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Evolutionary origins for ecological patterns in space

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Historically, many biologists assumed that evolution and ecology acted independently because evolution occurred over distances too great to influence most ecological patterns. Today, evidence indicates that evolution can operate over a range of spatial scales, including fine spatial scales. Thus, evolutionary divergence across space might frequently interact with the mechanisms that also determine spatial ecological patterns. Here, we synthesize insights from 500 eco-evolutionary studies and develop a predictive framework that seeks to understand whether and when evolution amplifies, dampens, or creates ecological patterns. We demonstrate that local adaptation can alter everything from spatial variation in population abundances to ecosystem properties. We uncover 14 mechanisms that can mediate the outcome of evolution on spatial ecological patterns. Sometimes, evolution amplifies environmental variation, especially when selection enhances resource uptake or patch selection. The local evolution of foundation or keystone species can create ecological patterns where none existed originally. However, most often, we find that evolution dampens existing environmental gradients, because local adaptation evens out fitness across environments and thus counteracts the variation in associated ecological patterns. Consequently, evolution generally smooths out the underlying heterogeneity in nature, making the world appear less ragged than it would be in the absence of evolution. We end by highlighting the future research needed to inform a fully integrated and predictive biology that accounts for eco-evolutionary interactions in both space and time.

eco-evolutionary dynamics | spatial ecology | local adaptation

Biologists since Darwin have proposed that evolution occurred slowly and across great distances (1). Consequently, many ecologists assumed that they could safely ignore evolution, especially at fine temporal and spatial scales (2). By the end of the last century, however, evidence had accumulated that populations could evolve on timescales fast enough so that evolution could influence ecological dynamics (3), resulting in the widespread realization that ecological thinking was incomplete without accounting for evolution. Subsequent studies contributed to the burgeoning field of

eco-evolutionary dynamics (3, 4), designated science's "newest synthesis" (5). However, most eco-evolutionary studies have focused on temporal dynamics (3, 4, 6).

Just as perceptions about the temporal scale of evolution have changed, new findings are challenging perceptions about the spatial scale of adaptation. Local adaptation refers to a pattern whereby natural selection increases the local frequency of genotypes with higher survival and fecundity [i.e., the fitness or long-term success of populations (7)] relative to foreign genotypes (8–10). Biologists often discover adaptive

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divergence not just across broad continental scales but at the fine spatial scales that characterize many ecological patterns, including population abundance, community diversity, and ecosystem function (11, 12). Fine-scaled, or microgeographic, adaptation can occur not just for small species and poor dispersers but also for larger-bodied and better-dispersing organisms (11) (Fig. 1). Locally adapted populations of these species, moreover, can alter the ecology of other species that are not adapting on fine scales. These realizations greatly expand the range of spatial scales, species, and ecosystems for which evolution might influence spatial ecological patterns.

Conceptual Framework for Ecoevolution in Space

We develop a new framework for understanding how evolution shapes ecological patterns, by extending an existing framework on phenotypic variation to variation in ecological impacts. In the phenotypic version, adaptive evolution dampens (countergradient) or amplifies (cogradient) the effect of environmental heterogeneity on phenotypic divergence in space (13). For example, low temperature usually slows growth, but populations from colder environments often evolve countergradient adaptations that dampen thermal impacts on growth rates (14). Less commonly, cogradient selection amplifies existing environmentally induced variation (15).

Evolution can affect spatial ecological patterns analogously by altering not just individual phenotypes but also the properties of populations, communities, and ecosystems (16). We propose a spatial eco-evolutionary framework that predicts when and how local adaptation alters ecological patterns relative to that expected without evolution, and then enumerate mechanisms that explain these patterns (Fig. 2). Applying this framework first requires understanding the null spatial ecological pattern expected without evolutionary divergence among populations, such that all populations are characterized by the same mean or ancestral trait. Then we compare the observed spatial ecological pattern (e.g., population abundance, community diversity, productivity) in the presence of evolution to this null pattern. Adaptive evolution can

dampen, amplify, or create new spatial ecological patterns relative to that expected in the absence of evolution. Maladaptive evolution (e.g., through drift or gene flow) will generally reverse the direction of these effects.

For example, let us assume that spatial environmental variation in temperature, nutrients, or predation risk increases an ecological property like population abundance, community diversity, or ecosystem productivity and generates a subsequent spatial pattern on the landscape. If populations along this environmental gradient evolve in ways to reduce the strength of that relationship, then evolution will dampen the original spatial pattern (Fig. 2, *Left*). Without accounting for local adaptation, a researcher might incorrectly conclude that the environment does not influence ecological patterns. Instead, the environment shapes ecological patterns so strongly that they initiate the adaptations that obscure them. This dampening scenario in space echoes cryptic eco-evolutionary dynamics in time that obscure predator–prey oscillations (17) and other ecological dynamics (18, 19). For example, stick insects evolve camouflage on alternative host plants, dampening the effects of heterogeneous predation risks among host plants and supporting more even population abundances and other associated ecological patterns (20).

Alternatively, populations might adapt in ways that strengthen the relationship between the environment and ecological responses, thereby amplifying the original spatial structure (Fig. 2, *Middle*). In this case, a researcher might incorrectly overestimate the ecological effects of the environmental gradient, because ecological and evolutionary effects operate jointly. For example, spotted salamanders evolve to forage more in low-resource environments, reducing resources further, and amplifying the original resource differences (21).

Spatial variation in genotypes also can create new ecological patterns where none existed previously or even create qualitatively different patterns, such as by altering species composition (Fig. 2, *Right*). More specifically, either adaptation to an environmental gradient unrelated to the ecological response or genetic diversity maintained through random processes can create new or qualitatively different ecological patterns compared to what existed in their absence. For instance, different plant genotypes located in close proximity often host different herbivorous species (16, 22).

Literature Review

We apply this framework to 500 studies published over the last century to interpret how evolution alters spatial ecological patterns (*SI Appendix, Table S1* and Fig. 3). We selected studies from a systematic keyword search followed by a backward review of cited literature of relevant publications (for details, see *SI Appendix*). To avoid the confounding effect of phenotypic plasticity, we only included studies that demonstrated a genetic basis for trait variation via common garden or reciprocal transplant experiments or an understanding of trait heritability or the genes underlying trait variation. We focused on natural populations and thus excluded studies on commercial, laboratory, or domestic cultivars, because we were specifically interested in understanding how evolution modifies spatial patterns in nature. We limited analyses to traits that affect ecological properties in space, such as those related to population fitness and abundance, species interactions, and ecosystem properties like biomass or nutrient uptake or retention. Using this published information, we compared spatial patterns with evolution to those expected without evolution. We then determined whether evolution dampens or

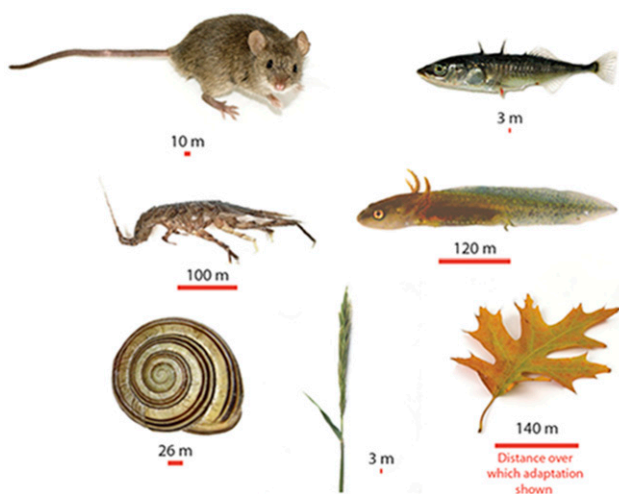


Fig. 1. Widespread evidence for microgeographic adaptation. Many species adapt at surprisingly fine scales as indicated by red lines, including (clockwise from bottom left) banding in land snails, camouflaged isopods, allele frequencies in mice, feeding morphology in fish, feeding behavior in salamanders, herbivore-defended trees, and toxin-tolerant grass.

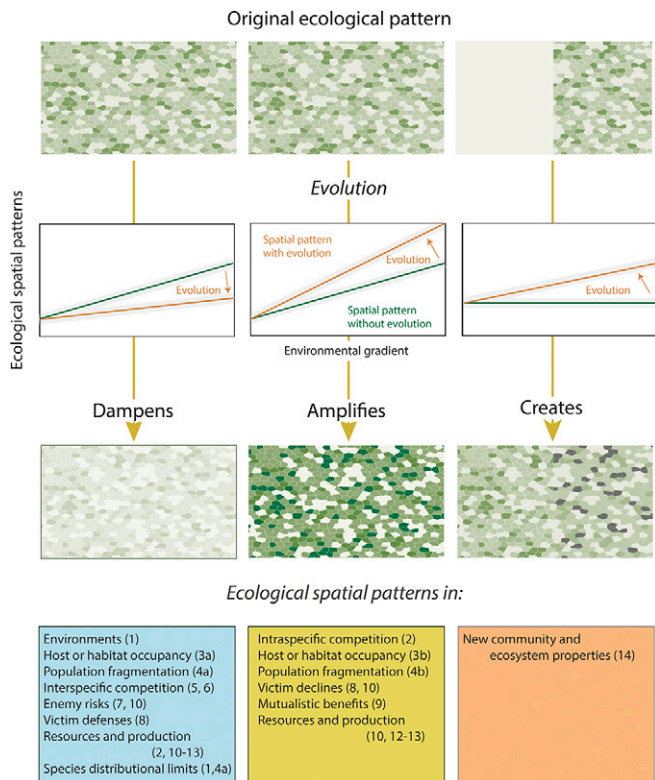


Fig. 2. Evolution can dampen, amplify, and create spatial ecological patterns, affecting everything from population abundances to species ranges. (Left) Evolution can dampen an existing ecological spatial pattern across an environmental gradient by reducing the slope. (Middle) Alternatively, evolution might amplify the original ecological spatial pattern. (Right) Evolution can also create a pattern where none existed before by creating a nonzero slope (changing unpatterned into patterned half) or completely novel patterns (e.g., new species composition indicated in purple patches). Numbered mechanisms correspond to those found in Table 1.

amplifies existing environmental heterogeneity or creates new spatial patterns entirely, according to our framework. We consider population adaptations across all temporal scales, ranging from short to long term, because evolution can alter ecological spatial patterns regardless of the speed with which they emerged.

Overall, we find that evolution dampens ecological patterns in space in 85% of studies, amplifies it in 13% of studies, and creates new patterns in 8% (Fig. 3). Percentages exceed 100% because, oftentimes, studies reveal more than one pattern. These effects were pattern-, trait-, and condition-specific: Adaptation of a given trait can dampen one ecological pattern while amplifying another, different traits can dampen or enhance the same pattern, and adapted traits can dampen a pattern in one region while amplifying it in another. Maladaptation through mutations, drift, or gene flow reverses the effect of adaptation on ecological patterns and produces a pattern more similar to or even exceeding the no-adaptation null pattern. The challenge is to discover general theories that predict these dependencies. Toward this end, we also identify 14 mechanisms from the reviewed literature that govern whether evolution dampens, amplifies, or creates spatial ecological patterns (Figs. 2 and 3 and Table 1, and italicized in the text below).

Population Abundances across Habitats

Local adaptation can enhance fitness in initially low-fitness habitats, thus *dampening fitness differences* across environments (23).

Local adaptation thereby provides a dominant mechanism that frequently evens out population abundances across environmental heterogeneity (24). For example, locally adapted three-spine sticklebacks (25) and bacteria (26) populations grew more abundant after adapting to local environments. The evolution of higher fitness occasionally equalizes abundances further by intensifying intraspecific competition and limiting large population sizes (27). Hence, local adaptation frequently dampens spatial variation in population abundances (94% of studies; Fig. 3) by equalizing population mean fitness across environments, weakens correlations between abundances and environmental gradients, and promotes colonization of marginal habitats.

In 1% of studies, local adaptation amplified, rather than dampened, differences in population abundances among habitats. *Density-dependent selection* can amplify resource-driven density differences by buffering the negative impacts from intraspecific competition and promoting even higher densities (28). For instance, guppies from a high-density population evolved to cope with intraspecific competition and reach higher densities than expected without evolution (29).

Metapopulation Patch Occupancy

At larger spatial scales, the balance between local extinction and regional colonization determines the proportion of occupied patches in a metapopulation. Increased extinction rates are expected to decrease patch occupancy (30). However, adaptation to local environments can decrease extinction rates, thereby expanding habitat use and patch occupancy and dampening environmental effects. For example, bacteria in an experimental metapopulation adapted to and colonized a novel environment, which expanded patch occupancy (31).

Dispersal also can elevate colonization rates and therefore increase patch occupancy in metapopulations. Theoretical models suggest that *dispersal can evolve* depending on kin competition, inbreeding, and spatiotemporal environmental variation (32–34). In particular, models indicate that spatial heterogeneity has contrasting effects on dispersal evolution, depending on the relative risks of dispersal and dispersing into lower-fitness habitats versus the benefits of avoiding local extirpation or environmental change (34–36). Under many conditions, habitat fragmentation is expected to select for higher dispersal (37), which would counteract the usually negative ecological impacts of fragmentation on colonization rates, occupancy levels, and metapopulation persistence. For example, fragmented landscapes selected for higher dispersal in Glanville fritillary butterflies and dampened fragmentation effects on patch occupancy (37, 38). However, if dispersal costs outweigh benefits, higher fragmentation can theoretically select for reduced dispersal, thereby decreasing occupancy, causing metapopulation collapse (39), and ultimately amplifying the original fragmentation effects, although support for this theoretical outcome is more limited.

Adaptation of habitat or host preference can dampen the effect of environmental variation on occupancy patterns by matching locally adapted phenotypes to specific habitat types (40). For example, Wrangler grasshoppers preferentially settle on substrates that match their camouflage (41). This habitat matching can support the adaptation of other traits associated with that habitat and increase patch occupancy beyond that expected from random dispersal. Also, the evolution of habitat generalists (42) would dampen effects on patch occupancy. In contrast, evolving a preference for the most frequent environment, especially at fine spatial scales (37), could instead amplify niche specialization, lower

How evolution affects ecological spatial patterns

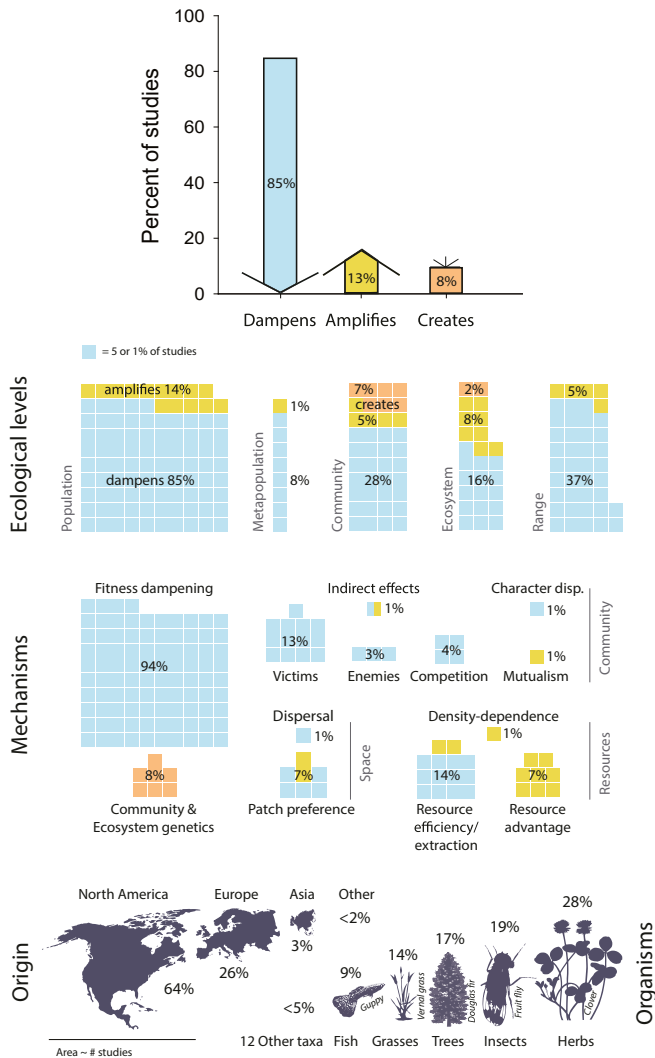


Fig. 3. Results from literature review including overall patterns, by ecological level, by mechanism, and by geographic origin and taxonomic group. Evolution usually dampens existing ecological patterns (blue), especially at population, metapopulation, and range levels. Evolution also can amplify existing patterns (yellow), especially for positive species interactions and resource-related ecosystem properties. Sometimes evolution creates new patterns (orange) when genetic variation within foundation or keystone species creates differences in dependent communities. Fourteen mechanisms grouped into five categories (details in Table 1) explain these divergent outcomes. We depict the dominant continental origins and taxonomic groups (most common species named) with icon size proportional to number of studies. Summed percentages exceed 100% because some studies include multiple effects. In waffle graphs, each block equals five studies or 1% of studies.

patch occupancy, and increase isolation. Thus, understanding when populations evolve to specialize on a subset of habitats or become generalists to multiple habitats can predict how adaptations in metapopulation traits modify environmental heterogeneity. Current information (SI Appendix, Table S1) suggests a slight trend toward dampening effects (5% vs. 2%; Fig. 3).

Both dispersal and habitat specialization might evolve jointly in response to spatial heterogeneity. In one model, low environmental heterogeneity selected for high-dispersing habitat generalists,

whereas higher heterogeneity selected for poor-dispersing habitat specialists (43). Additional models demonstrate the evolution of specialization and low dispersal with higher habitat heterogeneity under a larger parameter space (44). Thus, the joint evolution of higher dispersal and habitat generalists could further dampen environmental effects. Above a critical level of heterogeneity, the opposite pattern might result and further amplify already strong environmental heterogeneity.

Community Interactions, Composition, and Diversity

We find a general pattern in which *adaptation of victims* to enemies like predators, parasites, and pathogens weakens the strength of negative interactions (45, 46) and dampens the ecological impacts of patchily distributed enemies. For example, a marsh plant evolved less edible leaves in response to more intense herbivory, reducing leaf damage by 70% in high-herbivore regions (46). Populations also evolve to compete better against co-occurring species. Evening primrose evolved higher competitive ability against dandelions following experimental herbivore exclusion (47), thereby dampening differences in competitive outcomes between exclusion and control habitats.

Evolution also can dampen the impacts of interspecific competition on spatial productivity patterns. Competition normally limits productivity in diverse communities, but genotypes of different plant species that evolved together produced more overall biomass than genotypes of the same species evolving in isolation (48). *Character displacement*, where competing species evolve divergent resource use when together (49), can dampen diversity differences by allowing competing species to co-occur and dampen resource heterogeneity by more evenly redistributing attack rates among resources. For example, stickleback fish evolved preferences for pelagic rather than benthic invertebrates when co-occurring with benthic-feeding sculpin (50). Although less well documented, a few examples indicate that species can evolve *stronger mutualisms*. In one instance, legume populations evolved greater fitness benefits from local nitrogen-fixing bacteria (51), thereby amplifying the original mutualistic benefits. Overall, we find that adaptation usually dampens spatial patterns originating from negative interactions and amplifies those from positive interactions (52).

Another common finding is that genetic variation among individuals of keystone or foundation species frequently affects the diversity, abundances, and interaction networks of associated species (16, 53) through *community genetics* (16). Such evolved trait variation can alter communities as much as species introductions (54). In one experiment, differently adapted *Daphnia* influenced invertebrate community composition as much as adding predators and producers (55). In another example, salamanders evolved traits that dampened a top predator's negative effect on prey diversity (21).

In food webs, changes at one level, alternatively, can decrease and increase biomass in successive trophic levels via *indirect trophic effects*. If evolution dampens effects at one trophic level, it can amplify effects at the next level, dampen these effects at the third level, and so on. Divergent evolution of populations across habitats can thereby alter food web structures in space. For instance, guppies evolved divergent traits depending on predator community, and these traits altered nutrient cycling and algae and invertebrate biomass (56, 57) and amplified positive effects of top predators on basal resources (58). When stick insects evolved camouflage on host plants, they reduced predator abundances, which increased survival of co-occurring herbivores, and maintained similar grazing levels across host plant species (20). *Daphnia* populations that adapted to consume toxic cyanobacteria reduced lake

Table 1. Mechanisms of eco-evolution in space inferred from 500 eco-evolutionary studies on natural populations

Mechanism class	Mechanism	Ecological spatial pattern without evolution	Evolution of	Impact of evolution on spatial structure	Other ecological impacts	Example
Populations						
Environments	1. Fitness dampening	Uneven population abundances across environments	Higher fitness in alternative environments	Dampens environmental heterogeneity on population abundances	Dampens effects of population abundances on other ecological properties	Stream and lake stickleback fish reach higher abundances in respective environments (25)
Resources	2. Density-dependent selection	Uneven population densities	Less sensitivity to intraspecific competition in dense populations	Amplifies differences in population abundances	Dampens resource heterogeneity (if underlying abundance differences)	Evolution of guppies to have higher fitness at higher densities (29)
Metapopulations						
Spatial resources	3a. Adaptation to habitat or host preference	Low occupancy or abundance in nonpreferred or low-fitness patches	Expanded habitat or host use	Dampens effect of environment on population occupancy	Dampens effects of occupancy on other ecological properties	Grasshoppers prefer habitats that match their cryptic coloration (41)
Spatial resources	3b. Adaptation to habitat or host preference	Low occupancy or abundance in nonpreferred or low-fitness patches	Narrower preference for a subset of habitats or hosts	Amplifies effects when populations specialize on a subset of patches	Amplifies effects of occupancy on other ecological properties	Butterflies adapt to prefer the most common host plant (37)
Spatial resources	4a. Dispersal adaptation	Low occupancy of isolated or temporary habitats	Higher dispersal to colonize isolated habitats	Dampens effect of isolation on occupancy and range extent	Dampens effects of occupancy on other ecological properties	Cane toads evolve to disperse farther during invasion of Australia (85)
Spatial resources	4b. Dispersal adaptation	Low occupancy of isolated or temporary habitats	Reduced dispersal to avoid dispersal costs	Amplifies existing distribution limits	Amplifies effects of occupancy on other ecological properties	Evolution of lower dispersal in wind-dispersed plants on islands (96)
Communities						
Species interactions	5. Adaptation of competitors	Low abundance with competitors	Interspecific competition	Dampens effect of competitors on population abundances	Dampens variation in competitor densities	Primrose plant evolves tolerance to competition (47)
Species interactions	6. Character displacement	Low abundance with competitors and low resources in multicompetitor communities	Specialization on different resources	Dampens effects of competitors on population abundances	Dampens effects of joint consumption on shared resources	Stickleback in lakes with competing sculpin shift toward eating competitor's less preferred, pelagic prey (50)
Species interactions	7. Adaptation of victims	Low victim abundance with enemies	Defenses against predators, herbivores, pathogens, and parasites	Dampens effect of enemies on victim population abundances	Dampens variation in enemy densities	Evolution of camouflage in stick insects dampens population abundances, community diversity and food web abundances (20)
Species interactions	8. Adaptation of enemies	Low enemy abundance with defended victims	Countermeasures to victim defenses	Dampens effect of defended prey on enemy population abundances	Dampens or amplifies enemy's effect on victim population abundances, depending in part on coevolutionary dynamics	Evolution of toxin tolerance in <i>Daphnia</i> in response to toxic cyanobacteria (59)
Species interactions	9. Adaptation of mutualists	High abundances with mutualists	Stronger mutualistic relationships	Amplifies abundances with mutualists	Amplifies abundances with other mutualists	Legumes evolve greater symbiotic benefits in response to local N-fixing bacteria (51)
Species interactions	10. Indirect trophic effects	Variation in food chain lengths or abundances	Traits that alter abundance or occupancy of focal species	Dampens effect of environment on abundance or occupancy	Dampens or amplifies effect of one food chain level on others	<i>Daphnia</i> evolve higher fitness in lakes with anadromous fish, enhancing their density, and decreasing algae (97)
Ecosystems						
Resources	11. Resource efficiency	Uneven resources and low abundance or production with low resources	Less resource uptake or more efficient resource use in low-resource environments	Dampens effects of low-resource conditions on population abundances and production	Dampens resource heterogeneity	Tallgrass evolves greater interaction with mycorrhizae to extract nutrients under low-nutrient conditions (98)
Resources	12. Resource extraction	Uneven resources and low abundance and production with low resources	More resource uptake in low-resource environments	Dampens effect of low-resource conditions on population abundances and production	Amplifies resource heterogeneity	Hawaiian O'hia tree assimilates more nitrogen in low-nitrogen habitats (69)
Resources	13. Resource advantage	Uneven resources and higher production with higher resources	Greater production in high-resource environments	Amplifies production in high-resource environments	Dampens resource heterogeneity	Perennial plants evolve to grow longer and flower more with longer growing seasons (70)
Creating or unknown	14. Community and ecosystem genetics of foundation or keystone species	Homogeneous ecological patterns	Traits that affect other community or ecosystem properties	Usually unexplored	Creates new spatial heterogeneity in dependent species and ecosystems	Genetic variation in tree against beavers increases tannins in local waterbodies (75)

We highlight dampening (blue), amplifying (yellow), or creating (orange) mechanisms by color in a manner consistent with Figs. 2 and 3.

primary productivity by 95% and dampened toxic effects on other species and water quality via *adaptation of enemies* (59).

Evolution can modify classic ecological theories underlying community diversity. For example, the Janzen–Connell theory proposes that specialist enemies enhance species diversity by preferentially attacking dense hosts, thereby promoting rare competitors (60). Adaptation of pathogen host specialization, however, could increase local diversity, whereas adaptation of host defenses could decrease diversity by lessening negative density-dependent mortality (61). Adaptations of dominant competitors also can influence species diversity. For example, mustard plants use toxins to kill their competitors' root mutualists to form dense, single-species stands. However, as intraspecific competition increases, mustard plants evolve better intraspecific competitiveness but also lower toxins, which allows competing species to invade (62). The balancing effects of interspecific versus intraspecific selection can thus maintain spatial

heterogeneity in species composition. Niche-based theories of community assembly often assume communities assemble deterministically because environments sort species based on fixed traits (63). Yet, early colonists might adapt to novel conditions, alter assembly dynamics, and permanently alter spatial patterns of richness and composition (64, 65). See Table 1, *SI Appendix, Box 1*, and recent reviews for additional mechanisms not often found in reviewed empirical literature (4, 19, 66) because either our specific methods did not detect them, they have not been explored empirically, or they are truly rare in nature (e.g., evolution of neutrality, coevolutionary range boundaries, and evolution in metaecosystems).

Nutrients, Energy, and Biomass in Ecosystems

Although evolution mostly dampened ecosystem properties (59% of ecosystem studies), evolution also amplified ecosystem properties

in 32% of ecosystem studies, especially for traits related to energy and resource use (Fig. 3). When faced with lower resources, some organisms evolve more *efficient resource use*. For instance, prairie tallgrass in low-resource environments evolved with local mycorrhizal fungi to enhance their mutualistic exchange of nutrients and carbon (67). Efficient resource use might reduce demand in resource-poor environments and thereby weaken strong resource gradients. However, low resources also might select for *enhanced resource extraction*, which would then amplify existing resource heterogeneity. For example, spotted salamanders evolve to forage more intensely in low-resource ponds (68), and the Hawaiian O'hia tree evolves to assimilate more nitrogen in low-nitrogen habitats (69).

In high-resource environments, populations commonly evolve even higher fitness and biomass production (*resource advantage*) than afforded by ecology alone. For instance, the Heal-all herb evolved to grow larger and flower more in mild climates (70). Adaptation thus amplifies the existing productivity–resource gradient, while higher resource uptake in high-resource environments can dampen underlying resource gradients.

Evolution in foundation or keystone species can disproportionately affect ecosystem patterns, through *ecosystem genetics* and *indirect trophic effects*. Local adaptation commonly reduces phenotypic–environment mismatches in foundation species, increases performance under stressful conditions, and enhances fitness across a broader range of environments (71). For example, as trees adapt to cold, nutrient-poor, or dry environments, they can expand their latitudinal and elevational range, even switching treeless biomes to forested ones (72). Also, the evolution of fire-adapted, serotinous cones in lodgepole pines maintains forest in fire-prone regions (73). Thus, when local adaptation expands key species distributions, it subsequently dampens variation in dependent species and ecosystem processes. Genetic variation within these species creates new community and ecosystem patterns where none existed previously in 8% of studies (Fig. 3). In one such case, the evolution of tree tannin concentrations creates spatial heterogeneity in soil conditions, litter decomposition rates, and water quality (74).

Adaptation also can amplify energy or material flows between ecosystems by promoting regional heterogeneity or dispersal capacity. For example, beavers selected for higher defensive tannins in riparian poplars (75), which increased tannins in nearby streams and amplified water chemistry differences among ecosystems (76). Local adaptation of salmon to natal streams changes phenotypes in ways that can maximize abundance in each location, and thereby dampen spatial variation in the transfer of marine subsidies to the surrounding forest (77). Salmon adaptations to drainage-specific stream temperatures also increased interpopulation variance in migration timing (78), which stabilized salmon-derived ecosystem services (79) and dampened resource ephemerality for bears (80).

Species Ranges and Regional Diversity

We extend the insights gained from the local effects of fitness dampening and dispersal adaptation to the broader spatial scales that define species ranges and regional diversity patterns. Our review revealed that evolution usually dampened environmental effects on macroecological patterns (35% vs. 4%; Fig. 3). Without adaptation, a species declines in population growth rate across spatial environmental gradients until reaching a range limit where growth rate falls below replacement (81). Consequently, population abundances and patch occupancy are expected to decrease near range edges (82). Yet, local adaptation at the range edge can expand a species' niche and range extent, thereby

dampening the impact of environmental clines on species distributions (83). Both theoretical and empirical studies suggest that enhanced dispersal and rapid population growth are especially likely to evolve at range edges owing to the fitness benefits accrued by colonizing empty habitats (84–87). For example, dispersal adaptations can expand range boundaries by supporting sink populations through repeated immigration (88).

In contrast, maladaptation can amplify environmental effects on range properties. Gene flow from core habitats might spread maladapted genotypes into smaller edge populations, preventing adaptation and reducing fitness (89). Resultant maladaptation could decrease edge population abundances further, exaggerate maladaptive gene flow from core to edge habitats, and create a maladaptive feedback loop (90). Analogous to our understanding of population abundances and metapopulation occupancy, local adaptation at range boundaries likely dampens environmental impacts by expanding range extent and increasing edge population abundances, whereas maladaptive gene flow amplifies existing range constraints.

When to Expect Dampening, Amplifying, and Creating

Local adaptation dampened ecological patterns in 85% of studies and did so most especially for population abundances, community interactions, and range extent. Local adaptation often expands a species' niche by improving local fitness or expanding the environmental tolerance for populations, so that individual populations can overcome low-fitness environments, negative species interactions, and isolation. Populations also might evolve to specialize on frequent or high-fitness environments, thus amplifying the original ecological structure. Adaptation that expands a species' niche tends to dampen ecological structure, whereas adaptation toward specialization amplifies it. What adaptation accomplishes in terms of amplifying or dampening, maladaptation can undo (91). Hence, if adaptation usually dampens spatial patterns, then maladaptation will usually amplify them.

The effect of evolution on spatial ecological patterns also depends on whether populations adapt to other species or resources. Adaptation to abiotic, nonresource features usually homogenizes population abundances without altering the underlying environmental gradient. However, results are more complicated when dealing with interacting species and resources. Adaptation to negative species interactions usually dampens spatial structure, whereas adaptation to positive interactions can amplify it. Evolutionary impacts on populations and resources depend on whether populations in low-resource environments evolve to live on less or extract more. In the latter case, local adaptation amplifies resource extraction, productivity, and population densities.

In 8% of studies, local genetic variation, especially in foundation or keystone species, creates new spatial ecological structure by restructuring dependent species and ecosystem properties. As a caveat, some studies on community genetics have not yet discovered the selective agents that maintain this genetic variation, such that future work might reveal that genetic responses actually dampen or amplify these newly discovered selection gradients.

Future Work and Unresolved Questions

Although we highlight the 14 mechanisms revealed by a literature review, we recognize that more mechanisms exist. We hope that this review encourages the description of new mechanisms underlying ecoevolution in space and theories to predict their effects on ecological patterns. Although we focus on empirical patterns, we offer a brief overview of the intersections of

ecological, evolutionary, and eco-evolutionary theories about spatial patterns, in *SI Appendix, Box 1*.

To date, few empirical studies completely evaluate eco-evolutionary interactions in space through field manipulations, and fewer test for underlying mechanisms. Although often inferred, the cryptic influence of dampening eco-evolutionary effects is particularly difficult to detect by observing natural patterns. Future approaches could experimentally manipulate existing adaptations or the evolutionary process itself and then compare resulting ecological patterns, preferably under realistic conditions. Alternatively, or in addition, characterizing the genetic composition of populations before and after experimental manipulations could partition responses into ecological and evolutionary components.

In addition to adding to our fundamental knowledge on ecoevolution in space, we also highlight six important, but unresolved, questions at this eco-evolutionary interface. We use these questions to expand the focus of our conceptual framework to explore less understood aspects of spatial ecoevolution and also reach the various allied fields that are likely to be affected by these concepts.

- 1) How does the nature of eco-evolutionary feedbacks influence whether spatial patterns are amplified or dampened over long periods? Closed-loop or narrow-sense feedbacks, where trait evolution influences an ecological pattern that subsequently induces evolution in the original trait (19), might yield important space–time dynamics. Some loops are clearly reinforcing, such as when low resources select for greater resource extraction. Alternatively, some loops might cycle between dampening and amplifying, such as the ebb and flow of enemy and victim coevolution (92). Both theory and empirical experiments will be needed to disentangle the longer and more complicated feedbacks of ecoevolution in space and time.
- 2) When and where will evolutionary or ecological processes have the greatest influence on spatial patterns? Ecological responses (e.g., species colonization) are usually expected to supersede parallel evolutionary responses (e.g., niche expansion or adaptive radiation). Yet, our review suggests that evolution can shape many ecological processes. Evolution is predicted to play an especially important role in fragmented, species-poor regions with weaker environmental heterogeneity (66), where sufficient time exists for local adaptations to arise before preadapted species arrive and fill open niches. However, this view also assumes sufficient genetic variation to take advantage of ecological opportunities and that ecological—rather than genetic—constraints are more important. These assumptions likely depend on specific combinations of evolutionary rates, colonization rates, and niche redundancies among potential colonizing species.
- 3) Are coevolutionary effects among multiple species more likely to dampen or amplify spatial ecological patterns? Coevolution can create a more dynamic interplay of space, ecology, and adaptation. The patterns expected will change depending on the spatial pattern of evolution and coevolution (92) and number of potentially coevolving species (93). Adaptations in one species might commonly counteract adaptations of another species, thus providing a dampening feedback on interaction strengths in both space and time, but amplifying is also possible when one species adapts faster than the other (92). The added complexity of reciprocal selection among multiple species in space and time is likely to enrich the range of outcomes and place a premium on understanding relative rates of coevolutionary responses among interacting species.
- 4) How does the rate of adaptation interact with the spatial scale of ecological pattern formation? We might expect that rapid adaptation might be necessary to counteract equally rapid, fine-scaled spatial environmental change (e.g., biotic interactions), whereas selection might change more gradually at larger spatial scales (e.g., climate) and thus not require as rapid adaptive evolution to maintain spatial patterns. This matching-scales hypothesis likely misses interesting interactions, large-scaled human-induced changes, and further context dependencies that should be elucidated in future research.
- 5) Under what conditions will speciation convert evolutionary differences among populations into ecological differences among species? Local adaptation can enhance habitat specialization, which, we find, typically dampens ecological patterns. However, such population differentiation also can lead to reproductive isolation and even speciation, thereby converting intraspecific differences into interspecific ones. This longer-term perspective might reveal additional feedbacks between evolution and ecology through speciation, feedbacks which are not normally considered by ecologists thinking about contemporary timescales. Moreover, to what extent does it matter whether organisms are different species versus locally adapted populations, for the purposes of spatial ecological impacts? Speciation isolates sexually reproducing genotypes from the homogenizing effects of genetic exchange and allows them to diverge further, but the distinction matters much less for asexual organisms.
- 6) What are the consequences of losing intraspecific genetic diversity? Rates of intraspecific biodiversity loss are many times higher than rates of species loss (94, 95). Losing uniquely adapted populations and traits could revert ecological spatial patterns back to what is expected without evolution. Loss of genetic diversity could also hinder opportunities for future fine-scaled adaptation. Moreover, population extirpations reduce local species richness, which could open up ecological and evolutionary opportunities for remaining species. The degree to which existing ecological spatial patterns are resilient to anthropogenic disturbances will likely depend on the genetic variance and redundancy of less sensitive species.

Conclusion

Biologists increasingly recognize that evolution occurs across many spatial scales, including the finer scales that characterize many ecological patterns. Consequently, evolution does not just alter ecological patterns through time, but also in space. We demonstrate that local adaptation can alter everything from spatial variation in population abundances to ecosystem properties. Sometimes, evolution can amplify environmental variation, especially along resource gradients, where selection enhances resource uptake and exacerbates underlying resource deficiencies. The adaptation of preference for a dominant habitat or host and mutualisms also can amplify ecological structure. The evolution of foundation or keystone species can create ecological patterns where none existed originally. However, evolution generally dampens environmental heterogeneity by counteracting its associated fitness reductions. Consequently, we do not observe the complete spatial heterogeneity of nature, because evolution has smoothed it out and hidden its rough edges.

Identifying feedbacks between ecology and evolution along temporal and spatial scales has revealed broad new frontiers

in biology. Perhaps even more importantly, these insights are forcing us to reexamine foundational assumptions. Ecologists can no longer justify the assumption that evolution does not influence ecological patterns and processes. The challenge is to improve our ability to predict when and how evolution shapes both spatial and temporal ecological patterns so that we can create a truly integrated biology.

Data Availability. All of the data are included in the manuscript and *SI Appendix*.

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