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OPINION

Biodiversity change under adaptive community dynamics

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Abstract

Compositional change is a ubiquitous response of ecological communities to environmental drivers of global change, but is often regarded as evidence of declining "biotic integrity" relative to historical baselines. Adaptive compositional change, however, is a foundational idea in evolutionary biology, whereby changes in gene frequencies *within* species boost population-level fitness, allowing populations to persist as the environment changes. Here, we present an analogous idea for ecological communities based on core concepts of fitness and selection. Changes in community composition (i.e., frequencies of genetic differences *among* species) in response to environmental change should normally increase the average fitnessof community members. We refer to compositional changes that improve the functional match, or "fit," between organisms' traits and their environment as *adaptive community dynamics*. Environmental change (e.g., land-use change) commonly reduces the fit between antecedent communities and new environments. Subsequent change in community composition in response to environmental changes, however, should normally increase community-level fit, as the success of at least some constituent species increases. We argue that adaptive community dynamics are likely to improve or maintain ecosystem function (e.g., by maintaining productivity). Adaptive community responses may simultaneously produce some changes that are considered societally desirable (e.g., increased carbon storage) and others that are undesirable (e.g., declines of certain species), just as evolutionary responses within species may be deemed desirable (e.g., evolutionary rescue of an endangered species) or undesirable (e.g., enhanced virulence of an agricultural pest). When assessing possible management interventions, it is important to distinguish between drivers of environmental change (e.g., undesired climate warming) and adaptive community responses, which may generate some desirable outcomes. Efforts to facilitate, accept, or resist ecological change require separate consideration of drivers and responses, and may highlight the need to reconsider preferences for historical baseline communities over communities that are better adapted to the new conditions.

KEYWORDS

adaptive dynamics, anthropocene environments, community ecology, ecosystem function, environmental change, species turnover

1 | INTRODUCTION

The world's biota is in a state of flux. The broad agreement among scientists is that the composition of contemporary **ecological communities** (see glossary Box 1) is changing rapidly (Blowes et al., 2019; Dornelas et al., 2014; Hillebrand et al., 2018; Primack et al., 2018; Thomas, 2020), and that this change is driven to a substantial degree by human activities such as land-use conversion (Newbold et al., 2020), climate change (Feeley et al., 2020), and the human-aided dispersal of species (Pyšek et al., 2020). Conservation biologists are

BOX 1 Glossary (terms initially introduced in text as Bold).

Adaptive change: Change in the identities and/or abundances of alleles, genotypes, or species that increase mean fitness via improved matching between traits and the environment.

Community composition: Most often characterized by the identities and relative abundances of species found in a given place at a given time, in which case we would also refer to species composition. Composition may equally be characterized by trait distributions or other relevant community characteristics.

Community dynamics (adaptive or maladaptive): Changes in community composition, which are adaptive if they increase average fitness via improved trait–environment matching (i.e., improved fit), and maladaptive if they do the opposite.

Community state (adaptive or maladaptive): The relative degree of adaptation of a community, jointly determined by community composition and the environment.

Counterfactual: A state of the world that does not occur, but that could or would have occurred under different conditions.

Ecological community: A population, in the statistical sense, comprising all organisms across species in a given place at a given time. Communities may be subdivided for practical or scientific reasons into taxonomic (e.g., bird community), trophic (e.g., community of herbivores), or other useful subunits (e.g., feeding guild of granivorous rodents).

Ecosystem functions: Processes related to ecosystem-level transfers of energy and materials. Examples include primary production, water and nutrient regulation, decomposition, soil retention, and pollination. When humans benefit from an ecosystem function, it is often called an ecosystem service.

Environment: Physical and biological attributes of a location relevant to organismal fitness. While there are dynamic feedbacks between the success of organisms and the biotic environment subsequently experienced by the same organisms, here we focus primarily on physical attributes of the environment, such as the climate. Similar principles apply to the consideration of biotic environments. Environments can be characterized not only by average conditions (e.g., mean annual temperature) but also their variability (e.g., magnitude of temperature fluctuations).

Facilitate–Accept–Resist: Management framework under which desired combinations of environment and community composition are pursued through facilitating, accepting, or resisting change in the environment and/or community composition, following Thomas et al. (2022).

Fit: A functional match between traits and environmental conditions. Organisms, populations, or communities whose traits confer a good fit to a particular environment may be said to be well adapted to that environment and are expected to have high levels of fitness. As such, fit is not something that is measured directly, but rather inferred from studies of how fitness depends on traits and environment.

Fitness:

Individual level: The expected quantitative contribution of an organism to the future population or community of which it is part. Most used in evolutionary biology (i.e., for populations), where individuals are of comparable size and life history.

Genotype/Species level: The mean fitness across organisms (or units of biomass) of a given genotype (in a population-level study) or species (in a community-level study).

Population/Community level: The mean or sum of fitnesses across all organisms (or units of biomass) in the population or community. The fitness of a population is sometimes quantified as the per capita population growth rate (individuals/individual/time). Given vastly different individual sizes and life histories across species, the fitness of a community may be quantified as the growth rate in units of living biomass (mass/mass/time). This is equivalent to productivity expressed relative to initial biomass, and to the weighted average of individual species' productivities, with weights equal to initial biomass.

Selection: Deterministic fitness differences among organisms, genotypes, or species with different traits. In the adaptive community dynamics framework, the focus is on selection based on fitness differences among organisms of different species, not among entire communities.

often concerned about such changes, due, for example, to declines in the abundances of particular species—sometimes to the point of extinction (IUCN, 2021)—or of species associated with particular habitat types (e.g., Busch et al., 2020). Policy guidelines have thus commonly aimed to preserve and restore historical baseline states with respect to **community composition** (e.g., Steffen et al., 2015). However, if one accepts that environmental changes have occurred and will continue in the future (e.g., climate change), some compositional change will be *required* to maintain an adaptive **fit** between environmental conditions and the organisms that live in a given place (i.e., **adaptive change**; Godfrey-Smith,2014), particularly if the aim is to maintain **ecosystem functions** (Chesson et al., 2001; Harrison et al., 2022; Oliver et al., 2015).

Here, we outline a framework for understanding and studying **community dynamics**, whereby the ecological community is viewed as a population of organisms (of multiple species) in which **selection** occurs not only among genotypes within species but also among organisms of different species. Following the lead of evolutionary biologists, we define *adaptive community dynamics* as change in the composition of an ecological community that improves the fit between organisms' traits and the **environment**, thus increasing or maintaining average **fitness**. Our framework starts with the concepts of fitness and selection in single-species populations undergoing adaptive evolution, and extends them in two key ways: (1) We substitute "species" in place of "genotypes" as the biological units whose relative frequencies are of interest, and (2) we expand options for assessing fitness, which is often quantified as the rate of change in "abundance" (broadly defined) over time (see below). From this conceptual basis, we illustrate how adaptive, or maladaptive, **community states** can be altered by changes in the environment (e.g., climate or land use) and by changes in species composition (i.e., community dynamics). We highlight empirical evidence for adaptive community dynamics, and contrast this with the way community dynamics are often interpreted. Although the idea of adaptive community dynamics is often implicit in ecological and global change studies (e.g., the widely observed improved performance of warm-adapted species in response to climate change in temperate regions (Bowler et al., 2017; Feeley et al., 2020)), it is rarely discussed explicitly. We think this interpretation deserves broader discussion given its important consequences for both assessing and managing changes to ecological communities.

We stress from the outset that the word "adaptive" does not imply change that is necessarily "good." Adaptive community responses to environmental change may or may not be preferred by particular stakeholders (e.g., due to increased carbon storage vs. decreased abundance of native or endangered species), just as adaptive evolutionary responses within a species may or may not be preferred (e.g., evolutionary rescue maintaining harvested fish populations vs. smaller fish for fishers and consumers). Even if an environmental change is undesirable overall (e.g., climate warming), adaptive community dynamics in response to that change may promote certain desirable outcomes (e.g., maintained ecosystem function). At the very least, this should prompt us to reconsider conservation goals that are aimed by default at maintaining historical baseline states. Our framework highlights the importance of assessing the adaptive (or maladaptive) nature of community *responses* to environmental change separately from environmental change itself. Explicit recognition of adaptive community dynamics can help scientists inform appropriate interventions to **facilitate, accept or resist** ecological change under the reality of anthropogenic environments, given particular management or conservation goals (Thomas et al., 2022).

2 | ADAPTIVE COMMUNITY DYNAMICS IN THEORY

The ideas of selection and system-level adaptive change extend well beyond evolutionary biology (Godfrey-Smith, 2014), with applications in economics (Beinhocker, 2006), the social sciences (Hodgson & Knudson, 2010), and community ecology (Leibold & Norberg, 2004; Shipley, 2010; Vellend, 2016). Here, we are concerned with adaptive change in which organisms—subdivided by types (e.g., genotypes, species)—interact differentially with physical and biological processes, such that selection leads to changes in the relative frequencies of types (Matthen & Ariew, 2002; Pigliucci & Kaplan, 2006). It is therefore the relative degree of fit between organisms' traits and the environment which is the key determinant of whether change is adaptive (Figure 1; McGill et al., 2006; Shipley, 2010). In this section, we first give a brief overview of some core concepts underlying adaptive change in evolving populations, as well as introducing some conceptual issues that arise. We then show how the same conceptual scaffolding can be used to describe adaptive change in ecological communities.

2.1 | Fitness, selection, and adaptive change in populations: A very brief overview

As populations with genetically variable phenotypes interact with the environment, those individual, heritable characteristics that enhance survival and reproduction tend to increase in frequency, causing adaptive evolution. "Adaptedness," therefore, is context dependent—a "property-in-an-environment" (Brandon, 1995). As such, the extent to which a population is well adapted can be altered through change in either the environment or the composition of the population itself (Figure 1; Hendry & Gonzalez, 2008).

Adaptive evolution is caused by natural selection, which is in turn underpinned by fitness differences. Quantifying fitness is thus of central importance for evolutionary studies, but it is far from straightforward (Godfrey-Smith, 2014; Matthen & Ariew, 2002; Orr, 2009; Pigliucci & Kaplan, 2006). Fitness can be quantified at the level of individual organisms (e.g., counting offspring), or at the level of a biological "type" (e.g., a change in genotype frequency). A particular research question (or logistical limitation) might require a focus on particular components of fitness, such as survival or fertility, rather than "overall" fitness

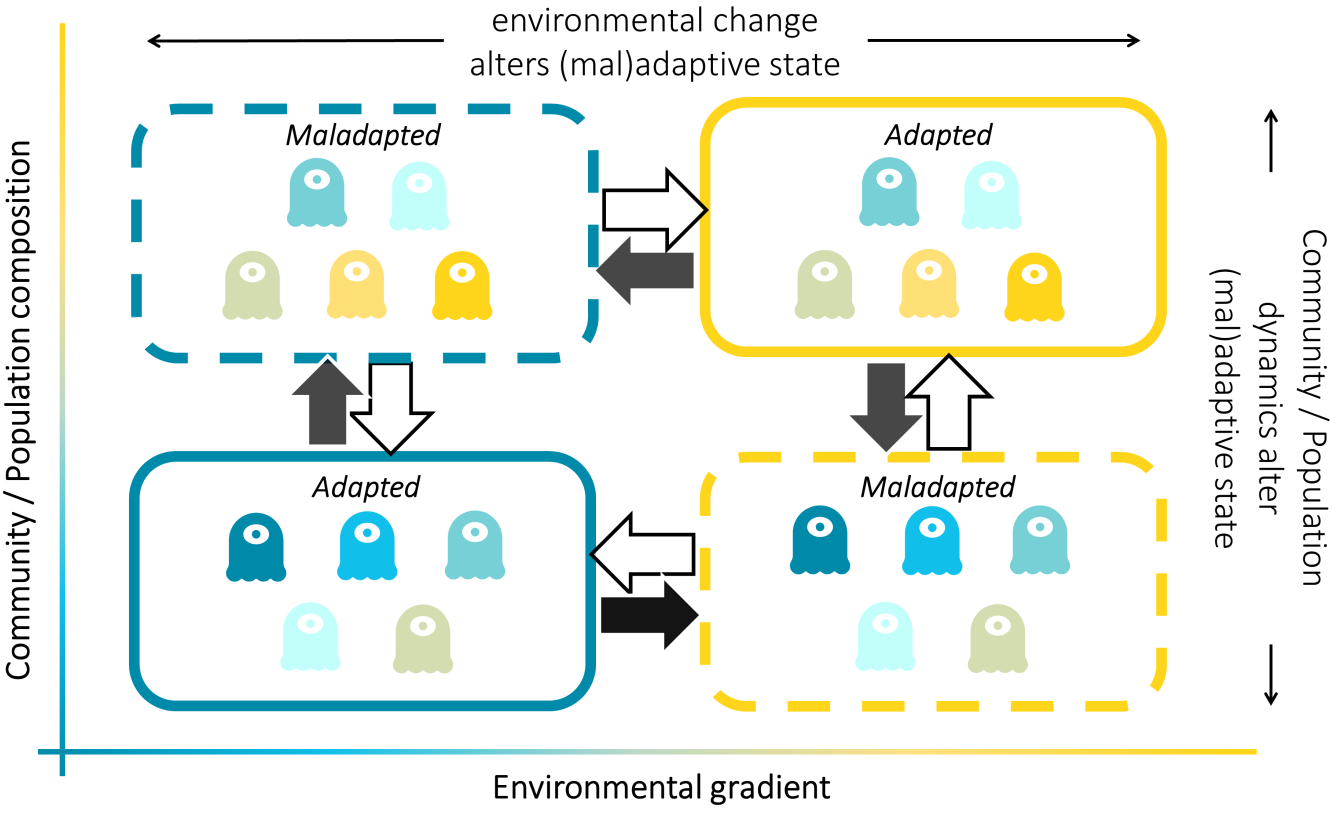

FIGURE 1 (Mal)adaptive states. The degree to which a community or population is well adapted (i.e., its (mal)adaptive state) is determined by the relative fit between the trait distribution of community (or population) members (*color of critters*) and local environmental conditions (*color of community/population outlines*). As such, changes in either the environment or species composition can cause a shift from a relatively well adapted to maladapted state, or vice versa. Here, thick *black arrows* denote shifts in environment (*horizontal*) or composition (*vertical*) which reduce trait–environment matching, and thick *white arrows* denote environmental/compositional shifts which improve trait–environment matching. We typically expect environmental change to reduce community/population-level adaptation initially, with selection leading to subsequent adaptive dynamics.

(Laughlin et al., 2020; Sober, 2000). Measures of absolute fitness may be required in some instances, while fitness relative to some reference population, individual or type will be required in others (Brady et al., 2019; Orr, 2009). There is also no single most appropriate time frame over which to quantify fitness—sometimes researchers estimate a population growth rate over many generations (e.g., for a bacterial genotype in the lab (Bell, 1990; Lenski et al., 1998)), and sometimes they estimate fitness components within a fraction of a generation (e.g., for trees in a forest). Many species produce multiple offspring types (e.g., clonal vs. sexual reproduction in many plants and fungi, and some animals) for which a simple sum of individuals is often of little meaning, and for which the difference between growth and reproduction can be ambiguous. Finally, to break the circularity in statements like "survival of the fittest," fitness is often defined as a *propensity* for survival and reproductive success (Sober, 2000), but most often we can only measure *realized* survival or reproduction. In short, evolutionary biologists continue to grapple with many conceptual and operational definitions of fitness (Kokko, 2021; Matthen & Ariew, 2002; Orr, 2009), united only by the notion of how much the different types of organisms that are present in a population at one point in time contribute to the population at some future time.

Evolutionary biologists face an additional challenge in using fitness to assess adaptation "after the fact"—that is, after environmental change has already induced selection and adaptation. Since the fitness of a biological entity (e.g., genotype, population, species) is specific to a particular environmental context (Figure 2a; Brandon, 1995), adaptive states can only be defined *relative* to specific alternative states (Brady et al., 2019). If adaptation has occurred (e.g., because the physical environment has changed), the relevant baseline against which to assess the new population is not the absolute fitness of the original population at time 1 (the historical state), but rather the **counterfactual** scenario of what the relative fitness of the population present at time 1 would be in the new environment (Figure 2b; Kokko, 2021). In nature, counterfactual ("original") populations with which to compare populations that have adapted to environmental change are expected to be transient. However, when environmental change is rapid, adaptive responses might lag far behind. This can happen, for instance, if organisms are long-lived or immigration of new types is slow to occur. Such conditions create "natural" experiments for testing adaptive community dynamics. For example, for a discrete environmental change (e.g., altered drainage) that affects only some sites, the transient state of historical composition + new environment (Figure 2b

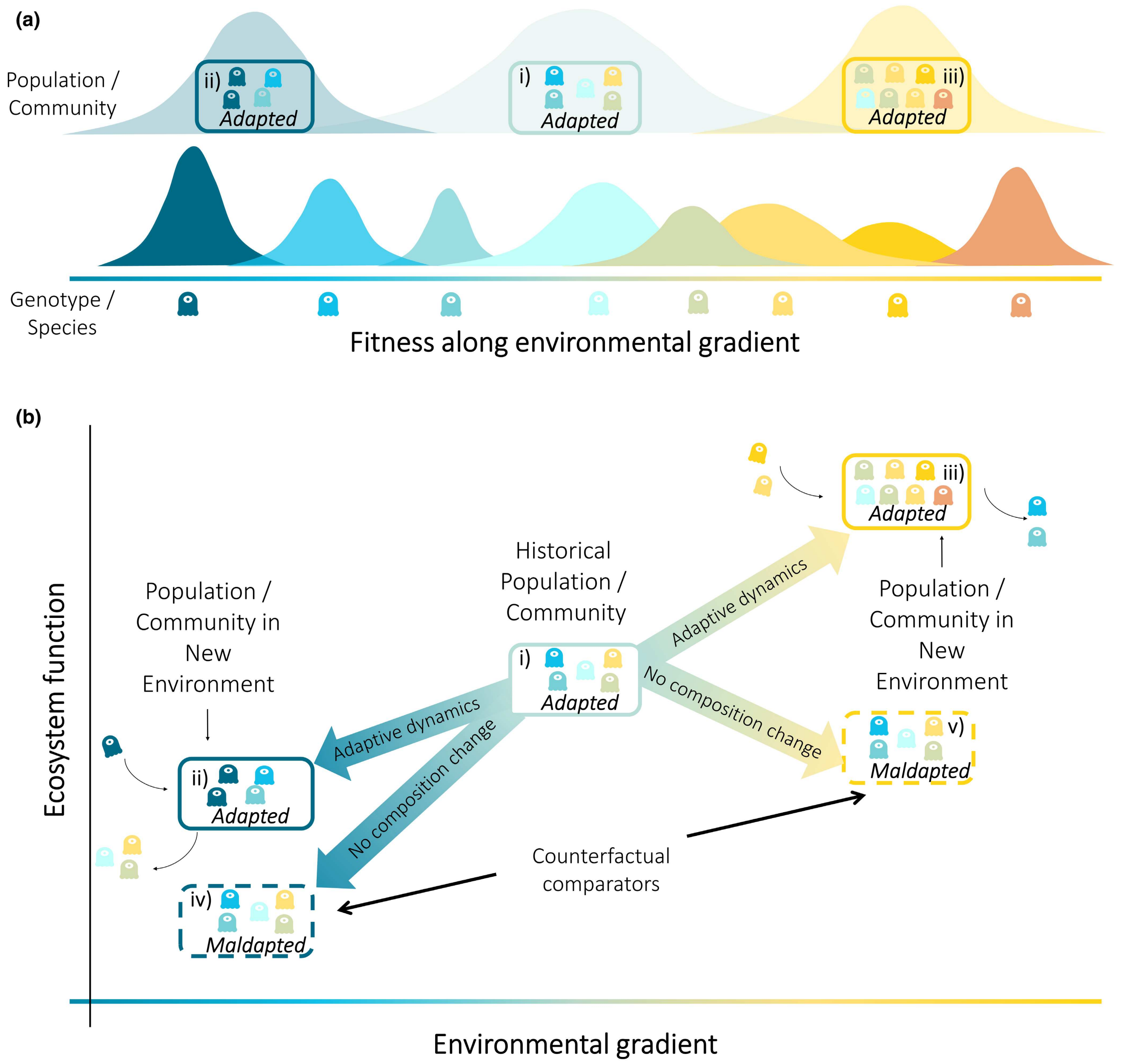

FIGURE 2 Fitness and function in differing environments. (a) The fitness of a biological entity (e.g., genotype, species, population, community), represented here by abundance functions along an environmental gradient, is specific to particular environmental contexts. (b) The relevant fitness benchmark for assessing whether *preceding* population or community dynamics were adaptive is not the fitness of the historical population/community in its previous environment (i), but rather the counterfactual situation of the historical population/ community inhabiting the new environment (*iv or v; bottom left/right*). Because an historical community is maladapted in the new environment, we would also expect decreased ecosystem function (e.g., biomass production or nutrient retention) due to low relative fitness of resident organisms (i.e., relative maladaptation). Resulting population changes, and thus compositional change, are expected to gradually restore ecosystem function. Since ecosystem function is limited not only by species composition but also by environmental factors (e.g., climate or resource availability), it can decline in magnitude over time even under adaptive dynamics (*movement to the left, from i to ii*). However, we predict that it should generally be higher relative to the counterfactual community–environment combination (*iv*).

iv and v) might persist long enough to permit comparisons with the historical composition + historical environment (i.e., in control sites, Figure 2b i), and also with the new composition + new environment after enough time has passed to allow composition to "catch up" (Figure 2b ii and iii). Such comparisons can also be made directly in laboratory experiments (Kassen, 2014) or indirectly through field-based reciprocal transplant experiments, in which individuals are moved between two or more environments, with the prediction that locally sourced individuals have higher fitness than those from elsewhere due to prior adaptation (Hereford, 2009).

2.2 | Adaptive change in ecological communities

The concept of adaptive turnover in ecological communities is a direct extension to the concept of adaptive change in evolving populations, and coherent with a view of communities in which species respond individualistically to environmental change (Gleason, 1926; Matthews, 1996). In populations, selection operates via deterministic fitness differences between individuals of different genotypes; in communities, selection operates *additionally* via fitness differences between organisms of different species (Shipley, 2010; Vellend, 2010, 2016). In both cases, selection is precisely the same process, involving differential fitness due to some aspects of the morphology, physiology, or behavior of organisms of different types and how they interact with the physical and biological environment. The extent to which a community is well adapted, therefore, is determined by the overall fit between the traits of community members and particular environmental contexts. As such, the (mal)adaptive state of a community (its degree of adaptation) can be altered via changes in (i) the environment and (ii) species composition (as with populations; Figure 1). We describe changes in species composition as community dynamics, which are adaptive if they increase average fitness via improved trait–environment matching (i.e., via improved fit), and maladaptive if they do the opposite.

In the context of an ecological community (i.e., a multi-species "population"; see glossary Box 1), most empirical data relate to the relative success (fitness) of collectives of individuals at the level of species populations (instead of genotypes) but, otherwise, the same concepts and challenges that arise in evolutionary biology apply. Applying the unifying notion of fitness articulated above, we are interested in the changing contributions of different species to a community over time. As in studies of fitness variation *within* many single-species populations (see above), counting individuals fails to capture such "contributions" in many communities or is operationally intractable (e.g., soil fungi). For maximum generality, we focus here on changing proportional contributions to the overall community in terms of biomass, for which relative differences among species will converge on estimates based on individuals in the special case where individuals are of comparable size and life-history characteristics across species. In this paper, our operational definition of fitness is the growth rate (per capita or per unit biomass) of a subpopulation of interest (i.e., genotype, phenotype, or species), which can be expressed relative to some references such as the mean growth rate within the population (Brady et al., 2019; Futuyma & Kirkpatrick, 2017; Kokko, 2021; Laughlin et al., 2020; Pigliucci & Kaplan, 2006). However, in specific contexts and to answer particular questions, researchers may find it convenient to use different measures or components of community-level fitness, just as evolutionary biologists do for studies within species (above).

From a mathematical perspective, there is nothing special about *community-level* adaptive change, such that evolutionary models for asexual haploid genotypes (Nowak, 2006) can be used "as is" to describe adaptive community dynamics, simply by replacing "genotype" with "species." Ecological models developed for interacting species that explore more complex scenarios may, in turn, provide important insights for population genetics (e.g., Ellner & Hairston Jr., 1994). Some aspects of empirical studies might actually be more straightforward in the community context, where measurement of fitness (e.g., biomass growth rates) should usually be easier than in evolutionary biology, as individuals of different species are generally easier to distinguish in the field than are different genotypes or phenotypes within species. In addition, a considerable range of existing frameworks (e.g., Harrison et al., 2022; Loreau, 2010; Suding et al., 2008) can be used to develop the link between adaptive dynamics and ecosystem function (*next section*).

Having built upon models for single species (in which individuals usually share a trophic position), the adaptive community dynamics framework is most easily envisioned for "horizontal" communities, in which organisms compete for space and resources and do not (in general) prey upon each other (e.g., guilds or assemblages; Fauth et al., 1996). However, the framework should apply equally, in theory, at the level of whole ecosystems, where the flux of energy among trophic levels is constrained by the relative abundance and fitness of component species (Naeem et al., 1994), which in turn are constrained by environmental conditions.

2.3 | From adaptive community dynamics to ecosystem function

We expect that adaptive community dynamics will usually enhance ecosystem functions. For instance, if an area becomes wetter (or drier), species of decomposer suited to wet (or dry) conditions should increase in absolute and relative abundance, thus increasing decomposition, nutrient regulation, and waste treatment. In the rest of the paper, our discussion of ecosystem functions focuses mainly on biomass production, for several reasons: (1) Ecosystem functions related to biomass production are by far the most commonly studied (van der Plas, 2019); (2) productivity is often used synonymously with ecosystem function in the literature; (3) many ecosystem functions and services (e.g., efficiency of nutrient use, forage production) are ultimately sustained through biomass production (Pettorelli et al., 2018); and (4) the relationship between biomass production and adaptive community dynamics is the most direct, via the survival, growth, and reproduction of community members. In general, we expect similar arguments to hold for other ecosystem functions and services, while recognizing that some (e.g., flower availability to pollinators, and so pollinator availability to nearby crops) could decline while productivity increases (e.g., if wind-pollinated grasses increase in dominance).

As with populations of single species, the adaptive state of a community cannot be judged through post hoc fitness comparisons between scenarios that vary in *both* community composition and environment. Because the average fitness of communities and their component species vary along environmental gradients (Figure 2a), inferring that the current community composition is the result of preceding adaptive dynamics requires a comparison of the contemporary community in the new environment with the counterfactual scenario of the historical community also in the new environment (Figure 2b). This exact logic is implicit (if not explicitly described) in theory that links biodiversity to ecosystem function, which invokes differential adaptive responses of species as underlying the stability of ecosystem function in response to environmental change (i.e., adaptive community dynamics) (Chesson et al., 2001; Harrison et al., 2022; Loreau, 2010; Loreau et al., 2021). Species that might be relatively poorly adapted to current conditions are expected to provide “insurance,” increasing in abundance when environmental conditions shift to suit them (Loreau et al., 2021). In such cases, attempts to restore the historical composition of a community (e.g., removing warm-adapted species from a climate-warmed community) without reversing the environment to its prior state (e.g., reverting to a pre-warming climate) would work *against* the goal of maintaining ecosystem function. Counterfactuals present a logistical challenge but can be addressed in several ways. Experimental environment reversals and reciprocal transplant experiments at the level of whole assemblages (e.g., Cui et al., 2018; Walker et al., 2022), or analysis of natural experiments as described earlier, can be used to assess community-level fitness (as well as resulting ecosystem-level effects) in community–environment combinations that we do not expect to see once adaptive dynamics have caught up to environmental change (such as those depicted in Figure 2).

Stabilizing effects of adaptive community dynamics on ecosystem functions and services may produce counterintuitive outcomes. For instance, environmental change combined with adaptive dynamics can lead to *lower* productivity than in the historical community–environment state if a direct negative effect of environmental change outweighs a positive effect of adaptive community dynamics (the left side of Figure 2b). For example, increased drought might reduce productivity regardless of community composition, but a drought-adapted community would still have a higher productivity than a (historical) wet-adapted community under the new drought conditions. In this case, the positive effect of adaptive community dynamics can only be detected with reference to the counterfactual (environmental change without community response). In other cases, the positive effect of adaptive dynamics can outweigh a negative influence of environmental change, resulting in an increase in productivity over time (right side of Figure 2b). In short, just as the mean fitness of populations and communities is constrained by environmental conditions and available organisms, productivity is constrained by the state of the environment (e.g., climate and soil characteristics; Grace et al., 2016) and the species pool. However, in general, we expect that adaptive community dynamics should usually lead to higher levels of ecosystem function *given a particular environmental context*.

2.4 | Community maladaptation

Importantly, community composition can also change maladaptively, such that the degree of match between traits and the environment sometimes declines (vertical black arrows in Figure 1). For example, species poorly adapted to local conditions can nonetheless colonize and maintain populations via dispersal (i.e., mass effects; Leibold & Chase, 2018). Species' abundances can also fluctuate stochastically with respect to trait–environment relationships, especially in small and isolated communities, which is the community-level equivalent of genetic drift within populations (i.e., Hubbell, 2001; Vellend et al., 2014). Limited dispersal into small and isolated communities (e.g., due to habitat fragmentation) can slow the arrival of adapted species, thereby also slowing adaptive dynamics that might counter maladaptive change. In addition, turnover that is adaptive with respect to one trait may be maladaptive with respect to another, leading to trade-offs or conflicts. For example, traits that facilitate immigration, such as large wings and flight muscles in insects, may, at least initially, result in reduced reproductive output following arrival (Simmons & Thomas, 2004; Thomas et al., 2001). In each of these cases, the dynamics of species turnover are at least partly maladaptive.

3 | EMPIRICAL EVIDENCE POINTING TO ADAPTIVE COMMUNITY DYNAMICS

Several components of what we now call adaptive community dynamics have been addressed by many empirical studies, but described using a wide variety of terms. First, many community-level experiments have manipulated environmental conditions in microcosms or mesocosms (Arnott et al., 2021), in agricultural settings (Guo et al., 2019; Silvertown et al., 2006), or in more “natural” habitats (Avolio et al., 2020, 2021; Komatsu et al., 2019). Such manipulations almost always elicit changes in community composition, and authors' interpretations about which species increase or decrease—sometimes based on a priori predictions—routinely invoke the concept of adaptive community dynamics (without using this term). Moreover, experiments investigating the stability of ecosystem function over time consistently find that asynchronous (complementary) changes in relative abundances of component species (adapted to differing environmental conditions) bolster the stability of ecosystem properties in response to environmental change (Allan et al., 2011; de Mazancourt et al., 2013; Hector et al., 2010; Hong et al., 2022; Leary & Petchey, 2009; Thibaut et al., 2012). This is in line with results from the many experiments that have manipulated community composition, both at the level of the whole community (e.g., biodiversity–ecosystem function experiments (Huang et al., 2018; Weisser et al., 2017)), and through introductions and removals of individual species (Silcock et al., 2019), which indicate that the composition of communities has a major influence on ecosystem function (Hooper & Vitousek, 1997; Huang et al., 2018; Pennekamp et al., 2018). Effects are routinely attributed to adaptive trait–environment matching (Cadotte, 2017; de Bello et al., 2021).

The burgeoning literature on how functional traits affect the distribution, abundance, and dynamics of populations and communities relies on much of the same underlying logic as the adaptive community dynamics framework (Adler et al., 2013; Diaz et al., 2004; Enquist et al., 2015; Green et al., 2022; McGill et al., 2006; Violle et al., 2007, 2014). Observational studies consistently find evidence of relationships between traits (within and across species) and environmental conditions; these results are described in various ways, including "species sorting" and "environmental filtering" (Chase et al., 2020; Leibold & Chase, 2018), or as manifestations of "selection" (Shipley, 2010; Vellend, 2016). At large spatial scales, such patterns are glaringly obvious: tall trees with no frost tolerance dominate the tropical rainforest while short-statured herbs and shrubs with cold-season dormancy dominate the tundra (Lomolino et al., 2017). At smaller spatial scales, observational data are also frequently used to test a priori predictions about community change based on traits expected to permit survival and reproduction in given environments. For example, increased disturbance predictably leads to plant communities dominated by relatively short-lived species with high seed production (Grime, 2001), nutrient addition or urbanization to dominance by fast-growing nutrient-demanding species (Bobbink et al., 2010; Williams et al., 2015), and warming to increases in species with distributions that historically lived closer to the equator or at lower elevations (i.e., thermophilization; Bowler et al., 2017; Feeley et al., 2020; Zellweger et al., 2020). All such cases are strongly suggestive of adaptive community dynamics.

A particularly promising approach that could be used to study adaptive community dynamics involves transplantation of entire communities (e.g., sections of herbaceous vegetation or "turf") among environments. Studies using this experimental approach have, for example, assessed effects of climate and other environmental changes (e.g., salinity, inundation) on community composition and ecosystem function (Cui et al., 2018; Peterson-Smith & Baldwin, 2006; Wetzel et al., 2004), finding environmental effects on species' relative abundances and community-level productivity. Some reciprocal community transplants have also been used to study effects of community compositional change on soil carbon storage (Walker et al., 2022) and CO_2 production (Juottonen, 2020). These transplant studies do not report results that can easily be interpreted in terms of the adaptive community dynamics framework (this was not their aim), due to the temporal resolution and detail with which results were reported. However, whole-community transplants such as these could be used to test the predictions of adaptive community dynamics (as shown in Figure 2) explicitly, in terms of both community dynamics and implications for ecosystem function. The framework predicts that fitness and ecosystem functions will initially decline, but then gradually increase in communities transplanted to different environments, primarily through resulting relative abundance changes (i.e., adaptive community dynamics). The same set of predictions of temporal dynamics applies to natural experiments in which some replicate communities are exposed to an abrupt environmental change, while others are not.

Importantly, while empirical evidence from many studies is strongly suggestive of adaptive community dynamics, an association between community composition and environment in a predicted direction (e.g., thermophilization) is not evidence that *all* community change is adaptive. Maladaptive change via drift or mass effects can be happening simultaneously, with a variety of methods proposed to detect their influence (Vellend et al., 2014), and causal effects can be difficult to infer from observational data (Arif & MacNeil, 2022). In addition, given ubiquitous time lags between environmental change and community responses (Jackson & Sax, 2010), most evidence does not imply that adaptive dynamics are "complete," in other words, that the community has achieved a new equilibrium. These results can only show that sufficient adaptive dynamics have occurred to *improve* trait–environment matching. Nonetheless, as for evolution in single-species populations, we expect that, under strong selection, concurrent maladaptive processes are more likely to slow or limit the magnitude of adaptive community dynamics, rather than to reverse them.

4 | THE ANTHROPOCENE ENVIRONMENT AND HUMAN INTERVENTION: TO FACILITATE, ACCEPT, OR RESIST ADAPTIVE DYNAMICS?

Anthropogenic activities are inducing a plethora of environmental and compositional changes within Anthropocene environments (Díaz et al., 2019; Thomas, 2020). Rapid environmental changes are likely to reduce the fit between the environment and community composition initially, and therefore to increase levels of maladaptation (Brady et al., 2019; Hendry & Gonzalez, 2008; Figure 3a). Subsequently, however, we generally expect community composition changes to reinstate (gradually or rapidly) the fit between species (traits) and the new environment via adaptive dynamics (Chesson et al., 2001).

In this context, one can view environmental management as largely (but not exclusively) concerned with first deciding which position in the environment–community composition space is desired, and then defining actions (or a lack thereof) that will help achieve the desired outcome given available resources (Figure 3b). The adaptive community dynamics framework is thus of obvious relevance in management. Faced with environmental and ecological change, managers effectively have three initial choices: They can attempt to facilitate, accept, or resist any given type of change (Millar et al., 2007; Schuurman et al., 2020; Thomas et al., 2022). Resisting change involves manipulating the environment (e.g., irrigating a drying wetland), the community composition (e.g., removing woody plants from the wetland), or both, in a manner whereby ongoing management interventions retain the existing community, or restore it to a preferred historical condition. For acceptance and facilitation, the target of actions is largely adaptive community dynamics itself, in both cases aiming to enable the community composition to adjust to the new environment.

Defining desired outcomes is fundamentally a question of values and can be independent of whether or not states are adaptive. People value nature for many reasons, some of which involve a preference for maladaptive states (Vellend, 2019). For example, maintaining targeted ecosystem services such as agricultural yields involves energy

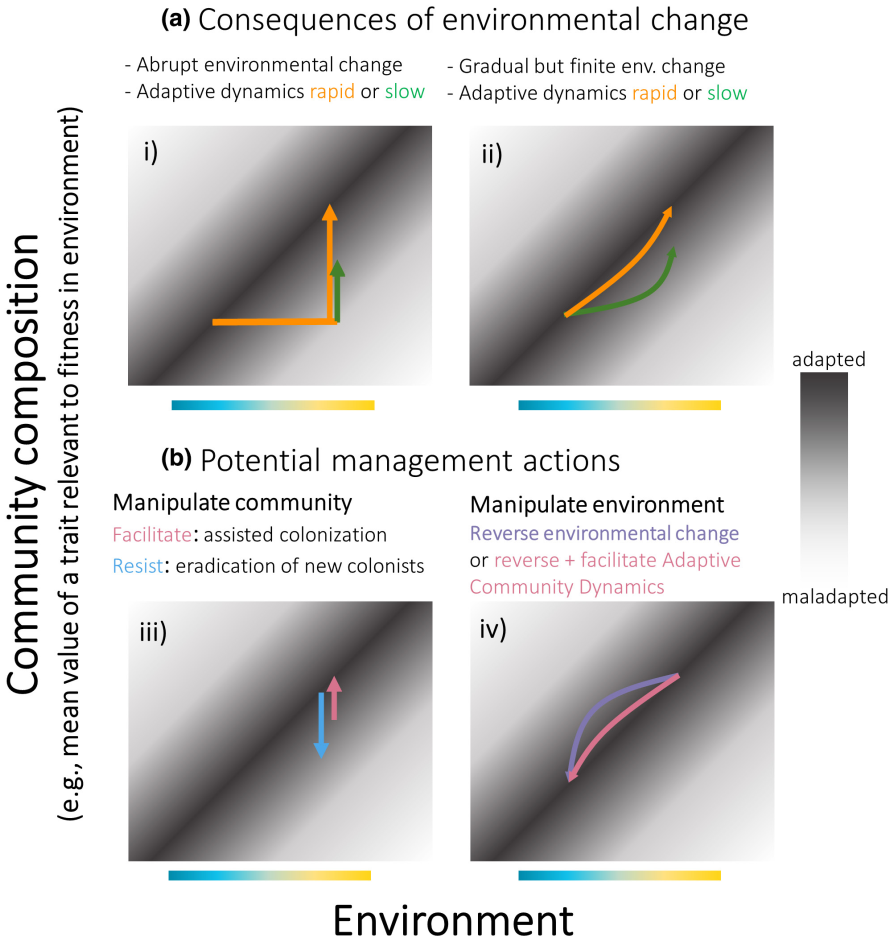

FIGURE 3 Hypothetical scenarios of environmental change, community responses, and potential management interventions. For illustrative purposes, community composition (typically multivariate) is represented here by a single axis, representing the mean value of a trait (e.g., optimal temperature for fitness) relevant to the environmental variable in question (e.g., temperature). (a) Human activities drive environmental change via abrupt events such as land-use change (i) or gradual processes such as climate change (ii). Resulting maladaptive states should elicit adaptive community dynamics in response. (b) Management interventions may involve resistance or facilitation of change and be implemented through actions to manipulate the community composition (iii) and/or to change the environment (iv).

inputs to resist adaptive community dynamics (e.g., keeping out weeds and pests), as do many actions aimed at conserving particular species (e.g., providing waterholes for large vertebrates or nest boxes for certain birds). The latter examples—waterholes and nest boxes—involve an environmental manipulation aimed at countering environmental states that are extremely difficult if not impossible to control at a local level, such as climate change (which might eliminate waterholes) or an absence of trees suitable for cavity nesting (if large tree holes take a century or more to form in a newly planted tree). For many reasons, people also aim to resist environmental change itself (e.g., reducing greenhouse gas emissions or nutrient input), in essence preventing "unwanted" adaptive community dynamics from occurring in the first place.

When environmental change has already occurred or is practically impossible to stop, achieving certain desired outcomes, such as the promotion of ecosystem function, is likely to require accepting or facilitating adaptive community dynamics. Resisting adaptive dynamics (e.g., eradicating undesired species) might work against such goals. For example, preventing shrub encroachment of grasslands (Redhead et al., 2012) might reduce overall biomass production and require increasing efforts over time as continued climate change strengthens selection. To facilitate adaptive dynamics that might naturally involve long time lags, managers can assist the migration of suitably adapted species to places that they are unable (or slow) to reach on their own (Thomas, 2017, 2020; Figure 3b iii). This may include reintroductions of previously persecuted species (e.g., wolves; Musiani & Paquet, 2004) which can once again thrive under the new environment generated by legal protection (Carter & Newbery, 2004; Gaywood, 2018), or entirely new colonists whose environmental requirements match altered local environments (Thomas, 2020). Such actions are, of course, not without risks (Pyšek et al., 2020), and care should be taken when evaluating candidate species. Managers can also promote dispersal by increasing connectivity between habitat patches (Resasco, 2019). In principle, such actions should not require increased efforts over time as they involve working with, rather than against, adaptive dynamics.

Overall, while resisting adaptive dynamics will be the appropriate option for some objectives, there is no reason that it needs to be the default strategy, as it often seems to be. A dominant thrust of the messaging from ecologists and conservation biologists is that change from the historical composition of ecological communities represents "collapse" (MacDougall et al., 2013), "disruption" (Trisos et al., 2020), "erosion of integrity" (Purvis et al., 2019), or declining "intactness" (Scholes & Biggs, 2005). This can be seen especially clearly in the 2019 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report, which is meant to represent a consensus statement from the scientific community, co-authored by >70 scientists from across the globe. The report states that: "Local communities are not on average showing rapid changes in species richness, but their *biotic integrity is being eroded* *rapidly by changes in which species are present and abundant*" (Purvis et al., 2019, p. 235; italics not in original). To support the portion of this statement about biotic integrity, the IPBES report exclusively cites studies that report declines in "biodiversity intactness indices" (Hill et al., 2018; Scholes & Biggs, 2005), which are based on changes in the abundances and identities of species compared to the assumed historical community (i.e., newly arriving species cannot increase intactness). The clear message is that compositional change relative to historical states is undesirable. Despite justified concern over native and endemic species declines (including extirpations and extinctions), the adaptive community dynamics framework suggests that blanket resistance to community change would likely come at a cost. Specifically, resisting community change might compromise the maintenance and stability of ecosystem functions such as productivity and carbon sequestration—which IPBES also highlight as fundamental to underpinning nature's contribution to people (Purvis et al., 2019, p. 215)—under further environmental change (Chesson et al., 2001; Loreau et al., 2021; Oliver et al., 2015).

5 | CONCLUDING REMARKS

The concepts of adaptive community dynamics and (mal)adaptive community states—determined by the fit between species traits and the environment—have great potential to help clarify links between global change and ecosystem function. Armed with these concepts, we can identify trade-offs involved in resisting versus facilitating or accepting adaptive community compositional changes, which can in turn help inform conservation. When making value statements about ecological change, it is important to distinguish between the drivers of turnover and the community response itself. Resisting adaptive community dynamics will often promote some management goals (e.g., protection of endangered species or bolstering agricultural yields), but combatting adaptive ecological responses rather than the drivers of change may also unwittingly compromise the functioning of Anthropocene ecosystems. Given the ubiquity of compositional change in contemporary ecological communities (Dornelas et al., 2019; Hillebrand et al., 2018), labeling altered communities as having reduced "integrity" without qualification seems potentially (if unintentionally) misleading if community change is usually adaptive. The adaptive community dynamics framework suggests two rules of thumb with potentially general applicability: (1) The further a desired community state is from the optimal trait–environment match, the more work will be required to achieve or maintain that state; (2) For a given environmental state, productivity and related ecosystem functions are likely to be increased if adaptive community dynamics are accepted or facilitated.

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The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

This is an 'Opinion' submission, and as such, has no associated data.

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