

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 largerbodied 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



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.

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 ecoevolutionary 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. 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.

(2, 10-13)

Species distributional limits (1,4a)

(10, 12-13)

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 noadaptation 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 threespine 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. Densitydependent 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



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 resourcerelated 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,



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

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Table 1.Mechanisms	of eco-evolution in s	pace inferred	from 500 eco-evolutionary	y studies on natural	populations
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		Ecological spatial pattern		Impact of evolution on		
Mechanism class	Mechanism	without evolution	Evolution of	spatial structure	Other ecological impacts	Example
Desculations						
Populations	1 Eitness damponing	Unaven pergulation	Higher fitness in alternative	Dampang anvironmental	Dompone offects of population	Stroom and Jako stickloback
Environments	1. Huless dampening	abundances	environments	heterogeneity	abundances on other	fish reach higher abundances
		across environments		on population abundances	ecological properties	in respective environments (25)
Resources	Density-dependent	Uneven population	Less sensitivity to intraspecific	Amplifies differences in	Dampens resource heterogeneity	Evolution of guppies to
	selection	densities	competition in dense populations	population abundances	(if underlying abundance differences)	have higher fitness at higher densities (29)
Metapopulations						J
Spatial resources	3a. Adaptation to habitat	Low occupancy or	Expanded habitat or host use	Dampens effect of environment	Dampens effects of occupancy	Grasshoppers prefer habitats
	or host preference	abundance		on population occupancy	on other ecological properties	that match their cryptic
		in nonpreferred or				coloration (41)
		low-fitness				
0		patches		A 10 00 - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 -	A 110 10 - 0	
Spatial resources	3D. Adaptation to nabitat	Low occupancy or	Narrower preterence for a subset of babitate or bosts	Amplifies effects when populations	Amplifies effects of occupancy on	Butternies adapt to
	or nost preference	in nonpreferred or	subset of habitats of hosts	specialize on a subset of patches	other ecological properties	host plant (37)
		low-fitness patches				
Spatial resources	4a. Dispersal adaptation	Low occupancy of isolated	Higher dispersal to colonize	Dampens effect of isolation on	Dampens effects of occupancy	Cane toads evolve to
		or temporary habitats	isolated habitats	occupancy and range extent	on other ecological properties	disperse farther during invasion
						of Australia (85)
Spatial resources	4b. Dispersal adaptation	Low occupancy of isolated	Reduced dispersal to	Amplifies existing	Amplifies effects of occupancy	Evolution of lower
		or temporary habitats	avoid dispersal costs	distribution limits	on other ecological properties	dispersal in wind-dispersed
Communities						plants on Islands (96)
Species interactions	5. Adaptation of competitors	Low abundance	Interspecific competition	Dampens effect of competitors	Dampens variation in	Primrose plant evolves
		with competitors		on population abundances	competitor densities	tolerance to competition (47)
Species interactions	6. Character displacement	Low abundance with	Specialization on different resources	Dampens effects of competitors	Dampens effects of joint	Stickleback in lakes with
		competitors		on population abundances	consumption	competing sculpin shift
		and low resources in			on shared resources	toward eating competitor's
		multicompetitor				less preferred, pelagic prey (50)
Species interactions	7 Adaptation of victime	communities	Defenses against produtors	Dompone offect of enemies	Dompone variation in	Evolution of computings in stick
species interactions	7. Adaptation of victims	with enemies	herbivores, pathogens,	on victim population abundances	enemy densities	insects dampens population abundances
			and parasites		,	community diversity and food web
			·			abundances (20)
Species interactions	8. Adaptation of enemies	Low enemy abundance	Countermeasures to	Dampens effect of defended prey	Dampens or amplifies enemy's effect	Evolution of toxin tolerance
		with defended victims	victim defenses	on enemy population abundances	on victim population abundances,	in Daphnia in response to
					depending in part on coevolutionary	toxic cyanobacteria (59)
Species interactions	9 Adaptation of mutualists	High abundances	Stronger mutualistic	Amplifies abundances	dynamics Amplifies abundances with	Legumes evolve greater
Species interactions	7. Adaptation of matualists	with mutualists	relationships	with mutualists	other mutualists	symbiotic benefits in response
						to local N-fixing bacteria (51)
Species interactions	10. Indirect trophic effects	Variation in food chain	Traits that alter abundance or	Dampens effect of environment	Dampens or amplifies effect of one	Daphnia evolve higher fitness
		lengths or abundances	occupancy of focal species	on abundance or occupancy	food chain level on others	in lakes with anadromous fish,
						enhancing their density, and
F .						decreasing algae (97)
Resources	11 Resource efficiency	Uneven resources and low	Less resource uptake or more	Dampens effects of low-resource	Dampens resource beterogeneity	Tallorass evolves greater interaction
nessarees	The Nebbarec enterency	abundance or production	efficient resource use	conditions on population	bampens resource neterogeneity	with mycorrhizae to extract nutrients
		with low resources	in low-resource	abundances		under low-nutrient conditions (98)
			environments	and production		
Resources	12. Resource extraction	Uneven resources and low	More resource uptake in	Dampens effect of low-resource	Amplifies resource heterogeneity	Hawaiian O'hia tree assimilates
		abundance and production	low-resource environments	conditions on population		more nitrogen in low-nitrogen
D	10.0	with low resources		abundances and production		habitats (69)
Resources	13. Resource advantage	Uneven resources and	Greater production in	Amplifies production in	Dampens resource heterogeneity	Perennial plants evolve to
		higher production with	mgn-resource environments	high-resource environments		grow longer and llower
		ingrier resources				seasons (70)
Creating or unknown	14. Community and ecosystem	Homogeneous	Traits that affect other	Usually unexplored	Creates new spatial heterogeneity	Genetic variation in tree
	genetics of foundation or	ecological patterns	community or ecosystem properties		in dependent species and ecosystems	against beavers increases
	keystone species					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

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To date, few empirical studies completely evaluate ecoevolutionary 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 matchingscales hypothesis likely misses interesting interactions, largescaled 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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