in a given population can substantially influence aspects of local biodiversity (Figure 1B). To develop this argument, we outline three basic steps that link rapid evolution to biodiversity via maladaptation (Figure 2). In developing this argument we use the term ‘(mal)adaptation’ to emphasize the continuum [18], and the terms ‘maladaptation’ and ‘adaptation’ when we refer to relative locations on, or directional movement across, that continuum.

In step 1, we highlight several mechanisms that can generate maladaptation, such as gene flow between populations adapted to divergent environments [17]. In step 2, we highlight how (mal)adaptation in one species can alter the abundances of other species in a community (‘species abundances’), according to theory on networks of ecological interactions, such as food webs [19,20]. In step 3, we emphasize how variation in species abundances arising from steps 1 and 2 can influence species richness through effects on extinction and colonization [21,22]. We then propose an eco-evolutionary theory of island biogeography [23,24] that incorporates (mal)adaptation, and suggest a research program for its study.

We use island biogeography as a predictive framework, as opposed to parallel concepts such as the metacommunity [25,26], because island biogeography is a well-known and intuitive simplification of natural ecological complexity. Moreover, it focuses explicitly on the roles of island isolation and area as factors that influence rates of extinction and colonization, and are also factors that can influence (mal)adaptation. Island biogeography thus provides an excellent starting point for extending our understanding of evolutionary mechanisms that drive patterns of biodiversity, and we anticipate that future work could allow a similar extension to be made to metacommunity theory.

Step 1: evolution drives (mal)adaptation

We provide a brief overview of how the four core evolutionary processes (genetic drift, gene flow, natural selection, and mutation) can generate quantitative variation in (mal)adaptation. We describe the basic ways in which (mal)adaptation is shaped by each mechanism, which often oppose one another, as well as relevant population demographic and geographic considerations, which become important for our arguments around island biogeography. Throughout this section we make the reasonable assumption that patch area and population size are positively related [27], and therefore imply effects of patch area when discussing effects of population size.

Genetic drift

Genetic drift is a stochastic process that can generate maladaptation by causing the spread and fixation of deleterious alleles. Although drift is expected to be strongest for neutral loci, it can also influence loci under selection, potentially compromising local adaptation. Similarly, founder effects can be expected to generate (mal)adaptation in newly colonized habitats. In addition, genetic drift and/or founder effects coupled with inbreeding can generate inbreeding depression, which can be manifested as generalized maladaptation unrelated to any particular ecological environment [28]. Genetic drift is most pronounced in small and isolated populations, and where gene flow from divergent populations is less likely (see also the next section). Thus, maladaptation arising from genetic drift will be greater, or more likely, in small and isolated populations than in large and well-connected populations.

Gene flow

Gene flow can both increase and decrease maladaptation, depending on whether migrants (dispersers) are locally adapted to different or similar environments. In the first case, gene flow is likely to be deleterious and cause maladaptation when metapopulations inhabit heterogeneous patch networks, wherein different alleles are favored in different environments [29–32]. In the second case, gene flow is likely to be beneficial in metapopulations inhabiting homogeneous patch networks, where it provides the raw material for adaptation [33,34] and can mitigate the depressive effects of inbreeding [28]. Importantly, these beneficial effects usually accrue at very low levels of gene flow, whereas deleterious effects are expected with higher levels of gene flow [35]. Given data on population sizes, patch spatial configuration, and patch-level phenotypes, it is possible to quantify the amount of gene flow from similar versus different environments, and thereby to predict expected levels of (mal)adaptation [31].

Natural selection and constraints on adaptation

Although the primary outcome of natural selection is to increase adaptation, several types of constraints can interact with natural selection to generate maladaptation [36]. First, genetic correlations among traits caused by pleiotropy or linkage disequilibrium [37,38] can result in maladaptation of particular traits, even while other traits are becoming better adapted. Second, evolutionary conflict can cause maladaptation. For example, sexual conflict can

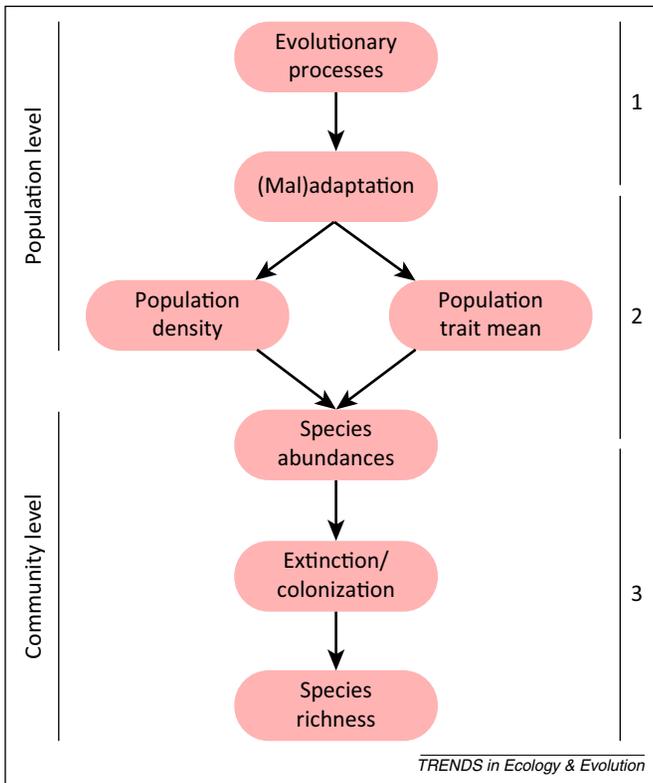


Figure 2. Schematic of the processes by which (mal)adaptation influences species richness. Evolutionary processes (selection, gene flow, drift) lead to (mal)adaptation in a focal species. (Mal)adaptation can influence species–interaction traits and/or population density of that species, either of which can then influence species abundances in a local community. Changes in the abundances of species in the community can influence extinction/colonization dynamics throughout the community, resulting in modified local diversity. Note that the arrows are drawn unidirectionally to highlight the mechanism of focus, but are not intended to indicate that effects may not flow up this chain of events. Numbers refer to the three main steps of the process as outlined in the main text, and annotations indicate the level of biological organization at which each process/concept focuses.

cause maladaptation in a trait for one sex that is driven by selection on that trait in the other sex [39,40]. Third, environmental change can generate temporally variable selection that contributes to maladaptation [41,42]. Although patch connectivity and area have been investigated as important consequences for divergent selection in the context of adaptive radiation [43,44], future research will be necessary to determine whether connectivity and area can have direct consequences for selection generally.

Mutation

Mutation is the ultimate source of new genetic variation. Mutation can thus generate maladaptation directly through the production of deleterious alleles. These negative effects will be stronger in smaller populations, which are more prone to chance fixation of deleterious alleles [45,46]. Mutation is also a source of novel beneficial alleles, and the rate of their production can limit adaptation, particularly in small populations ([46], but see [47]).

Step 2: (mal)adaptation can influence species abundances

We outline here how (mal)adaptation within one species can influence the abundance of other species in a local

community (‘species abundances’) through species interactions. To begin, we emphasize that (mal)adaptation refers to variation in the fit of traits to the environment of organisms expressing them. However, for (mal)adaptation to influence species interactions, those traits must either be important to species interactions themselves (‘species–interaction traits’) or directly cause changes in population density of the focal species (Figure 3). Although changes in species–interaction traits can often be concurrent with changes in population density, this is not inevitably so. For instance, densities can change due to (mal)adaptation in traits not related to species interactions, such as temperature tolerance (Figure 3, ‘other traits’), and species–interaction traits can change without altering population density, as in the case of soft selection [48,49].

Following established concepts in food web ecology [19,20], the effects of (mal)adaptation on species–interaction traits and/or population density can propagate through entire species–interaction networks, influencing the population density and/or species–interaction traits of other species (Figure 3; ‘Species 2’). Expanding Figure 3 to a large network of interacting species (not pictured), (mal)adaptation can drive variation in species abundances for entire communities.

To demonstrate the various ways in which (mal)adaptation can influence species abundances, we offer a three trophic level predator–herbivore–plant system as an example. In this example, inbreeding-based (mal)adaptation in a predator, causing reduced population density of the predator, might result in a higher abundance of the herbivore species on which it feeds. Alternatively (or additionally), gene flow between predator populations might lead to suboptimal predator foraging traits, which could similarly result in a higher abundance of the herbivore species. Furthermore, these direct effects of (mal)adaptation on adjacent species (predator–herbivore) might affect non-adjacent members through indirect interactions (predator–plant). Continuing the example above, maladaptation in a predator that increases herbivore abundance might cause a trophic cascade, thereby lowering the abundance of plant species on which they feed [50].

Step 3: (mal)adaptation can influence extinction and colonization

We draw here on recent theoretical work which combines food-web theory with the classic equilibrium theory of island biogeography [23,24], to illustrate mechanisms through which (mal)adaptation that changes species abundances can influence species richness. In classical island biogeography, increasing island area and increasing connectivity to the mainland both increase colonization rates and decrease extinction rates, yielding higher equilibrium species richness (Figure 4A) [23]. In the ‘trophic theory of island biogeography’, extinction/colonization rates are additionally modified by food-web structure and species abundances, shifting predictions of equilibrium species richness [21,22].

For example, the likelihood of a predator successfully colonizing and persisting on an island should increase with the abundance its prey species, and should decrease with the abundance of its competitors (although the likelihood of

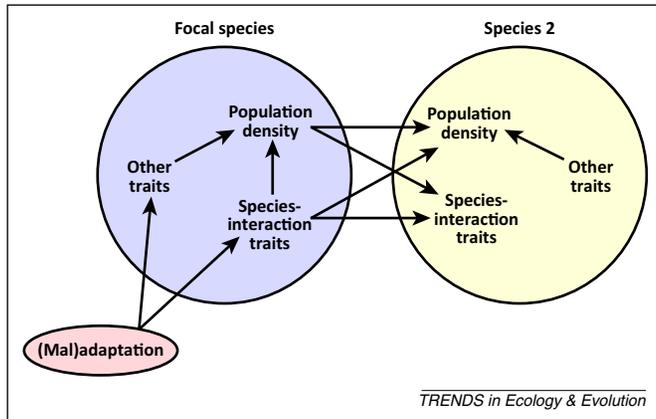


Figure 3. Conceptual diagram of step 2: how (mal)adaptation can influence species abundances. (Mal)adaptation, here specifically the process by which evolution moves a population along the (mal)adaptation continuum, influences the traits of a focal species. Those traits might be related to species interactions ('species-interaction traits') or related to other aspects of the environment ('other traits'). Both species-interaction traits and other traits might influence the population density of the focal species. Effects of (mal)adaptation on the focal species can propagate through a species interaction network because population density and/or species-interaction traits in the focal species influence those of other species. Note: all arrows are unidirectional, but many species properties might well be drawn with bidirectional arrows.

an individual propagule arriving should be unaffected by resident community structure). Using knowledge of interaction strengths between the predator and its competitors, together with the abundances of each interacting species, it is possible to predict the colonization and extinction rates for the predator above and beyond those predicted using classical island biogeography.

In step 2, we showed how density- or trait-based (mal)adaptation can influence species abundances through well-defined pathways in species interaction networks. Because the trophic theory of island biogeography demonstrates how variation in species abundances can modify extinction/colonization dynamics, the trophic theory supports the notion that (mal)adaptation can influence colonization and extinction rates as well. Hence, (mal)adaptation can influence species richness. For example, a maladapted predator with inefficient foraging might increase the species richness of an assemblage on which it preys by increasing the likelihood of successful prey colonization, and by decreasing the likelihood of prey extinction.

Eco-evolutionary island biogeography

Integrating the above steps, we now outline a framework for eco-evolutionary island biogeography that incorporates (mal)adaptation. In classical island biogeography, connectivity and area can influence species richness through niche-neutral and stochastic effects on colonization/extinction dynamics. In addition, connectivity and area can influence (mal)adaptation through their effects on a variety of evolutionary processes (step 1). Thus, combining steps 1–3, connectivity and area can influence species richness through their effects on (mal)adaptation. In short, there are two independent pathways by which connectivity and area can influence species richness, both mediated by effects on colonization/extinction dynamics. We argue that predictions of equilibrium species richness will be most accurate

when considering an eco-evolutionary island biogeography that integrates the traditionally considered effects of patch connectivity and area (Figure 4A) with their effects via (mal)adaptation (Figure 4B,C).

In any given metacommunity, the traditional and (mal)adaptation-mediated effects of connectivity and area on species richness might operate alone or in concert. If both pathways are operating simultaneously, they very well might have effects on species richness of contrasting magnitude, and might even have effects in contrasting directions. For example, in any scenario where connectivity increases maladaptive gene flow, and maladaptation leads to reduced species richness, traditional and (mal)adaptation-mediated effects of connectivity on species richness should oppose one another. We therefore argue that it is valuable (and possibly essential) to evaluate the effects of both mechanisms because eco-evolutionary island biogeography can yield predictions of species richness that equal, exacerbate (Figure 4B), nullify, or even invert (Figure 4C) traditionally recognized effects of patch connectivity and area. Two empirical examples from recent eco-evolutionary research highlight these effects and support their general application.

Timema cristinae stick insects

Gene flow between *T. cristinae* populations locally adapted to different host-plant species causes populations to become poorly camouflaged (maladapted) on their resident host plants [31]. Thus, connectivity among populations on different host-plant species strongly influences the degree of camouflage maladaptation [51]. Recent experiments show that camouflage maladaptation has the ecological consequence of decreasing the species richness of cohabitating arthropods, such as caterpillars and beetles, because avian predators that eat stick insects are attracted to host-plant patches harboring maladapted *Timema* [9].

In this scenario, the (mal)adaptation-mediated effect of connectivity is to decrease equilibrium species richness, opposing the traditionally predicted effect of connectivity (Figure 4A). If the (mal)adaptation-mediated effect outweighs the traditional effect, equilibrium arthropod species richness could actually be lower on well-connected patches in nature (Figure 4C). Further landscape-scale experimentation and observation will be necessary to determine whether natural patterns reflect the findings of the experiments, and to compare the magnitude and direction of the multiple effects of connectivity.

Threespine stickleback

Gene flow between lake and stream populations of threespine stickleback (*Gasterosteus aculeatus*) causes maladaptation in foraging morphology [52], and some evidence suggests it might reduce stickleback population density [53]. In a stream habitat, where well-adapted stickleback feed on benthic macroinvertebrates, maladaptive gene flow from lake populations should relax predation pressure by decreasing foraging efficiency on the benthos. This effect could increase successful macroinvertebrate colonization from nearby streams and reduce the likelihood of extinction, yielding higher equilibrium species richness for this guild.

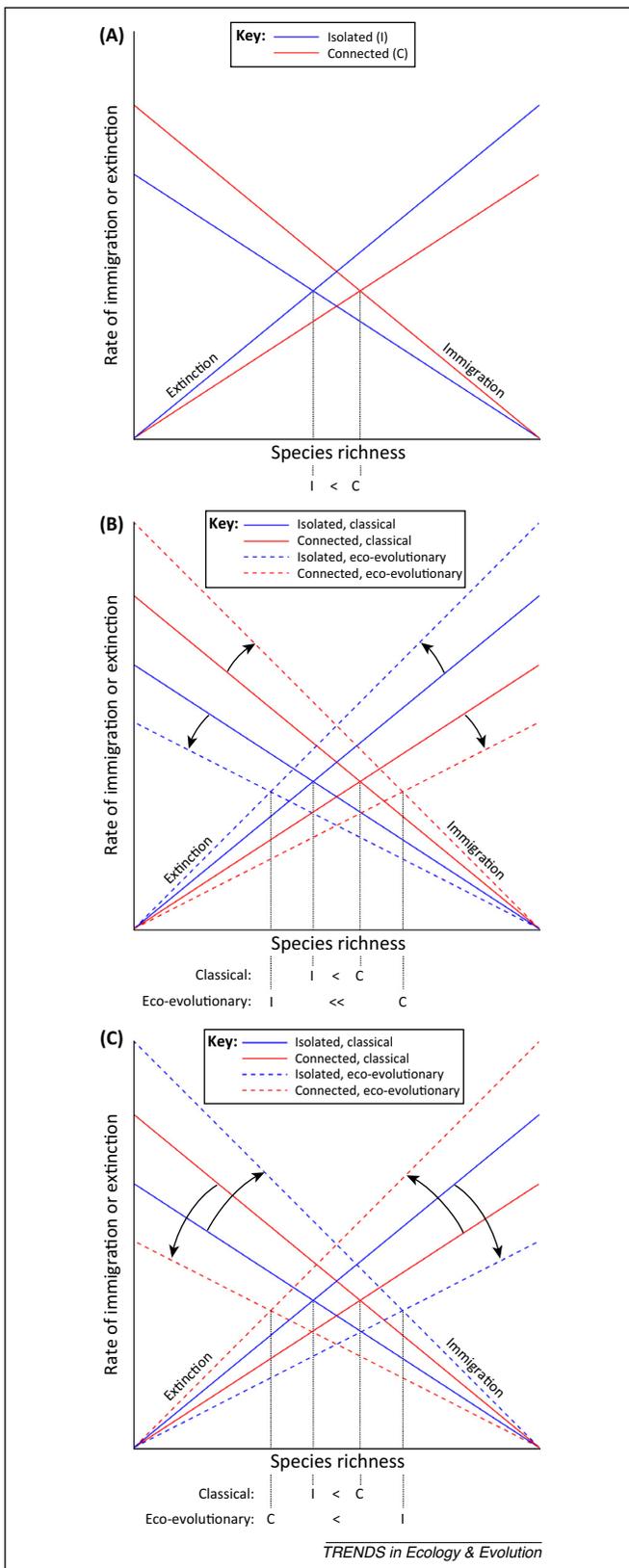


Figure 4. Consequences of (mal)adaptation for predictions of island theory. **(A)** Classical island theory predicts that island isolation will decrease immigration rates (downward-sloping curves), and increase extinction rates (upward-sloping curves) [59]. Consequently, equilibrium levels of species richness are predicted to be lower for isolated islands than for well-connected islands. **(B)** (Mal)adaptation can exacerbate the negative effects of isolation on equilibrium species richness, further constraining colonization and promoting extinction. **(C)** Alternatively, (mal)adaptation might invert classically predicted effects of isolation on equilibrium species richness, potentially promoting colonization and reducing extinction. Whether maladaptation will exacerbate

Contrary to the previous example, the (mal)adaptation-mediated effect of connectivity on species richness should exacerbate, rather than oppose, the traditional effect, such that the two effects combine to increase species richness (at least of benthic macroinvertebrates) in well-connected systems with more gene flow (Figure 4B). Although empirical work demonstrating links between gene flow and invertebrate species richness in stickleback has yet to be conducted, the above hypothesis demonstrates how considering (mal)adaptation can provide a set of interesting predictions about equilibrium species richness. With these motivating examples, we can now elaborate on how more generally to test predictions of eco-evolutionary biogeography.

Testing the theory

Investigations into eco-evolutionary island biogeography should ultimately be focused on understanding the relative contribution of traditional versus (mal)adaptation-mediated effects of patch connectivity and area to patterns of species richness. In the following we suggest methods for testing individual components of the theory, as well as more comprehensive tests that might capture the entirety of eco-evolutionary island biogeography. We refrain from offering detailed predictions for the methods described below because they will invariably be dependent on the specific processes at play in any given study system. We stress that the issue is not that detailed predictions are impossible, but rather that they will be system-specific, and direct the reader back to the two examples above for ideas on how to generate such predictions. As eco-evolutionary research accumulates both within and across systems, it will be fruitful to employ meta-analyses to gain an understanding of how important (mal)adaptation is for driving natural patterns of biodiversity.

(Mal)adaptation and species richness

An initial step in researching eco-evolutionary island biogeography is to evaluate the effects of (mal)adaptation on species richness, holding connectivity and area constant if possible. If (mal)adaptation does not itself influence species richness, the (mal)adaptation-mediated pathway from connectivity and area to species richness cannot operate. To do so, researchers could perform experiments that directly manipulate (mal)adaptation in the lab or field, and measure the effects on species richness (e.g., [9]). Experiments of this type should be complemented with observational studies, which could correlate natural levels of (mal)adaptation with species richness. Observational studies are highly valuable because they can help determine whether otherwise-unexplained natural patterns of biodiversity can be explained by rapid evolution.

Connectivity, area, and (mal)adaptation

Similarly, the (mal)adaptation-mediated pathway to species richness cannot operate if patch connectivity and/or

(B) or invert (C) the effects of isolation is highly context-specific, and requires detailed knowledge of a system in which (mal)adaptation is appreciable (see main text).

area do not influence (mal)adaptation. Effective experiments to evaluate the influence of connectivity and area on (mal)adaptation are more difficult than those evaluating the influence of (mal)adaptation on species richness, because they rely on evolution as a consequence of connectivity and area. Nevertheless, evolution can occur very rapidly when generation times are short and/or evolutionary forces are strong [54], and thus laboratory or even field experiments should be achievable on reasonable timescales in many systems. Such experiments could manipulate connectivity and area by varying the distance between habitat patches in heterogeneous environments as well as the size of those habitat patches, and then compare (mal)adaptation across levels of connectivity and patch area. Because of time constraints imposed by the process of evolution, observational studies to complement experiments are even more important here because they may capture the effects of connectivity and area on (mal)adaptation that have been occurring over longer timescales.

A holistic approach

Evaluating the relative roles of traditional and (mal)adaptation-mediated pathways from connectivity and area to species richness might be achievable with single experiments. One possible approach uses meso/microcosm experiments with metacommunities in heterogeneous patch networks. We suggest crossing a manipulation of patch connectivity (and/or area) with a manipulation of genetic diversity in the focal community member, thus changing the potential for (mal)adaptive responses (e.g., as in [55,56]). The effects of connectivity (and/or area) on species richness without a (mal)adaptive response could then be compared with the effect of connectivity in scenarios showing a (mal)adaptive response to tease apart the relative influences of traditional and (mal)adaptation-mediated effects. As above, such experiments would ideally be conducted in nature, logistics and ethics permitting.

Concluding remarks

Our suggested fusion of eco-evolutionary dynamics and island biogeography theory adds to a growing body of literature aimed at unifying predictive theories at small (genetic) and large (community) scales [6,43,57,58], where island biogeography and related concepts play a central role. We anticipate that our modifications of current theory to include several evolutionary mechanisms contributing to (mal)adaptation will help to resolve questions about the processes driving patterns of biodiversity. We furthermore hope that our ideas will help to stimulate and direct future research toward an investigation of the role of (mal)adaptation in driving ecological patterns, and encourage researchers with appropriate systems to apply them toward this end.

Acknowledgments

We thank Ilkka Hanski, Blake Matthews, Rudiger Riesch, Moritz Muschick, Victor Soria-Carrasco, Aaron Comeault, Gabriela Montejokovacevich, and Emma Curran for helpful comments on the manuscript. Rebecca Safran and the University of Colorado are thanked as an academic host to T.E.F. The European Research Council (ERC Starter Grant NatHisGen R/129639 to P.N.), the Royal Society of London

(University Research Fellowship to P.N.), and the British Ecological Society (Research Grant 4878-5918 to T.E.F.) are thanked for funding.

References

- 1 Darwin, C. (1859) *On The Origin of Species*, John Murray
- 2 Coyne, J.A. and Orr, H.A. (2004) *Speciation*, Sinauer Associates
- 3 Hairston, N.G. *et al.* (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8, 1114–1127
- 4 Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329–332
- 5 Thuiller, W. *et al.* (2013) A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol. Lett.* 16, 94–105
- 6 Urban, M.C. *et al.* (2008) The evolutionary ecology of metacommunities. *Trends Ecol. Evol.* 23, 311–317
- 7 Hendry, A. (2013) Eco-evolutionary dynamics: community consequences of (mal)adaptation. *Curr. Biol.* 23, R869–R871
- 8 Johnson, M.T.J. *et al.* (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 1593–1605
- 9 Farkas, T.E. *et al.* (2013) Evolution of insect camouflage drives rapid change of ecological communities. *Curr. Biol.* 23, 1835–1843
- 10 Urban, M.C. (2013) Evolution mediates the effects of apex predation on aquatic food webs. *Proc. R. Soc. B: Biol. Sci.* 280, 20130859
- 11 Whitham, T.G. *et al.* (2006) A framework for community and ecosystem genetics: From genes to ecosystems. *Nat. Rev. Genet.* 7, 510–523
- 12 Hersch-Green, E.I. *et al.* (2011) Community genetics: what have we accomplished and where should we be going? *Philos. Trans. R. Soc. B: Biol. Sci.* 366, 1453–1460
- 13 Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429
- 14 Kinnison, M.T. and Hairston, N.G. (2007) Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct. Ecol.* 21, 444–454
- 15 Fussmann, G.F. *et al.* (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21, 465–477
- 16 Pelletier, F. *et al.* (2009) Eco-evolutionary dynamics. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 1483–1489
- 17 Crespi, B.J. (2000) The evolution of maladaptation. *Heredity* 84, 623–629
- 18 Hendry, A.P. and Gonzalez, A. (2008) Whither adaptation? *Biol. Philos.* 23, 673–699
- 19 Pimm, S. (2002) *Food Webs*, University of Chicago Press
- 20 Ohgushi, T. *et al.* (2012) *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives*, Cambridge University Press
- 21 Holt, R.D. (2010) Toward a trophic island biogeography: Reflections on the interface of island biogeography and food web ecology. In *The Theory of Island Biogeography Revisited* (Losos, J.B. and Ricklefs, R.E., eds), pp. 143–185, Princeton University Press
- 22 Gravel, D. *et al.* (2011) Trophic theory of island biogeography. *Ecol. Lett.* 14, 1010–1016
- 23 Schoener, T.W. *et al.* (2010) The MacArthur–Wilson equilibrium model: a chronicle of what it said and how it was tested. In *The Theory of Island Biogeography Revisited* (Losos, J.B. and Ricklefs, R.E., eds), pp. 52–87, Princeton University Press
- 24 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 25 Leibold, M.A. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613
- 26 Holyoak, M. *et al.* (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*, University of Chicago Press
- 27 Sandoval, C.P. (1994) The effects of the relative geographic scales of gene flow and selection on morph frequencies in the walking-stick *Timema cristinae*. *Evolution* 48, 1866–1879
- 28 Keller, L.F. and Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends Ecol. Evol.* 17, 230–241
- 29 Barton, N. and Hewitt, G. (1989) Adaptation, speciation and hybrid zones. *Nature* 341, 497–503
- 30 Nosil, P. *et al.* (2005) Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* 59, 705–719
- 31 Bolnick, D.I. and Nosil, P. (2007) Natural selection in population subject to migration load. *Evolution* 61, 2229–2243

- 32 Hanski, I. *et al.* (2010) Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. *Am. Nat.* 177, 29–43
- 33 Feder, J.L. *et al.* (2003) Allopatric genetic origins for sympatric host-plant shifts and race formation in *Rhagoletis*. *Proc. Natl. Acad. Sci.* 100, 10314–10319
- 34 Barrett, R.D.H. and Schluter, D. (2008) Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44
- 35 Garant, D. *et al.* (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct. Ecol.* 21, 434–443
- 36 Arnold, S.J. (1992) Constraints on phenotypic evolution. *Am. Nat.* 140, S85–S107
- 37 Agrawal, A.F. and Stinchcombe, J.R. (2009) How much do genetic covariances alter the rate of adaptation? *Proc. Biol. Sci.* 276, 1183–1191
- 38 Hansen, T.F. and Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. *J. Evol. Biol.* 21, 1201–1219
- 39 Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
- 40 Gosden, T.P. *et al.* (2012) The B-matrix harbors significant and sex-specific constraints on the evolution of multicharacter sexual dimorphism. *Evolution* 66, 2106–2116
- 41 Siepielski, A.M. *et al.* (2009) It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol. Lett.* 12, 1261–1276
- 42 Bell, G. (2010) Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 87–97
- 43 Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature* 408, 847–850
- 44 Kisel, Y. and Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* 175, 316–334
- 45 Burt, A. (1995) The evolution of fitness. *Evolution* 49, 1
- 46 Eyre-Walker, A. and Keightley, P.D. (2007) The distribution of fitness effects of new mutations. *Nat. Rev. Genet.* 8, 610–618
- 47 Barton, N. (2010) Understanding adaptation in large populations. *PLoS Genet.* 6, e1000987
- 48 Wade, M.J. (1985) Soft selection, hard selection, kin selection, and group selection. *Am. Nat.* 125, 61–73
- 49 Saccheri, I. and Hanski, I. (2006) Natural selection and population dynamics. *Trends Ecol. Evol.* 21, 341–347
- 50 Terborgh, J. and Estes, J.A., eds (2010) *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, Island Press
- 51 Nosil, P. (2009) Adaptive population divergence in cryptic color-pattern following a reduction in gene flow. *Evolution* 63, 1902–1912
- 52 Moore, J.S. and Hendry, A.P. (2005) Both selection and gene flow are necessary to explain adaptive divergence: evidence from clinal variation in stream stickleback. *Evol. Ecol. Res.* 7, 871–886
- 53 Moore, J.-S. and Hendry, A.P. (2009) Can gene flow have negative demographic consequences? Mixed evidence from stream threespine stickleback. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 1533–1542
- 54 Hendry, A.P. and Kinnison, M.T. (1999) The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53, 1637–1653
- 55 Yoshida, T. *et al.* (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424, 303–306
- 56 Turcotte, M.M. *et al.* (2011) The impact of rapid evolution on population dynamics in the wild: Experimental test of eco-evolutionary dynamics. *Ecol. Lett.* 14, 1084–1092
- 57 Vellend, M. (2003) Island biogeography of genes and species. *Am. Nat.* 162, 358–365
- 58 Jordi Moya-Laraño, J.R.B.-C. (2014) Eco-evolutionary spatial dynamics: Rapid evolution and isolation explain food web persistence. *Adv. Ecol. Res.* 50, 75–143
- 59 Brown, J.H. and Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449