

Feedbacks link ecosystem ecology and evolution across spatial and temporal scales: Empirical evidence and future directions

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Abstract

1. Unifying ecosystem ecology and evolutionary biology promises a more complete understanding of the processes that link different levels of biological organization across space and time. Feedbacks across levels of organization link theory associated with eco-evolutionary dynamics, niche construction and the geographic mosaic theory of co-evolution.
2. We describe a conceptual model, which builds upon previous work that shows how feedback among different levels of biological organization can link ecosystem and evolutionary processes over space and time. We provide empirical examples across terrestrial and aquatic systems that indicate broad generality of the conceptual framework and discuss its macroevolutionary consequences.
3. Our conceptual model is based on three premises: genetically based species interactions can vary spatially and temporally from positive to neutral (i.e. no net feedback) to negative and drive evolutionary change; this evolutionary change can drive divergence in niche construction and ecosystem function; and lastly, such ecosystem-level effects can reinforce spatiotemporal variation in evolutionary dynamics. Just as evolution can alter ecosystem function locally and across the landscape differently, variation in ecosystem processes can drive evolution locally and across the landscape differently.
4. By highlighting our current knowledge of eco-evolutionary feedbacks in ecosystems, as well as information gaps, we provide a foundation for understanding the interplay between biodiversity and ecosystem function through an eco-evolutionary lens.

KEYWORDS

eco-evolutionary feedbacks, ecosystem function, geographic mosaic theory of co-evolution, niche construction

1 | INTRODUCTION

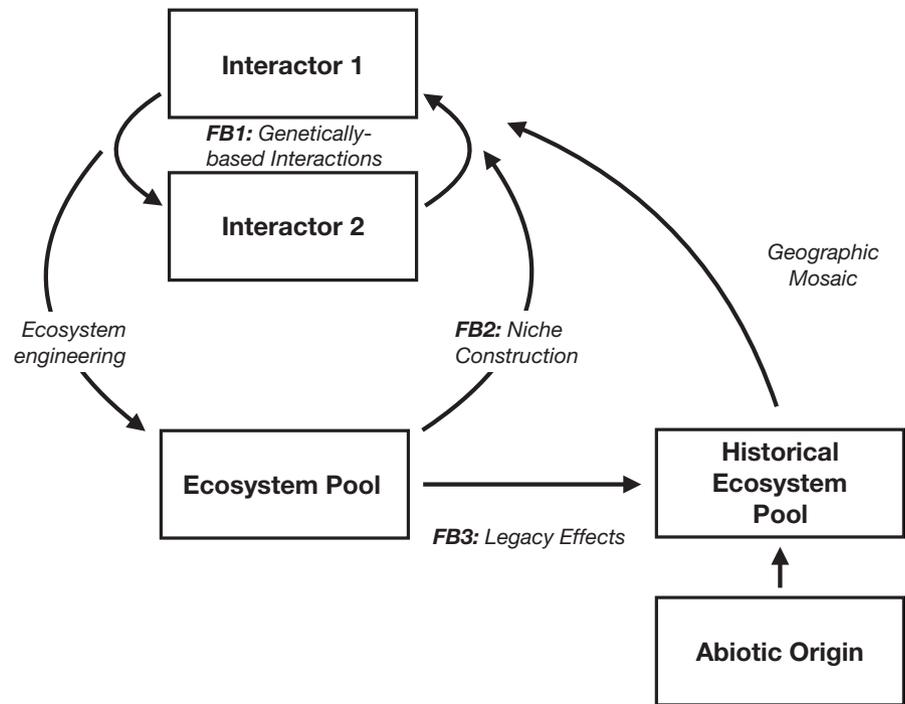
A critical challenge in biology is to understand the reciprocal interactions (hereafter, *feedbacks*) between ecological and evolutionary processes. Evolution in a focal organism can alter processes occurring at the population, community and ecosystem levels, which in turn can feed back to alter subsequent evolution of the focal organism (Hendry, 2017). This eco-evolutionary (eco-evo) feedback occurs because evolution can shift phenotypic variation in populations, which can alter species interactions and ecosystem processes, such as energy flow and nutrient cycling (Jones, Lawton, & Shackak, 1994; Lindeman, 1942). Further, these changes to energy flow and nutrient cycling can vary spatially and temporally in strength and direction, can persist for generations via *legacy effects* and can feed back to shape future species interactions. Numerous examples suggest that eco-evo dynamics are ubiquitous; however, detecting them remains challenging because the net result of interacting feedbacks could

range from positive to negative, and cumulatively appear neutral (Kinnison, Hairston, & Hendry, 2015; Schweitzer, Juric, Voorde, Clay, & Bailey, 2014). Further, the drivers and consequences of variation in eco-evo feedbacks across levels of biological organization, spatial scales and time are unclear. Here, we integrate the temporal dynamics of *niche construction* theory (NCT), the spatial scale of *geographic mosaic theory of co-evolution* (GMT) and energy and nutrient dynamics of classic ecosystem ecology (circa Jenny, 1941; Lindeman, 1942; Chapin, Matson, & Vitousek, 2012), to provide a conceptual framework to link ecosystem ecology and evolution (terminology defined in Box 1). The framework presented here builds upon previous work (Matthews et al., 2014; Van Nuland et al., 2016; Post & Palkovacs, 2009) in three significant ways: first, we expand a conceptual model, showing three levels of feedback that incorporate temporal and spatial scales that are explicitly related to *ecosystem state factors* and the legacy effects of past species interactions; second, we provide some empirical examples across multiple terrestrial and aquatic systems

Box 1 Definitions of terms

Eco-evolutionary feedback	Feedback describes a sequence of interactions in which the result of a process affects the conditions that initially generate the process / eco-evolutionary feedbacks are the cyclical interaction between ecology and evolution such that changes in ecological interactions drive evolutionary change in organismal traits that, in turn, alter the form of ecological interactions, and so forth.
Genetically-based species interactions	Genetically-based phenotypic interactions within populations or among species.
Phenotype	The physical appearance or biochemical characteristic of an organism as a result of the interaction of its genotype and the environment.
Population	A group of organisms of one species that interbreed and live in the same place at the same time.
Community	An association of interacting species that live in a particular area.
Ecosystem	Ecological system consisting of all the organisms in an area and the physical environment with which they interact.
Ecosystem pool	Quantity of energy, material, or nutrients in an ecosystem compartment.
Ecosystem state factors	Independent variables that control the characteristics of ecosystems (climate, parent material, topography, potential biota, time; sensu Jenny 1941).
Ecosystem processes	Inputs or losses of materials and energy to and from the ecosystem and the transfers of these substances among components of the ecosystem; ecosystem processes include decomposition, production, nutrient cycling, and fluxes of nutrients and energy.
Ecosystem engineering	Modifications to the environment by a species that affects resource availability for another species.
Niche construction	The process whereby organisms actively modify their own and each other's evolutionary niches.
Legacy effects	The phenotypic effects of an organism that extends beyond the life of the organism // an indirect effect that persists for a long time period in the absence of the causal species, or after this species has ceased the causal activity.
Ecological inheritance	The persistence of environmental modifications by a species over multiple generations to influence the evolution of that or other species.
Abiotic origin	The initial conditions, climate and other factors which were present when the eco-evo dynamics "started".
Historical contingency	The evolutionary effects of the ecosystem pool which remains constant over ecological timescales but change over longer time periods due to gradual accumulation of changes (i.e., abiotic and biotic environmental effects) happening every generation.
Environmental context	The biophysical environment consisting of biotic and abiotic components surrounding a population or interacting populations.
Coevolutionary hotspots	Interactions are subject to reciprocal selection only within some local communities. These coevolutionary hotspots are embedded in a broader matrix of coevolutionary coldspots, where local selection is nonreciprocal.
Geographical mosaic hypothesis	States that because species interactions vary geographically, a mosaic of population genetic structure will result that leads to different evolutionary trajectories.

FIGURE 1 A conceptual illustration of interacting feedbacks linking genetically based interactions, niche construction, ecosystem dynamics and the geographic mosaic of co-evolution. Individual components within each feedback are defined conceptually to express how each feedback operates. *FB1* represents reciprocal, genetically based interactions. *FB2* shows how these genetically based interactions can influence ecosystem engineering and niche construction. *FB3* shows how historical contingency of past ecosystem-level feedbacks (i.e. temporal dynamics inherent to niche construction) and underlying abiotic origin (e.g. climatic gradients) can interact and feed back to influence strength and reciprocity of genetically based interactions in *FB1* (i.e. integrating NCT and the GMT)



that indicate generality of this conceptual framework; and third, we examine potential macroevolutionary consequences of this conceptual framework.

Niche construction is the process by which organisms modify and create their own niche or that of other interacting organisms (Odling-Smee, Laland, & Feldman, 2003). Niche construction varies across populations due to variation in phenotypes that directly or indirectly affect environments through genetically based species interactions. *Ecosystem processes* cumulatively represent niche construction because they control the input, loss and transfer of materials and energy to and from the ecosystem, are mediated by phenotypic interactions within communities and can reinforce patterns of phenotypic interactions on the landscape (Genung, Bailey, & Schweitzer, 2013), all of which can alter pattern selection. For example, ecosystem processes such as energy flow across trophic levels and nutrient cycling (e.g. decomposition rates in soils, nitrogen and phosphorous immobilization in soils) in terrestrial ecosystems occur over short to long time-scales and can shift in response to genetic variation in interacting phenotypes (Bailey et al., 2014; Schweitzer et al., 2014). Interactions among phenotypes (and underlying genotypes), therefore, play an integral role in niche construction by altering communities and ecosystems in ways that produce legacy effects and long-term changes in ecosystem pools over time (Bailey et al., 2009). Complementing NCT, the GMT explores the same genetically based interactions driving niche construction but along landscape-level environmental gradients such as climate, other organisms, relief and parent material (i.e. ecosystem state factors; Benkman, 1999; Brodie, Ridenhour, & Brodie, 2002; Chapin et al., 2012; Parchman, Buerkle, Soria-Carrasco, & Benkman, 2016; Van Nuland, Bailey, & Schweitzer, 2017). Geographic variation in genetically based species interactions, gene flow and natural selection leads to different evolutionary

outcomes across spatial scales (e.g. *co-evolutionary hot spots and cold spots*; sensu Thompson, 1998, 2005). However, ecosystem-level consequences and their potential feedbacks to population dynamics are rarely considered as a consequence of co-evolutionary interactions across spatial scales. Integrating these two established bodies of theory may help our understanding of how different feedbacks emerge across multiple levels of biological organization, further linking population, community and ecosystem processes across space and time.

2 | EXTENDING A CONCEPTUAL FRAMEWORK

We use an eco-evolutionary framework to show synthesis between NCT and GMT by incorporating feedbacks from multiple levels of organization to link scales of space and time (modified from Van Nuland et al., 2016; Figure 1). This builds upon and reconciles previous work in community and ecosystem genetics (Bailey et al., 2009; Des Roches et al., 2018; Schweitzer et al., 2012; Whitham et al., 2006), eco-evolutionary dynamics (Genung et al., 2011; Hendry, 2017; Matthews et al., 2014; Post & Palkovacs, 2009), niche construction theory (Kylafis & Loreau, 2008; Odling-Smee, Erwin, Palkovacs, Feldman, & Laland, 2013) and the geographic mosaic theory of co-evolution (Thompson, 1998). Together, these fields show how genetically based species interactions at different scales generate reciprocal feedbacks that may drive ecological (including ecosystem) functions through time, as well as alter evolutionary processes across the landscape. This synthesis shows the common elements in these areas of study can be merged theoretically and empirically to quantify when and how genetically based feedbacks can occur

among species across space and time to influence both ecosystem and evolutionary processes.

In the simplest case, our conceptual model shows two interacting species (co-)evolving through time and along abiotic gradients of ecosystem state factors (space) (Figure 1: *FB1*, genotype \times genotype [$G \times G$] interactions and reciprocal selection; Janzen, 1980). The boxes in *FB1* represent heritable trait variation for each interactor (i.e. individual traits, trait covariances or community-level trait matrices). The evolutionary consequences of *FB1* can vary within and among communities and geographically, ranging from non-evolving interactions to tightly coevolving interactions (Thompson, 2005). On this spectrum, the majority of eco-evolutionary interactions are likely the product of diffuse (co-)evolution, and this heterogeneity in $G \times G$ interactions along abiotic gradients will produce variation in the strength and reciprocity of selection across the landscape. The same genetically based species interactions drive variation in energy flow and nutrient cycling through processes such as trophic interactions, decomposition and nutrient transformation (i.e. ecosystem engineering). Niche construction occurs when the abiotic environmental variation (i.e. energy and nutrients) that is the result of species interactions over time (i.e. legacy effects) feeds back to affect contemporary population and community dynamics in the next generation (*FB2*). For example, genetically based species interactions lead to changes in trophic dynamics and nutrient cycling influencing the processes that build a niche (alteration of physical or chemical conditions) and change natural selection across temporal scales. Because the cumulative effects of *FB1* and *FB2* (i.e. species interactions, their ecosystem effects and feedbacks) can vary geographically in strength and direction along environmental gradients representative of ecosystem state factors, the conceptual model directly integrates the temporal dynamics of NCT with the spatial scale of the GMT. Finally, NCT and GMT can be further integrated by the cumulative effects of past species interactions (*FB3*). Feedback 3 starts with the original abiotic gradient of ecosystem state factors that underlie *FB1* and *FB2*. Feedback 3 is driven by and can change due to the slow alteration of the *ecosystem pool* from the legacy effects of *FB1* (Van Nuland, Ware, Bailey, & Schweitzer, 2019; Vitousek, 2004; Wooliver, Pfennigwerth, Bailey, & Schweitzer, 2016; Wooliver et al., 2018; Figure 1). The ecosystem pool is composed of the abiotic factors (e.g. nutrient pools, pH) that change over time and vary across spatial scales and is affected by the initial conditions, climate and other factors that were present when the eco-evo dynamics “started” (e.g. *abiotic origin*). The historical ecosystem pool can change through time due to gradual effects of past species interactions related to *FB1* and *FB2*, as the ecosystem pool and the historical ecosystem pool covary (Van Nuland et al., 2019; Vitousek, 2004). The eco-evo feedback at this scale can be thought of as *historical contingency* because contemporary interactions are contingent on the ecosystem-wide effects of prior interactions that vary geographically (Van Nuland et al., 2017, 2016; Senior et al., 2018). First, the interactions that constitute *FB1* (Figure 1) are not restricted to populations of different species but can also occur among individuals within a population (e.g. Turcotte, Reznick, & Hare, 2011) or among populations

(e.g. assortative mating). Second, the diffuse nature of coevolving ecological interactions on the landscape is a product of gene flow among populations, spatial structure of genetically based interactions (e.g. regional species pools) and the reciprocity of selection in those genetically based interactions. This diffuse (co-)evolutionary dynamic gives rise to a geographic mosaic of “hot spots” and “cold spots” of co-evolution (Thompson, 2005); however, we know little about how variation in *FB1* might shape the functions of ecosystems (Bailey et al., 2014; Schweitzer, Nuland, & Bailey, 2018).

Empirical evidence of these points furthers our understanding of eco-evolutionary dynamics as well as the genetic and environmental factors that determine phenotypes over time and space. We use three examples from terrestrial and aquatic systems to demonstrate the broad applicability of these concepts and which of the three feedbacks from Figure 1 have been demonstrated empirically to date. Further, we identify and explore research frontiers to demonstrate paths forward in understanding how eco-evo feedbacks link population, community and ecosystem-level processes across space and time.

3 | EVIDENCE OF ECO-EVOLUTIONARY FEEDBACKS ACROSS TERRESTRIAL AND AQUATIC SYSTEMS

3.1 | Ecosystem effects of evolution in plant-herbivore interactions

Evolution resulting from plant-herbivore interactions is likely to shape ecosystems when the genetic variation mediating the interaction is correlated with both fitness and ecosystem-level effects. Direct evidence and indirect evidence of the co-evolutionary dynamic of plant-herbivore interactions (Figure 2: *FB1*) exist, but empirical evidence of ecosystem feedbacks resulting from plant-herbivore interactions (*FB2*) remains scarce. However, studies investigating the ecological importance of genetic variation in plants and herbivores provide compelling evidence that contemporary evolution as a result of plant-herbivore interactions can have ecosystem-level effects (Figure 2: ecosystem engineering side of *FB2*). For example, Classen, Chapman, Whitham, Hart, and Koch (2007), Classen, Chapman, Whitham, Hart, and Koch (2013) demonstrated that piñon pine (*Pinus edulis*) susceptibility to a scale insect herbivore is correlated with plant traits that increased nitrogen (N) cycling through litter decomposition but reduced N and carbon (C) accumulation in soil over decades. Additionally, selective consumption of particular plants (e.g. Bailey et al., 2004; Belovsky & Slade, 2000; Yang & Gratton, 2014), induction of defence compounds (Katayama, Silva, Kishida, & Ohgushi, 2013; Schweitzer, Bailey, Hart, & Whitham, 2005), herbivore genetics (Kant, Sabelis, Haring, & Schuurink, 2008; Turley & Johnson, 2015; Zytynska et al., 2016) and differences in the quality of insect herbivore excretions can influence soil N availability and even feedback to influence plant production (Kagata & Ohgushi, 2013). Finally, interacting organisms from different trophic groups (e.g. predators (Schmitz et al., 2008), or soil micro-organisms

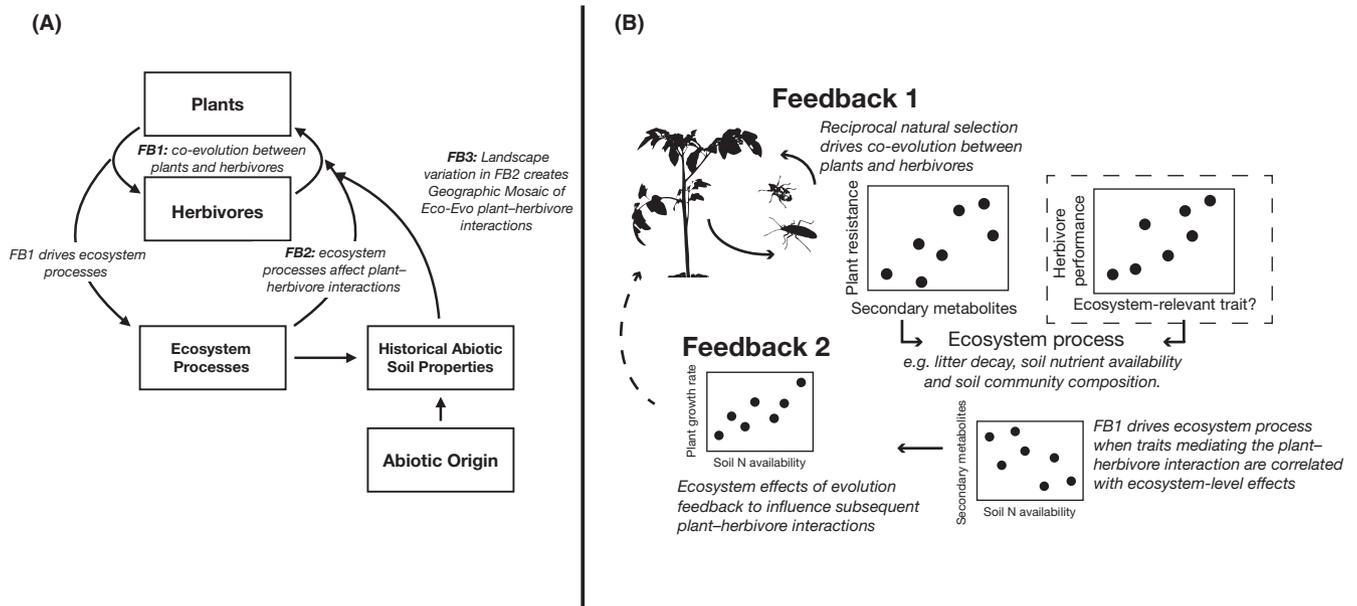


FIGURE 2 A conceptual illustration of the various feedbacks occurring between plants, herbivores and ecosystems. Feedback 1 (Panel a: *FB1*) is the co-evolution between plants and herbivores caused by reciprocal natural selection. *FB1* can alter ecosystem processes because heritable traits mediating plant–herbivore interactions are often correlated with ecosystem-level effects (Panel b: secondary metabolite production in plants alters soil N availability; e.g. Schweitzer et al., 2004). The ecosystem-level effects of plant defence evolution can feed back to influence subsequent plant–herbivore interactions, due to the effects of altered ecosystem processes on plant performance (Panels a and b: *FB2*; e.g. Fitzpatrick et al., 2015). In addition to local ecosystem processes, plant–herbivore interactions, and the feedbacks they initiate, are affected by variation in the abiotic and biotic environments across the landscape (Panel a: *FB3*). Edaphic features, climate and biotic factors, such as community composition and, over longer time-scales, the regional rates of speciation and extinction, cause this landscape-level variation in the environment. Dashed lines highlight current knowledge gaps in this system

(Pineda, Dicke, Pieterse, & Pozo, 2013)), could indirectly mediate the ecosystem effects of herbivory (Utsumi, 2011). Taken together, these studies suggest that genetic variation mediating the interaction between plants and herbivores can exhibit feedbacks to ecosystem processes.

Growing empirical evidence is showing ecosystem effects resulting from evolution in plant–herbivore interactions. For example, replicate populations of *Oenothera biennis* (a North American biennial forb) exposed to either ambient or reduced herbivory diverged in genotypic compositions after 5 years (Agrawal, Hastings, Johnson, Maron, & Salminen, 2012). Using the same experimental evolution study, Fitzpatrick et al. (2015) found significant effects of both the direction and the magnitude of plant evolution on litter decomposition and soil N mineralization rates occurred within experimental plots. Evidence of evolutionary divergence on *O. biennis* seedling performance in soil collected from each of the experimental plots was found, suggestive of an eco-evo feedback (Figure 2: *FB2*). From the herbivore side, although a long history of investigating contemporary evolution exists (especially in an agricultural context; Gould, 1991; Via, 1990), the effects of herbivore evolution on ecosystem processes are unclear. The evolution of traits that increase herbivore population growth would be expected to increase plant consumption. This could result in increased herbivore-derived resources or induced plant defences, both of which could have ecosystem effects (Yang & Gratton, 2014). In the green peach aphid, Turcotte et al. (2011)

found that evolution of increased population growth rates did not affect host plant biomass, while Turley and Johnson (2015) found negative effects dependent on host plant species. These few studies provide direct evidence that evolution resulting from plant–herbivore interactions can have ecosystem-level consequences. Even less is known about how landscape-level variation in the strength of plant–herbivore interactions may drive eco-evo feedback (Figure 2: *FB3*). The necessary ingredients for *FB3* exist: geographic clines in both heritable plant defence traits (e.g. Anstett et al., 2015) and the strength of plant–herbivore interactions (e.g. Benkman, 1999; Pennings & Silliman, 2005). Thus, landscape-level variation in eco-evo feedback due to plant–herbivore interactions is likely common. Our conceptual approach highlights a way forward for examining how plant–herbivore interactions (*FB1*) shape ecosystem pools and processes that may feedback (*FB2*) to influence ecosystem-level evolutionary effects at landscape scales (*FB3*).

3.2 | Ecosystem consequences of evolution in aquatic systems

Eco-evolutionary feedbacks in aquatic ecosystems have been studied primarily through the perspectives of trophic interactions and nutrient recycling (Matthews, Narwani et al., 2011b; Post & Palkovacs, 2009; Schoener, 2011). The presence of eco-evo feedbacks in aquatic microcosms is now incontrovertible with evidence

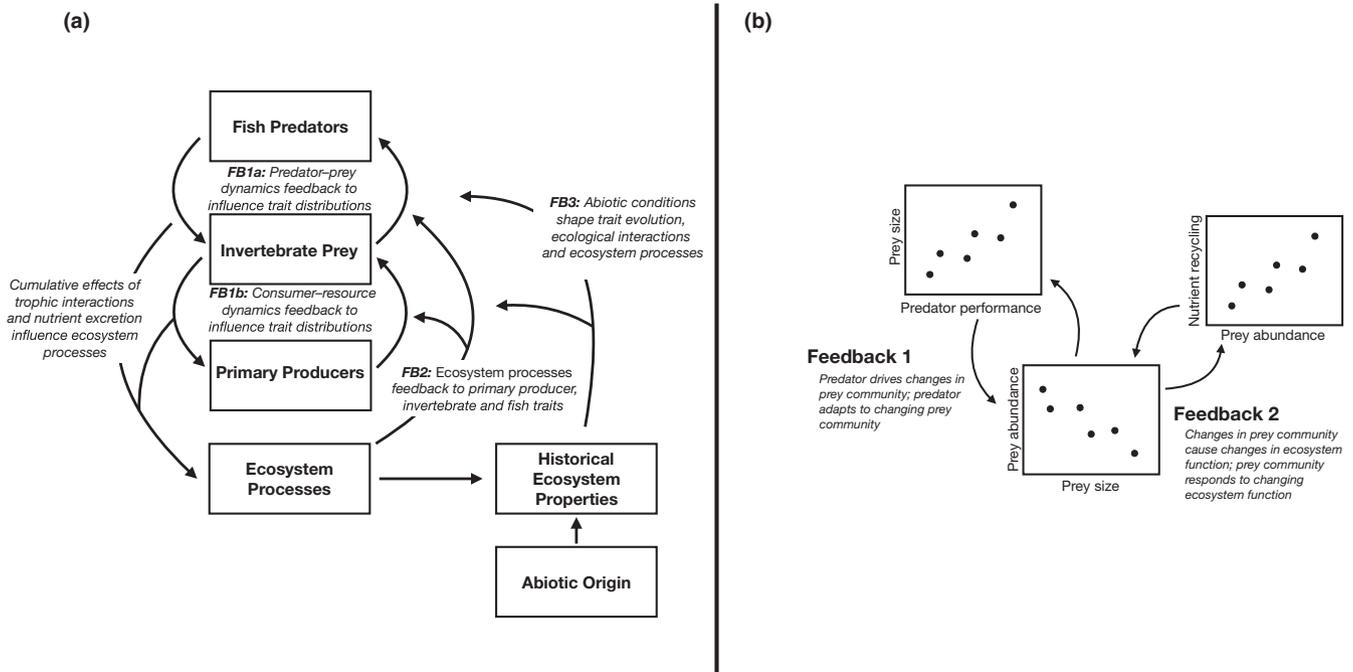


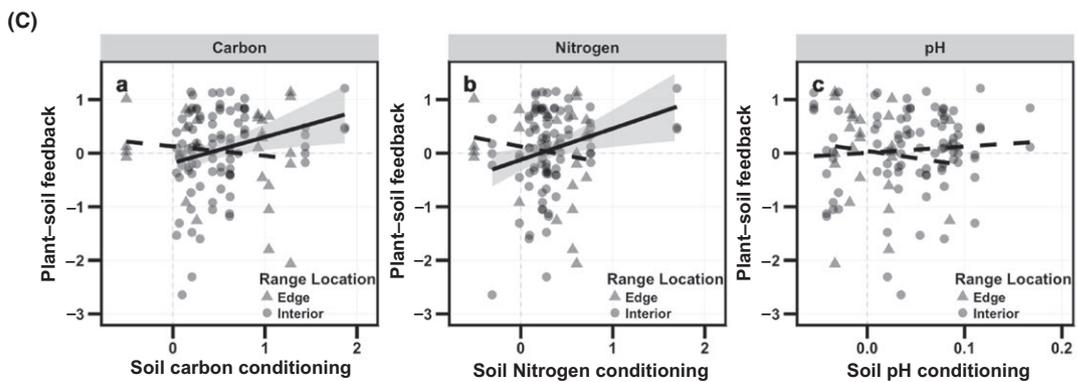
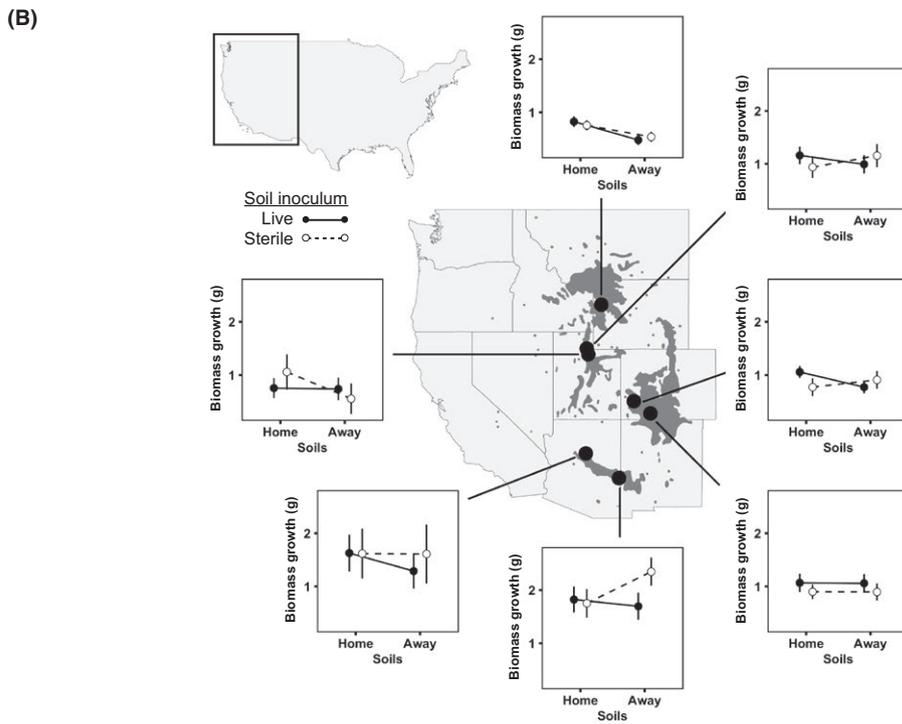
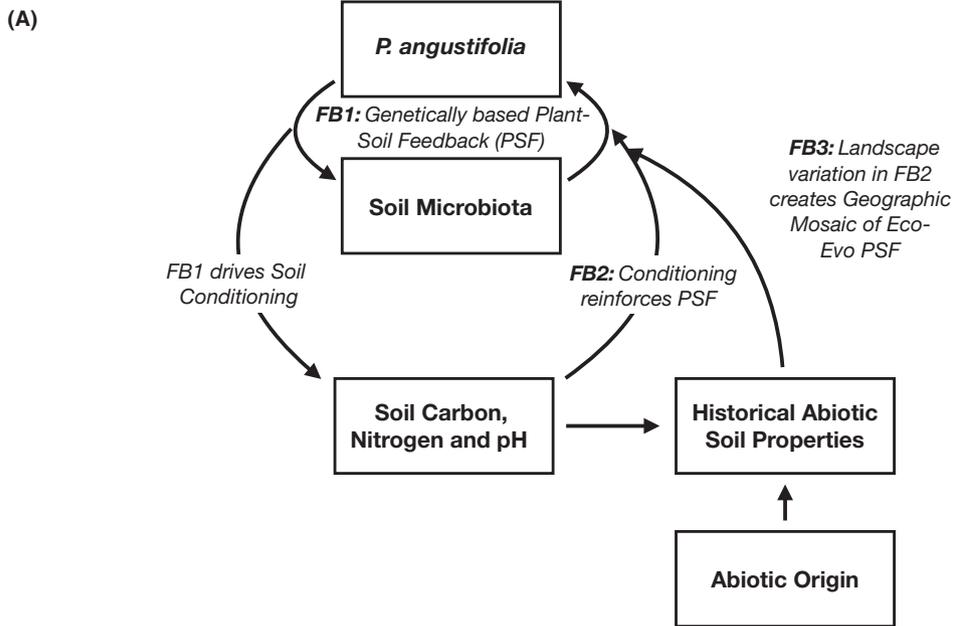
FIGURE 3 A conceptual illustration of the various feedbacks occurring between fish predators, invertebrate prey and primary producers in aquatic ecosystems. Feedback 1a and 1b (Panel a: *FB1a* & 1b) represents the evolutionary interactions driven by predator-prey and consumer-resource dynamics. Cumulative effects of the trophic interactions and nutrient excretions represented in *FB1* can alter ecosystem processes and feed back to influence changes to aquatic prey community (see Panel a: *FB2*; Panel b *FB1* and 2). Hypothetical data in Panel b are representative of findings from the Trinidadian guppy system (*FB1a*: Reznick et al., 1990; Reznick et al., 1996; Palkovacs et al., 2011; Zandonà et al., 2011; *FB1b*: Palkovacs et al., 2009; Bassar et al., 2010; Bassar et al., 2013; *FB2*: El-Sabaawi et al., 2015)

for eco-evo effects outside of laboratory experiments for a wide variety of aquatic taxa, including zooplankton (Matthews, Hausch, Winter, Suttle, & Shurin, 2011a; Miner, Meester, Pfrender, Lampert, & Hairston, 2012), aquatic macroinvertebrates (Ousterhout, Graham, Hasik, Serrano, & Siepielski, 2018), amphibians (Reinhardt, Steinfartz, Paetzold, & Weitere, 2013; Urban, 2013) and fishes (Auer et al., 2018; Carlson, Quinn, & Hendry, 2011; Fryxell & Palkovacs, 2017; Tuckett, Simon, & Kinnison, 2017). Here, we detail evidence for feedbacks in three fish study systems—alewife, guppies and threespine stickleback in the context of Figure 1.

It is clear that species interactions and trophic position can drive eco-evo feedback in multiple fish systems (Figure 3: *FB1*; Palkovacs & Post, 2008, Post, Palkovacs, Schielke, & Dodson, 2008). For example, the evolution of freshwater resident alewife populations shapes the seasonality of predation on zooplankton

communities. Year-round predation reduces zooplankton body size, thereby creating an eco-evo feedback that selects for smaller alewife gape and gill raker spacing (Palkovacs & Post, 2008). The ecological effects of alewife divergence also have impacts on the evolution of alewife prey (Walsh & Post, 2011), competitors (Huss, Howeth, Osterman, & Post, 2014) and predators (Brodersen, Howeth, & Post, 2015). In guppy populations, fish predators increase mortality rates and decrease guppy densities (Figure 3: *FB1a*; Reznick, Bryga, & Endler, 1990; Reznick, Butler, Rodd, & Ross, 1996). These ecological changes shape guppy feeding traits (Palkovacs, Wasserman, & Kinnison, 2011; Zandonà et al., 2011), which in turn alter invertebrate and periphyton abundances (Figure 3: *FB1b*; Palkovacs et al., 2009; Bassar et al., 2010). Changes in guppy density and resource availability appear to underlie the evolution of guppy life-history traits, including age and

FIGURE 4 A conceptual illustration of various feedbacks occurring between *Populus angustifolia*, tree-associated soil microbiome and local to landscape-level environmental contexts. Feedback 1 (Panel A: *FB1*) is the genetically based plant-soil feedback between plant traits and soil microbiota. Feedback 1 can alter ecosystem processes as both plants and soil microbes directly (Panel C: *FB1* and *FB2*, Van Nuland et al., 2017) alter soil nitrogen pools, soil carbon pools and soil pH, which in turn reinforces geographic variation in plant-soil feedback (Panel A: *FB2*). Feedback 3 (Panel A: *FB3*) is exhibited by showing geographic variation in existing PSF (*FB1*) across home and away soil inoculation treatments (Panel B, *FB1* and *FB3*: Schweitzer et al., 2018), likely driven by differences in abiotic and biotic environmental contexts. Panel c shows how plant-soil feedbacks (PSF) are related to the strength of soil conditioning across elevation gradients. The effect of (a) soil carbon (C) and (b) soil nitrogen (N) conditioning (i.e. the standardized difference between conditioned and unconditioned soil locations, *ecosystem engineering* (*FB2*), positively relates to feedback effects (*FB1* & *FB2*) for interior trees, but not edge trees (geographic variation resulting from *FB3*). Soil pH conditioning (c) did not predict interior or edge PSF. Solid lines depict significant regressions with grey areas representing 95% confidence interval, and dashed lines represent insignificant regressions



size at maturity (Bassar, Lopez-Sepulcre, Reznick, & Travis, 2013). This change in body size, in turn, alters nutrient recycling rates (Figure 3: *FB2*; El-Sabaawi et al., 2015). In stickleback populations, fish predators specialized on either pelagic or littoral prey reshape prey community structure through alternative feeding preferences (Des Roches, Shurin, Schluter, & Harmon, 2013; Harmon et al., 2009). Stickleback specialized on either stream or lake habitats reduce their favoured prey, causing a negative eco-evo feedback in mesocosms that favours the alternative type (Matthews, Aebischer, Sullam, Lundsgaard-Hansen, & Seehausen, 2016). Further, a recent mesocosm experiment showed how patterns of phenotypic variation between lakes can lead to differential prey depletion and ecosystem modification, feeding back into selection regimes (Best et al., 2017). Similarly, several studies have shown how environmental context, such as nutrient environment, influences *FB1* (see Brunner, Anaya-Rojas, Matthews, & Eizaguirre, 2017; Declerck et al., 2015; Tuckett et al., 2017). The presence of sticklebacks has been shown to influence aquatic food webs and ecosystem pools (see Limberger et al., 2018), and if similar ecological and ecosystem dynamics could feed back to have evolutionary ramifications across trophic levels and vary geographically (similar to Best et al., 2017), *FB3* may arise. As with plant-herbivore interactions, little information currently exists regarding how *FB1* and *FB2* may vary across environmental gradients to generate variation in ecosystem pools and processes that may drive and reinforce *FB3*. Understanding how the legacy effects of *FB1* and *FB2* influence *FB3* represents an important future research challenge in aquatic systems.

3.3 | Ecosystem consequences of evolution in plant-soil feedbacks

Plants alter the soils in which they grow, and evidence that these modifications can feed back to influence the same or different plants represents a rich and growing mechanism for a variety of ecological phenomena (Van der Putten, Bradford, Brinkman, Voorde, & Veen, 2016; Schweitzer et al., 2012). Within *Populus* (and many other plant taxa), population-level approaches show evidence that tree genotypes condition and host distinct microbial communities (Figure 4A: *FB1*), and differentially influence soil nutrient dynamics (Cregger et al., 2018; Schweitzer et al., 2008, 2004), which can feed back to influence plant productivity and performance (Figure 4B; *FB1* & *FB2*). Further, as plant-driven soil nutrient conditioning increases, so does the strength of plant-soil feedback, which demonstrates that *FB1* and *FB2* are related and vary geographically, directly linking populations, communities and ecosystems (Figure 4C, Van Nuland et al., 2017). When this occurs over long time periods across environmental gradients (Figure 1: *FB3*), ecosystem processes can drive population-level divergence. The best observational example for *FB3* is evidenced by the long-term soil nutrient gradient across the Hawaiian Islands in which divergent populations of *Metrosideros polymorpha* resulted from differences in litter traits that accelerated or slowed nutrient cycling depending on their position along a

soil fertility gradient (Treseder & Vitousek, 2001; Vitousek, 2004). However, Van Nuland, et al. (2019) provide further direct evidence integrating *FB*'s 1–3 across a landscape-level soil fertility gradient.

Together, these empirical results in both terrestrial and aquatic systems show unequivocally that the ecosystem consequences of genetic-based species interactions and niche construction vary (or will likely vary) across spatial environments. They provide evidence for multiple types of feedback, primarily through the evolution of trophic interactions. Although the means and specific evolutionary mechanisms differ among plants and herbivores, among predators and prey, and with both trophic and non-trophic interactions among plants, micro-organisms and soils, feedbacks over time connect populations, communities, and ecosystem pools and processes across space.

4 | CONCLUSIONS AND FUTURE DIRECTIONS

Here, an expanded conceptual framework links ecosystem ecology and evolution by integrating genetically based species interactions, NCT and GMT to highlight feedbacks over time and space. To date, empirical evidence and theoretical evidence show that feedbacks from multiple levels of organization can vary in strength and reciprocity and may be mediated by both direct and indirect interactions and by the environmental context in which such interactions take place. The examples outlined above show that genetically based species interactions (*FB1*) have consequences for both ecosystem and evolutionary processes. Though there is little direct evidence of *FB2* in the plant-herbivore example, the aquatic predator-prey-producer and plant-soil-microbe examples show patterns of ecosystem-level effects that directly alter evolutionary processes. Limited empirical information currently exists for *FB3* in both plant-herbivore interactions and aquatic trophic dynamics, but we show direct evidence that ecosystem-level effects of plant-soil-microbe interactions vary geographically, reinforcing *FB1* and *FB2* and providing examples of context dependency in feedbacks supporting this conceptual framework.

As outlined above, growing empirical evidence is beginning to clarify linkages between evolving trophic dynamics and differences in nutrient cycling rates. In all three systems, improving knowledge of environmental context (*FB3*) is critical for understanding the strength and reciprocity of ecological and evolutionary dynamics in experimental (and natural) settings. For example, eutrophication levels are being included as treatments in many aquatic studies to examine how ecosystem-level differences and environmental context may mediate eco-evo dynamics (Brunner et al., 2017; Declerck et al., 2015; Tuckett et al., 2017). In terrestrial systems, growing evidence shows the importance of ecosystem legacy effects in plant-herbivore and plant-soil interactions (e.g. Fitzpatrick et al., 2015; Pregitzer, Bailey, Hart, & Schweitzer, 2010, Van Nuland et al., 2017, 2019). Further integrating large-scale, geographic approaches with ecosystem perspectives (including ecosystem state factors) will

likely improve our understanding of how the interplay among phenotypes, trophic dynamics and environmental context influences both ecosystem and evolutionary processes in aquatic and terrestrial ecosystems.

Demonstrating *FB*'s 1–3 at macroevolutionary scales will improve understanding of how feedbacks across time and space (Figure 1) have long-term consequences for patterns of biodiversity (Weber, Wagner, Best, Harmon, & Matthews, 2017). For example, Wooliver et al. (2017) showed that *Eucalyptus* spp. species differ in their capacities to use N for growth. Such evolutionary divergence across species was found to be associated with both genetic variation in root function and soil N levels in their home ranges, whereby species occurring in higher nutrient soils have evolved greater specific root length and nutrient use capacities. This demonstrates that soil N has been a strong selective agent for plant function in this plant group that can in turn drive soil nutrient pools. Further, co-evolution with root symbionts seems to play a key role in driving nutrient use within the Tasmanian eucalypts (Wooliver et al., 2018). Overall, this work in plant–soil interactions demonstrates that natural variation in soil nutrient pools can drive feedbacks between plants and their soil microbial communities that vary from positive to negative depending on environmental context (GMT) and are phylogenetically based. From a plant–herbivore perspective, considering that plants have faced herbivory since their colonization of terrestrial Earth over 400 MYA (Labandeira, 2007), this ancient interaction was likely responsible for the development of complex food webs (Olson, 1966; Sues & Reisz, 1998) and is also attributed with giving rise to the rich arsenal of physiological, chemical and mechanical plant defences found today as well as the diversification of numerous plant and animal lineages (Becerra, Noge, & Venable, 2009; Futuyama & Agrawal, 2009; Wiens, Lapoint, & Whiteman, 2015). Thus, using recently developed phylogenetic tools and other comparative approaches to demonstrate the role of NCT and GMT across landscapes will be important to demonstrate the concepts in Figure 1 and their consequences in terrestrial ecosystems.

Our comparative approach highlighted, conceptually and empirically, how feedbacks can link ecosystem ecology and evolution by merging concepts of NCT and GMT over time and space. We showed multiple examples of genetically based species interactions (*FB*1) and how these interactions lead to niche construction over time, altering physical or chemical conditions to impact natural selection (*FB*2). In a plant–soil system, we showed how *FB*'s 1 and 2 can be examined across gradients and spatial scales (*FB*3) that may overall have macroevolutionary consequences. Overall, this approach indicates similarities and linkages among independent lines of research/theory (NCT and GMT), highlights research gaps and reveals many testable hypotheses. Testing these will progress the synthesis showing the ecological and evolutionary relationships between patterns of biodiversity and ecosystem function. Exciting work awaits.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the development of this conceptual synthesis, as well as the subsequent literature search, writing and revision of this manuscript.

DATA ACCESSIBILITY

This manuscript does not use data. All data presented in figures are cited within the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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