The Importance of Eco-evolutionary Potential in the Anthropocene

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Humans are dominant global drivers of ecological and evolutionary change, rearranging ecosystems and natural selection. In the present article, we show increasing evidence that human activity also plays a disproportionate role in shaping the eco-evolutionary potential of systems—the likelihood of ecological change generating evolutionary change and vice versa. We suggest that the net outcome of human influences on trait change, ecology, and the feedback loops that link them will often (but not always) be to increase eco-evolutionary potential, with important consequences for stability and resilience of populations, communities, and ecosystems. We also integrate existing ecological and evolutionary metrics to predict and manage the eco-evolutionary dynamics of human-affected systems. To support this framework, we use a simple eco–evo feedback model to show that factors affecting eco-evolutionary potential are major determinants of eco-evolutionary dynamics. Our framework suggests that proper management of anthropogenic effects requires a science of human effects on eco-evolutionary potential.

Keywords: conservation, disturbance ecology, ecology, evolution

Eco-evolutionary dynamics—the ongoing reciprocal interactions between evolution and ecology (Post and Palkovacs 2009, Hendry 2016)—have become an important paradigm for understanding both ecological and evolutionary change (Schoener 2011). Eco-evolutionary dynamics (see box 1 for glossary) are of particular applied interest in human-affected systems, because they can amplify or extend the effects of anthropogenic perturbations across natural systems (Palkovacs et al. 2012, Loeuille 2019). For example, contemporary evolution in response to human activities can generate novel, ecologically important traits that amplify or extend anthropogenic impacts to new populations, species, or habitats (Palkovacs et al. 2012, Hendry et al. 2017). Therefore, understanding the role of humans in generating or facilitating eco-evolutionary dynamics is key to forecasting human impacts on the biosphere.

Because humans adeptly cause both ecological (Vitousek et al. 1997, Estes et al. 2011) and evolutionary change (Palumbi 2001, Hendry et al. 2017, Pelletier and Coltman 2018), it is natural to expect human influences on eco-evolutionary dynamics (Alberti 2015). Most work on eco-evolutionary dynamics has been focused on anthropogenic perturbation (Palumbi 2001, Western 2001, Palkovacs et al. 2012, Alberti 2015, Hendry et al. 2017, Mimura et al. 2017); either humans manipulate some aspect of the environment, leading to evolutionary change (Hendry et al. 2008, Fugère and Hendry 2018), or humans generate evolutionary change in some population, leading to ecological change (Turcotte et al. 2017, Wood et al. 2019).

Humans directly cause evolutionary perturbation in both captive and wild organisms through intentional and unintentional artificial selection—for example, harvest-induced evolution and domestication (Palumbi 2001, Price 2002, Darimont et al. 2009, Zeder 2016). Humans also directly cause evolution through introduction of domesticated or transgenic organisms into wild gene pools (Naylor et al. 2005, Ellstrand 2018). When anthropogenic evolution changes ecologically relevant functional traits—particularly those related to diet and life history—ecological change and eco-evolutionary dynamics can result (Hendry et al. 2017, Mimura et al. 2017, Des Roches et al. 2018, Start 2018, Wood et al. 2018, 2019).

Anthropogenic ecological perturbations are also numerous. In particular, anthropogenic perturbations of ecosystems through species introductions and removals can rearrange entire food webs (Pace et al. 1999, Ripple et al. 2016, Tylianakis and Morris 2017). Both introductions and removals of top predators have been shown to have cascading food web impacts that alter the course of contemporary evolution in lower trophic levels (Mooney et al. 2010, Palkovacs et al. 2011, Wood et al. 2018). Similarly, the introduction and the removal of competitors have also caused significant niche evolution in wild organisms (Eastwood et al. 2007, Moran and Alexander 2014). Therefore, humans may spark eco-evolutionary dynamics by introducing or removing key predator, prey, and competitor species.

The abiotic frame has also been altered significantly by human activities. Pollution by diverse media (nutrient,

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Box 1. Glossary.

Eco-evolutionary dynamics. Contemporaneous interactions between evolution and ecology. Can include eco-to-evo and evo-to-eco processes (weak dynamics), as well as eco-evolutionary feedbacks (strong dynamics), for which eco-evolutionary dynamics are often confused.

Eco-evolutionary feedbacks. Contemporaneous, reciprocal interactions between the same ecological and evolutionary processes; for example, evolution in one population leads to ecological change, which generates further evolution in the same population.

Eco to evo. Ecological change that leads to contemporary evolutionary change.

Evo to eco. Evolutionary change that leads to contemporary ecological change.

Eco-evolutionary potential. The combined properties of an eco-evolutionary system determining the realized likelihood of an ecological or evolutionary change generating eco-evolutionary dynamics. Eco-evolutionary potential is the net combination of all coupling between ecological and evolutionary components of a system, minus their inherent resilience.

Pulse disturbance. A single-event ecological disturbance.

Press disturbance. A sustained or iterative ecological disturbance.

Resilience. The inherent tendency of a system to revert toward an initial state.

Coupling. The degree to which two processes reciprocally influence each other.

Contemporary evolution. Evolution on time scales similar to ecological processes, also called “rapid” evolution.

Functional traits. Organismal traits that affect performance or fitness across taxa. **Ecologically relevant functional traits** (ERFTs) are functional traits that also have a strong role in shaping the environment

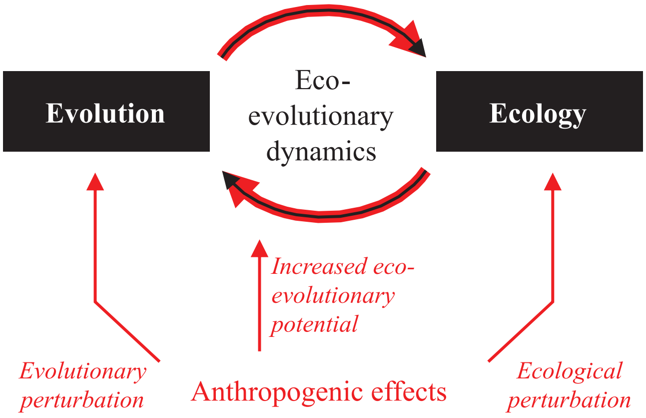
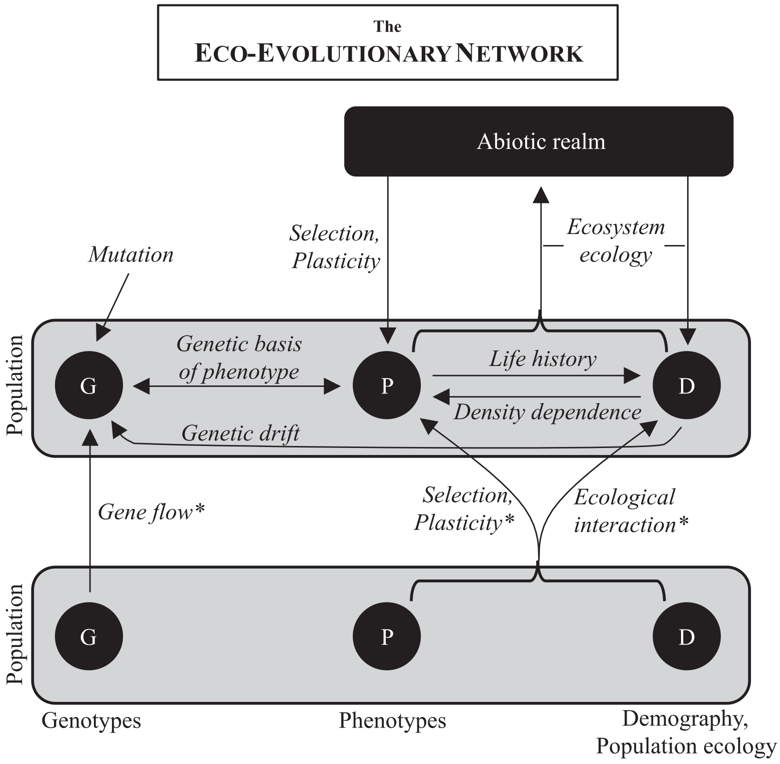


Figure 1. Anthropogenic impacts on eco-evolutionary dynamics. Eco-evolutionary dynamics are contemporaneous, often reciprocal interactions between evolution and ecology. Humans can drive eco-evolutionary dynamics, not only by perturbing ecology and evolution, but also by changing eco-evolutionary potential—the degree to which evolutionary change leads to ecological change and vice versa.

chemical, light, sound, material) can fundamentally alter ecosystems by changing nutrient fluxes, habitability, physical structure, and sensory efficacy of organisms, to name a few examples (Gaston et al. 2013, Arenas-Sánchez et al. 2016, Råman Vinnå et al. 2017). These alterations of the abiotic frame can generate novel contemporary evolution, either increasing tolerance to the pollutant itself or responding to pollution-mediated ecological change (Whitehead et al. 2012, Johnson and Munshi-South 2017, Tuckett et al. 2017, Wood et al. 2020b). Again, such contemporary evolution can potentially spark eco-evolutionary dynamics.

Beyond perturbation

Although all of the above examples represent ways that humans can spark eco-evolutionary dynamics, we suggest a sole focus on ecological or evolutionary perturbation by humans is incomplete. A more complete understanding of human effects on eco-evolutionary dynamics requires examining anthropogenic impacts on eco-evolutionary potential, which we define as the degree to which ecological change results in evolutionary change and vice versa (figure 1). As will be explained later, eco-evolutionary potential is the complex combination of all coupling between ecological and evolutionary components of a system, minus their inherent resilience. The current, perturbation-focused approach assumes that eco-evolutionary potential does not change, and anthropogenic influences on eco-evolutionary dynamics rest solely on the strength and frequency of anthropogenic perturbations to ecology and evolution (Pelletier and Coltman 2018). However, anthropogenic changes to eco-evolutionary potential could generate much larger changes to eco-evolutionary dynamics. If humans decrease eco-evolutionary potential, many eco-evolutionary dynamics would shrink or disappear, with ecological change failing to generate evolutionary change and vice versa. But, if humans increase eco-evolutionary potential—which, as we



Definitions

Selection. The effect of environment (other individuals, populations, and abiotic conditions) on the phenotypes of a population via differential survival and reproduction

Plasticity. Changes in individual phenotypes in response to environmental conditions

Genetic basis of phenotype The degree to which phenotypes are influenced by genotypes

Life history. Phenotypes that influence the life events and development of individuals, and therefore population demography

Density dependence The effect of demography on individual phenotypes, by either plasticity or selection

Genetic drift Random changes in population genetic makeup, particularly at small population size

Mutation. Random generation of new genetic alleles

Gene flow. Exchange of genetic alleles between two populations

Ecological interaction Effects of one population on the abundance and demography of another, including competition, predation, etc.

Ecosystem ecology Interactions between populations and abiotic factors

Figure 2. Eco-evolutionary networks. Eco-evolutionary networks consist of interacting genotypes, phenotypes, populations, communities, and ecosystems. For any population, interactions with other populations and the abiotic realm can lead to interlinked demographic, phenotypic, and genetic change. The avenues for the environment to affect a population's phenotypic makeup (P) are numerous, as are the avenues for a population's phenotypic makeup to affect the environment (i.e., other populations or the abiotic realm). Interactions between the two populations are shown as unidirectional for simplicity but are likely bidirectional. The two populations could be the same species or different species; in the latter case, gene flow would be considered horizontal gene transfer or hybridization.

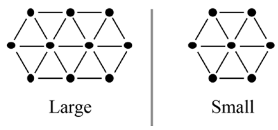
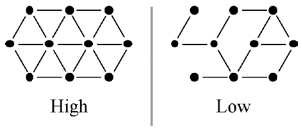
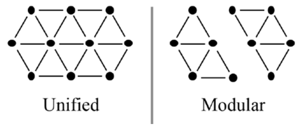
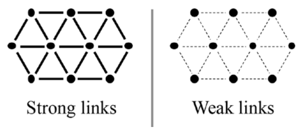
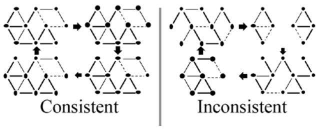
argue in the present article, is more likely—then new and stronger (i.e., faster, more dynamic, and producing greater degrees of change) eco-evolutionary dynamics would result. Importantly, these dynamics need not be sparked by anthropogenic perturbation; human changes to eco-evolutionary potential could lead to new dynamics facilitated by increased eco-evolutionary potential but not kicked off by humans (as in Hiltunen et al. 2014). Eco-evolutionary dynamics can be a source of instability: generating oscillations and crashes in population size (Abrams and Matsuda 1997, Kasada et al. 2014), amplifying ecological change (Ruokolainen et al. 2009), and extending ecological change to new populations (Palkovacs et al. 2012, Hendry et al. 2017). Therefore, understanding anthropogenic effects on eco-evolutionary potential and eco-evolutionary dynamics is a key element to studying and managing human impacts on the biosphere.

In the present article, we undertake four steps toward understanding the role humans play in shaping eco-evolutionary potential. First, we use an eco-evolutionary network approach to describe the numerous ways in which humans likely alter complex systems to affect eco-evolutionary potential. Second, we apply this approach to a handful of well-studied examples to illustrate its utility. Third, we use simple eco-evolutionary models to examine when and how human modifications of eco-evolutionary potential are likely to have negative consequences for communities and ecosystems. Fourth, we outline experimental and analytical methods for examining eco-evolutionary potential in future studies.

A network approach to eco-evolutionary potential

Here we propose a systems framework for examining eco-evolutionary potential on the basis of characteristics of an interacting network. Networks consist of players and their connections to each other, called nodes and links, respectively. We note that at first glance, networks will look familiar to readers in discipline-specific ways: Ecologists may see them as food web diagrams, whereas evolutionary biologists may see them as selection topologies or gene networks. However, the players in an eco-evolutionary network are diverse, including genes, populations, and ecosystem compartments, and their potential connections are geometrically more diverse (figure 2). For example, they could be

Table 1. Eco-evolutionary networks.

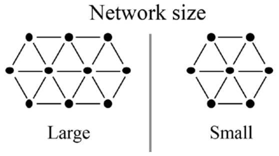
Network aspect	Description	Examples	Eco-evolutionary potential[a]	Metrics[b]
Network size  	Humans alter network size by adding or removing players (nodes).	Smaller food webs	⬆↓	N_C, N_T
		Simpler selection	⬆↓	$-\gamma, \sigma_\beta^2$
Network connectivity  	Humans alter network connectivity by adding or removing connections (links).	Omnivory	↑⬇	$\overline{L_{pred,\,prey}}$
		Novel interactions	↑⬇	$\bar{L}$
Network modularity  	Humans alter network modularity by breaking up networks into multiple modules or connecting disparate modules.	Modularized food webs	⬆↓ (local)	Q, ρ_M, σ_D^2
		Decreased gene flow	⬆↓ (local)	F_{STn}, R_I, R_M
Network intensity  	Humans alter network intensity by strengthening or weakening connections (links).	Changes in ecological interaction strength	⬆⬇	$\frac{\partial N_1}{\partial N_2}$
		Decreased age structure, generation time	⬆↓	$\bar{A}, \bar{A_P}$
		Altered trait variation, plasticity	⬆⬇	$\pi, F_{IS}, \sigma_G^2, \frac{\partial X}{\partial E}$
Network consistency  	Humans alter network consistency by varying network properties over time or canalizing networks.	More frequent disturbance	⬆↓ (short term)	f_Y
		System canalization	↑⬇	σ_Y^2

Examples of anthropogenic effects on eco-evolutionary potential, as well as metrics for measuring them. *Note:* [a]The larger arrow indicates predominant effect of humans on eco-evolutionary potential via each given example alone. [b]See the text for equation legends.

individuals with different traits competing in a population to determine population growth, they could be species with different functional traits interacting to determine community composition, or they could be different pieces of an ecosystem interacting to determine the transfer of energy and nutrients. Essentially, each node in the network can be described by a set of functionally important features that influence its interactions with other nodes.

Ecological and evolutionary networks have been analyzed in innumerable ways (Proulx et al. 2005, Almaas 2007, Bascompte 2007, Borgatti and Halgin 2011, Deng et al. 2012); here we have summarized five network properties that are likely to influence eco-evolutionary potential (table 1). These properties all address complexity: complexity of players (network size), complexity of interactions (network connectivity), complexity across patches (network modularity), complexity of interaction strengths (network intensity), and complexity over time (network consistency). As such, these five properties lead to a similar conclusion: Simpler networks—including smaller, more strongly interacting, and more consistent networks—are more likely to exhibit eco-evolutionary potential. Importantly, we argue that the tendency for human effects on these networks is often toward simplification, generally increasing the potential for eco-evolutionary dynamics, with a few notable exceptions. We also provide examples and metrics for measuring each network aspect.

Network size: Altering number of players. Humans affect the size of networks, either by adding or removing players. Network size can determine the stability of ecosystems in the face of trait change (Neutel et al. 2002, Gross et al. 2009, LeCraw et al. 2014, Zhao et al. 2019) and the sensitivity of populations to changes in selection regimes (Barton and Partridge 2000), affecting the potential for eco-evolutionary dynamics.

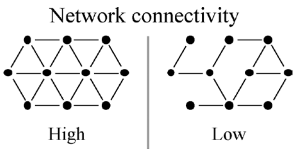


By directly and indirectly causing population and species losses, humans often shrink food webs, the ecological components of eco-evolutionary networks (Estes et al. 2011, Peipoch et al. 2015). Human dominated environments generally support fewer species—for example, through monocultures such as agriculture (Matson et al. 1997) and facilitation of generalist species (see the “Network connectivity” sections below), humans disrupt and remove specialists, thereby shrinking food webs (Strong and Frank 2010). Even additions of invasive species often eventually lead to a functionally smaller network because of the ensuing loss of native species (Doherty et al. 2016). Smaller food webs are less stable and more susceptible to perturbation because of decreased redundancy and decreased diffusing capacity, i.e., the potential for disturbance to be divided and absorbed across a broad network, rather than affecting a single population (Gross et al. 2009, LeCraw et al. 2014, Zhao et al. 2019). Furthermore, in a smaller food web, the distance (in terms of the shortest number of successive links) between any two populations is smaller, meaning a change in one population is more likely to affect any given other population (Neutel et al. 2002). Therefore, if humans shrink food webs, ecologically relevant functional trait evolution in one population is more likely to affect ecological change (and therefore eco-evolutionary dynamics) in another.

In a similar vein, humans also tend to simplify evolutionary processes. Wild organisms typically face a tangled web of numerous, conflicting selection pressures. Such complex selection landscapes reduce the likelihood of strong responses to any individual selection pressure, such as environmental change (Schluter et al. 1991, Barton and Partridge 2000). However, as humans remove interacting species such as predators and competitors or override limiting factors such as nutrients, various forms of competing selection and trade-offs are relaxed (Fugère and Hendry 2018). Therefore, by simplifying the selection landscape, humans can make wild populations more likely to evolve in the face of environmental change and therefore increase the likelihood of eco-evolutionary dynamics.

Metrics for examining network size. Food web size can be measured in numerous ways, including the number of populations or ecosystem compartments (N_C), or number of trophic levels (N_T). Selection complexity can be examined by quantifying the net stabilizing selection pressure on a population ($-\gamma$), or by examining variation in directional selection gradients (σ^2_β).

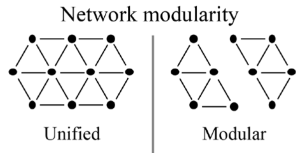
Network connectivity: Altering link complexity. Humans can also alter the connections within networks, adding or removing links without changing the host of players. These links include the effective addition or loss of ecological interactions between species, selection pressures, or effects of traits on ecology. Whereas increases in network connectivity might be predicted to favor stabilizing eco–evo dynamics through processes such as redundancy and competing feedback loops (Landi et al. 2018), loss of network connectivity might be predicted to generate destabilizing eco–evo dynamics by allowing some connections to dominate system function.



One example of humans altering network connectivity is a bias in human-dominated systems toward generalists and omnivores (Fedriani et al. 2001, Gutiérrez-Cánovas et al. 2013). Novel, human-dominated systems (e.g., cities) rarely support specialists and tend to be populated by more flexible generalists (Gruber et al. 2019). Therefore, a network of generalists, particularly omnivores, has a much higher density of links per player than a network of specialists. This increased network connectivity could ultimately become a source of ecological stability (Landi et al. 2018) in some human dominated systems, when compared to similar size networks of specialists, but getting to that point could involve strong transient eco-evolutionary dynamics as generalists and omnivores are substituted for specialists. Therefore, changes in network connectivity may increase or decrease eco-evolutionary potential.

Through landscape disturbances, humans also force players that would not normally directly interact to do so. By restricting habitat size, altering habitats entirely, monopolizing resources (e.g., water), or generating unusual conditions (e.g., artificial light), humans can bring species together (Hobbs et al. 2009). This activity can generate new ecological interactions—particularly competition and predation—and, with it, new selection pressures and new eco-evolutionary dynamics.

Metrics for examining network connectivity. Network connectivity can be measured by examining the average number of links per individual, $\bar{L}$.

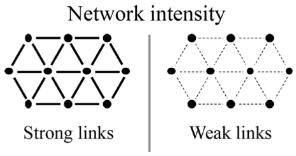


Network modularity: Altering metasystem complexity. Human activities can affect the modularity of systems, in some cases breaking large systems into numerous smaller modules, and, in others, increasing connectivity across systems (Sebastián-González et al. 2015, Takemoto and Kajihara 2016). Because connectivity to broader metacommunities and metapopulations can determine the sensitivity of communities to trait change and the sensitivity of populations to changes in selection regimes (Urban et al. 2008), changes in system modularity can alter eco-evolutionary potential.

Humans can increase modularity by weakening or eliminating interactions between species or other ecosystem components. For instance, in food webs, humans can break trophic links, reducing the web into smaller, more isolated interacting parts. Humans can also increase modularity by fragmenting ecosystems spatially (Fischer and Lindenmayer 2007, Lindenmayer and Fischer 2007), physically dividing ecosystems into more numerous, smaller modules. Another form of modularization happens when humans cut or overwhelm flows of nutrients and energy between spatially separated modules (Buckner et al. 2018). By isolating modules, humans reduce the capacity of the broader metasystem to disperse or dilute the local ecological effects of trait change, in turn intensifying interactions within the local module. Such isolation therefore increases the chance of trait change leading to ecological change in any given module (Urban et al. 2008, Legrand et al. 2017). Moreover, this lack of connectivity between models decreases the likelihood of eco-evolutionary dynamics in one module affecting another, making it more likely that modules will show locally nuanced, idiosyncratic dynamics.

Humans also have strong impacts on genetic metapopulation structure, in some cases increasing gene flow (translocation, homogenization; Crispo et al. 2011) and in others decreasing gene flow (fragmentation, modularization; Legrand et al. 2017). Decreasing gene flow can facilitate evolution by isolating populations from maladaptive gene flow (Haldane and Ford 1956, Polechová and Barton 2015), but also limits inputs of novel genetic variation, reducing the potential extent of evolution where such genetic variation is limiting. Conversely, when humans increase maladaptive gene flow, the flow of alleles can overwhelm any potential natural selection, preventing an evolutionary response to ecological change and reducing eco-evolutionary potential (Garant et al. 2007). Anthropogenic movement of adaptive alleles, or alleles that are adaptive with some combination of local alleles, can provide a lifeline for populations with low standing genetic variation that are experiencing strong selection (Lenormand 2002). Therefore, the effect of humans on eco-evolutionary potential via gene flow will depend on the level of standing genetic variation in the receiving population and the degree to which gene flow is adaptive. Overall, given that contemporary evolution is most often fueled by standing quantitative trait variation, which is often difficult to significantly deplete, the dominant effect of modularization on evolution is apt to be facilitation of stronger local adaptation and associated eco-evolutionary dynamics.

Metrics for examining network modularity. Modularization might be measured by rates of energy or nutrient flow across modules (Q) or autocorrelation between modules (ρ_M). Because modularized metacommunities have numerous strong (within modules) and weak (across modules) interactions, modularization might also be measured as the variation in interaction strengths across a metacommunity (σ_D^2). Gene flow can be quantified across modules by examining neutral genetic divergence (F_{STn}) or rates of immigration and emigration (R_I, R_M).



Network intensity: Altering link strength. In addition to adding and removing connections, human activities alter the strength of connections within networks. Although similar to network connectivity above, this pattern includes strengths of ecological and evolutionary interactions, and strengths of interactions between evolution and ecology.

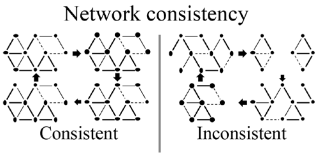
Human effects on ecological interaction strengths are mixed. On one hand, by virtue of their smaller size (in space and number of players, see the “Network size” section), food webs created by humans are more likely to have strong interactions (Neutel et al. 2002). On the other hand, these food webs are more likely to be populated by generalists (see the “Network connectivity” section), which have weaker interactions with their many food items (Wootton and Stouffer 2016). More intense interactions tend to generate flashier, less-stable systems, and stronger instances of selection (Legrand et al. 2017). Stronger links therefore generally lead to less-stable systems (Neutel et al. 2002), increasing eco-evolutionary potential.

Anthropogenic changes to age structure might also increase eco-evolutionary potential. Human activities—for example, harvest—increase mortality rates of wild organisms. Increases in mortality rates, even when not age selective, necessarily decrease the average age of a population (Kuparinen et al. 2016a, Palkovacs et al. 2018). Decreasing the age structure of a population tends to generate more chaotic abundance dynamics and make the population more susceptible to external perturbation (Audzijonyte et al. 2013, 2014, Kuparinen et al. 2016b), functionally increasing link strength. Therefore, populations with younger average ages are likely to be more sensitive to (i.e., have stronger links with) functional trait evolution in their predators and prey. Population responses to selection are also dependent on age structure, with shorter generation times allowing for faster responses to selection (Hendry and Kinnison 1999). Humans reduce generation times through both ecological (i.e., individuals only have offspring when they are young, before they die; Kuparinen et al. 2016a, Palkovacs et al. 2018) and evolutionary (i.e., selection for earlier reproduction; Stearns 1989, Heino et al. 2015) mechanisms. Populations with shorter generation times are more likely to have evolutionary responses that are contemporaneous with environmental change, allowing for eco-evolutionary dynamics.

Humans can also influence eco-evolutionary potential by increasing or decreasing heritable trait variation in populations. Heritable trait variation is a key component of evolution in response to natural selection (Fisher 1930). Evolution by natural selection can only proceed as far as standing heritable variation allows (Cortez 2016), after which it is limited by rates of mutation, which are generally too slow to allow for evolution at contemporary times scales to ecological processes for all but the most multilocus traits. Humans generally decrease genetic variation by shrinking and fragmenting populations, as well as exposing populations to acute bouts of strong, hard selection that result in genetic bottlenecks (DiBattista 2008). Therefore, human impacts on populations are likely to reduce evolutionary responses (i.e., the evolutionary link strength between populations and their environment) to environmental change via reductions in genetic variation. One caveat to this pattern is when humans increase gene flow by translocating organisms (see the “Network modularity” section), supplying additional genetic variation.

Humans can also facilitate genetic evolution by pushing populations beyond their plastic adaptive capacity. Phenotypic plasticity can buffer organisms against environmental change, allowing them to persist without necessarily requiring genetic evolution (Price et al. 2003). Because humans are adept at creating environmental conditions well beyond those typically experienced by organisms—even over long evolutionary timescales—humans may reduce organisms’ capacity for plastic adaptation, thereby causing contemporary genetic evolution even in otherwise highly plastic organisms (Dewitt et al. 1998, Reed et al. 2011). Included in this new genetic evolution is evolution for increased plastic responses to environmental change (Diamond et al. 2018). In this way, limiting plasticity increases the strength of the links between ecological change and genetic evolution, although they may be transient in the case of evolution of increased plastic responses. Therefore, by pushing organisms beyond the range of plastic adaptation to environmental change, humans may make evolutionary responses to environmental change, and eco-evolutionary dynamics, more likely.

Metrics for examining network intensity. Age structure can be quantified through life tables, or simply through average age of a population ($\bar{A}$). Generation time can be calculated as the average age of parents at reproduction ($\bar{A}_P$). Interaction strengths can be measured in numerous ways (Paine 1980, Berlow et al. 1999); the simplest is the change in abundance of one taxon in response to another ($\frac{\partial N_1}{\partial N_2}$), but similar metrics are available for the change in the trait of one taxon as a response to a change in the trait or abundance of another. Genetic variation within a population can be measured at a per-locus basis (π, F_{IS}), or for a quantitative trait with a genetic basis (σ_G^2). Plasticity can be quantified as the intragenerational sensitivity of a phenotype to environmental change ($\frac{\partial X}{\partial E}$).



Network consistency: Altering temporal complexity. Humans can also alter the temporal variation in systems, by increasing the likelihood of rapid, large-magnitude changes in particular components (i.e., making systems “flashier”), or by canalizing temporal variation (Rohr and Raffel 2010, Bowman et al. 2011). Systems that naturally face periodic severe storms, for example, might be considered inherently inconsistent, but humans can still disrupt such systems by affecting the frequency or severity of such storms (e.g., through climate change) or imposing other temporal drivers. Inconsistent networks are inherently less likely to exhibit stabile eco-evolutionary dynamics in the long term, and instead may be more sensitive to perturbation in the short term, because inconsistency keeps resetting the network and eco-evolutionary dynamics far from any stable equilibria (Weese et al. 2011). With this in mind, more consistent human-dominated systems, such as agroecosystems, may be places of continually strong eco-evolutionary dynamics.

Metrics for examining network consistency. Metrics for network consistency include frequency of disturbance in a network attribute (f_Y) and temporal variation in a network attribute (σ_Y^2).

Interactions between network properties. As highlighted above, network properties determining a system’s eco-evolutionary potential are not necessarily independent, and effects of human activities on one property may extend to other properties. For example, reductions in connectivity may also result in increases in modularity and decreases in network size if enough connections are lost to fragment the network into multiple smaller modules (Fagan 2002). This example also highlights the interdependence of network size and network modularity. Changes in network size can also affect network intensity if added or removed players have skewed interactions strengths (e.g., removal of weakly interacting players or addition of strongly interacting players; Berlow 1999, Darimont et al. 2009). Furthermore, link strength and link consistency may be related, with weaker links (low intensity) leading to decreased network connectivity and consistency if weak links are transient (Kokkoris et al. 2002). Therefore, we stress that a network approach to eco-evolutionary potential should be overarching, and avoid a singular focus on a single network aspect.

Examples: Anthropogenic impacts on eco-evolutionary potential in fishes

Although a complete example of humans altering eco-evolutionary potential in a single study system has not been documented, a holistic look at eco-evolutionary dynamics in fishes reveals tentatively strong anthropogenic impacts on eco-evolutionary potential. Here we use our heuristic approach outlined earlier to examine eco-evolutionary potential in three model fish systems.

Plague minnows: Mosquitofish (*Gambusia* spp.). Mosquitofish—primarily *Gambusia affinis* and *Gambusia holbrooki*—have become a model system of eco-evolutionary dynamics because of their invasive nature, persistence in a diverse range of human-altered environments, and penchant for contemporary evolution. Mosquitofish have been buffeted by predator introductions, climate warming, and urbanization, and shown evolutionary responses to all three (Meffe et al. 1995, Langerhans et al. 2004, Wood et al. 2020a, 2020b). Furthermore, humans have directly meddled with their evolution, domesticating mosquitofish and altering their gene flow (Wood et al. 2019).

Humans have also likely increased the eco-evolutionary potential of mosquitofish in numerous ways, and this high eco-evolutionary potential may explain why mosquitofish have become such a model taxon for eco-evolutionary dynamics. First, although humans initially introduced and translocated mosquitofish indiscriminately (for their perceived utility in removing mosquito larvae), probably facilitating gene flow, mosquitofish systems today tend to be small, isolated systems with very limited gene flow, with droughts and dams further isolating populations (Stearns 1983, US Fish and Wildlife Service 2009). This reduction in mosquitofish gene flow has probably facilitated local adaptation from their and has fed the diverse eco-evolutionary dynamics noted above in mosquitofish (changes to network modularity and intensity).

Furthermore, mosquitofish exist in small, simple, strongly interacting environments, favoring further eco-evolutionary potential. Mosquitofish systems are typically dominated by mosquitofish and their piscine predators, which are also typically invaders (Pyke 2008). These systems have few players and links (network size and connectivity), but these links are strong (network intensity), showing large selection gradients and fast responses to evolution (Santi et al. 2020). Furthermore, mosquitofish are generalist zooplanktivores (network connectivity), leading mosquitofish trait evolution to have strong ecological impacts on lower taxa (Hurlbert et al. 1972, Hurlbert and Mulla 1981).

Harvested fish. Harvested marine populations also have significant potential for human-driven eco-evolutionary dynamics. Ecologically, humans have drastically reduced the abundance, size structure, and age structure of many marine taxa; evolutionarily, humans have generated incredible size selectivity and genetic bottlenecks in marine stocks (Conover and Munch 2002, Hutchings and Fraser 2008).

But, again, the human impact on eco-evolutionary dynamics in marine fish likely runs much deeper than these perturbations. The marine ecosystems in which harvested fish live are often made fundamentally simpler, in part because of the marine food web being fished down (network size; Pauly et al. 1998). These simpler ecosystems make evolution—in fished species and in others (Wood et al. 2018)—more likely. Furthermore, the decreased admixture of dwindling stocks (network modularity) and decreased age structure of harvested stocks (network intensity) make rapid eco-evolutionary responses to locally intense fishing more likely (Audzijonyte et al. 2013, 2014, Heino et al. 2015).

On the other hand, multiple selection pressures (e.g., from ocean warming and acidification) and multiple stressors may limit the extent of contemporary evolution in harvested species (network size, connectivity; Dunlop et al. 2015). Furthermore, the stronger the declines in harvested species abundance, the weaker the interactions between it and other species and the lower the potential for eco-evolutionary dynamics (Wood et al. 2018).

Benthivores: White perch (*Morone americana*) and threespine stickleback (*Gasterosteus aculeatus*). A common axis of ecologically relevant contemporary evolution in fishes is benthivory. In addition to bottom-feeding behaviors, evolution of benthivory can involve significant morphological change, including mouth, eye, and fin placement (Schluter 1993, Willacker et al. 2010, Lundsgaard-Hansen et al. 2013, Tuckett et al. 2013). Benthic feeding can release nutrients into the water column, both through disturbance of the benthos and excretion, leading to algae blooms and decreased water clarity (Vander Zanden and Vadeboncoeur 2002, Wahl et al. 2011, Lundsgaard-Hansen et al. 2014, Tuckett et al. 2017). Decreased water clarity caused by cultural eutrophication can then feed back to select for further benthivory (Persson and Nilsson 2007, Wanink et al. 2008, Tuckett et al. 2013), generating the potential for a positive eco-evolutionary feedback. Feedback potential here can be mediated by numerous natural factors. Conflicting natural selection (e.g., from predation; Reznick and Ghalambor 2001, Palkovacs et al. 2011), limits to standing genetic variation (Bell 2013), and gene flow can stall contemporary evolution (Polechová and Barton 2015, Ellstrand and Rieseberg 2016). In the same vein, ecological connectedness (e.g., residence time; Romo et al. 2013) and ecological buffering capacity—for example, a compensatory response in algivorous zooplankton (Wood et al. 2019)—can limit the impact of benthivory on lake clarity.

Humans can make this eco-evolutionary feedback more likely, both by intensifying the feedback and increasing the reciprocal impacts of ecology and evolution—that is, eco-evolutionary potential. Humans may facilitate contemporary evolution, both by reducing conflicting selection pressures (network size, connectivity; Fugère and Hendry 2018; e.g., removing predators; Estes et al. 2011) and by shortening generation times through processes such as harvest (Huusko and Hyvärinen 2005; network intensity). Alternatively, in some species humans may prevent contemporary evolution by adding new conflicting selection pressures—for example, introducing invasive predators (Barton and Partridge 2000)—and creating genetic bottlenecks (DiBattista 2008). Anthropogenic landscape fragmentation can cut off gene flow (network modularity), facilitating local adaptation (Crispo et al. 2011, Polechová and Barton 2015). In the ecological realm, humans may make communities more sensitive to contemporary evolution by reducing ecological buffering capacity—for example, humans could reduce zooplankton diversity or facilitate blooms of inedible, toxic algae, reducing the potential for a compensatory response in zooplankton (network complexity; Bell 2002, Sommer et al. 2003, Finke and Denno 2004). In addition, humans can isolate lakes (network modularity; Crook et al. 2015), increasing water residence time (Romo et al. 2013) and facilitating faster nutrient cycling, (Paerl and Scott 2010) making communities much more likely to change in response to contemporary evolution. Therefore, in this example, perturbation by humans is only the tip of the iceberg, because humans likely have a strong influence on the potential for destabilizing eco-evolutionary dynamics.

Table 2. Eco-evolutionary model equations.

	Constant resilience		**Decreasing, limited resilience**	
	Pulse disturbance	**Press disturbance**	**Pulse disturbance**	**Press disturbance**
$G_0 =$	0			
$E_0 =$	d			
$G_{t+1} =$	$(1 - r) * (G_t + \nu E_t)$		$\left(1 - \frac{r}{1+\lvert G_t \rvert}\right) * (G_t + \nu E_t)$	
$E_{t+1} =$	$(1 - r) * (E_t + \nu G_t)$	$(1 - r) * (E_t + d + \nu G_t)$	$\left(1 - \frac{r}{1+\lvert E_t \rvert}\right) * (E_t + \nu G_t)$	$\left(1 - \frac{r}{1+\lvert E \rvert}\right) * (E_t + d + \nu G_t)$

Note: All models begin with the evolutionary trait (G) equal to zero and the ecological trait (E) equal to disturbance strength (d). Pulse disturbance models also have the disturbance added to the ecological trait very time step. E and G positively feed back to influence each other; the strength of this feedback is determined by the eco-evolutionary coupling variable v. In the constant resilience models, resilience (r) is a constant proportion of G and E (e.g., an r of 0.1 reduces G and E by 10% each time step). In the decreasing limited resilience models, the effect of r decreases as E and G are further from zero. The subscripts indicate time (t).

Instability as a consequence of increased eco-evolutionary potential

In the previous two sections, we have highlighted many of the ways humans increase (or decrease) eco-evolutionary potential, making systems more likely to exhibit eco-evolutionary dynamics. But how does increased eco-evolutionary potential translate to system stability—the persistence of rare species, consistency of food webs, and the ability of ecosystems to withstand human perturbations? To investigate this question, we built a model of positive eco-evolutionary feedbacks, which are a type of eco-evolutionary dynamic that can generate instability and amplify human perturbations and are therefore cause for conservation concern (Kinnison and Hairston 2007, Palkovacs et al. 2012, Loeuille 2019). We examined the role of eco-evolutionary potential in generating unstable positive eco-evolutionary feedbacks, which could lead to population extirpation or collapse of an ecosystem.

Modeling effects of eco-evolutionary potential on network stability. We sought to create a simple model of eco-evolutionary dynamics with which to examine the effects of eco-evolutionary potential on eco-evolutionary network stability. We modeled a positive eco-evolutionary feedback, in which ecology and evolution reinforce each other. Such feedback loops have the potential to amplify human disturbances and are therefore an ideal focus for this study (Kinnison and Hairston 2007). We created the simplest possible network representation of an eco-evolutionary feedback with an ecological variable (E) and evolutionary variable (G). Post and Palkovacs (2009) mathematically define an eco-evolutionary feedback as the following:

$$\frac{dG}{dt} = f\,(\mathrm{G}, E) \qquad (1)$$

$$\frac{dE}{dt} = f\,(G, E) \qquad (2)$$

We created an expanded, iterative model from these equations:

$$G_{t+1} = (1 - r)\,(G_t + \nu E_t) \qquad (3)$$

$$E_{t+1} = (1 - r)\,(E_t + \nu G_t) \qquad (4)$$

Where v is intrinsic eco-evolutionary coupling—the degree to which the ecological and evolutionary variables inherently reinforce each other—and r is resilience, or the tendency of G and E toward zero.

Eco-evolutionary potential is the net combination of all coupling between ecological and evolutionary components of a system, minus their inherent resilience. Technically eco-evolutionary potential here has two components: coupling (v) and resilience (r). For example, when a population experiences natural selection as the result of ecological change, the strength of the selection is the coupling component (v), and any factors that prevent a response to selection (e.g., confounding selection, lack of genetic variation, lack of heritability) constitute the resilience component (r). Eco-evolutionary potential here—the response of a population's phenotype to ecological change and vice versa—is therefore the combination of both antagonistic components. Although this level of detail is necessary to build a working model (as the model has no stable outcomes when v is positive and r is not included), in wild systems separating v and r is likely to prove difficult and unnecessary.

Thus far, our model assumes that resilience is unlimited; that is, it is a constant proportion of G and E regardless of how extreme G and E become. This assumption is fairly unrealistic, particularly in human-affected ecosystems (Kinzig et al. 2006, Baho et al. 2017, Dakos et al. 2019). In reality, resilience can be viewed more as a ball in a pit; within the pit, the ball will roll toward the center, but outside of the pit, the ball is unlikely to roll

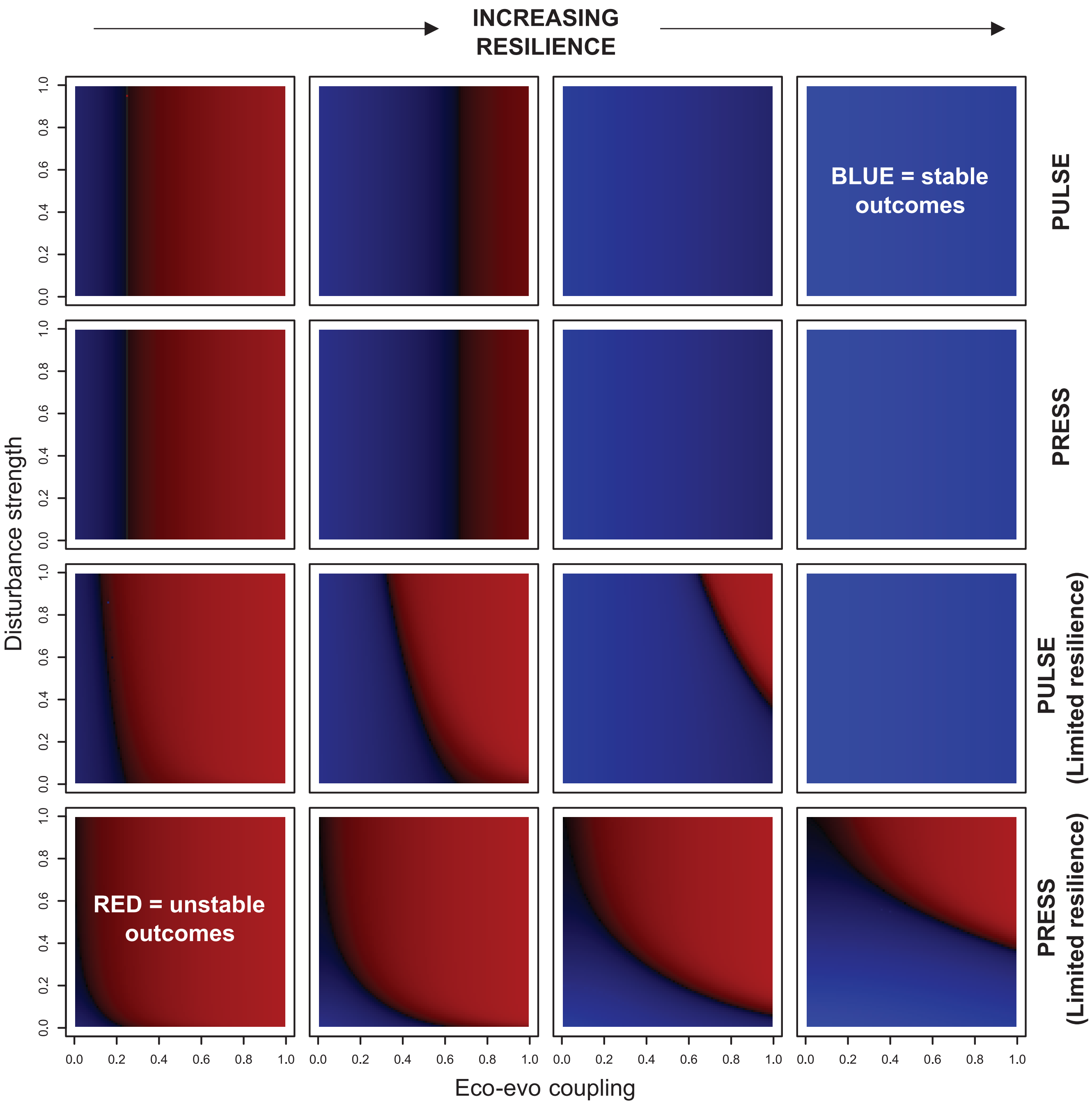


Figure 3. Eco-evolutionary potential and network stability. Increasing eco-evolutionary coupling decreases the stability of eco-evolutionary networks, particularly when resilience is low or limited. Results here are from an eco-evolutionary feedback model with four parameters: eco-evolutionary coupling (the x-axis), disturbance strength (the y-axis), inherent network resilience (horizontal panel arrangement), and the type of disturbance (vertical panel arrangement). The resilience values, from left to right, are 0.2, 0.4, 0.6, and 0.8. See table 2 for model formulations and definitions.

toward the pit (Peterson et al. 1998, Beisner et al. 2003). We therefore also modeled a decreasing or “limited” resilience scenario, replacing $1 - r$ from equations 3 and 4 with, respectively

$$\left(1 - \frac{r}{1+|G_t|}\right), \left(1 - \frac{r}{1+|E_t|}\right) \qquad (5)$$

We disturbed each model, increasing its ecological variable (E) by a given amount (d), either initially or repetitively at each iteration—representing a pulse or press disturbance, respectively (Bender et al. 1984). Because E and G interact reciprocally, there is no net difference in the model outcome if we disturb E or G; we are not implying that humans only disturb E. For full model equations, see table 2.

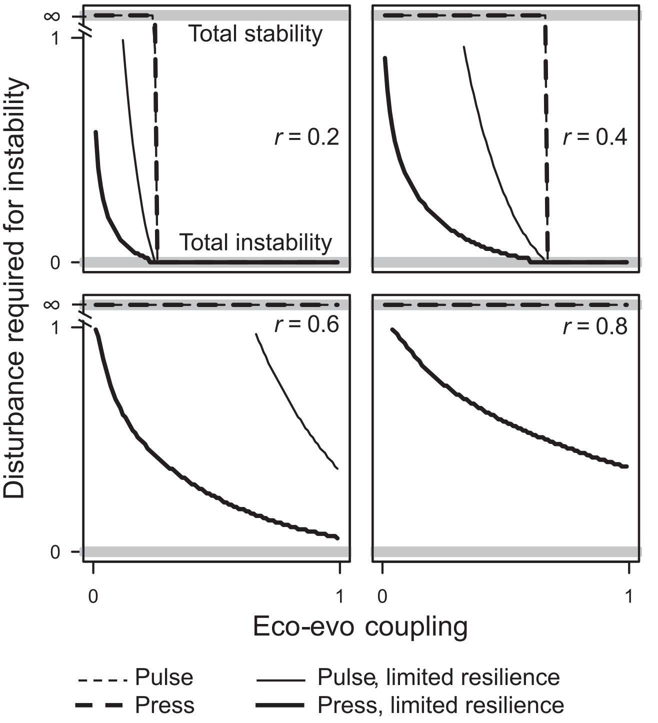


Figure 4. Disturbance required to destabilize an eco-evolutionary network. Increasing eco-evolutionary coupling decreases the amount of disturbance necessary to destabilize an eco-evolutionary network, particularly when resilience (r) is low or limited. Results here are from an eco-evolutionary feedback model; see table 2 for model formulations and definitions. The outcomes for pulse and press disturbances are the same for the highest resilience (r = 0.8) scenario.

We calculated the stability of the eco-evolutionary system (S) by examining the relative rate of change of E and G over time.

$$S = -\underset{t}{\text{median}}\left(\ln\left(\frac{0.5\,(E_t + G_t) - 0.5\,(\mathrm{E}_{t-1} + \mathrm{G}_{t-1})}{0.5\,(E_{t-1} + G_{t-1}) - 0.5\,(E_{t-2} + G_{t-2})}\right)\right) \quad (6)$$

Negative values of S indicate that change in the system is increasing (i.e., accelerating), and therefore demonstrate instability. Positive values indicate that change is decreasing (i.e., decelerating), therefore demonstrating stability. We examined the outcomes of the model over the range of parameters $0 < \{r, d, v\} < 1$ for four disturbance types: pulse or press × constant or limited resilience.

Model results. System stability was highly dependent on eco-evolutionary potential; increasing eco-evolutionary coupling across all types of resilience and disturbance led to decreased stability (figure 3). When resilience was constant, increasing eco-evolutionary coupling, but not disturbance strength, lowered system stability, with higher resilience requiring greater eco-evolutionary coupling to destabilize the system (figure 4). With the more realistic decreasing resilience model, increasing eco-evolutionary coupling also lowered the amount of disturbance necessary to generate system instability, especially for press disturbances (figure 4).

We also generated equations that approximated system stability, with $R^2 > .996$ for all models (table 3). In all models, stability (S) corresponded with eco-evolutionary coupling (v) and system resilience (r):

$$\mathrm{S} \propto -\ln((1 + v)\,(1 - r)), \quad (7)$$

with negative values of S indicating instability, and positive values of S indicating stability. In models with limited resilience, S also decreased logistically with d (table 3). This finding indicates increasing eco-evolutionary coupling, as well as decreasing system resilience, drive system instability. Because both v and r dictate the net response of ecology to evolution and vice versa, and v and r will be challenging to disentangle in nature, we can define net eco-evolutionary potential (Z) as the following:

$$Z = (1 + v)\,(1 - r) \quad (8)$$

These results indicate that eco-evolutionary potential—the realized net effect of ecology on evolution and vice versa—has the key role in determining the stability of eco-evolutionary dynamics, either by setting system stability alone or by regulating the level of disturbance that can destabilize a system. Although we did not investigate negative eco-evolutionary dynamics in the present article, increasing eco-evolutionary potential intuitively must provide at least some system stability when eco-evolutionary dynamics are negative (Hendry 2016).

Our model suggests that the role of humans in generating eco-evolutionary dynamics—particularly those that destabilize communities—is likely strongly determined by eco-evolutionary potential (Z, equation 8), or the net reciprocal impact of ecology and evolution. Therefore, as theorized earlier, an added focus on eco-evolutionary *potential* is necessary for a full picture of anthropogenic impacts on eco-evolutionary dynamics.

Quantifying anthropogenic effects on eco-evolutionary potential

In order to quantify the effects of humans on the stability of eco-evolutionary systems, we must both be able to estimate eco-evolutionary potential and determine the effect of humans on eco-evolutionary potential.

Here, we present two metrics to evaluate the strength of eco-evolutionary dynamics. Both are expressed in terms of linked variation between an ecological and organismal trait variable and range from 0 to 1. Because the two components of eco-evolutionary potential described in our models, eco-evolutionary coupling and inherent resilience, are difficult to tease apart, here we focus on net eco-evolutionary potential, or the combined effects of coupling and resilience. The first metric identifies the degree to which trait variation and ecological variation are correlated, without confirming

Table 3. Stability equations for eco-evolutionary models.

Disturbance	Stability equation
Pulse	$\boldsymbol{e}^{S} \cong -(1+v)(1-r)$
Press	$\boldsymbol{e}^{S} \cong -(1+v)(1-r)$
Pulse (limited resilience)	$\boldsymbol{e}^{S} \cong -(1+v)(1-r)-(1+v)(r)\,\text{logit}^{-1}(\boldsymbol{\psi})$
	$\boldsymbol{\psi} = -14.9 + 19.0v - 39.6r^2 + 16.1\sqrt{d}$
Press (limited resilience)	$\boldsymbol{e}^{S} \cong -(1+v)(1-r)-(1+v)(r)\,\text{logit}^{-1}(\boldsymbol{\psi})$
	$\boldsymbol{\psi} = (-12.2 + 13.9v - 38.0r^2 + 26.5\sqrt{d} + 11.4r^2\sqrt{d})\,\text{logit}^{-1}(\boldsymbol{\phi})$ $(-0.59 + 6.9v - 5.0r^2 + 6.6\sqrt{d} + 4.4r^2\sqrt{d})\ 1-\text{logit}^{-1}(\boldsymbol{\phi}))$
	$\boldsymbol{\phi} = (0.80 + 0.39r^2 + 9.3\sqrt{d} - 8.0r^2\sqrt{d})\,(\boldsymbol{\theta})$
	$\boldsymbol{\theta} = v - 0.49 - 1.4r^2 + 1.1\sqrt{d} + 0.42r^2\sqrt{d}$
	$\text{logit}^{-1}(X) = \frac{1}{1+e^{-X}}$

Note: ψ, φ, and θ refer to nested portions of the equations. *Abbreviations:* *d*, disturbance strength; *r*, system resilience; *S*, stability (equation 6); *v*, eco-evolutionary coupling.

reciprocal interactions, and is therefore practical for observational studies:

$$P = \max_x((\rho_{G_t,\,E_{t+x}})^2) \tag{9}$$

P is the net eco-evolutionary potential (0 to 1); $\rho_{G_t,\,E_{t+x}}$ is the correlation between a genetic trait (*G*) and an ecological trait (*E*) at time *t*. The maximum function allows a time lag of *x*, because reciprocal interactions between evolution and ecology are unlikely to be instantaneous (DeLong et al. 2016). Squaring the correlation coefficient keeps *P* between 0 and 1 and retains consistency with our earlier model and the following metric. A negative value of *x* allows the causation to proceed in either direction.

The second metric identifies the net degree to which trait variation and ecological variation are reciprocally interacting, and therefore requires experimental manipulation of both the trait and the environment:

$$P = \sqrt{\max_x(\eta_{G_{t+x},E_t}) * \max_x(\eta_{E_{t+x},G_t})} \tag{10}$$

P is the net eco-evolutionary potential (0 to 1); η_{G_{t+x},E_t} is the (partial) R^2 of a regression of a genetic trait (*G*) on an ecological trait (*E*) when *E* is manipulated at time *t*, allowing for a time lag of *x*; η_{E_{t+x},G_t} is the (partial) R^2 of a regression of an ecological trait (*E*) on a genetic trait (*G*) when *G* is manipulated at time *t*, allowing for a time lag of *x*. Because *P* is the geometric mean of the partial R^2 of traits on ecology and ecology on traits, for *P* to be greater than 0, both partial R^2 values must be greater than 0.

We can use these two metrics of the strength of eco-evolutionary dynamics to measure the effect of humans on eco-evolutionary dynamics. First, through experimentation or observation, we can relate change in *P* (see above) with changes in evolutionary or ecological parameters (*M*).

$$\frac{\Delta P}{\Delta M} \text{ or } \beta_{P,M} \tag{11}$$

$\Delta P/\Delta M$ is the change of either of our metrics of eco-evolutionary potential above (equations 9 and 10) with respect to any evolutionary or ecological parameter (see the equations in table 1), determined via a factorial design; $\beta_{P,M}$ is the slope of a regression of *P* on *M*.

Finally, we can calculate the anticipated or realized net effect of humans on eco-evolutionary potential (Ω):

$$\Omega = \sum_z \left(\frac{\Delta P}{\Delta M_z} * \widehat{\Delta M_z} \right) \text{ or } \sum_z \left(\beta_{P,M_z} * \widehat{\Delta M_z} \right) \tag{12}$$

$\Delta P/\Delta M_z$ is the change of either of our eco–evo potential metrics above (equations 9 and 10) with respect to each ecological or evolutionary parameter (see the equations in table 1), determined via a factorial design; β_{P,M_z} is the slope of a regression of *P* on M_z; $\widehat{\Delta M_z}$ is the anticipated or realized change in each ecological or evolutionary parameter because of humans.

Conclusions

Humans have profound impacts on both ecology and evolution, and these impacts likely extend beyond simple perturbations of eco-evolutionary systems to changes in eco-evolutionary potential in complex systems. Eco-evolutionary potential is an empirically measurable component of eco-evolutionary systems, and has likely already played a role in key focal systems in the field. Because eco-evolutionary potential—perhaps even more than perturbation strength—drives the severity and stability of eco-evolutionary dynamics, failure to incorporate eco-evolutionary potential into assessments of human impacts ignores a major component of risk from human activities on evolutionary ecology.

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