An evolving meta-ecosystem framework

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Abstract

Eco-evolutionary dynamics can shape populations and communities, but their impact on ecosystems remains underexplored. At the same time, ecosystem ecology emphasizes how energy and nutrients flow across spatial boundaries, linking multiple ecosystems into meta-ecosystems. Here, we synthesize these disciplinary perspectives into the evolving meta-ecosystem (evome) framework, building from metapopulation and metacommunity theories. We posit that locally evolving populations that disperse regionally will influence ecosystem and landscape biogeochemical cycling across multiple spatial and temporal scales. We present six testable hypotheses illustrating how selection, local adaptation, dispersal, gene flow, and species traits interact to drive meta-ecosystem resource heterogeneity, dynamics, and resilience. Applying this evome framework can inform future theoretical advancements and empirical research while also guiding the management of interconnected ecosystems undergoing environmental change.

Keywords: meta-ecosystem, eco-evolution, trophic subsidies, rapid evolution, ecosystem resilience, landscape ecology

Combining evolution, space, and ecosystems

Evolutionary adaptation can occur rapidly and across fine spatial scales, compelling a paradigmatic shift toward recognizing evolution's ability to shape ecological dynamics and patterns [1-3]. Although eco-evolutionary interactions have been convincingly demonstrated, less attention has focused on ecosystems [1, 4]. We explore how integrating the traditionally disconnected disciplines of eco-evolution and ecosystem science could inform both fundamental and applied aspects of evolution and ecosystem ecology.

Ecosystem ecologists increasingly appreciate the importance of connectivity between similar and different ecosystems [5-7]. The cross-ecosystem exchange of energy and nutrients often connects ecosystems, and these **trophic subsidies** (see Glossary) can substantially alter recipient ecosystems, often increasing productivity [5]. The **meta-ecosystem** framework adopts this broader view by evaluating the local and regional dynamics of interconnected ecosystems [6, 8]. Research suggests that ecosystem connections can boost resilience and the subsidies that maintain species and ecosystem functions in lower-resourced ecosystems [8-10]. At the same time, ecosystem functions are emergent properties of the species and their interactions with the environment. A conceptual framework is needed that incorporates relationships between ecosystem function and constituent individuals' vulnerability and functional traits, which evolution can alter.

Integrating ecology and evolution and ecosystem ecology represents two important advances, but research combining them remains limited. We define the **evolving meta-ecosystem,** or **evome** [ee-VOHM], as a set of interconnected ecosystems in which populations can evolve and influence ecological and evolutionary dynamics at multiple spatial and temporal scales (Fig. 1). Evolution can be adaptive, when mediated by natural selection, or non-adaptive, when originating through genetic drift, high gene flow, and some forms of sexual selection. Evolution can depend on both local standing genetic variation and natural selection as well as regional genetic variation distributed via gene flow and selection operating at the metapopulation scale on dispersal ability and habitat selection [2, 11, 12].

Here, we review progress in understanding eco-evolutionary dynamics and meta-ecosystems, combine these approaches to define the evome concept, present original hypotheses emanating from the evome concept, and indicate potential applications and future directions. Our overarching goal is to advance new understanding about how evolution affects ecosystems and the flow of energy and nutrients across landscapes.

Conceptual progress in eco-evolution and meta-ecosystems

Eco-evolutionary ecosystem advances

Adaptive evolution can occur over just a few generations and thereby alter contemporary ecological dynamics. For example, some monkeyflower plant populations adapted to extreme drought over several generations, allowing their population abundances to rebound [13]. Adaptations can also occur at fine spatial scales via strong selection or barriers to gene flow [14], as exemplified by salamanders that adapted to a cline in predation in a single pond [15]. Overall, evolution might commonly affect ecology by promoting **evolutionary rescue** or persistence during environmental change, stabilizing species interactions, creating priority effects in communities, and altering spatial ecological patterns [3, 16-18].

Evolution can also affect ecosystem properties, often through the evolution of foundation or keystone species, which already disproportionately affect ecosystems [19-22]. Examples include Trinidadian guppies that affect production, decomposition, and nutrient flux [23, 24], cottonwood trees with different leaf chemistries that affect soil nutrient pools and cycling [25], and the examples listed in Figure 2. More generally, the ecological impacts of intraspecific variation, underlain at least partially by evolution, can be as strong as interspecific variation [26, 27]. Intraspecific variation can also affect primary productivity and nutrient cycling more than population characteristics [27].

Empirical evidence suggests that evolution often dampens ecological dynamics and patterns. For instance, predation rates increased when either predatory damselflies or their Daphnia prey were not adapted to urban heat, but rates were lower when both species adapted [28]. Evolution can also amplify or create new ecological dynamics and patterns. However, empirical work suggests that dampening usually prevails, likely because adaptation often reduces fitness differences in time and space, which can also have the effect of dampening differences in associated ecological properties [3].

Meta-ecosystem advances

Meta-ecosystem dynamics depend not only on the passive movement of energy and nutrients (e.g., seaweed washing up on islands) but also on active movement and habitat selection by individuals [29, 30]. These resources can move long distances, with effects on recipient ecosystems that sometimes outpace local contributions [31]. For instance, seabirds transport marine nutrients far from the ocean to island colonies, producing some of the highest nutrient concentrations on Earth [32]. Such **teleconnections,** which link

ecological processes over large distances [33], require considering much larger spatial scales to understand local ecosystem dynamics. In addition, **cross-scale interactions** over space or time can influence ecosystem dynamics [34] by constraining local processes [35] or generating non-linear dynamics [36]. Spatial variation in these processes can also create biogeochemical hotspots or control points such that localized inputs or conditions generate disproportionately high rates of ecosystem processes or exert outsized effects on ecosystem-level fluxes [37].

Generally, high-resource ecosystems are expected to subsidize low-resource ecosystems [9], and these asymmetric flows can homogenize differences among connected ecosystems. For example, migrating salmon transport marine nutrients into less productive rivers and riparian ecosystems [38]. Spatial flows might also enhance overall meta-ecosystem function by redistributing resources to the ecosystems that best utilize them. In theory, higher primary production in terrestrial systems can subsidize aquatic system production, which then subsidizes terrestrial production with nutrients [39]. **Stoichiometric quality** of subsidies also matters. Subsidies with higher nutrient-to-carbon ratios often have stronger impacts than higher total resources [10, 40]. For example, salmon strongly affect inland ecosystems when they are phosphorus-poor.

Understanding the origins and consequences of trait variation requires elucidating how ecological and evolutionary processes generate and maintain trait variation across multiple spatial scales and levels of ecological organization. For instance, divergent phenologies within and among species can ensure a regular supply of resources over time (Fig. 1) [41], and diverse traits across or within species (e.g., leaf chemistry) can promote complementary ecosystem functions [42]. These flows can occur through passive transport of detritus or nutrients or via distinct individual foraging behaviors, life-history habitat transitions, seasonal migration, or dispersal [36, 43, 44]. For example, individuals that select specific habitats will link similar ecosystems, potentially over larger distances, whereas passive transport is more likely to link neighboring, disparate ecosystems indiscriminately [8].

The evome

The evome framework builds on these advances and draws inspiration from analogous multi-scale eco-evolutionary frameworks, including metapopulation genetics, evolving metacommunities, and macrosystems [2, 12, 31]. Evomes couple evolution and gene flow with the movement of organisms, energy, and nutrient flows, mechanisms often

considered separately [43]. Hence, evomes bridge the divide between the eco-evolution of interacting populations and landscape-scale biogeochemical cycling.

Ecosystems can be altered by both local evolution and selection and movement, gene flow, and selection operating across broader landscapes. For example, adaptation to local conditions can create maladaptive or adaptive gene flow into nearby ecosystems, depending on how well source and recipient environments match [45, 46]. Such eco-evolutionary interactions can involve the same ecosystems (e.g., stream-to-stream) or divergent ecosystems (e.g., stream-to-terrestrial). These dynamics can occur across finer scales, such as from a stream to its riparian zone, or entail large-scale teleconnections when long-distance dispersers link faraway ecosystems.

Evolution can alter demographic traits like population growth rates, individual dispersal propensity and distance [47], as well as **ecosystem impact traits** like body size, edibility, and nutrient stoichiometry. These traits can affect both local and distant ecosystems (Fig. 1). To illustrate, salmon that normally migrate between the ocean and freshwater habitats have repeatedly evolved permanent freshwater resident populations [48]. Losing this migratory behavior eliminates the existing marine-to-freshwater nutrient subsidies.

Overall, the evome concept elicits new ways to think about the relationships between ecology and evolution and forces one to consider how these processes play out over multiple spatial and temporal scales. The framework also offers insights into how spatial flows of energy, nutrients, and genes maintain **ecosystem resilience** (Box 1).

Hypotheses

Here we highlight six hypotheses, building on recent advancements in eco-evolution and meta-ecosystems and extending concepts from metapopulation and metacommunity frameworks.

H1: Eco-evolutionary decay

Trait evolution can alter ecosystems directly via ecosystem impact traits or indirectly by altering population abundances. One hypothesis is that when evolved differences in population abundances affect ecosystem properties, these impacts will be weaker because additional noise-prone links reduce the correlation between genotype and ecosystem impact [1, 4]. For instance, a host's evolved immunity could reduce parasite load and increase overall host abundance (assuming hard selection), which might

indirectly alter primary production by changing prey densities. Alternatively, the host might evolve enhanced immunity that alters its stoichiometry or nutrient excretion, which directly affects ecosystem properties.

Hypothesis 2: Local adaptation subsidizes other ecosystems

We hypothesize that local adaptation in time and space of key species might not only increase local ecosystem productivity but also subsidize less-adapted populations and less productive ecosystems, promoting cross-ecosystem resilience to disturbances. We also predict that higher gene flow will increase maladaptation in the recipient population, making associated ecosystems increasingly reliant on cross-ecosystem subsidies and susceptible to disruptions in flow.

H3: Evolution of Dispersal

Dispersal is a trait, like any other, that can evolve through natural selection, for instance, to avoid inbreeding, competition, or enemies, or exploit resources elsewhere [47, 49]. Increasing dispersal propensity or distance could increase cross-ecosystem subsidies. Increasing fragmentation, however, can select for reduced dispersal to avoid dispersing into the void, thereby reducing the trophic subsidies that support resource-poor habitats.

H4: Evolution of habitat selection

Habitat selection can evolve when certain phenotypes settle in habitats where they have higher fitness. For example, color-polymorphic grasshoppers actively choose different substrates that maximize their crypsis [50], which can drive genetic divergence between microhabitats, reduce predation rates and energy flows, and ultimately strengthen links between similar ecosystems. Such tight ecosystem-to-ecosystem linkages might be disrupted if a habitat-specific phenotype is lost, lowering subsidies and augmenting resource heterogeneity across the landscape.

H5: Top-down versus bottom-up processes

We hypothesize that ecosystem processes will be most sensitive to evolution in top consumers or primary producers depending on whether top-down predation or bottom-up nutrient and energy limitations dominate in a particular ecosystem. However, more generally, because plants directly influence processes like productivity and nutrient ratios,

218 we suspect that plant evolution might affect meta-ecosystems more than higher trophic
219 levels. Indeed, a meta-analysis found that intraspecific variation in primary producers
220 affected ecosystem properties more strongly than for consumers [27]. However, evolution
221 might be more important for top consumers that readily move between ecosystems and
222 disproportionately affect ecosystems through top-down effects. For example, the
223 evolution of a keystone predator might reduce herbivore densities and thereby increase
224 primary production.

225

226 *H6: Dampening landscape ecosystem heterogeneity*

227 Adaptation often dampens ecosystem dynamics and patterns in space and time because
228 local adaptations usually reduce fitness variation and its associated ecological impacts
229 [3]. Hence, we might expect that adaptation will reduce resource heterogeneity between
230 ecosystems. This prediction, however, depends on how populations adapt to low-resource
231 environments. Local adaptation might decrease resource differences among ecosystems
232 if it selects for higher resource extraction. However, if populations adapt to use resources
233 more efficiently or switch to alternative resources, then resource heterogeneity might
234 decrease. If evolution generally dampens resource heterogeneity, then adaptation might
235 tend to increase ecosystem resilience by countering changes in space and time. However,
236 time lags between selection changes and adaptive responses over multiple generations
237 could generate important transient dynamics.

238

239 Roadmap for the future

240 New theories and experimental tests are needed to test these hypotheses, generate more
241 hypotheses, and further develop the evome conceptual framework.

242

243 *Theory*

244 Besides developing the six previously highlighted hypotheses, additional theories might
245 examine how evolution and community assembly interact to determine meta-ecosystem
246 structure [51], how evolution affects food web dynamics and subsidies [52], how
247 perceptions and imperfect information affect movement decisions and ecosystem flows
248 [53], and how dispersal evolution and landscape fragmentation interact to alter meta-
249 ecosystem flows [49]. From a dynamic perspective, future models should examine when
250 evolution can maintain existing ecosystem properties during environmental change,

including in response to synchronous/non-synchronous disturbances and correlated/non-correlated patterns of habitat loss. Theory should also be expanded to explore broader spatial and temporal scales, such as biogeographical processes and the longer scales of extinction and speciation, which are usually difficult to explore experimentally [54].

Experimental tests

Eco-evolutionary tests have generally focused on how evolution affects populations, sometimes communities, but rarely ecosystems. Our goal is to inspire empiricists to fill this gap and explore how genetic variation affects ecosystems and meta-ecosystems and vice versa. Toward this end, we provide a set of suggested tests of the six presented hypotheses in Box 2. Understanding which ecosystem properties are regulated by genetic impacts on population abundances versus ecosystem impact traits will be critical for developing a more mechanistic understanding. Detecting evolution's effects in nature requires associating genetic and trait variation with observed changes in ecosystems and meta-ecosystems. For instance, one could evaluate how variation in a genetically controlled trait like nutrient stoichiometry affects natural ecosystems [55, 56]. If possible, it would be ideal to manipulate evolution or traits in natural ecosystems experimentally. For example, one could add live organisms or detritus from organisms that vary in ecosystem impact traits and evaluate impacts on the resident community and ecosystem [57]. Alternatively, barriers could be deployed to reduce existing cross-ecosystem flows to evaluate their impacts [58-60]).

Applications

Ecosystem properties are often tightly linked to human benefits, making meta-ecosystem dynamics highly relevant to society. For instance, agriculture might benefit from natural predators and pollinators dispersing from nearby undisturbed land, which might then enhance agricultural productivity. Evolution might enhance or diminish these functions [61], requiring careful thought about how such integrated systems should be designed and managed for eco-evolutionary resilience. For example, if species adapted to native habitat evolve reduced dispersal in agriculturally fragmented landscapes, then this might undermine natural subsidies to agriculture. Other human-nature ecosystem interfaces like fisheries, invasive species management, and urban ecosystems also could benefit from emerging insights [62].

Understanding evolving meta-ecosystem dynamics is likely to improve conservation. Yet, most mitigation or restoration plans either ignore evolution or ignore the ecosystem implications of evolution. By recognizing the importance of cross-ecosystem connections and that evolutionary dynamics can alter them, the evome concept suggests multiple ways to improve meta-ecosystem resilience to anthropogenic disturbances (Box 1). For instance, warmer climates often select for smaller body sizes, which could reduce subsidies to recipient ecosystems, such as fisheries. This information would argue for enhancing connectivity or population abundances to compensate. Evolutionary tools such as assisted gene flow can be designed to alter ecosystem impact traits to facilitate population and ecosystem protection and recovery.

Concluding remarks

We seek to broaden the meta-ecosystem framework to include eco-evolutionary dynamics and inspire new research avenues. The evome concept highlights how ecology and evolution could interact at local and landscape scales to alter ecosystem energy and nutrients and their cross-ecosystem exchanges, both near and far. The framework makes unique predictions (see Outstanding Questions) that need to be developed into full theories and tested empirically. Given the proximate implications of ecosystem changes to people, insights on evolving meta-ecosystems are likely to inform applications to conservation, agriculture, fisheries, and cities.

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Declaration of interests

The authors declare no competing interests.

Boxes

Box 1: Mechanisms of evome resilience

Evomes offer insights into the spatial and temporal dimensions of ecosystem-evolutionary dynamics, especially how spatial flows of energy, nutrients, and genes enhance **ecosystem resilience,** the maintenance or recovery of ecosystem properties in response to environmental change. Following disturbance, an ecosystem could recover to a previous state through ecological and evolutionary mechanisms at both local and landscape scales (Table i), as well as interactions among these mechanisms. In particular, the evome framework emphasizes the joint processes that maintain a diverse portfolio of species and genotypes in the meta-ecosystem and their redistribution following local disturbances to ensure maintenance of ecosystem properties. For example, theory on **spatial insurance** posits that diverse species will stabilize ecosystem functions if disturbances are asynchronous across patches and immigration from undisturbed patches can restore function in disturbed habitats [63-65]. Evolution can promote the same stability by maintaining or creating asynchrony or functional compensation through changes in trait distributions.

Table i: Examples of ecological and evolutionary modes that can enable ecosystem resilience at local or landscape scales.

	Spatial scale	
	Local	**Landscape**
Ecological	Trait plasticity (demography, phenology, behavior) Community change (functional shifts)	Ecological rescue (immigration) Community assembly (functional substitution)
Evolutionary	Evolutionary rescue (local adaptation) Evolution of impact traits Indirect evolutionary rescue (mediated by species interactions)	Evolutionary rescue (adaptive gene flow) Metapopulation adaptation (dispersal or habitat selection evolution)

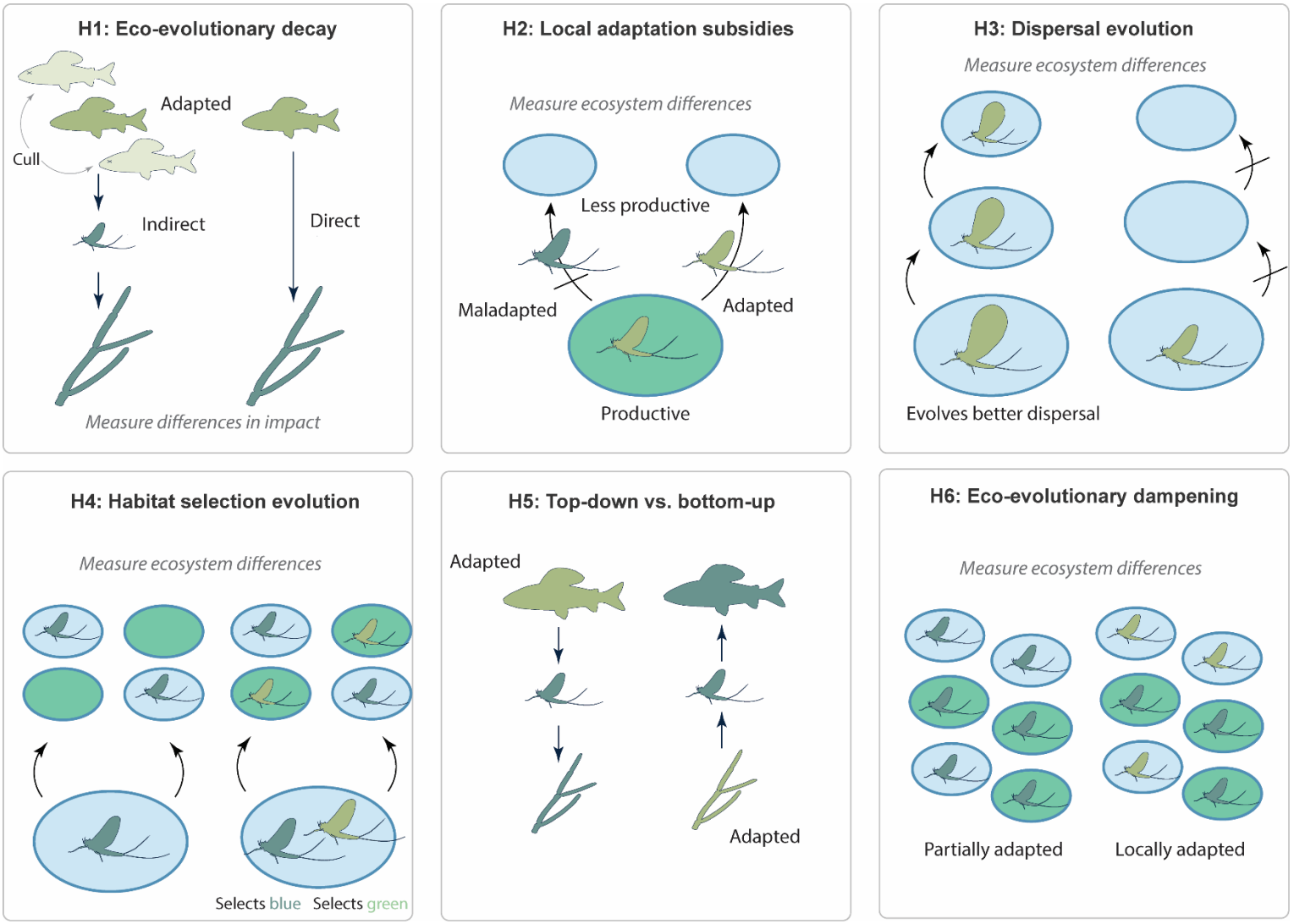
Ecological rescue can occur through phenotypic plasticity, such as via environmentally induced changes in demography, phenology, or behavior, that maintains local fitness. Also, the distribution of local species abundances might change in ways that stabilize ecosystem properties, as when a species better adapted to new conditions replaces a functionally similar, but declining species. Alternatively, ecosystem functions might be maintained through regional immigration of individuals that rescue a declining population or regional colonization of a new species that replaces ecosystem function.

Evolutionary rescue, whereby adaptive evolution allows a population to recover from an environmental change, can occur through selection on local mutations and standing genetic variation or via regional gene flow. Moderate gene flow can increase overall genetic diversity, especially when recombined to create novel, adaptive genotypes or originating from a matching environment. However, too much gene flow can reduce local adaptations that maintain ecosystem functions. Both processes can also lead to the evolution of **ecosystem impact traits**, which directly alter ecosystems by affecting processes like primary production or decomposition. Ecological rescue might also be mediated by species interactions. **Indirect evolutionary rescue** happens when the evolution of an interacting species facilitates a population's recovery from environmental change [66]. For instance, immigrating hosts or prey with limited defenses against local pathogens or predators can drive up infections or mortality (**spatial genetic subsidies** [67]) which could affect ecosystem properties. **Metapopulation adaptation**, or an adaptation in response to selection at the landscape scale [11], involves traits like dispersal propensity or distance and habitat selection. These adaptations can directly alter cross-ecosystem subsidies.

Box 2: Key hypotheses and potential tests

We suggest possible ways to test the six hypotheses in the main text which take a multi-scale approach to understand evolution's impact on ecosystem and meta-ecosystem dynamics.

Fig. i. Potential tests of six evome hypotheses. See text for detailed descriptions.



H1: Eco-evolutionary decay – Measure how ecosystem properties are altered by differently adapted populations in experiments or nature and if these impacts are mediated by population abundances or ecosystem impact traits. Causal inference testing methods may be needed to partition these mechanisms, as they are likely to covary dynamically. One could also design experiments that isolate these factors, for instance by culling to maintain a steady population density, thereby excluding numerical effects.

H2: Local adaptation subsidizes other ecosystems – Evaluate local adaptation across ecosystems and if those with strongly adapted populations contribute immigrants that subsidize other ecosystems. One could artificially block this immigration and observe if the recipient ecosystem declines in markers like total productivity. Alternatively, one could mimic a subsidy by seeding ecosystems with adapted or maladapted populations and measure the recipient ecosystem's properties.

H3: Evolution of dispersal – Identify genotypes that vary in dispersal propensity or distance or alter dispersal experimentally and evaluate impacts on ecosystems at varying distances. For example, arrays of habitats could be set at varying distances from each other or their connections altered to enable or disable dispersal and then seeded with genotypes that vary in their movement rates.

H4: Evolution of habitat selection – Similar to H3, but design arrays of heterogeneous habitats and seed them with genotypes that evolved to select one or the other habitat or both and measure impacts on ecosystem connections and properties.

H5: Top-down versus bottom-up processes: Identify the dominant direction of trophic control and observe whether adapted primary producers or top consumers affect ecosystems the most. Experiments might include communities with factorial combinations of locally adapted/maladapted producers and adapted/maladapted consumers.

H6: Dampening landscape ecosystem heterogeneity – Assess how local adaptation vs. maladaptation of populations distributed across ecosystems in a landscape affects the spatial variance in ecosystem properties. For example, create arrays of two different habitats and then seed some with genotypes only adapted to one habitat (partially adapted) or match each genotype to its optimal habitat (locally adapted). Comparing the spatial variation in ecosystem properties between these two treatments would reveal if local adaptation dampened or amplified the original spatial variation.

Image credits: Baetis Nathan Jay Baker https://www.phylopic.org/images/9e0ee363-98ac-4270-a236-0ada224cfa1d/baetis-rhodani, Grayling Johannes Radinger https://www.phylopic.org/images/2b26fca9-33c3-42e3-9704-b569ecb165a0/thymallus-thymallus, Cladophora Sergio A. Muñoz-Gómez https://www.phylopic.org/images/03abc638-50f8-496d-aa96-0d16e1abaa91/cladophora-glomerata

Figures

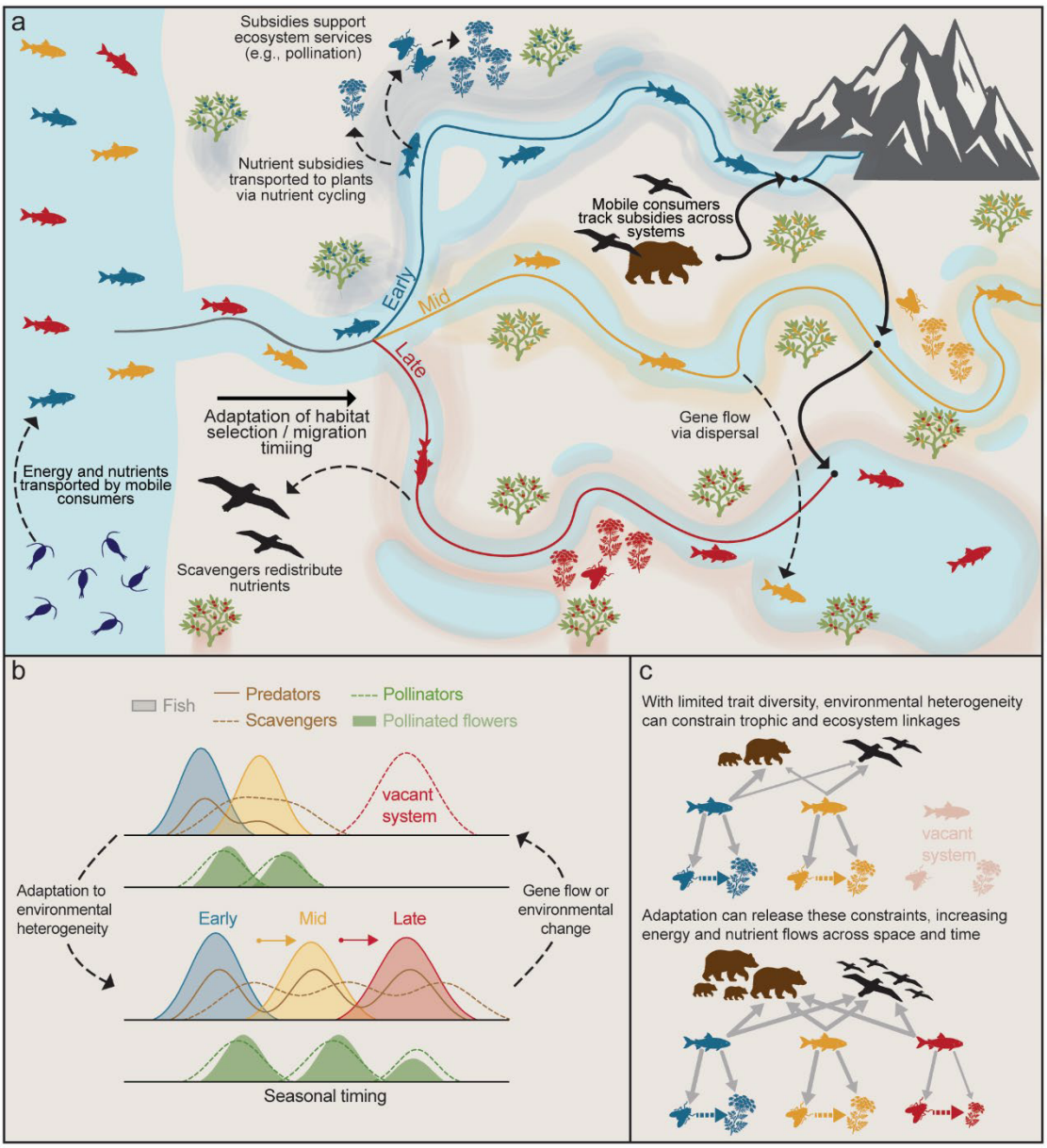


Fig. 1: Illustration of evolving meta-ecosystem framework. The figure demonstrates how an evolving meta-ecosystem approach can be applied to understand how local and landscape variation in populations can alter ecosystem properties and dynamics. (a) Salmon can adapt the seasonal timing of breeding to maximize their fitness in different habitats (colored fish represent different genotypes). These fish spawn, die, and decompose in rivers, supplying energy and nutrients to the rivers, terrestrial plants, their pollinators, and mobile consumers that span river ecosystems and redistribute sea-

derived nutrients. (b and c) With minimal local adaptation, the overall seasonal duration of spawning is limited, some habitats such as the lake system (lower, red) remain unoccupied, and trophic subsidies and ecosystem linkages are constrained. However, if some salmon adapt to breed later and colonize the new system, the resources are distributed across space and time, contributing to increasing subsidies that better support higher trophic levels than without adaptation. Straying fish can colonize new habitats, but also facilitate gene flow, causing maladaptation that could lower fish fitness and ultimately cause extirpation.

Fig. 2: Examples of evolutionary impacts on ecosystem and meta-ecosystem properties.



Ecosystem impact: Sockeye salmon (*Oncorhynchus nerka*) adapt different migration and spawning phenology in response to changing water temperatures, which alters the delivery of nutrient-rich carcasses to terrestrial ecosystems and terrestrial consumer abundance [41].

Meta-ecosystem impact: Predators and scavengers track spawning sockeye salmon across tributaries within a watershed, shifting nutrient uptake and ecosystem processes both temporally and spatially.



Ecosystem impact: Stick insects (*Timema cristinae)* adapt camouflage in response to differently patterned host plants, which reduces predation on this species as well as other insect species, thereby enhancing local consumer biomass.

Meta-ecosystem impact: Gene flow of maladapted color morphs to the incorrectly matched host plant species attracts birds, increases predation, and thereby reduces consumer biomass [64].



Ecosystem impact: Duckweed (*Lemna minor*) is a widespread invasive species that adapts, along with its microbial symbionts, to alter ecosystem primary productivity [68].

Meta-ecosystem impact: Duckweed removal selects traits that increase its invasiveness, amplifying its impacts on ecosystem productivity. Evolution by associated microbes also enhances population growth and ecosystem effects [69].



Ecosystem impact: The wild yeast species (*Hanseniaspora uvarum*) can exhibit either local adaptation or maladaptation to cultivated apples, depending on the orchard and apple variety.

Meta-ecosystem impact: Adaptation by wild yeast influences the composition of the larger microbial community and the rate of fruit decomposition [70]. These differences in decomposition likely alter the supply of nutrients from apples to the soil.

Image credits: sockeye salmon: Jonny Armstrong, stick insect: Aaron Comeault, duckweed: Barbarossa~commonswiki, apples: Daniel Bolnick.

Glossary

Cross-scale interactions: the interplay between processes at different spatial and temporal scales that can result in non-linear dynamics. Processes at larger scales often constrain the processes at lower scales.

Ecological rescue: Ecosystem recovery that can occur through local phenotypic plasticity responding to environmental change or through regional immigration of individuals that rescue a declining population.

Ecosystem impact traits: Characteristics of organisms that directly affect ecosystem properties.

Ecosystem resilience: the maintenance or recovery of ecosystem properties in response to environmental change.

Evolutionary rescue: The recovery of a population declining in response to maladaptation to an environmental change through adaptive evolution.

Evome (Evolving meta-ecosystem): A set of interconnected ecosystems in which populations can evolve and thereby influence ecological and evolutionary dynamics at multiple spatial and temporal scales.

Indirect evolutionary rescue: a declining population recovers from a disturbance due to the evolution of an interacting species.

Meta-ecosystem: A set of ecosystems connected by the flow of energy and nutrients.

Spatial genetic subsidies: Maladapted prey with limited defenses against local enemies immigrate to a new patch and provide a naïve and easily extracted resource to consumers.

Spatial insurance: A form of resilience whereby biodiversity stabilizes ecosystem functions via asynchronous compensatory dynamics, which can also be promoted by evolution and ecosystem flows.

Stoichiometric quality: A higher ratio of nutrients to carbon, which is considered a better resource for consumers.

Teleconnections: Phenomena which link ecological processes over large distances, often requiring a consideration of processes operating over much larger spatial scales than usually considered to understand local ecosystem dynamics.

Trophic subsidies: The flow of energy and nutrients across ecosystems that can substantially alter recipient ecosystems.

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Outstanding Questions

1. Does local adaptation in one ecosystem subsidize other ecosystems?
2. When does evolution affect ecosystem properties indirectly through changes to population abundances versus direct ecosystem impact traits?
3. Do ecosystem impacts vary based on the trophic level of the adapting species?
4. When does adaptation dampen spatial heterogeneity in ecosystems and when does it amplify or create new spatial patterns?
5. How often does dispersal evolution alter meta-ecosystem dynamics?
6. How does the colonization of new species and the local adaptation of resident species interact to fill empty niches and support ecosystem properties?
7. How does evolution in food webs alter subsidies to other ecosystems?
8. How does evolution of immunity (by hosts) and immune evasion (by parasites) alter infection rates, epidemiology, dispersal, and ecosystem consequences of infection?
9. Can sexual selection affect traits with ecosystem consequences?
10. How do perception and behavioral responses affect movement patterns and the subsequent quantity and quality of ecosystem flows?
11. How do landscape fragmentation and the evolution of dispersal alter ecosystem flows?
12. Are tipping points triggered when cross-ecosystem subsidies decrease that lead to local co-extinctions, and how do these co-extinctions affect ecosystems?
13. To what degree can asynchronous responses through movement or evolution generate a form of spatial insurance to disturbances?
14. To what degree could network theory be applied to understand the various contributions of complex interacting networks of interacting and evolving species?
15. What is the best way to identify the most important traits that connect a species' vulnerability to environmental change with the ecosystem consequences of losing that species?
16. How can the evome framework be extended to provide novel insights across biogeographic and macroevolutionary scales?