

Review

Geo-evolutionary feedbacks: integrating rapid evolution and landscape change

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We develop a conceptual framework for geo-evolutionary feedbacks which describes the mutual interplay between landscape change and the evolution of traits of organisms residing on the landscape, with an emphasis on contemporary timeframes. Geo-evolutionary feedbacks can be realized via the direct evolution of geomorphic engineering traits or can be mediated by the evolution of trait variation that affects the population size and distribution of the specific geomorphic engineering organisms involved. Organisms that modify their local environments provide the basis for patch-scale geo-evolutionary feedbacks, whereas spatial self-organization provides a mechanism for geo-evolutionary feedbacks at the landscape scale. Understanding these likely prevalent geo-evolutionary feedbacks, that occur at timescales similar to anthropogenic climate change, will be essential to better predict landscape adaptive capacity and change.

Bridging geomorphology and evolutionary biology

Biological processes affect almost all **landscapes** (see [Glossary](#)) on Earth [1]. Their effects are perhaps most prominent in **biogeomorphic landscapes** such as coastal wetlands, sand dunes, and peatlands. These landscapes are globally important because of their transport and storage of water, sediments, and carbon, but are also highly vulnerable to climate change [2]. The field of biogeomorphology has been built on observations of the strong influence of organisms on landscapes; however, biogeomorphic models seldom consider genetic or phenotypic changes of organisms (*cf* [3]) because evolution is perceived to take place slowly and across great distances. Thus, geomorphologists have often assumed that they could safely ignore evolution, especially at fine temporal and spatial scales. However, evidence from evolutionary biology has accumulated that populations can evolve meaningful changes on the same timescales at which they modify the landscape [4,5]. Failing to consider evolution in **contemporary time** (ranging from decades to a few hundred years, where absolute timespan translates differently to species based on generation time and effective population size [6]) poses significant uncertainties in predicting landscape responses to anthropogenic climate change.

Looking at this knowledge gap from the other side, evolutionary biology often does not consider the effect of landscape dynamics on biological evolution. Although the effects of landscape changes on speciation in geological time are relatively well studied [7–11], synergistic interactions between evolution and landscape change in contemporary time have not been embodied in evolutionary biology. For instance, the theory of **niche construction** addresses the evolutionary consequences of how organisms modify their environment and **niche**; however, it does not consider simultaneous landscape development [12]. Such persistent disciplinary barriers have impeded the development of a much-needed integrative theory. We propose such an integration of geomorphology and evolutionary biology to better understand ecosystem vulnerabilities and adaptive capacities against a backdrop of global change.

Highlights

Organisms can modify landscapes. Because the evolution of organisms is often perceived to take place slowly, geomorphologists have assumed that they could safely ignore evolution in understanding landscape change, especially in contemporary time.

Evidence has accumulated that populations can evolve rapidly on timescales congruent to that of landscape change. The resulting landscape change can in turn affect the evolution of these organisms.

We provide a conceptual framework for these geo-evolutionary feedbacks that describes the interplay between landscape change and the evolution of organisms residing on the landscapes.

Geo-evolutionary feedbacks are probably common – they can occur at patch or landscape scales and can be realized by direct or indirect pathways.

Failure to consider geo-evolutionary feedbacks may limit our ability to predict landscape and population responses to modern global change.

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The key realization to our argument is that evolutionary dynamics and landscape change can occur at congruent timescales, thus forming an interplay between the evolution of populations and the dynamics of landscapes on which those populations reside. We define such reciprocal effects as **geo-evolutionary feedbacks** [13] (Figure 1A), which can take some guidance from the rapidly progressing field of **eco-evolutionary feedbacks** [4,5]. Eco-evolutionary dynamics considers contemporary interactions between ecology and evolution, where 'ecology' refers to population (e.g., organismal abundance), community (e.g., species richness), and ecosystem attributes (e.g., resource levels [14]). Geo-evolutionary feedbacks instead pertain to the interplay between evolution and landscape change – the theater in which ecological dynamics occur – and thus complement eco-evolutionary feedbacks. We first describe the pathways and conditions under which geo-evolutionary feedbacks occur. We then describe the spatiotemporal scales of geo-evolutionary feedbacks, their expected mechanisms at local and landscape scales, and the environmental factors that would influence feedbacks. Finally, we propose methods to test the presence and strength of geo-evolutionary feedbacks.

Direct versus indirect geo-evolutionary feedbacks

Geo-evolutionary feedbacks describe the reciprocal interactions between evolution and landscape change. 'Landscape change' refers to changes in landscape morphology or other geophysical properties (e.g., soil porosity, sediment size, slope stability). Geomorphic processes leading to landscape change include processes induced ultimately by gravitational or molecular stress and by chemical reactions [15]. Stress-induced processes lead to erosion and material disintegration, transport, and deposition. Chemical processes refer to weathering, namely the attrition of mineral surfaces and lowering of rock surfaces by chemical reactions. Crucially, all these processes are subject to organismal modifications. For instance, organisms can impede energy

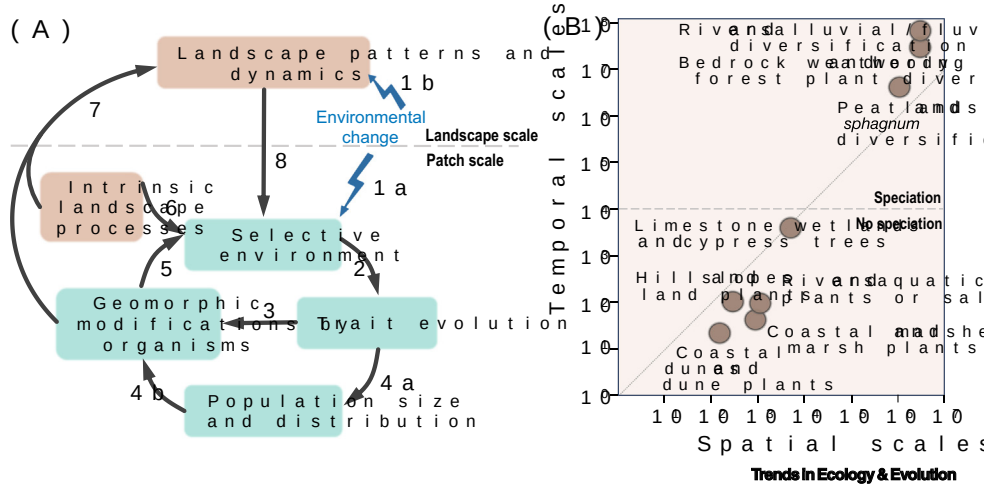


Figure 1. Mechanisms of geo-evolutionary feedbacks and examples across a range of spatiotemporal scales. (A) Geo-evolutionary feedbacks unfold when (i) environmental change causes changes in the local selective environment that are directly (arrow 1a; e.g., warming affects the water temperature of rivers) or indirectly mediated by landscape patterns and dynamics (arrow 1b; e.g., sea-level rise affects the elevation of coastal marshlands); (ii) an altered selective environment can induce trait evolution (arrow 2); (iii) trait evolution can lead to changes in organismal geomorphic effects directly by altering the population mean per-capita size of organisms (arrow 3), or indirectly by altering the population size or spatial/temporal distributions of an organism capable of geomorphic modifications (arrows 4a and 4b); and (iv) the evolution-caused changes in local geomorphic modifications interact with the intrinsic landscape processes and alter the selective environment directly (arrows 5 and 6), or first affect the landscape-scale emergent properties, via landscape spatial self-organization (arrow 7), which then affect the selective environment (arrow 8). (B) Examples of geo-evolutionary feedbacks occur across a range of spatiotemporal scales (circles; Table 1 for detailed information about each example).

Glossary

Biogeomorphic landscapes:

landscapes where the interactions between biological and geomorphic processes play a significant role in shaping the landscape morphology and dynamics (e.g., tidal marshes, mangroves, coastal dunes, river deltas).

Contemporary time:

a timespan ranging from a few decades to a few hundred years, where absolute timespan translates differently to species, depending on their generation time and effective population size. In this timeframe, evolutionary dynamics typically involve the evolution of trait variation of a population, without speciation.

Eco-evolutionary feedback:

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.

Emergent property:

a macroscale entity that results from microscale interactions but is characterized by properties that cannot be directly associated with the microscale (i.e., 'the whole is greater than the sum of its parts').

Geo-evolutionary feedback:

the cyclical interaction between landscapes and evolution such that changes in landscape morphology or other geophysical properties drive evolutionary change in the organismal traits that, in turn, alter the landscape.

Geomorphic engineering:

alteration of the landscape geomorphology by organisms; geomorphic engineering traits are organismal traits that enable modification of the physical landscape.

Landscape: an area that is spatially heterogeneous in at least one factor of interest. This flexible definition is applicable across scales and is adaptable to different systems.

Landscape energy: erosive forces driven by pressure gradients (e.g., wind, water) or solely by gravity. It reflects the physical capacity of the landscape to perform geomorphic work (e.g., particle entrainment, transport of sediments) in the absence of organisms.

Locality: a specific area or habitat where particular species or community of organisms lives and thrives (e.g., a coastal marshland, a dune field).

Morphodynamics: the process by which landscape morphology affects physical or biological processes in such

and material transport (e.g., root sediment trapping) and can accelerate material disintegration and chemical weathering [1]. Furthermore, biomass accrual can directly modify a landscape (e.g., peat accumulation) [16]. The altered landscape morphology and dynamics might, in turn, affect evolution, thus forming geo-evolutionary feedbacks.

Following from a distinction in eco-evolutionary dynamics, geo-evolutionary feedbacks can be realized by either 'direct' (i.e., 'per capita') or 'indirect' (i.e., via changes in abundance and distribution) pathways. The direct pathway involves evolutionary changes (e.g., in the mean and variance) of **geomorphic engineering** traits such as plant morphological **traits** (e.g., stem density, diameter) that modify sediment transport. [Box 1](#) provides a concrete example where increased anthropogenic nitrogen input causes changes in stem thickness and root-to-shoot ratio of *Schoenoplectus americanus*, a dominant sedge in North American coastal marshes [3]. Evolutionary changes in these morphological traits reduce the rate of sediment accumulation and make marshlands more susceptible to sea-level rise. The resulting increased exposure to sea-level rise forms a new selective pressure (e.g., inundation) that can elicit evolutionary responses in other relevant traits of *S. americanus* (e.g., inundation tolerance) [17], forming a geo-evolutionary feedback. In such cases geo-evolutionary feedbacks involve the evolution of traits with direct geomorphic consequences: that is, changes in the per-capita effects of organisms on the environment.

Alternatively, geo-evolutionary feedbacks can be mediated by ecological dynamics without requiring the evolution of geomorphic engineering traits; instead, effects are driven by the evolution of traits that affect species abundance and distribution. For instance, with the rise of sea level, the salinity tolerance of *S. americanus* populations has evolved over the past few decades [17] ([Box 1](#)). Salinity tolerance mainly involves physiological adaptations; for example, root Na⁺ exclusion capacity and tissue tolerance to accumulated Na⁺ by intracellular partitioning [18]. Although these traits do not directly engage in geomorphic modifications, salinity adaptations affect plant fitness in the changing environment. Increases in growth and abundance can enhance the accrual of sediments and organic matter, forming indirect geo-eco-evolutionary feedbacks (arrows 4a and 4b, instead of arrow 3, in [Figure 1A](#)). Indirect geo-evolutionary feedbacks can also be mediated by the evolution of traits that affect population distribution in space and time. For instance, life-history and dispersal traits influence when in landscape development and where on the landscape organisms exert geomorphic effects, respectively, both of which can lead to significant landscape consequences [19,20].

Overall, we might expect geo-evolutionary feedbacks to most readily involve the indirect pathway, given that evolution clearly influences organismal abundance, which can strongly affect geomorphic processes, and geomorphic changes can impose selection on organisms. However, the direct pathway is perhaps more compelling because it involves evolution that results in changes to the per-capita geomorphic effects of organisms. Indeed, most studies of eco-evolutionary dynamics are focused on this direct pathway, such as experiments that manipulate the genotypes or phenotypes of focal organisms while maintaining their densities at constant levels [21]. Hence, most of our discussion focuses on this direct pathway, while acknowledging that the indirect pathway is likely to be more prevalent.

General requirements for geo-evolutionary feedbacks

Geo-evolutionary feedbacks focus on ecological variables associated with landscape morphology and dynamics (e.g., water availability affected by landforms that set the distance to groundwater, nutrient limitations that are affected by bedrock weathering), which share several general requirements with eco-evolutionary feedbacks [5,22]. For example, if geo-evolutionary feedbacks are to occur, evolution and landscape change need to co-occur on congruent timescales.

a way as to influence the further development of the morphology.

Niche: the sum of all natural selection pressures experienced by a population.

Niche choice: the mechanism by which an individual selects an environment, resulting in a change in the phenotype–environment match, fitness, and individualized niche of an individual.

Niche conformance: the mechanism by which an individual adjusts its phenotype, resulting in a change in the phenotype–environment match, fitness, and individualized niche of an individual.

Niche construction: the mechanism by which an individual makes a change to its environment, resulting in a change in the phenotype–environment match, fitness, and individualized niche of an individual.

Patch scale: the spatial scale of a relatively homogeneous area within a landscape that differs from its surroundings. 'Patch scale' is relative to 'landscape scale'. Because the size of a landscape is specific to the focal study, the size of a patch could also vary with the focal landscape and the focal environmental variable(s) used to quantify heterogeneity.

Spatial self-organization: the process of local interactions among agents in a system that spontaneously give rise to pronounced macroscale spatial patterns from disordered initial configurations.

Trait: any morphological, physiological, or phenological feature measurable at the individual level, from the cell to the whole-organismal level, without reference to the environment or any other level of organization.

Box 1. Geo-evolutionary feedbacks in coastal salt marsh landscapes

Responding to an array of anthropogenic environmental changes (e.g., sea-level rise, warming, elevated atmospheric CO₂, and increased nutrient loading), the mean and variance of many traits in the coastal marsh sedge *Schoenoplectus americanus* have evolved in contemporary time (arrow 1 in Figure 1). Indeed, 'resurrected' cohorts of *S. americanus* from a time-stratified seed bank reveal a century-long record of heritable variation in salinity tolerance [17] driven by the selective pressure of shifting estuarine conditions under a changing climate. Similarly, Vahsen *et al.* [3] found heritable changes in an additional seven traits they measured, including root depth distribution, root-to-shoot ratio, rooting depth, stem height, stem density, stem width, aboveground biomass, and belowground biomass. For instance, rooting depth has become shallower and the root-to-shoot ratio has declined. These shifts are likely a response to increased anthropogenic nitrogen loading since the mid-20th century because excess nitrogen may have alleviated nutrient limitation, thus reducing the need for plants to invest in traits that improve access to belowground resources [74]. Of the seven traits, five have further evolved greater adaptive plasticity (i.e., enhanced sensitivity to exposure) over the past century [75].

The evolution of salinity tolerance allows the population to grow better under rising sea levels, maintaining its geomorphic effects (arrow 2). The seven traits measured in [3] all directly affect sediment trapping, and their evolution alters the mean per-capita size of geomorphic modifications (arrow 2). Furthermore, the evolution of trait adaptive phenotypic plasticity causes geomorphic consequences both directly (by plastic responses of geomorphic traits) and indirectly (by allowing the plant to maintain its abundance under a changing environment) (arrow 2).

These plant geomorphic modifications then feed back to affect the evolution of plants at both the local patch scale and the landscape scale. At the patch scale, local environmental conditions affect the immediate selective environment of the plant (arrow 3). At the landscape scale, the evolutionary change of the population, including its mean and variation of traits, abundance, and spatial distribution, will affect landscape spatial self-organization and the broader-scale emergent properties (arrow 4), such as the structure of a tidal creek network, which then affect landscape sediment trapping, and hence the vulnerability of coastal marshes to sea-level rise [3], thus forming a new selective pressure that can feed back to affect the evolution of plants (arrow 5) to generate geo-evolutionary feedbacks at the landscape scale.

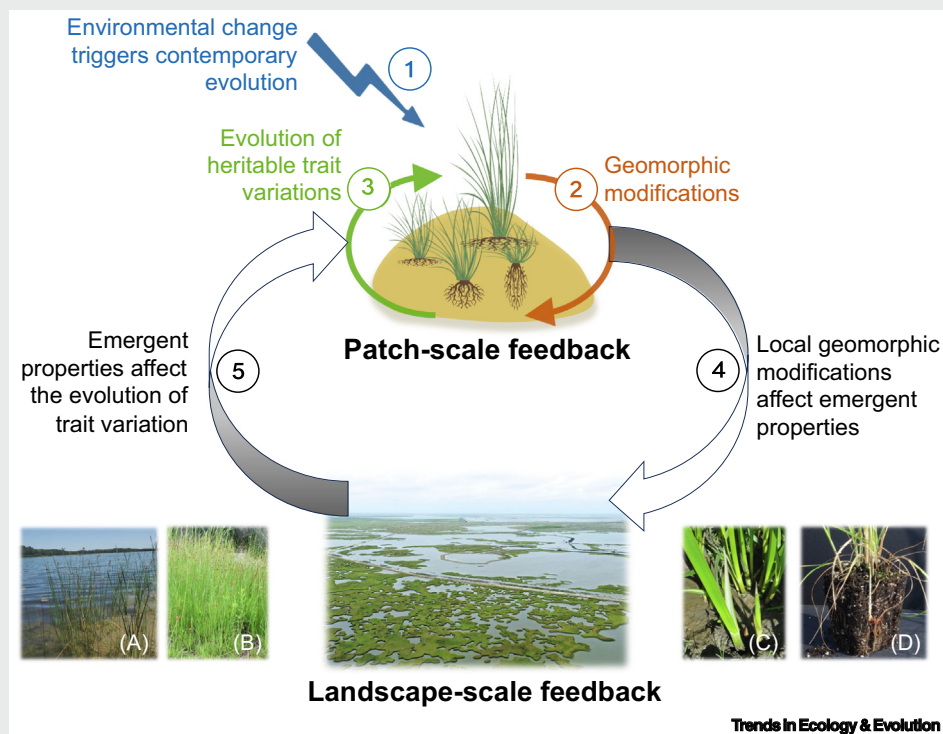


Figure 1. Geo-evolutionary feedbacks using the example of coastal salt marsh landscapes. Panels (A) and (B) at the foot of the figure show different stem densities of *Schoenoplectus americanus* – a dominant sedge in North American coastal marshes. (C) Shows plant trapping sediments. (D) Shows the root biomass of *S. americanus*, where greater root biomass leads to greater sediment-trapping capacity.

Furthermore, organismal geomorphic modifications must cause selection on the population, which must have sufficient genetic capacity to evolve in response to the geomorphic change [22,23]. These conditions are not a given. For instance, organismal modifications do not always lead to changes in the selective environment [24]. In such cases, organisms can change the landscape but the geomorphic consequences are merely a side effect (e.g., altered soil erosion by cattle trampling). However, for all cases of organismal geomorphic engineering, some degree of feedback, involving a chain of interacting species or multiple intermediate traits and variables, probably occurs, at least in some contexts [25]. A majority of those effects are likely minor – we focus on feedbacks that are strong and consistent.

Spatiotemporal scales of geo-evolutionary feedbacks

One of the key issues in considering geo-evolutionary feedbacks is their scale – both temporal and spatial – because scale is inherent to the concept of 'landscape' [26]. A 'landscape' is broadly defined as a spatially heterogeneous area [27], the size of which is specific to the focal study. The timescale relevant to the dynamics of a given landscape increases with landscape size [28]. Small landscapes equilibrate rapidly with the environment. Large landscapes require a longer time to equilibrate because the timescale of the response to new conditions depends on the amount of material that must be transformed or transported [29]. Because of the correlation between the size of a landscape (spatial scale) and its rate of change (timescale), for evolution and landscape change to occur on congruent timescales, the spatial scale of a landscape of interest dictates the timescale of evolutionary change.

Landscapes at the **locality** scale (a specific area or habitat; e.g., a coastal dune) change rapidly, and geo-evolutionary feedbacks will therefore involve correspondingly rapid evolutionary change. In such cases we are not so much interested in the evolution of new traits (i.e., the origin of the beaver's teeth) but instead in changes in the mean and variance of existing traits (i.e., changes in the size of teeth) in contemporary time. [Box 1](#) provides such an example involving *S. americanus* in coastal marsh landscapes. We focus on geo-evolutionary feedbacks at the locality scale in contemporary time – the temporal window where the mutual interplay between landscapes and evolution has been rarely studied but is most relevant to anthropogenic climate change.

Although our primary focus is on relatively small spatial scales and contemporary time, geo-evolutionary feedbacks obviously also occur on larger scales ([Table 1](#) and [Figure 1B](#)) – biogeomorphologic macroevolution [30]. At the scale of geographic regions, for landscape change and evolution to occur at similar timescales, speciation and diversification must couple with landscape development over millions of years. For example, facilitated by enhanced resource limitation caused by a decline in atmospheric CO₂ in mid to late Cretaceous [31], thinner roots began to evolve [32,33]. The evolution of fine roots allowed plants to forage for water and nutrients from bedrock more efficiently and created landscape patches varying in soil thickness and nutrient conditions [34], which accentuated landscape heterogeneity and the radiation of land plants [35].

Landscape cross-scale interactions and emergent properties

As discussed previously, geo-evolutionary feedbacks can occur in landscapes of vastly different sizes, ranging from small habitats (localities) to large geographic regions. Regardless of the absolute size of a landscape, organismal modifications typically occur locally (**patch scale**). However, local dynamics may cascade to the broader scale and induce landscape-scale geo-evolutionary feedbacks. This scaling up occurs by **spatial self-organization**, a process where broad-scale **emergent properties** or patterns – such as rhythmic patterns on sandy beaches [36], and

Table 1. Examples of potential geo-evolutionary feedbacks in contemporary time and in geological time^a

Geo-evolutionary feedbacks in contemporary time at the locality scale				
(1) Environmental change/stress →	(2) Contemporary evolutionary responses →	(3) Geomorphic modification at the patch scale →	(4) Consequences at the landscape scale →	(5) Contemporary evolutionary response to geomorphic modifications
Ocean warming; altered regime of upwelling (nutrient supply); ocean acidification reducing food availability; altered hydrological and temperature regime of stream water, etc.	Salmon in rivers (e.g., <i>Oncorhynchus tshawytscha</i> , <i>Oncorhynchus nerka</i>): evolution of the variation of traits relevant to heat tolerance and to upstream migration and spawning dates [76]	Population size and temporal distribution of organismal modifications: disturb the channel substrate in redd excavation, which increases the fine sediments to be carried downstream; and the delivery of nutrients from the carcasses of mass spawning salmon populations to riparian vegetation, which affects sediment deposition and trapping [77]	Modify total sediment transport rates, alter typical alluvial reach- and subreach-scale morphology (forming hummocky surface), hydraulics, and stability [78]. Possibly modify longitudinal topographic profile of rivers [79]	Changes to the longitudinal topographic profile of rivers potentially lead to changes to the size and amount of sediment on the channel bed, which could feed back to affect redd building behavior or the spatial distribution and abundance of salmon
Warmer water temperature, ocean acidification	Mussels in coasts: adaptive genetic variation associated with seawater temperature (<i>Mytilus galloprovincialis</i>) [80] and ocean acidification (<i>Mytilus edulis</i>) [81]	Population size: reduces the efficiency of coastal rock breakdown processes and reduces wave turbulence at the rock surface [82]	Increase the stability of rocky coasts [82]	Increases in the population size and frequency of traits that adapt to the initial environmental changes (e.g., warmer, and more acidic ocean water) as a result of stable habitat (rocky coasts)
Warmer temperature	Mountain plants: early flowering of <i>Boechera stricta</i> , a mustard native to the US Rocky Mountains, by directional selection [83]. Reduction in the climate-related genetic variation in natural populations, for example <i>Betula pendula</i> (European white birch) [84]	Population size: affects soil cohesion and strength, with roots penetrating the soil mantle and anchor the soils into more stable substrate [85]	Modify the stability of hillslopes [86]	Changes in soil and slope stability potentially feed back to alter the genetic variations of traits that responded to the initial environmental change (i.e., warming)
Intense ivory poaching	Elephants on land surfaces (<i>Loxodonta africana</i>): frequency of tusklessness increases in the population [87]	Per-capita effect: reduced capacity to dig wells, smooth rock surfaces, and peel bark [88]	Tusklessness may affect rates of bioturbation and induce changes in plant communities [88], although the effects are often localized, with limited effects at the landscape scale [88]	Likely negligible effects on the contemporary evolution of elephants, although potentially could have large, diffuse effects on other species on the same landscape [89]
Sea-level rise, warming, elevated atmospheric CO ₂ , increased nutrient loading	Saltmarsh plants (e.g., <i>Schoenoplectus americanus</i> , <i>Spartina</i>): evolution of the variation of morphological traits [3], salinity tolerance [17,90], and phenotypic plasticity [75]	Per-capita effect and population size: change the rates of sediment trapping and organic matter accrual (Box 1)	Modify tidal creek channel structure and the resilience of marshlands to sea-level rise	Modified landscape resilience to sea-level rise potentially feeds back to affect the evolution of variation of traits relevant to the altered risk of inundation and exposure to high salinity
Increased wind speed and sand burial rate, reduced nutrient availability	Coastal dune plants (e.g., <i>Ammophila brevifolula</i> , <i>Uniola paniculata</i> , <i>Arctotheca populifolia</i>): variation of morphological traits – stem length, ratio of length to height (lateral vs vertical growth form), leaf thickness, and leaf shape [91]	Per-capita effect: affects sand deposition rate and pattern	Affect dune shape and resilience to dune overtopping by storms	Altered sand deposition likely feeds back to affect the variation of physiological traits that determine the capacity of plants to withstand burial; modified risk of dune overtopping potentially induces the evolution of trait variations relevant to the new selective environment

Table 1. (continued)

Geo-evolutionary feedbacks in contemporary time at the locality scale				
(1) Environmental change/stress →	(2) Contemporary evolutionary responses →	(3) Geomorphic modification at the patch scale →	(4) Consequences at the landscape scale →	(5) Contemporary evolutionary response to geomorphic modifications
Increased water temperature	Aquatic plants in rivers: evolution of variation of (i) traits relevant to thermal adaptation by downregulating respiration relative to photosynthesis [92], and (ii) traits allowing greater photosynthetic capacity and reduced susceptibility to photoinhibition [93]	Population size: affects sediment deposition rate and transport pattern	Modify river channel geomorphology and stability	Potentially feeds back to affect the evolution of genetic variation in traits that adapted to the initial environmental change (warmer water) because of altered channel stability
Mid- to late-Holocene El Niño-Southern Oscillation leading to the establishment of cypress trees in South Florida (USA), with plant growth stressed by water in the dry season [94]	Cypress tree (<i>Taxodium distichum</i>) in coastal wetlands: evolution of the variation of traits affecting CO ₂ at the bedrock surface (e.g., root morphology and biomass allocation to roots)	Per-capita effect: CO ₂ from root respiration and organic matter decomposition accelerates limestone weathering by ~20-fold and forms weathered limestone depressions [53]	Self-organize into evenly spaced depressions across the landscape [54]	Evolution of the variation of root traits that affect CO ₂ at the bedrock surface; self-organized spatial patterning can modify gene flow among cypress subpopulations in a spatially structured population
Geo-evolutionary feedbacks in geological time at the regional scale				
(1) Environmental change/stress →	(2) Geological evolutionary responses →	(3) Geomorphic modification at the patch scale →	(4) Consequences at the landscape scale →	(5) Geological evolutionary response to geomorphic modifications
The decline of atmospheric CO ₂ , that began in the Cretaceous probably caused water to become more limiting and nutrients more bound to organic matter [32]	Woody forest plants: emergence of fine root traits such as increased specific root length and reduced root diameter during the Cretaceous period (~145–65 Myr ago) [32]	Per-capita effect: accelerated rates of bedrock chemical and physical weathering	Create heterogeneous landscape varying in regolith and soil thickness and in geochemical conditions	Speciation and acceleration of diversification of woody forest plant species during the Cretaceous period [33]
Likely stressed by water as plants move from swampy lowlands to drier alluvial settings [95]	Land plants in fluvial and alluvial environments: emergence of wood and well-developed extensive root systems that penetrated deeply into the soil [95]	Per-capita effect: enhanced formation of pedogenic clay minerals, promotes channel avulsion by large woody debris, and reduces erosion and sediment transport by root binding	Form channelled- and island-braided rivers, meandering and anabranching rivers, and stable muddy floodplains [43,95]	Speciation and acceleration of diversification of alluvial and fluvial plants over the 120 Myr interval from the Devonian through to the Carboniferous [43,95,96]
Likely Miocene climatic cooling in the northern hemisphere [97]	Peat mosses (<i>Sphagnum</i>): emergence of traits affecting organic matter decay rate, for example the content of sphagnum, phenolics, and Klason lignin, and traits adapting to the cold, acidic, low-nutrient, and anoxic environments of peatlands [98]	Per-capita effect: accumulation of organic matter and peats	Form hummock-hollow landscape spatial patterning [16]	Speciation and acceleration of diversification of <i>Sphagnum</i> 7–20 Myr ago [97]

^aFrom the first to the last columns in the table, we outline the sequential steps involved in full-circle geo-evolutionary feedbacks. Environmental stress/change (column 1) triggers evolutionary responses by focal trait(s) (column 2), which then lead to geomorphic consequences at the local scale (column 3) and the landscape scale (column 4). Geomorphic consequences, at the patch or landscape scale, might invoke subsequent evolutionary response by the focal organism (column 5), bringing geo-evolutionary feedbacks full circle. Note that the evolutionary responses that lead to geomorphic consequences at the patch or landscape scale can be the evolution of variation in geomorphic engineering traits that primarily affect per-capita size, or the evolution of variation in performance traits that primarily affect the population size and distribution of the geomorphic engineering organism.

regular patterns in peatlands produced by interactions among flow, sediments, nutrients, and plants [16,37] – are formed solely by internal feedbacks [38,39]. For instance, plant recruitment strategies affect river channel networks [40]: slow and patchy vegetation colonization leads to more extensive channel networks with shorter unchanneled path lengths (indicating that channels have higher efficiency to drain a watershed) than a fast and homogeneous colonization strategy. In another example, adaptations of dune plants to sand burying affect the shape of coastal dunes. Dense and clumped shoots of *Ammophila breviligulata* (American beachgrass) coupled with rapid lateral spread give rise to wide foredunes, whereas *Uniola paniculata* (sea oats), with fewer, taller shoots and slower lateral spread, tends to form narrower, steeper dunes [41].

The next question is how such emergent broad-scale patterns shaped by trait variation can in turn affect trait evolution at the local scale (arrow 8 in Figure 1A), thus fulfilling the largest promise of geo-evolutionary feedbacks. We can see several routes to such an outcome. First, landscape patterns can constrain the local environment that organisms occupy [42]. As an example, plants promote channel stability by increasing bank cohesion through the binding power of roots [43,44]. Consequently, plants tend to 'corral' the water into a single dominant channel [45]. This modification leads to the formation of single-thread, deep channel systems with rapid flows, which in turn increase the rate of plant removal. A new steady-state is achieved when the removal rate is eventually as fast as the rate of plant expansion. This example indicates that the broad-scale patterns emerging from local adaptation surely feed back to reduce fitness of organisms. Second, emergent properties can affect the resilience of the landscape that organisms reside on [38]. In tidal creek networks, plant traits shape the development of network complexity [19,46]. The emergent network complexity, rather than plant traits directly, then determines the sedimentation rate of the system and therefore the resilience of marshlands to sea-level rise and further evolution of marsh plants. In coastal dunes, plant traits shape dune morphology, which alters dune vulnerability to overtopping by storm-induced waves [47]. Notably, organismal adaptation to the local environment does not necessarily increase landscape resilience [48]. Third, the spatial characteristics of emergent patterns can affect evolution. For instance, environmental heterogeneity across microhabitats can drive genetic differentiation of subpopulations [49]. Patch configuration affects the strength of local adaptation by affecting gene flow across habitats [50]. Low levels of habitat aggregation weaken local adaptation because gene flow between habitats can overwhelm selection [51,52].

An example of how geo-evolutionary feedbacks merge patch and landscape scales can be seen in wetlands of South Florida. CO₂ from cypress (*Taxodium distichum*) root respiration accelerates the limestone weathering by ~20-fold, creating weathered depressions (radius >80 m with center >1.5 m deep) [53]. The duration of surface water in depressions extends with depression size, feeding back to enhance cypress fitness in the water-limited system. This dynamic forms geo-evolutionary feedbacks at the patch (depression) scale. The formation of depressions modifies surface and subsurface water flow, triggering complex feedbacks between hydrology, weathering rate, and plant growth that give rise to strikingly evenly spaced depressions across the landscape [54,55]. This emergent spatial patterning can induce geo-evolutionary feedbacks at the landscape scale by setting the characteristic distance between cypress subpopulations, each of which is confined within depressions where surface water accumulates, and thereby affecting the gene flow of the meta-population. Patterns of gene flow have a variety of effects on contemporary evolution [52].

Other factors influencing geo-evolutionary feedbacks

The emergence of broad-scale properties and landscape-scale feedbacks can be affected by landscape heterogeneity because heterogeneity constrains the effectiveness of internal

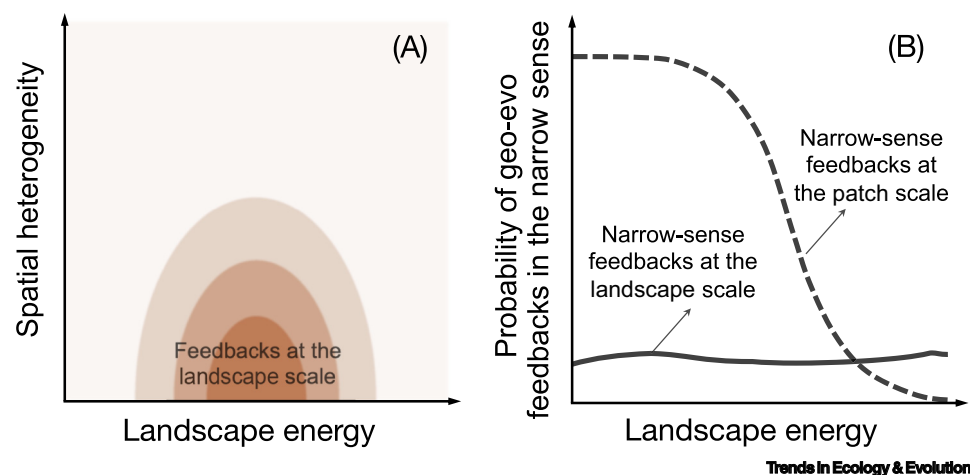


Figure 2. Variables expected to affect geo-evolutionary feedbacks. (A) Geo-evolutionary feedbacks at the landscape scale likely occur when landscape spatial heterogeneity is low and landscape energy (the erosive force on landscapes that is driven by wind, water, and gravity) is neither too high nor too low (a darker brown color denotes a higher probability of landscape-scale geo-evolutionary feedbacks). The occurrence of feedbacks at the patch scale may not be sensitive to landscape energy or spatial heterogeneity. (B) Landscape energy further affects the probability that feedbacks are present in the narrow sense. At a low energy level (but sufficient for biogeomorphic processes [99]), patch-scale feedbacks (dashed line) are likely to be in the narrow sense. As the energy level increases (e.g., strong waves or winds, steep slopes), patch-scale feedbacks are more likely to be present in the broad sense. The probability that geo-evolutionary feedbacks at the landscape scale (solid line) will be present in the narrow sense is likely to be low and is not affected by landscape energy.

feedbacks and spatial self-organization [56] (Figure 2A). A common example of landscape heterogeneity is the variation in substrate. The regular patterning of limestone depressions in South Florida can be formed because the landscape features an approximately homogeneous environment. Landscapes with highly variable lithology will not exhibit such self-organization [54]. Heterogeneity increases with spatial scale. Considering a geographic region as a landscape, its lithology varies markedly [57]. Deep roots evolve in bedrock patches of low resistance (e.g., limestone), thereby increasing rock porosity and regolith thickness. These geomorphic changes create soil pockets to store resources, causing subsequent selection for deep roots [58]. In weathering-resistant patches (e.g., ironstones), limited weathering produces thin soils. As a result, shallow roots that prioritize lateral expansion evolve to explore a large rock surface to acquire resources [59], which in turn limits the weathering rate and soil accumulation. In this case geo-evolutionary feedbacks occur largely at the patch scale – patches change relatively rapidly, coupled with corresponding rapid evolution of trait variation on the congruent timescale. However, interactions among patches are limited by the heterogeneity of lithology. Consequently, such patch-scale feedbacks accentuate the existing heterogeneity and accelerate plant diversification. By contrast, in the example of cypress limestone depressions described in the preceding text, homogeneous substrates allow among-patch interactions such that organismal traits can propagate to affect emergent landscape patterning, making geo-evolutionary feedbacks at the landscape scale possible.

The likelihood of landscape-scale feedbacks is further affected by how much energy drives the landscape (**landscape energy**) (Figure 2A). Calm or frequent stormy conditions can lead either to a lack of energy or to the dominance of a forced process that overwhelms the possibility for internal feedbacks to take over ([38] and references therein). Landscape self-organization occurs between these extreme conditions when energy is sufficient to override the underlying heterogeneity to allow local processes to propagate across the landscape and form broad-scale patterns. For landscape-scale geo-evolutionary feedbacks to occur, sufficient energy is required to drive **morphodynamics**,

and organismal modifications need to generate equally significant effects. Low-relief fluvial landscapes are a class of landscapes that meet this requirement and allow abundant vegetation to develop and form complex flow–vegetation feedbacks that give rise to emergent geomorphology [2].

It is also useful to consider the likelihood of two basic classes of geo-evolutionary feedbacks, sometimes referred to in the eco-evo literature as narrow (or closed) versus broad (or open) [5]. Broad-sense geo-evolutionary feedbacks form (i) when change in one aspect of a landscape (e.g., caused by endogenous landscape dynamics) affects evolution, which then influences a different landscape variable, or (ii) when evolution of a given trait (e.g., caused by warming) affects landscape change, which in turn influences the evolution of a different trait of the same species. Narrow-sense feedbacks instead occur when landscape and evolutionary change reciprocally affect each other through the same traits and same landscape variables. Note that both broad- and narrow-sense feedbacks can either affect traits that influence the per-capita geomorphic effects of organisms (direct geo-evolutionary feedbacks) or traits that affect the abundance and distribution of organisms (indirect feedbacks).

Landscape-scale geo-evolutionary feedbacks are clearly most likely in the broad sense because the likelihood that the emergent property will affect the evolution of the original trait is low – by definition, emergent properties cannot be anticipated by local processes or features. Narrow-sense feedbacks are more likely at the patch scale but will depend on factors such as landscape energy (Figure 2B). In a relatively calm environment, organisms can actively change their physical environment to achieve a phenotype–environment match (niche construction, *sensu* [60]). For instance, faced with soil toxicity and low oxygen associated with waterlogging, *Carex stricta*, a common tussock sedge in freshwater marshes of North America, evolved concentrated shallow rooting which captures and retains sediments on which roots continue to grow and build hummocks [61,62]. Such geomorphic engineering alleviates waterlogging stress, causing subsequent evolution of the original trait, hence forming narrow sense feedbacks (Figure 2B). When the energy level is high, under strong mechanical stress (e.g., floods, wind gusts), the capacity of organisms to modify the physical habitat becomes limited because the outcome of niche construction can be easily swamped or countered (e.g., *C. stricta* sediment capturing and hummock building will not be effective at very high flow rates). The strategy organisms adopt often shifts from niche construction to adjusting their phenotypes to conform to existing niches (**niche conformance**, *sensu* [60]) or to selecting the environment to which they are best suited (**niche choice**, *sensu* [60]). As an example of niche conformance, adapting to the drag force exerted by flowing water, aquatic emergent plants often possess remarkable mechanical strength to resist breakage and uprooting [63]. An example of niche choice is provided by the adaptation of dune plants to sand burial [64] by rapid vertical elongation of tillers or lateral spread of rhizomes to escape burial [41]. In both examples, accidental geomorphic consequences occur. For instance, stem mechanical strength affects the dissipation of hydrodynamic forces, where stiff stems cause higher energy dissipation and hence higher sediment accretion [65]. However, unlike in niche construction, the resulting geomorphic consequences (altered sediment deposition around plant stems) do not alleviate the original stress acting on the plants (drag force or sand burial rate) to prompt subsequent evolution of the original trait (stem mechanical resistance or rate of escaping burial). Thus, in landscapes with high energy, patch-scale feedbacks, if present, will likely operate in the broad sense (Figure 2B).

Testing geo-evolutionary feedbacks

We expect that readers will find our arguments and examples plausible, but they may be struck by the apparent rarity of concrete demonstrations of geo-evolutionary feedbacks. Indeed, this gap is perhaps where effort should next be directed. We suspect that geo-evolutionary feedbacks are reasonably common (but certainly not universal) and we therefore need clear empirical

Box 2. Quantifying the strength of geo-evolutionary feedbacks

Several statistical and mathematical approaches have been developed to organize and quantify eco-evolutionary effects and feedbacks [100]. We show here – for illustrative purposes – how one of those approaches (based on [4]) could be applied to geo-evolutionary feedbacks (Figure I). We start by assuming that the rate of change in a landscape variable (L) over time (t) is a function of change in intrinsic landscape processes (G_i) and organismal modifications (G_o); that is, $L(t) = L[G_i(t), G_o(t)]$. In continuous time, differentiation by the chain rule yields:

$$\frac{dL}{dt} = \frac{\partial L}{\partial G_i} \frac{dG_i}{dt} + \frac{\partial L}{\partial G_o} \frac{\partial G_o}{\partial Z_G} \frac{\partial Z_G}{\partial K} \frac{dK}{dt} + \frac{\partial L}{\partial G_o} \frac{\partial G_o}{\partial N} \frac{\partial Z_{NG}}{\partial K} \frac{dK}{dt} \quad [I]$$

In Equation I, the change in the landscape variable (L) is partitioned into effects due to:

- (i) The first term = changes in the landscape intrinsic processes (G_i).
- (ii) The second term = changes in the organismal modifications that result from evolution of a geomorphic trait (Z_G) caused by changes in the external local environment (K).
- (iii) The third term = changes in the organismal geomorphic modifications (G_o) that result from changes in population size of a focal species (N) that results from evolution of a non-geomorphic trait (Z_{NG}) caused by changes in the external local environment (K).

Equation II quantifies the evo-to-geo effects. Geo-evolutionary feedbacks require landscape change to cause further evolutionary response. The evolutionary response by the phenotypic trait (Z) caused by a landscape change can be quantified as:

$$\frac{dZ}{dt} = \frac{\partial Z}{\partial K} \frac{\partial K}{\partial L} \frac{\partial L}{\partial G_i} \frac{dG_i}{dt} + \frac{\partial Z}{\partial K} \frac{\partial K}{\partial L} \frac{\partial L}{\partial G_o} \frac{dG_o}{dt} + \frac{\partial Z}{\partial K} \frac{\partial K}{\partial G_o} \frac{\partial G_o}{\partial t} + \frac{\partial Z}{\partial K} \frac{\partial K}{\partial G_i} \frac{dG_i}{dt} \quad [II]$$

In Equation II the evolutionary change in the trait phenotype (Z) is partitioned into effects due to:

- (i) The first term = evolutionary responses to the broad-scale landscape changes (L) caused by intrinsic landscape processes (G_i).
- (ii) The second term = evolutionary responses to the broad-scale landscape changes (L) caused by organismal landscape modifications (G_o).
- (iii) The third term = evolutionary responses to organismal landscape modifications locally (G_o).
- (iv) The fourth term = evolutionary responses to local landscape changes caused by intrinsic landscape processes (G_i).

We highlight a few features of geo-evolutionary feedbacks: (i) geo-to-evo effects can operate at the local (third and fourth terms in Equation II) or landscape scale (first and second terms in Equation II). (ii) $\frac{\partial L}{\partial G_i}$ and $\frac{\partial L}{\partial G_o}$ (in Equation I) describe the emergence of the broad-scale patterns from local processes. Emergence does not occur in all landscapes (Figure 2B), and the relationship between local processes and emergent properties varies significantly across landscapes. (iii) The extent to which geomorphic changes ($\frac{\partial K}{\partial G_o}$, $\frac{\partial K}{\partial G_i}$, and $\frac{\partial K}{\partial L}$ in Equation II) can lead to changes in the selective environment affects the strength of the geo-evolutionary feedbacks.

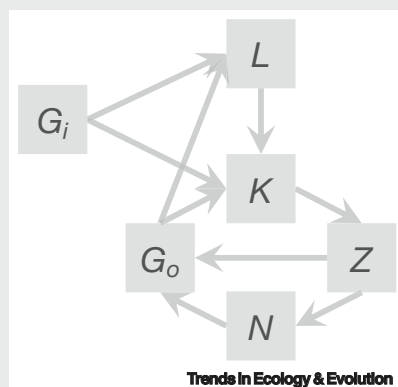


Figure I. Path diagram representations of landscape changes (L) caused by changes in the intrinsic landscape processes (G_i) and/or organismal modifications (G_o). Landscape changes (L) can affect the external local environment (K), relevant traits of an organism (Z), and its population size (N). These changes can further affect organismal modifications of the landscape (G_o).

demonstrations or refutations of the suggestions outlined in the preceding text. Fortunately, the literature on eco-evolutionary dynamics provides some evidence of how empirical demonstrations might proceed [66].

A foundational approach to investigate eco-evolutionary feedback centers around what are sometimes called 'common gardening' experiments (*sensu* [67]). That is, different genotypes or phenotypes of organisms are placed into the same 'arena' (laboratory or field) to structure their environment. The original organisms are then removed, and the full suite of genotypes or phenotypes is placed into both structured environments – to measure the performance and fitness of each genotype in the environment structured by each genotype. For geo-evolutionary dynamics, analog landscapes, such as meandering rivers or deltas, could be developed in experimental fields or laboratory facilities. The landscapes would commence with a common initial condition and be seeded with organisms of divergent phenotypes as experimental treatments. This approach would allow us to observe how populations of different genotypes affect landscape morphology. We could then later place populations of equal genotypic frequencies onto these different landscapes to determine the effects of landscape morphology on selection.

Moving beyond 'analog' environments, ecological restoration provides opportunities to test geo-evolutionary feedbacks in the real world. On the one hand, reintroducing species of significant geomorphic effects, such as mussels [68], salmon [69], and beavers [70], allows us to test the evo-to-geo effect by manipulating the genotype of introduced organisms [71]. On the other hand, habitat restoration, for example by designing channel morphology in river restoration [72], allows us to demonstrate the geo-to-evo effect by creating geomorphic features that may create a new selective environment.

When manipulative experiments are not possible, we can take a modeling approach. Vahsen and colleagues recently incorporated empirically quantified rates of evolution and heritable trait variation into coastal marsh landscape models [3]. Comparing the results from models with and without considering trait variations allows us to identify landscape and genetic signatures of geo-evolutionary feedbacks [13]. Expected signatures can be validated by empirical data – landscape changes can be inferred from time-series remote sensing imagery, and evolution from genotypes of the historical populations 'resurrected' from time-stratified seed banks. When time-series data are limited, space-for-time substitutions with careful validations of space-time equivalence and transferability [73] are another option. Empirically derived parameter values can be used to estimate the strength of geo-evolutionary feedbacks (Box 2).

Concluding remarks

Although concrete examples demonstrating the full circle of geo-evolutionary feedbacks remain scarce, it is apparent that organismal evolution and landscape change can occur in contemporary time and elicit feedbacks. Integrative approaches will thus be increasingly useful as anthropogenic change continues to challenge our ability to forecast landscape resilience and design sustainable ecological restorations. The geo-evolutionary feedbacks described here provide a framework for integrating genetic variation and landscape dynamics. More work will be necessary to determine when and where such feedbacks operate and how effective they are in mediating the response of landscapes and populations to modern global change (see Outstanding questions).

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Outstanding questions

Many variables related to biological organisms and physical landscapes are expected to affect the strength of geo-evolutionary feedbacks. What are the most common or most impactful variables that determine feedback strength?

Limited by empirical studies, the extent to which geo-evolutionary feedbacks are prevalent across various landscapes remains unclear. To what extent do geo-evolutionary feedbacks affect landscape responses to anthropogenic environmental change in contemporary time? How much are we missing by not considering geo-evolutionary feedbacks in predicting landscape change and in ecosystem management and restoration?

Quantification of geo-evolutionary feedbacks relies on measurements of many variables (Box 2). Is there a predictive framework to infer the effect size of geo-evolutionary feedbacks? What are the key elements of such a framework?

Under what conditions do geo-evolutionary feedbacks enhance population and landscape resilience, and under what conditions might they accelerate population and landscape collapse? The answer to this question might partly resemble that of eco-evolutionary feedbacks; however, some features might be unique to geo-evolutionary feedbacks.

How do we integrate geo-evolutionary and eco-evolutionary feedbacks to form a unified theory that considers the feedbacks among the change of geomorphic landscapes, the evolution of organisms residing on the changing landscape, and the ecological dynamics at population and community levels?

Landscapes bear an unmistakable stamp of life. As life simultaneously evolves to cope with changing landscapes, what topographic features reflect this evolution – namely the topographic signatures of evolution? In other words, how do geo-evolutionary feedbacks shape landscape patterns?

Declaration of interests

The authors declare no competing interests.

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