Humans as the world's greatest eco-evolutionary force

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ABSTRACT

Humans are dominant global drivers of ecological and evolutionary change, rearranging ecosystems and natural selection in many ways. Here, we show increasing evidence that human activity also plays a disproportionate role in shaping the eco-evolutionary potential of systems. We suggest the net outcome of human influences on trait change, ecology, and the feedbacks that link them, will often (but not always) be to increase the intensity of eco-evolutionary coupling, 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-impacted systems. To support this framework, we use a simple eco-evo feedbacks model to show that factors affecting coupling strength 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.

BACKGROUND

Eco-evolutionary dynamics—the ongoing reciprocal interactions between evolution and ecology [1,2]—have become an important paradigm for understanding both ecological and evolutionary change [3]. Eco-evolutionary dynamics are of particular applied interest in human-impacted systems, as they can amplify or extend the effects of anthropogenic perturbations across natural systems [4,5]. For example, contemporary evolution in response to human activities can generate novel, ecologically-relevant traits that amplify or extend anthropogenic impacts to new ecosystem compartments [5,6].

As humans are adept at causing both ecological [7,8] and evolutionary change [6,9], it is natural to expect that human actions can influence eco-evolutionary dynamics [10]. In the most widely studied class of anthropogenic effects, humans directly change the course of both ecology and evolution [5,6,9–12]. Many examples of contemporary evolution and eco-evolutionary dynamics involve perturbations—either humans manipulate some aspect of the environment, leading to evolutionary change [13,14], or humans generate evolutionary change in some organism, leading to ecological change [15,16]. Humans directly cause evolution in both captive and wild organisms through intentional and unintentional artificial selection (e.g. harvest) [9,17] and domestication [18,19]. When artificial selection results in changes in ecologically relevant functional traits—particularly what, where, and how much an organism eats or is consumed—ecological change and eco-evolutionary dynamics can result [6,11,20–22].

Anthropogenic ecological disturbances are also prolific. In particular, anthropogenic perturbations of ecosystems through species introductions and removals can rearrange entire food webs through trophic cascades [23–25]. 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 [22,26,27]. Introductions and removal of competitors has also caused significant niche evolution in wild organisms [28,29]. Therefore, humans may spark eco-evolutionary dynamics by introducing or removing key predator and prey species. The abiotic frame has also been altered significantly by human activities. Pollution by diverse media (nutrient, 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 [30–32]. These alterations of the abiotic frame—as well as their resulting changes in species distributions—have been shown to generate numerous examples of contemporary evolution [33–35], thereby potentially sparking eco-evolutionary dynamics.

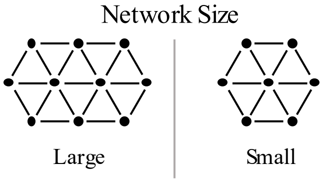
Beyond perturbation.

While all of these examples represent ways that humans might affect eco-evolutionary dynamics, we suggest a focus on perturbations affecting selection or functional trait effects is likely incomplete. We suggest that understanding human effects on eco-evolutionary dynamics requires examining anthropogenic impacts on “eco-evolutionary potential” – which we define as the degree to which various system properties determine the strength of ecological and evolutionary coupling. Eco-evolutionary potential likely plays a major governing role in the scope and pattern of ensuing eco-evolutionary dynamics, and affects the stability of eco-evolutionary systems (Figure 1; also see later analysis).

A NETWORK APPROACH TO ECO-EVOLUTIONARY POTENTIAL

Here we propose a network framework for examining eco-evolutionary potential. 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, while evolutionary biologists may see them as selection topologies. 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 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 functional trait compartments of an ecosystem interacting to determine the transfer of energy and nutrients. Essentially, the nodes in the network have functionally important features that influence their interactions with other nodes.

Networks have been analyzed in innumerable ways; 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 strength (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. Indeed, most examples of strong eco-evolutionary dynamics have been found in simple, strongly interacting systems. Importantly, we argue that the tendency for human effects on these networks is generally towards simplification, generally increasing the potential for eco-evolutionary dynamics, with a few notable exceptions. We also provide examples and metrics for measuring these network aspects.



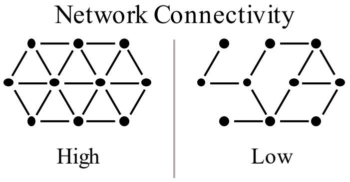
Network size – altering number of players

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 [36–39] and the sensitivity of populations to changes in selection regimes [40], thus affecting the potential for eco-evolutionary dynamics.

By directly and indirectly causing species losses, humans shrink food webs, the ecological components of eco-evolutionary networks [8,41]. Smaller food webs are less stable and more susceptible to perturbation due to decreased redundancy and decreased diffusing capacity [36–39]. Even additions of invasive species often eventually lead to a functionally smaller network due to the ensuing loss of native species [42]. Smaller food webs are more likely to exhibit strong ecological responses to changes in constituent population functional traits because a greater proportion of those functional interactions are either direct or involve fewer intermediaries. Indeed, many foundational examples of eco-evolutionary dynamics are in simple, strongly-interacting predator-prey systems [43,44].

By the same process, 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 [40,45]. However, as humans remove interacting species like predators and competitors or override limiting interactions like nutrients, various forms of competing selection and tradeoffs are relaxed [14]. Thus, by simplifying the selection landscape, humans can make wild populations more likely to evolve in the face of environmental change, and thus increase the likelihood of eco-evolutionary dynamics.

Food web size can be measured in numerous ways, including the number of populations or 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_β^2).



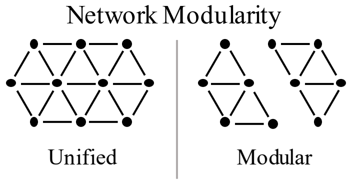
Network connectivity – altering link complexity

Humans can also alter the connections within networks, adding or removing links without changing the number of players. These links include new (or lost) ecological interactions between species, new selection pressures, and new evo-to-eco effects. Whereas increases in network connectivity might be predicted to favor stabilizing eco-evo dynamics through processes like redundancy and competing feedbacks [46], 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 towards generalists and omnivores [47,48]. Novel, human-dominated systems (e.g., cities) rarely support specialists, and tend to be populated by more flexible generalists [49]. Thus, 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 [46] 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 substitute 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 [50]. 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 eco-evolutionary potential. Network connectivity can be measured by examining the average number of links per individual, $\bar{L}$.



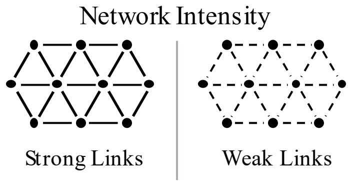
Network modularity – altering metasystem complexity

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 [51,52]. As 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 [53], changes in system modularity can alter the potential for eco-evolutionary dynamics.

Humans can increase modularity by weakening or eliminating interactions between species or other ecosystem components. For instance, in food webs, humans can break trophic linkages, reducing the web into smaller, more isolated interacting parts. Humans can also increase modularity by fragmenting ecosystems spatially, decreasing connectivity between ecosystem components because of decreased connectivity among spatial modules [54,55]. Another form of modularization happens when humans reduce or overwhelm abiotic subsidies between spatially separated modules (ecosystems) [56]. By isolating modules, humans reduce the capacity of the broader metasystem 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 [53,57]. 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 showed locally nuanced dynamics.

Humans also have strong impacts on genetic metapopulation structure, in some cases increasing gene flow (translocation, homogenization) [58] and in others decreasing gene flow (fragmentation, modularization) [57]. Decreasing gene flow can facilitate evolution by isolating populations from maladaptive gene flow [59,60], but also limits inputs of novel genetic variation, reducing the potential extent of evolution where such genetic variation is limiting. . Given that contemporary evolution is most often fueled by standing quantitative trait variation, which is often difficult to significantly deplete, the dominant effect of modularlization on evolution is apt to be facilitation of stronger local adaptation and associated eco-evolutionary dynamics.

Metrics for examining eco-evolutionary potential. Modularization can be measured by rates of energy or nutrient flow across modules (Q) or autocorrelation between modules (ρ_M). As modularized metacommunities have numerous strong (within modules) and weak (across modules) interactions, modularization can 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).



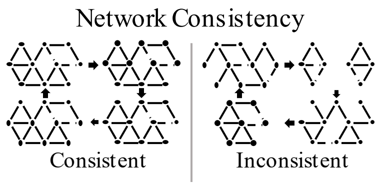
Network intensity – altering link strength

In additions to adding and removing connections, human activities alter the strength of connections within networks. While similar to network connectivity above, this pattern includes strengths of ecological interactions, and strengths of interactions between evolution and ecology. Human-dominated environments tend to have more intensely interacting species. These more intense interactions tend to generate flashier, less-stable systems, and stronger instances of selection [57]. Stronger links therefore generally lead to less-stable systems [37], increasing the potential for eco-evolutionary dynamics.

Anthropogenic changes to age structure can 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 [61,62]. Decreasing the age-structure of a population tends to generate more chaotic abundance dynamics and make the population more susceptible to external perturbation [63–65], functionally increasing link strength. Thus, populations with younger average ages are likely to be more sensitive to functional trait changes in their predators and prey. Organisms' response to selection are also dependent on age structure, with shorter generation times allowing for faster responses to selection [66]. Humans reduce the generation time through both ecological (i.e. individuals only have offspring when they are young, before they die [61,62]) and evolutionary (i.e. selection for earlier reproduction [67,68]) mechanisms. Organisms 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 [69]. Evolution by natural selection can only proceed as far as standing genetic variation allows [70], after which it is limited by rates of mutation, which are generally too slow to allow for contemporary evolution. Humans generally decrease genetic variation by shrinking and fragmenting populations, as well as exposing populations to strong, hard selection that results in genetic bottlenecks [71]. Thus, human impacts on populations are likely to reduce evolutionary responses to environmental change via reductions in genetic variation. One caveat to this pattern is when humans increase gene flow by translocating organisms, thus 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, thus allowing them to persist without necessarily requiring genetic evolution [72]. As 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 [73,74]. This pattern thereby increases the strength of links between ecological change and genetic evolution. Thus, 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 eco-evolutionary potential. 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 ($\overline{A_P}$). Interaction strengths can be measured in numerous ways [75,76]; 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 (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 humans or other drivers canalizing temporal variation [77,78]. 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 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, as inconsistency keeps resetting the network and eco-evolutionary dynamics far from any stable equilibria [79]. With this in mind, human dominated systems, like agro-ecosystems, may be places of continually strong eco-evolutionary dynamics.

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

EXAMPLES: ANTHROPOGENIC IMPACTS ON ECO-EVOLUTIONARY POTENTIAL IN FISHES

While 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 *G. affinis* and *G. holbrooki*—have become a model system of eco-evolutionary dynamics due to 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 [80–83]. Furthermore, humans have directly meddled with their evolution, domesticating mosquitofish and altering their gene flow [16].

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, while 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 [84,85]. This reduction in mosquitofish gene flow has probably facilitated local adaptation from their initially diverse and relatively homogenous gene pool, and fed the diverse eco-evolutionary dynamics documented in mosquitofish (changes to network modularity and intensity).

Furthermore, mosquitofish exist in small, simple, strongly-interacting environments, maximizing their eco-evolutionary potential. Mosquitofish systems are typically dominated by mosquitofish and their piscine predators, which are also typically invaders [86]. 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 [87]. Furthermore, mosquitofish are generalists (network connectivity), leading mosquitofish trait evolution to have strong ecological impacts on lower taxa [88,89].

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 [90,91].

But again, the human impact on eco-evolutionary dynamics in marine fish likely runs much deeper than these perturbations. The marine ecosystems in which cod and salmon live are fundamentally simpler, in part due to “fishing down” of the marine food web (network size) [92]. These simpler ecosystems make evolution—in fished species and in others [22]—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 [63,65,68].

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) [93]. 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 [22].

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 [94–97]. 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 [33,98–100]. Decreased water clarity can then feed-back to select for further benthivory [97,101,102], 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 [26,103]), limits to standing genetic variation [104], and gene flow can stall contemporary evolution [60,105]. In the same vein, ecological connectedness (e.g. residence time [106]) and ecological buffering capacity—e.g. a compensatory response in algivorous zooplankton [16]) can limit the impact of benthivory on lake clarity.

Humans can make this eco-evolutionary feedback more likely, both by sparking the feedback and increasing the reciprocal impacts of ecology and evolution—i.e. eco-evolutionary potential. Initial cultural eutrophication can catalyze selection for benthivory [33,97]. Humans may facilitate contemporary evolution, both by reducing conflicting selection pressures (network size, connectivity) [14] (e.g. removing predators [8]) and by shortening generation times through processes like harvest [107] (network intensity). (Alternatively, in some species humans my prevent contemporary evolution by adding new conflicting selection pressures—e.g. introducing invasive predators [40]—and creating genetic bottlenecks [71].) Anthropogenic landscape fragmentation can cut off gene flow (network modularity), facilitating local adaptation [58,60]. 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) [108–110]. In addition, humans can isolate lakes (network modularity) [111], increasing water residence time [106] and facilitating faster nutrient cycling, [112] making communities much more likely to change in response to contemporary evolution. Thus, in this example, perturbation by humans is only the tip of the iceberg, as humans likely have a strong influence on the potential for destabilizing eco-evolutionary dynamics.

INSTABILITY AS A CONSEQUENCE OF INCREASED ECO-EVOLUTIONARY POTENTIAL

But how important are human alterations to eco-evolutionary potential versus human perturbations? Based on our framework and examples above, we investigated the role of eco-evolutionary potential in destabilizing simple eco-evolutionary systems via positive eco-evolutionary feedbacks. We created a simple model examining the stability of eco-evolutionary systems based on three parameters: eco-evolutionary coupling, perturbation strength, and inherent system resilience. We examined the effect of pulse and press disturbances, as well as constant resilience and decreasing or limited resilience models, the latter of which assumed that system resilience became weaker as the system was moved farther from its initial state.

Modeling eco-evolutionary dynamics

We iteratively modeled an ecological (*E*) and evolutionary variable (*G*), which interacted in a positive feedback. Positive values for either variable would increase the value of the other in the following model iteration; the strength of this increase was dependent on an eco-evolutionary coupling variable (*v*). The system had a resilience parameter (*r*) which pulled both *E* and *G* back towards zero each iteration. Resilience could function as a constant proportion (i.e. an *r* of 0.5 means that both *E* and *G* will be reduced by 50% each iteration) or could be limited, with resilience decreasing as *E* and *G* move away from zero. This limited resilience scenario represents a more realistic, possibly stressed ecosystem, which is unlikely to exhibit inexhaustible resilience [113–115]. We disturbed each system, increasing its ecological variable (*E*) by a given amount (*d*), either initially or repetitively at each iteration—representing a pulse or press disturbance, respectively. As *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.

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

(1)

$$S = -\underset{t}{\operatorname{median}}\left(\ln\left(\frac{0.5(E_t + G_t) - 0.5(E_{t-1} + G_{t-1})}{0.5(E_{t-1} + G_{t-1}) - 0.5(E_{t-2} + G_{t-2})}\right)\right)$$

Negative values of *S* indicate that change in the system is increasing (i.e. accelerating), and thus demonstrate instability. Positive values indicate that change is decreasing (i.e. decelerating), thus 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 coupling across all types of resilience and disturbance, with higher eco-evolutionary coupling leading to decreased stability (Figure 3). When resilience was constant, increasing eco-evolutionary coupling, but not disturbance strength, lowered system stability, with higher resilience requiring higher 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 $R^2 > 0.996$ for all models (Table 3). In all models, stability (S) corresponded with eco-evolutionary coupling (v) and system resilience (r):

(2)

$$S \propto -\ln\big((1+v)(1-r)\big)$$

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. As 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 (P) as:

(3)

$$P = (1 + v)(1 - r)$$

These results show that eco-evolutionary dynamics, when mutually reinforcing, can be a source of system instability, and in many cases can facilitate destabilizing environmental responses to disturbance. Furthermore, these results indicate that the ratio of eco-evolutionary coupling to system resilience—i.e. eco-evolutionary potential, the realized net effect of ecology on evolution and vice-versa—has the key role in determining system stability, either by setting system stability alone or by regulating the level of disturbance that can destabilize a system. Though we did not investigate negative eco-evolutionary dynamics here, eco-evolutionary potential intuitively must provide at least some system stability when eco-evolutionary dynamics are negative [1]. However, most work on eco-evolutionary dynamics to date has focused on the role of disturbance, not the role of eco-evolutionary potential [5,6,9]. 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 (P, Eqn. 3), 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 coupled, without confirming reciprocal interactions, and is therefore practical for observational studies:

(4)

$$P = \max_{x}\left(\left(\rho_{G_t,E_{t+x}}\right)^2\right)$$

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*, as reciprocal interactions between evolution and ecology are unlikely to be instantaneous [116]. 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:

(5)

$$P = \sqrt{\max_{x}\left(\eta_{G_{t+x},E_t}\right) * \max_{x}\left(\eta_{E_{t+x},G_t}\right)}$$

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*. As *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*).

(6)

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

$\Delta P/\Delta M$ is the change of either of our metrics of eco-evolutionary potential above (Eqns. 4 and 5) with respect to any evolutionary or ecological parameter (see the equations in Table 4), 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 coupling (Ω):

(7)

$$\Omega = \sum_{z}\left(\frac{\Delta P}{\Delta M_z} * \widehat{\Delta M_z}\right) \text{ or } \sum_{z}\left(\beta_{P,M} * \widehat{\Delta M_z}\right)$$

$\Delta P/\Delta M_x$ is the change of either of our eco-evo coupling metrics above (Eqns. 4 and 5) with respect to each ecological or evolutionary parameter (see the equations in Table 4), determined via a factorial design; β_{P,M_x} is the slope of a regression of P on M_z; ΔM_z-hat is the anticipated or realized change in each ecological or evolutionary parameter due to 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 the very coupling of evolution and ecology in complex systems. As the net coupling between ecology and evolution—not disturbance strength alone—drives the potential for eco-evolutionary feedbacks, failure to consider the effects of humans on this characteristic of eco-evolutionary networks ignores a major component of risk from human activities on evolutionary ecology.

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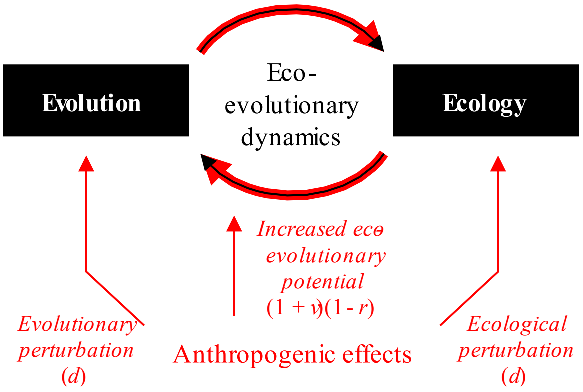
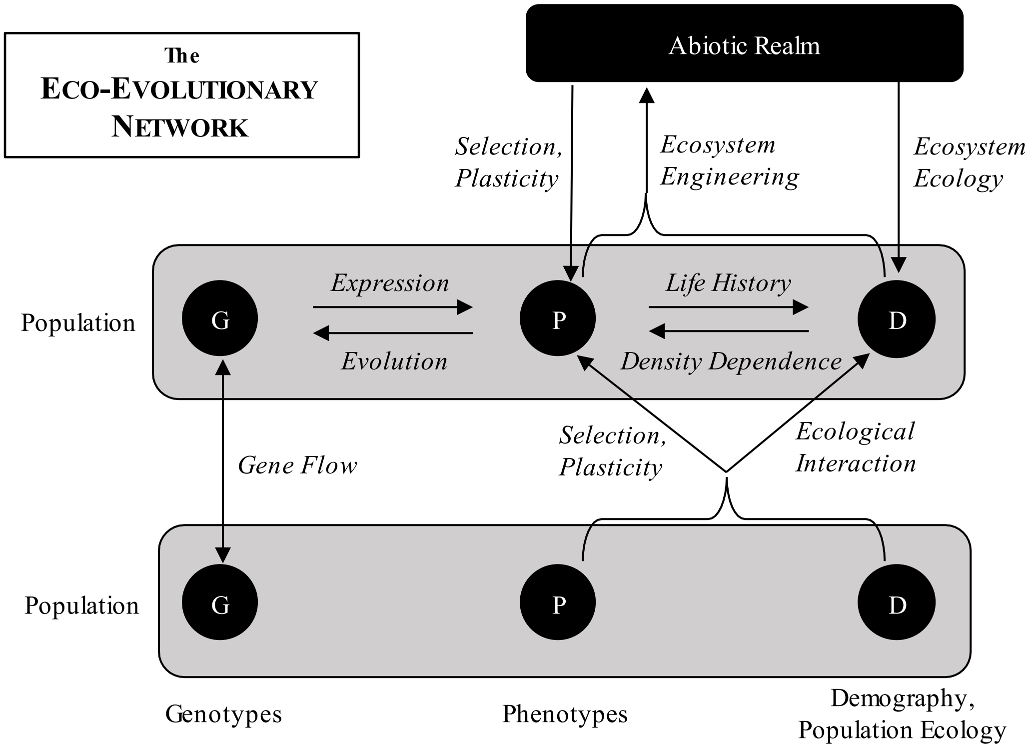
EPP, MTK, ZTW, and BJO designed the review. ZTW conducted model analyses. ZTW led writing; all authors contributed.

Figure 1: Anthropogenic impacts on eco-evolutionary dynamics.



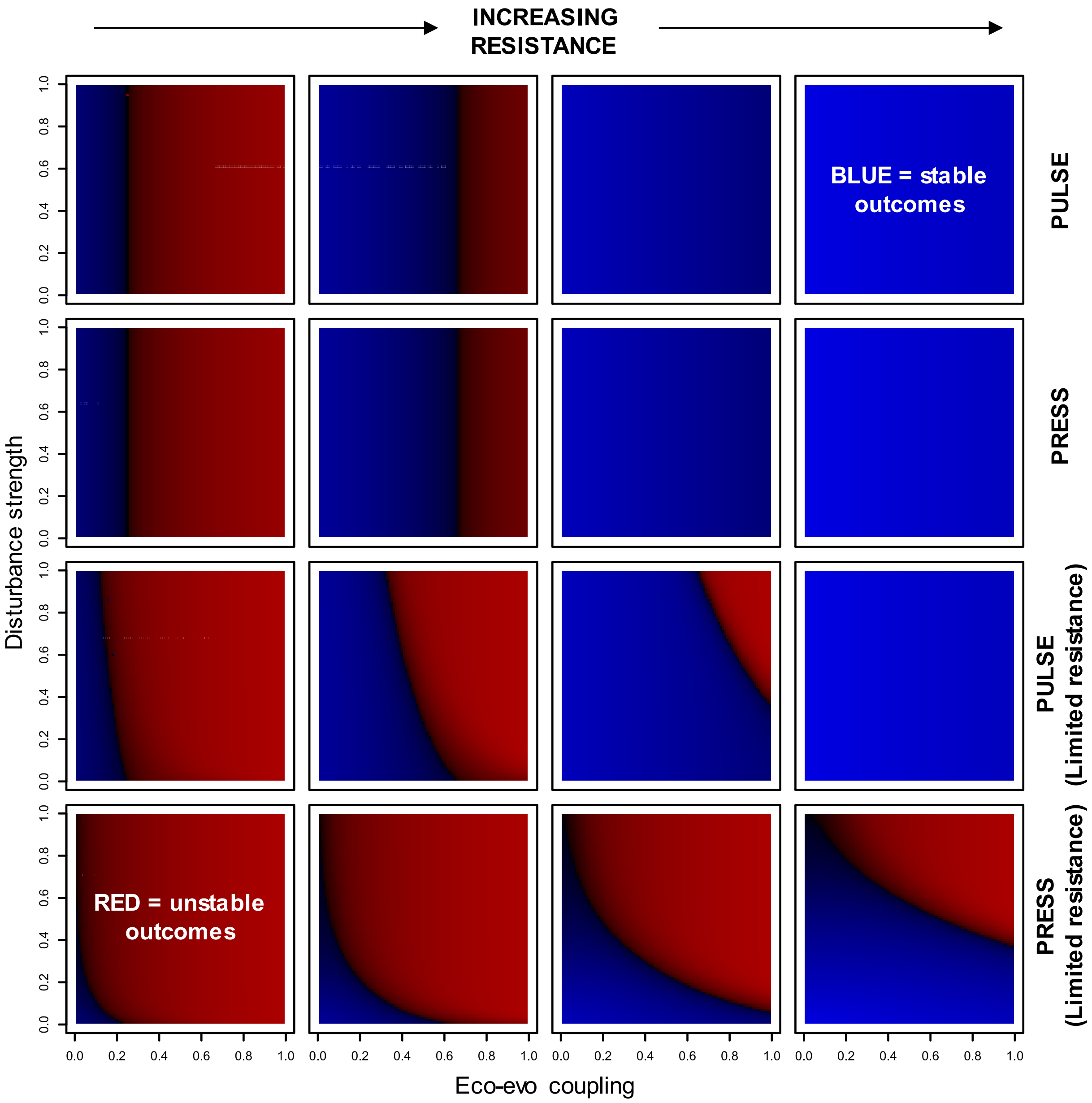
Humans can facilitate eco-evolutionary dynamics not only by disturbing systems, but by increasing eco-evolutionary potential: strengthening eco-evolutionary coupling and weakening inherent resilience. Letters refer to model equations (see later analysis).

Figure 2. Eco-evolutionary networks.



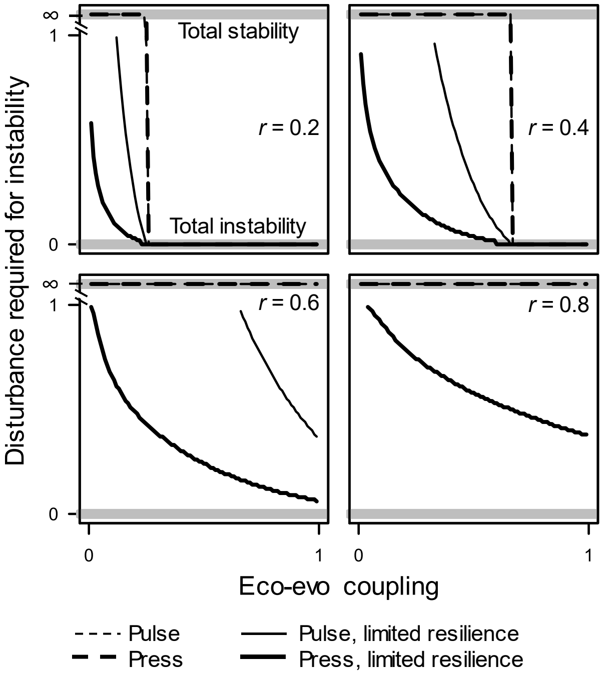
Eco-evolutionary networks consist of interacting genotypes, phenotypes, populations, communities, and ecosystems.

Figure 3. Eco-evolutionary model stability.



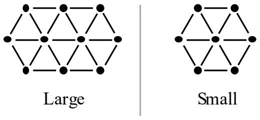
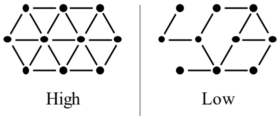
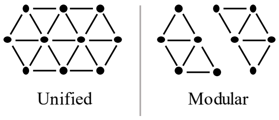
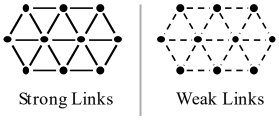
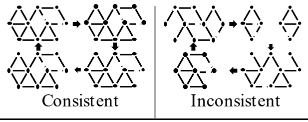
Increasing eco-evolutionary coupling (*v*) and decreasing resilience (*r*) decreases both the stability of eco-evolutionary systems and the amount of disturbance (*d*) needed to destabilize systems. See Table 1 for model formulations and definitions and Eqn. 1 for stability calculation.

Figure 4. Disturbance required to destabilize an eco-evolutionary model.



Increasing eco-evolutionary coupling (*v*) and decreasing resilience (*r*) decreases both the stability of eco-evolutionary systems and the amount of disturbance (*d*) needed to destabilize systems. See Table 2 for model formulations and definitions.

Table 1. Eco-evolutionary networks.

Network Aspect	Description	Examples	Eco-Evolutionary Potential	Metrics
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).	Stronger ecological interactions	⬆↓	$\frac{\partial N_1}{\partial N_2}$
		Decreased age structure, generation time	⬆↓	$\bar{A}, \overline{A_P}$
		Altered trait variation, plasticity	⬆⬇	$F_{IS}, \sigma_G^2, \frac{\partial X}{\partial E}$
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. See text for metric equation legends.

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			
$G_{t+1} =$	$(1 - r) * (G_t + vE_t)$		$\left(1 - \frac{r}{1 + \lvert G_t \rvert}\right) * (G_t + vE_t)$	
$E_{t+1} =$	$(1 - r) * (E_t + vG_t)$	$(1 - r) * (E_t + d + vG_t)$	$\left(1 - \frac{r}{1 + \lvert E_t \rvert}\right) * (E_t + vG_t)$	$\left(1 - \frac{r}{1 + \lvert E \rvert}\right) * (E_t + d + vG_t)$

G = evolutionary trait; *E* = ecological trait; *d* = disturbance strength; *r* = system resilience; *v* = eco-evolutionary coupling; subscripts indicate time (*t*).

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

S = stability (Eqn. 1); *v* = eco-evolutionary coupling; *r* = system resilience; *d* = disturbance strength.

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