

IDEA AND PERSPECTIVE

Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (CAFE) approach

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Abstract

The research of a generation of ecologists was catalysed by the recognition that the number and identity of species in communities influences the functioning of ecosystems. The relationship between biodiversity and ecosystem functioning (BEF) is most often examined by controlling species richness and randomising community composition. In natural systems, biodiversity changes are often part of a bigger community assembly dynamic. Therefore, focusing on community assembly and the functioning of ecosystems (CAFE), by integrating both species richness and composition through species gains, losses and changes in abundance, will better reveal how community changes affect ecosystem function. We synthesise the BEF and CAFE perspectives using an ecological application of the Price equation, which partitions the contributions of richness and composition to function. Using empirical examples, we show how the CAFE approach reveals important contributions of composition to function. These examples show how changes in species richness and composition driven by environmental perturbations can work in concert or antagonistically to influence ecosystem function. Considering how communities change in an integrative fashion, rather than focusing on one axis of community structure at a time, will improve our ability to anticipate and predict changes in ecosystem function.

Keywords

Biodiversity, community assembly, composition, dispersal, ecosystem function, metacommunity, Price equation.

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INTRODUCTION

One of the most popular areas of ecological research over the past few decades is the study of biodiversity's effects on ecosystem function. Species impact ecosystem functions in

many ways as they search for and consume resources from their environment and convert those resources into new biomass through individual growth or reproduction. Through these activities species contribute to standing biomass and productivity, nutrient cycling and many other ecosystem

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properties and services (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2012). Based on empirical evidence and theoretical reasoning, ecologists hypothesised that ecosystems containing more species would be more stable (MacArthur 1955; Elton 1958; McNaughton 1977) and exhibit higher levels of ecosystem functions (Darwin 1872; Margalef 1963). Although species can interact differently with their environment, these predictions assume species overlap enough to provide some redundancy and buffer ecosystem functions against extinctions. We now know after decades of rigorous experimental and theoretical research across many taxa and ecosystems that the number of species (i.e. species richness, independent of species identity) does indeed impact the level of ecosystem function that a community provides (Balvanera *et al.* 2006; Cardinale *et al.* 2011, 2012; Naeem *et al.* 2012; Tilman *et al.* 2014). This body of research into the biodiversity–ecosystem function relationship is often referred to by the acronym BEF, a convention we follow hereafter.

The number of species is an important determinant of ecosystem function, but so is the identity of those species (Diaz & Cabido 2001; Wardle *et al.* 2011). Species differ in their impact on nutrient flow, productivity and energy flow because they differ in morphological, behavioural or physiological traits that influence resource acquisition, use and allocation (Diaz *et al.* 2013; Faucon *et al.* 2017). Consequently, the processes that determine which species are in a community will also impact ecosystem function (Leibold *et al.* 2017). Community assembly describes how processes at different spatial and temporal scales interact to determine both the species composition and local biodiversity of a community (Chase & Myers 2011; HilleRisLambers *et al.* 2012; Kraft & Ackerly 2014; Vellend 2016; Leibold *et al.* 2017). The processes of community assembly are varied; community assembly is impacted by both intraspecific (e.g. Allee effects) and interspecific interactions (e.g. competition, predation, mutualism). These processes occur at a variety of spatial and temporal scales (e.g. dispersal, evolution) and are subject to varying degrees of determinism or stochasticity (Cabral & Kreft 2012; Cabral *et al.* 2017). Regardless of which processes are operating, community assembly determines the presence and abundance of species in a community. Community assembly can influence ecosystem function because changes in species composition also affect species, functional and phylogenetic diversity and species abundance distributions (Magurran & Henderson 2003; Harpole & Tilman 2006; McGill *et al.* 2007).

While some theoretical and conceptual work recognises that community assembly processes can impact BEF relationships (e.g. Bond & Chase 2002; Mouquet *et al.* 2002; Loreau *et al.* 2003; Gross & Cardinale 2007; Ptacnik *et al.* 2010; Jaillard *et al.* 2014; Leibold *et al.* 2017), few empirical studies have considered the effects of community assembly on ecosystem function explicitly (Fukami & Morin 2003; Fukami *et al.* 2005, 2010; Matthiessen & Hillebrand 2006; Thompson & Gonzalez 2016). Separating species richness effects on ecosystem function from composition effects is empirically difficult because changing richness also changes the composition of the community through the gain or loss of particular species and the unique set of traits and functions they contribute (but also see Schmid *et al.* 2017). Experimentally isolating the effects of composition

and richness on ecosystem function requires either (1) fully factorial designs where the occurrence and abundance of each species are separate experimental factors, or (2) multiple ‘replicates’ for each level of species richness that randomise the identity and relative abundances of species. These randomly assembled communities are necessary to isolate the species richness effect and eliminate natural community reorganisation via assembly processes. Differences in species composition between randomly assembled BEF communities can significantly impact ecosystem function (e.g. Hobbie 1992; Hooper & Vitousek 1997; Tilman *et al.* 1997; Kirwan *et al.* 2009; Hector *et al.* 2011) suggesting that processes determining species composition could significantly impact expectations from biodiversity–ecosystem relationships. However, it remains unclear from this previous experimental work how important community assembly is in natural communities where species compositions are unlikely to be random (Turnbull *et al.* 2005; Petermann *et al.* 2010; De Laender *et al.* 2016; Wardle 2016). Community assembly processes are likely to lead to particular assemblages that emerge from both local species interactions and colonisation from a regional species pool (Ricklefs 1987; Vellend 2016; Leibold *et al.* 2017). This raises the possibility that species gains may functionally compensate for species losses or that non-random shifts in composition may reinforce or undermine the effects of the random species losses studied in most BEF experiments (Fig. 1). Integrating non-random community assembly into our empirical studies of BEF relationships is critical because many real world scenarios have intertwined impacts on both species richness and composition (e.g. species invasions, extinctions of native species and range shifts caused by environmental change; De Laender *et al.* 2016; Eisenhauer *et al.* 2016; Wardle 2016; Leibold *et al.* 2017).

In this paper, we develop a community assembly based perspective for studying ecosystem function, which we refer to as CAFE (Community Assembly and the Functioning of Ecosystems; *sensu* Leibold *et al.* 2017). We see this approach as an expansion of and complement to the existing BEF framework. The CAFE perspective explicitly recognises that changes in ecosystem function arise due to both biodiversity change (through species gains and losses) and changes in the relative abundances and functions of resident species across space/time (cf. Wardle *et al.* 2011; Wardle 2016). We use an ecological application of the Price equation to study how changes in species richness and community assembly work together to impact ecosystem function (Price 1970, 1972; Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012). The Price equation supports broad empirical examinations of how both aspects of community assembly (species gains, losses and relative abundances) and changes in species number influence ecosystem function. In the following, we describe the CAFE framework for integrating community assembly with ecosystem function research and explain how to use the Price equation to empirically assess the impact of species richness and community assembly dynamics on ecosystem function. We also introduce a new graphical method to represent the components of the Price equation that facilitates the interpretation of these patterns. Finally, we contrast two different ways to view the Price components that emphasise either assembly or diversity effects and apply these approaches to three empirical datasets

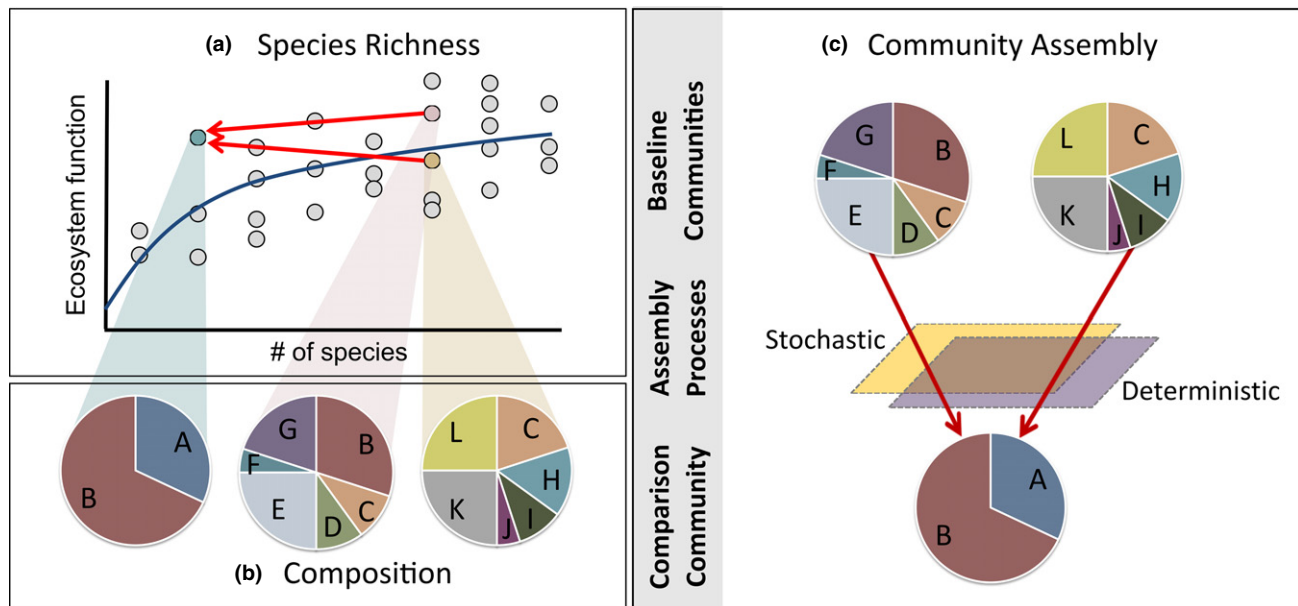


Figure 1 Community assembly and the functioning of ecosystems (CAFE) concept figure. The relationship between ecosystem function and species richness is composed of three key interrelated components: (a) The general increasing trend of ecosystem function with increasing number of species. Each circle is a community. The red arrows indicate transitions of a community from one state to another, which might result from community assembly, driven by an external perturbation or internal dynamics (panel c), leading to changes in community composition and species richness. (b) The species composition of each community and each species' contribution to total ecosystem function for that community. Each species is denoted by a letter and colour, and each species' contribution to ecosystem function is represented by the size of the pie slice. (c) The community assembly processes that lead to changes in community composition, structure and species richness along the red arrows in panel a (between temporally or spatially separated communities; i.e. baseline vs. comparison communities). For example, deterministic assembly processes could shape community composition through physiological constraints and biotic interactions, and/or stochastic assembly processes could shape community composition through environmental stochasticity, random dispersal patterns and random mortality due to perturbation.

that illustrate distinct scenarios involving various types of environmental perturbations.

THE CAFE APPROACH

The CAFE approach (Leibold *et al.* 2017) is based on the fundamental concept that natural communities are assembled through a variety of processes that result in non-random community structure. Community structure consists of the identity, traits and abundances of species in a community. It is determined by a combination of deterministic and stochastic processes; a suite of local niche-based (e.g. physiological constraints, resource competition, stress tolerance, predator–prey relationships, dispersal ability) and landscape processes (e.g. dispersal from a regional species pool, environmental oscillations, resource dynamics, disturbance regimes, topological complexity) (Violle *et al.* 2007; Cabral & Kreft 2012; HilleRisLambers *et al.* 2012; Cabral *et al.* 2017). Therefore, assembly is driven by the internal ecological dynamics of communities and by external drivers, both of which can lead to gains or losses of individuals and/or species in communities (Chase 2003). These cascading changes caused by community assembly alter both the species richness and species composition of ecosystems with consequences for their function. If these community-level changes are large enough they may both exacerbate or ameliorate predicted changes in function based only on losses in richness (Fig. 1).

While integrating community assembly into our understanding of ecosystem function is important, it is also difficult: community assembly is complex and composition is multi-dimensional. Part of the utility of the BEF framework is that it reduces this complexity by focusing primarily on changes in the number of species (and functional groups). Similarly, reducing community assembly to quantifiable emergent features will facilitate a better integration of community assembly processes into our understanding of ecosystem function. The CAFE framework posits that we can reduce the complexity of community assembly, while obtaining important insights, by focusing on three key features: (1) species loss, (2) species gain and (3) changes in the abundance or function of resident species. From these three features of community assembly, changes in community structure emerge: changes in species richness, distributions of functions and traits and species composition. Regardless of the specific mechanisms driving community assembly, we argue that some combination of local extinctions, colonisations or changes in the abundance of resident species will occur. Indeed, these three features arise from different classes of community assembly models and are empirically observed as communities reorganise in response to species extinctions (e.g. Fargione *et al.* 2003; Petermann *et al.* 2010), colonisations (e.g. response to invasives: Pfisterer & Schmid 2002) or environmental changes (e.g. Leibold *et al.* 2004; Suding *et al.* 2008). Linking species losses, species gains and resident responses to changes in ecosystem function is an important step towards integrating community assembly into

our understanding of the functioning of ecosystems (Avolio *et al.* 2015; Thompson & Gonzalez 2016; Leibold *et al.* 2017).

To empirically study and integrate community assembly effects on ecosystem function with our current understanding of the importance of species richness changes, we require an analytical approach that can link changes in overall species richness, impacts of losses and gains and changes in resident species to changes in ecosystem function (*sensu* Fox & Kerr 2012). Such a tool should ultimately be able to disentangle the impacts of species richness changes on ecosystem function from those caused by the changes in community structure and be applicable to less controlled experimental settings or observational studies. Understanding the impact of natural community assembly processes requires allowing communities to reorganise, and thus is not a question that can be explored in tightly controlled biodiversity experiments. Consequently, an ideal approach would not require the stringent experimental control necessary for BEF studies, but be flexible enough to study natural community assembly processes. We propose that one way to do this analytically is using variants of the ecological version of the Price equation pioneered by J. Fox (Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012) and originally used to study evolution (Price 1970; Frank 1997). At its core, the Price equation quantifies how individual species contribute to the differences in ecosystem function between two communities (a baseline and a comparison). These species-level effects can then be grouped in different ways to highlight the relative contributions of different community-level changes to overall ecosystem function (i.e. species richness *vs.* compositional effects, effects of colonisations *vs.* extinctions *vs.* changes in resident species). Below, we offer an intuitive explanation of the Price equation that is based on considering the effects of individual species. We then illustrate how different arrangements of the Price equation quantitatively link the outcomes of community assembly to both changes in ecosystem function and species richness.

UNDERSTANDING SPECIES-LEVEL EFFECTS ON THE RICHNESS AND FUNCTION OF COMMUNITIES

Any community can be represented by a point in two-dimensional space (Fig. 2; Appendix S1) defined by the number of species it contains (Species richness) and the total amount of function it produces (Ecosystem function). We begin by comparing two communities, A and B; one we call the baseline community and the other is the comparison community (*sensu* Fox & Kerr 2012). For now, which community is used as the baseline is arbitrary; later we will see how the appropriate choice of baseline communities depends upon the research question being addressed. Generally, baseline communities might be experimental controls, or communities prior to an environmental perturbation, whereas comparison communities are separated in time and/or by virtue of receiving particular treatment(s) (see Appendix S2 for more details). The relative position of these two different communities, which we might capture by a single vector linking points A and B, reveals differences in the diversity and function between our baseline and comparison community. We can gain significant insight into the causes of these

differences by considering all of the changes necessary to move from one community to the other (e.g. from baseline A to comparison B), one species at a time. Specifically, a single species can affect the richness and function of community A in three mutually exclusive ways that can each be represented by vectors in this space (Fig. 2a).

i. Shared species (Vector C)

A species that is a member of both the baseline and comparison community may provide more or less function in community B than it does in community A. This occurs when the species changes its abundance, its per capita function, or both (Fox 2006). This effect can be captured using a vertical vector (C, purple), which indicates a change in the function, but not in the richness, of the baseline community (community A). The illustrated example shows the focal species increasing its function in the comparison community (community B; C vector points up), but this effect may be positive, negative or zero.

ii. Lost species (Vector L)

A species that occurs in community A but not in community B is 'lost' as we transition from the baseline community to the comparison community. Losing a species affects both species richness (decreasing the species richness of community A by one) and ecosystem function (through the loss of any contributions that species had to ecosystem function). This effect can be captured by a single vector (L, red), which points down and to the left of the baseline community's origin. If we want to know if this particular species' effect on ecosystem function was higher or lower than the loss of an average species occurring in community A (i.e. is the loss of this species more or less influential than we might expect), this single vector can be decomposed into two vectors (\hat{L} and \bar{L}). \hat{L} represents the amount of function that would be lost if the focal species were a perfectly average representative of baseline community A. \bar{L} then corrects for the difference between this average value and the actual function lost with the focal species. Although this correction can be either positive or negative, this example illustrates a positive value, indicating that the focal species was lower functioning than average.

iii. Gained species (Vector G)

Finally, a species that does not occur in the baseline community (A) but appears in the comparison community (B) is 'gained'. This effect is captured by a single vector (G, blue), which points up and to the right of the baseline community's origin: the presence of the species adds to both species richness and function. As with the loss vector, the gain vector can also be decomposed into two additional vectors (\hat{G} and \bar{G}). \bar{G} represents the amount of function that the focal species contributes to the comparison community B, assuming that it is a perfectly average representative of all the species in B. \hat{G} then corrects for the difference between this average value and the actual function of the focal species. In this example the correction is positive, which indicates that the focal species had

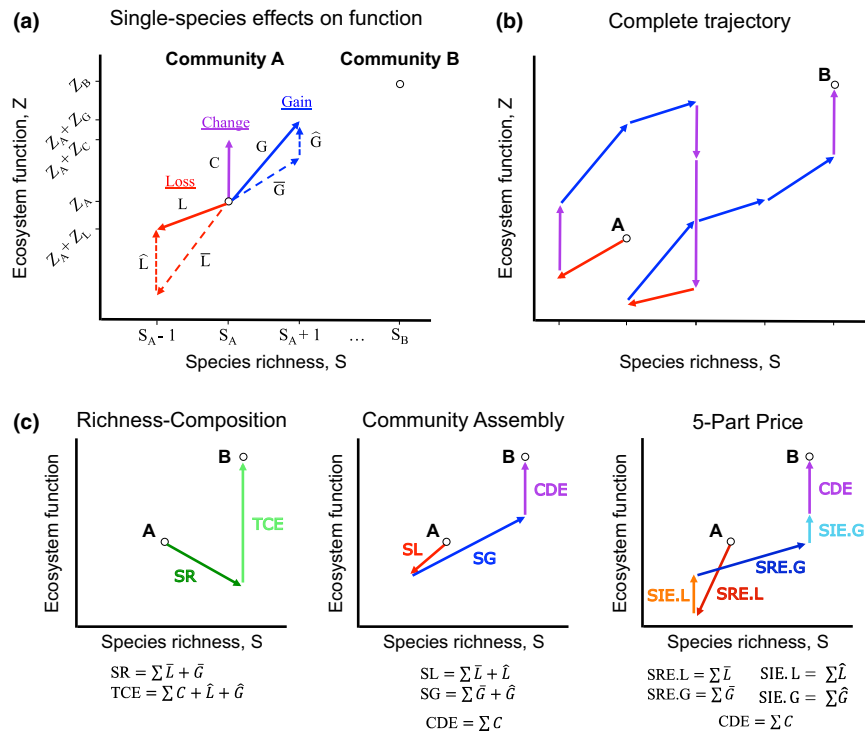


Figure 2 (a) Communities (such as A and B) can be oriented as points (circles) in the space defined by axes of their species richness and their total ecosystem function. The net difference between these two communities can be decomposed into the effects of individual species, which are either lost or gained (here, arbitrarily viewed from the perspective of community A) or, when shared by both communities, may change their function. These effects can be represented as vectors in richness-function space. As described in the text, grouping these vectors together in different ways and adding them up generates various metrics that offer insights into how compositional changes affect ecosystem function. (b) Hypothetical complete trajectory of species-level vectors accounting for the net differences between the total ecosystem function observed in community A and community B. Colours of the lines are identical to panel 'a'. (c) Three different arrangements of summed species-level effects on ecosystem function offer different insights into the causes of changes in ecosystem function. The Richness-Composition arrangement emphasises the effects of net changes in species richness and shifts in composition, while the Community Assembly and 5-part Price arrangements focus on the effects of gaining and losing species, offering additional information on the consequences of turnover and changes in species identity and community composition on ecosystem function. Abbreviations and Colours: L, effect of losing a species; \bar{L} , effect of losing an average species from community A; \hat{L} , difference between losing an average species and a specific species from A; G, effect of gaining a species; \bar{G} , effect of gaining an average species in community B; \hat{G} , difference between gaining an average species and a specific species in B; C change in the function of a species from A to B; SR, Species Richness effect (dark green); TCE, Total Composition effect (light green); SL, Species Loss effect (red); SG, Species Gain effect (blue); CDE, Context-Dependent effect (purple); SRE.L, Species Richness Effect of species Loss (red); SIE.L, Species Identity Effect of species Loss (orange); SRE.G, Species Richness Effect of species Gain (dark blue); SIE.G, Species Identity Effect of species Gain (light blue). Connections between the notations used in Box 1 and Fig. 2 are provided in Appendix S1.

above average function. However, this value can be positive or negative depending on the species in question.

In this manner, we can account for the effects of every species appearing exclusively or jointly in the baseline and comparison communities – each species must have one of the three effects described above. If we chain together the effects of each species, one after the next, we obtain a series of vectors that trace out a path from community A to community B. Adding up the effects of all species on the richness and function of the baseline community results in a single vector that recovers the net change in function and richness between baseline and comparison.

What insights do we gain with this approach? At the simplest level, a single vector connecting the baseline and comparison communities simplifies the complex suite of species responses by focusing on just the net change in species richness and the net change in ecosystem function. However, it loses the information of why this relationship emerges. At the other extreme, the complete set of individual effects of a

potentially large number of species is an overwhelming amount of information. Some intermediate level of simplification is required. The ecological application of the Price equation offers one way to rearrange and simplify the species-level vectors (Box 1; Appendix S1; Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012). There are also other arrangements that can be used to highlight different aspects of how changes in species composition and richness contribute to changes in ecosystem function. We present three of a myriad of possibilities here; each depends on rearranging and combining species vectors in different ways (Fig. 2b).

i. Richness composition

For some questions, we may want to quantify how much of our change in ecosystem function emerges from shifts in species richness relative to changes in the identity and functions of species. To do this, we can combine our vectors in ways that isolate the effects of changes in numbers of species from

Box 1 The ecological application of the Price equation

The Price equation (Price 1970, 1972) is a tool in evolutionary biology that quantifies how trait or gene frequency changes over time as a result of natural selection and gene transmission. Fox (Fox 2006; Fox & Harpole 2008; Fox & Kerr 2012) adapted the Price equation to compare ecosystem function between a baseline and comparison site (denoted with 'superscript on variables), separated in space and/or time. It relates ecosystem function differences to differences in species-level contributions to ecosystem function. This approach can be used if a community's total ecosystem function (T and T' in Fig. 3) is the sum of the contributions of the species in the community (z and z' in Fig. 3; e.g. community biomass = sum of population biomasses).

At its core, the ecological Price equation (Fig. 3), uses the number of species in each community (s and s'), the number of species shared (s_c), the average species-level function in each community (\bar{Z} , \bar{Z}') and the function of species shared by the baseline and comparison communities (\bar{Z}_c , \bar{Z}'_c). These variables are used to partition differences in ecosystem function between sites into five components (Fig. 3):

- (1) The species richness effect of losses (SRE.L): reflects the impact of the loss in species on ecosystem function, assuming species are lost randomly with respect to functional contribution.
- (2) The species richness effect of gains (SRE.G): same as SRE.L, but for the species gained by the comparison site.
- (3) The species identity effect of losses (SIE.L): If species lost tend to be higher or lower than average functioning species then this is reflected in the SIE.L.
- (4) The species identity effect of gains (SIE.G): same as for SIE.L but for the species gained by the comparison site.
- (5) The context-dependent effect of the resident or shared species (CDE): reflects resident species changes in their contributions to ecosystem function (e.g. a species increases its biomass with the loss of a dominant species)

An important note is that SIE and SRE are calculated relative to the community the species are lost from or gained into. Thus, the loss of two average species from the baseline community may not have the same ecosystem function impact as gaining two average species into the comparison community (i.e. \bar{Z} and \bar{Z}' may differ in their values). This is an expected consequence of community assembly – as the distribution of traits and contributions to functions changes with assembly, so too does the average species' value.

other compositional changes (identities, abundances). We can add together all of the vectors that affect species richness (both loss and gain terms) to obtain a net 'richness effect', which assumes that all gained or lost species are perfectly average. Mathematically, $SR = \sum(\bar{L} + \bar{G})$. Adding together all of the remaining vectors provides a second term capturing the totality of any effects that have to do with species' identity

as either high or low functioning species, as well as changes in their function across communities. Mathematically, this total composition effect, or $TCE = \sum(C + \hat{L} + \hat{G})$. Together the sum of the SR and TCE terms, which contain all the relevant vectors, recovers the net change in function and richness between A and B. The strengths of this approach include isolating the pure effects of the net change in richness between the baseline and comparison communities, while suppressing details on compositional differences to focus on the net compositional effect.

ii. Community assembly

The Richness-Composition approach highlights how community assembly processes impact ecosystem function through its impacts on the number of species and composition of those species. To gain more insight into the signatures of community assembly we could instead focus on the separate effects of gaining and losing species, incorporating both the effects of the number of species gained/lost and whether they are high or low functioning. To do so we could add together the effects of all of the lost species, and separately all of the gained species. Mathematically, this yields two vectors $SL = \sum(L)$ and $SG = \sum(G)$. The sum of the remaining vectors, which consist of changes in the function of shared species, yields the total effect of species shared between communities, also called the context dependence effect ($CDE = \sum(C)$). Again, as these terms collectively include all of the effects of the individual species of A and B, their total recapitulates the net change in richness and function between the baseline and comparison communities.

iii. 5-part price

Finally, we separate out the contributing species richness and species identity vectors, which are summed together to produce L and G vectors. This would provide separate terms indicating the effect of losing the appropriate number of perfectly average species from baseline A ($SRE.L = \sum(\bar{L})$), or gaining the appropriate number of perfectly average species in comparison B ($SRE.G = \sum(\bar{G})$). The effects of losing or gaining non-average species would also be captured by two separate terms, $SIE.L = \sum \hat{L}$ for losses and $SIE.G = \sum \hat{G}$ for gains. Finally, changes in the function of species shared by the baseline and comparison communities would be captured by a context dependence effect as in method (ii), where $CDE = \sum(C)$. The resulting set of five terms exactly reproduces the ecological Price equation partition first introduced by Fox & Kerr (2012). Note that we have chosen to re-name Fox & Kerr's (2012) 'Species Composition Effect (SCE)' to 'Species Identity Effect (SIE)'. We believe this word choice better reflects the actual interpretation of the SIE terms because the SIE terms depend on how the specific species that are gained or lost differ in function from the average functioning of all species in their origin community. Therefore, the SIE terms tell us something about the consequences of particular species being gained or lost, hence their identity matters. The 5-part Price arrangement offers a more detailed view of the source of differences between the richness and function of the A and B communities than the Richness-Composition or the Community Assembly

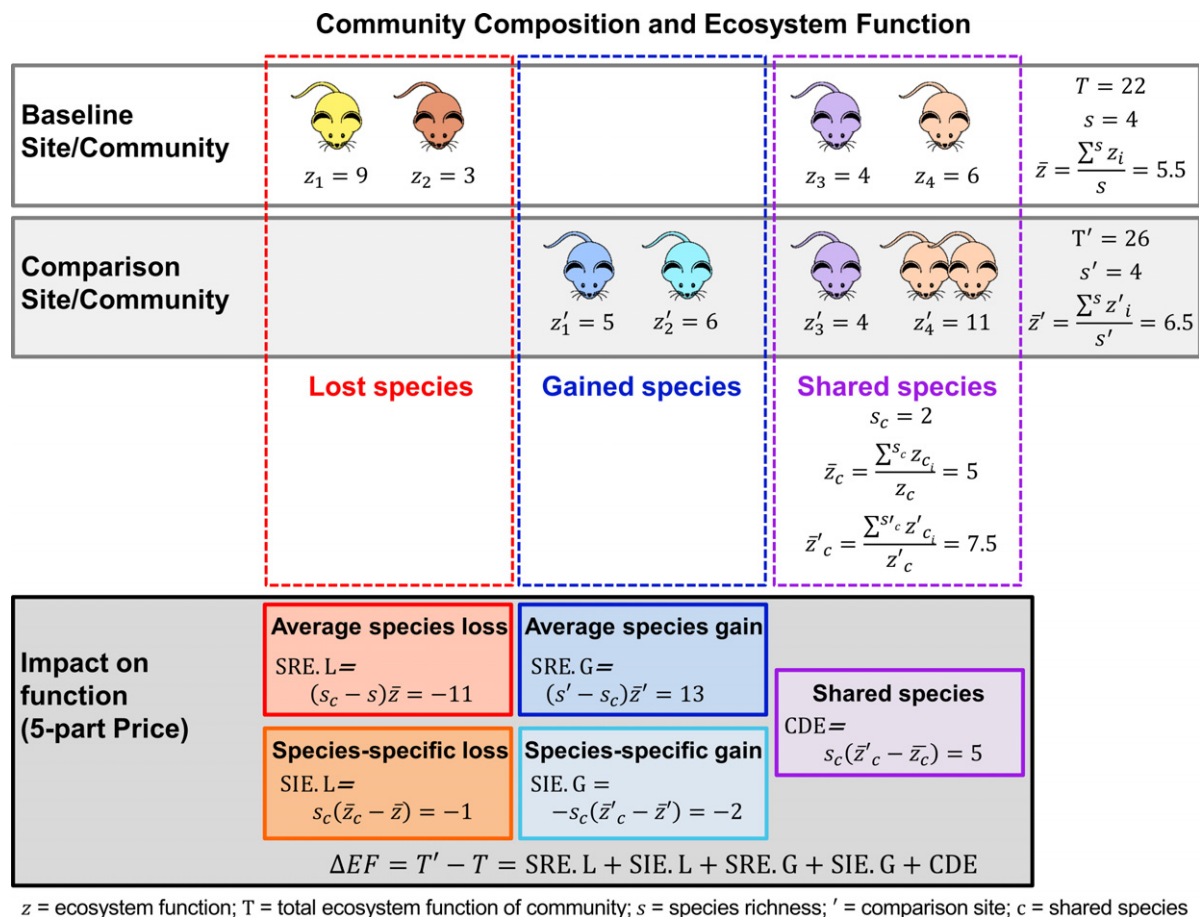


Figure 3 Schematic illustration of the ecological version of the Price equation as suggested by Fox & Kerr (2012). See detailed text in Box 1. More details on the linkages between the mathematical notations in Box 1 and Fig. 2 are provided in Appendix S1.

methods, while still suppressing species-level details. The Fox & Kerr (2012) version of the Price equation is also the mathematical framework upon which the Richness-Composition and the Community Assembly configurations are based. For more information on the Price Equation and interpretation of the components SRE.G, SRE.L, SIE.G, SIE.L and CDE, see Box 1, Fig. 3, Appendix S1 and Appendix S2 (including a link to our [R] code).

In the following sections, we provide three case studies exploring how biotic and abiotic perturbations (resulting from invasive species and a flood) trigger both compositional and species richness changes and how those changes impacted ecosystem function. We use each of the three vector approaches described above (Richness-Composition, Community Assembly, 5-part Price) to show how they offer different insights into the influence of assembly processes on the composition, the diversity and ultimately the function of ecosystems.

EMPIRICAL EXAMPLES OF COMMUNITY ASSEMBLY AND THE FUNCTIONING OF ECOSYSTEMS

To better understand assembly's role in ecosystem function, it is essential to quantitatively determine the extent to which ecosystem changes depend on richness alone, and when

composition also makes important contributions. We next show how arrangements of the Price equation, applied to empirical examples from marine and terrestrial ecosystems, offer new insights into how community assembly influences ecosystem function. In particular, we use three experiments where perturbations resulted in changes in relative abundance, species composition and ecosystem function to see how species richness and composition interact. Our examples include: (1) the invasion of a novel plant species into a forest community, (2) the recovery of a marine macroalgal community after the removal of an invasive species and (3) the response of a desert rodent community to a flash flood. For each example, we use the Richness-Composition, Community Assembly and 5-part Price equation approaches to understand the underlying community assembly processes influencing ecosystem function. In the section above, we explained the Price equation by assuming there were only two communities being compared (separated in space and/or time). However, these experiments contain replicate experimental plots. If the data were available, we used the full set of replicates (i.e. multiple control and treatment plots or multiple control plots that can be compared before and after an event) to examine all possible pairs of baseline and comparison plots. In this section, the vectors on our graphs (Figs 4 and 5) represent the mean Price component values.

Invasive species examples

Invasive species colonise, survive and reproduce at multiple sites and habitats outside of their native range (Blackburn *et al.* 2011). Typically, invasive species dominate the local communities they invade, causing decreased native species abundances and diversity (e.g. Vilà *et al.* 2011; Wardle *et al.* 2011). Consequently, the ecosystem function contributed by native species is expected to decrease, but expected to be high for the invasive species itself, which may result in a net gain in ecosystem function for the community. What might we expect to see, using the vector approaches outlined in this manuscript? The Richness-Composition approach focuses on the impact on ecosystem function due to changes in species richness relative to compositional effects. The SR vector (the effect of species richness changes assuming that species gained or lost were average in their function) will be the combination of the gain of 1 species (the invasive), additional colonisations and the loss of any natives. The gain of a single average functioning species (if the invasive species is average and is not accompanied by additional colonisers) should have minimal effect on ecosystem function, thus the Richness-Composition SR effect should be driven primarily by species loss. But if an invasive species is not an average functioning species, its compositional effect and any other impact on ecosystem function (selective loss of non-average species or changes in resident species' functions) not accounted for by the simple species richness effect is relegated to the TCE component of the Richness-Composition configuration (Fig. 2b). In contrast, the Community Assembly configuration focuses on the role of species gains and losses on ecosystem function. The gain of an invasive species (and its non-average impact on ecosystem function) will be expressed directly in the Species Gain component (SG) and indirectly through its impacts on extinction events in the Species Loss (SL) component. If the invasive species also suppresses the function of persistent resident species, this would show up in the CDE component of the Community Assembly configuration or the 5-part Price configuration. The 5-part Price approach will additionally provide information on whether gained or lost species differ from average species in the comparison or baseline community, in the SIE.G and SIE.L components, respectively. We investigate the contribution of invasive species to ecosystem function with two invasion experiments.

Adding an invasive species to a community

We use composition and biomass data (Flory 2016) from Flory & Clay's (2010) study of forest succession and invasion by a non-native grass, *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass). The experiment consisted of 32 tilled 5.25×5.25 m plots spaced 2.5 m apart. Plots were fenced to prevent seed dispersal between plots although some colonisation of unplanted species did occur (Flory & Clay 2010). Seeds of native herbaceous species were added to all plots and seeds of *Microstegium vimineum* to half of the plots, resulting in 16 uninvaded control plots (baseline) and 16 experimental plots (comparison). Aboveground dry-weight biomass, the ecosystem function of interest, was measured 1 year after invasion by *M. vimineum*. From the Richness-

Composition configuration (Fig. 4a, left panel), the plots invaded by *M. vimineum*, as expected, experienced a net loss of species, after only 1 year, which negatively impacted ecosystem function (SR, dark green vector). However, this loss in function was compensated for by an increase in ecosystem function through the combined composition effects of the lost, gained and/or resident species (TCE, light green vector). While there was a net decline in species richness, the Community Assembly configuration (Fig. 4a, middle panel) highlights that colonisations of invaders and other species also occurred and positively impacted ecosystem function. A loss in ecosystem function due to the loss of species (SL, red vector; $\bar{x} = 18 \pm 7$ species), was more than recovered through the gained species (SG, blue vector; $\bar{x} = 9 \pm 5$ species). The decreased performance of the resident species led to a very small net change in ecosystem function from the starting (baseline) condition (CDE, purple vector). The 5-part Price approach reveals that, while the extinction impacts on ecosystem function are as expected from species loss (i.e. the orange SIE.L vector is miniscule), the colonisation impacts on ecosystem function were increased by a strong species-specific effect (i.e. a substantial light blue SIE.G vector) of the gained species (including the invasive *Microstegium* species; Fig. 4a, right panel). In this experiment, both species richness and community turnover impacted ecosystem function, but these impacts opposed each other to result in little overall change in ecosystem function, despite a net loss of species.

Removing an invasive species from a community

Using experimental removals, Casas *et al.* (2004) found that an invasive kelp (*Undaria pinnatifida* (Harvey) Suringar) native to northeast Asia had strong negative effects on native seaweed richness in Argentina. To examine community recovery after the removal of an invasive, we used the mean wet biomass [g/m^2] of seaweed species aggregated across treatment quadrats [10 quadrats where *U. pinnatifida* was present (baseline) compared to 10 quadrats where it was removed (comparison)] as our measure of ecosystem function (Fig. 4b). Overall, removing the invasive species caused a 3-fold decrease in total ecosystem function, despite the net gain of a proportionally large number of species (13 species). The Richness-Composition configuration shows that a net gain of species richness (SR) resulted in a slight loss of ecosystem function and that most of the 3-fold decrease in ecosystem function was caused by removing the invasive species was due to compositional effects (TCE). The Community Assembly configuration shows that the net gain of species resulted in a negative contribution to ecosystem function because the contributions of the gained species (SG) could not offset the decrease in ecosystem function caused by the loss of two species (SL), one of which was the dominant invasive species. The recovery of the resident communities resulted in a very small increase in ecosystem function (CDE). The 5-part Price configuration separates out the identity effect of the species lost or gained (SIE.L, SIE.G) revealing that the largest loss in ecosystem function was due to the lost species being strongly above average in their contribution to function (large negative displacement of SIE.L). This strong SIE.L effect was mostly due to the disproportionate effect of removing the invasive species

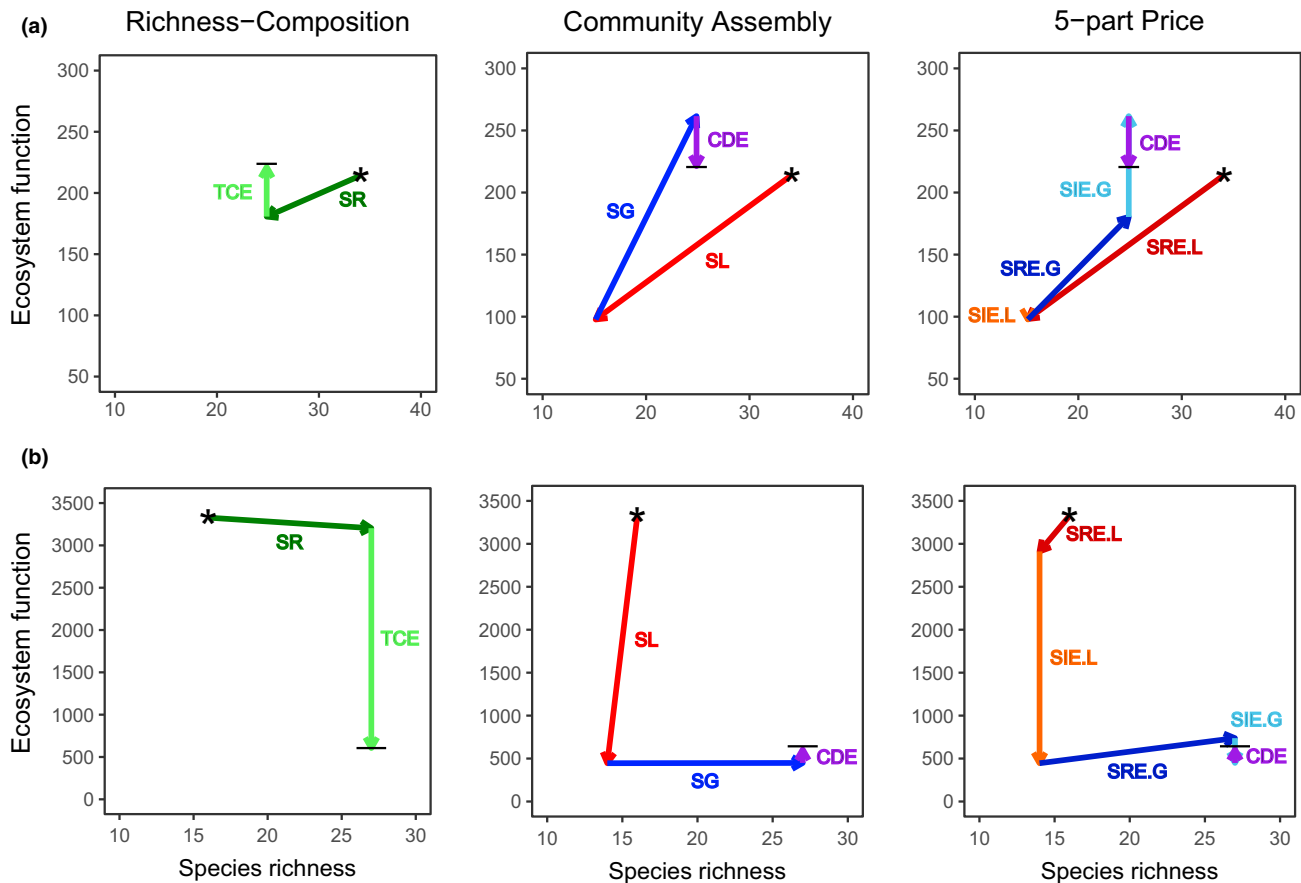


Figure 4 Vector plots comparing the Richness-Composition, Community Assembly and 5-part Price configurations for invaded communities. Vectors link the average community state of the baseline (*) and comparison (o) communities. (a) *Microstegium vimineum* grass species invasion effects on forest succession (Flory & Clay 2010). Average changes in ecosystem function (dried aboveground biomass (g)) across 16 plots in 2007 with *M. vimineum* absent (baseline) and 16 plots with it introduced (comparison) are presented. (b) Marine *U. pinnatifida* removal experiment (Casas *et al.* 2004). Average changes in ecosystem function [wet biomass (g m^{-2})] across 10 quadrats with *U. pinnatifida* present (baseline) and 10 quadrats with it removed (comparison) are presented. Abbreviations: See Fig. 2.

because it existed at a much higher biomass ($\bar{x} = 2881.6 \text{ g m}^{-2}$) than the other species lost ($\bar{x} = 0.104 \text{ g m}^{-2}$). Together, these configurations suggest that recovery of the community (during the experiment) was limited primarily to an increase in the number of species in the community. However, neither these newly gained species, as suggested by the Richness-Composition configuration, nor the resident species could compensate for the ecosystem function lost with the removal of the invasive, previously dominant species.

Disturbance impacts and recovery example

A particular strength of the vector representations of the CAFE framework is visualising how communities and their function change through time, such as before and after a perturbation or disturbance. Disturbances that cause large-magnitude mortality events, by definition, have large immediate impacts on ecosystem function. Following massive declines in populations, we would expect most impacts on ecosystem function to occur through extinctions or suppression of resident species. This effect should show up in the Richness-Composition configuration in both the SR component as the

number of species declines and in the TCE component as the function of resident species decreases. The Community Assembly configuration should show a strong negative impact of species losses (SL component) and resident responses (CDE component), but a weak or non-existent colonisation effect (SG component). Whether a disturbance removes weakly functioning or strongly functioning species probably depends in part on the type of disturbance and the traits of the species, so there is no *a priori* expectation of how the SIE components in the 5-part Price should respond.

Recovery from a disturbance can occur either through colonisation or the response of the surviving (i.e. resident) species. Colonisation effects will show up in the SR component of the Richness-Composition configuration, the SG component of the Community Assembly configuration, and the SRE.G component of the 5-part Price configuration. If colonising species are high or low functioning species, colonisation effects will also show up in the TCE component of the Richness-Composition configuration and the SIE.G component of the 5-part Price, and will contribute to the SG component of the Community Assembly configuration. Resident species responses will show up solely in the TCE component

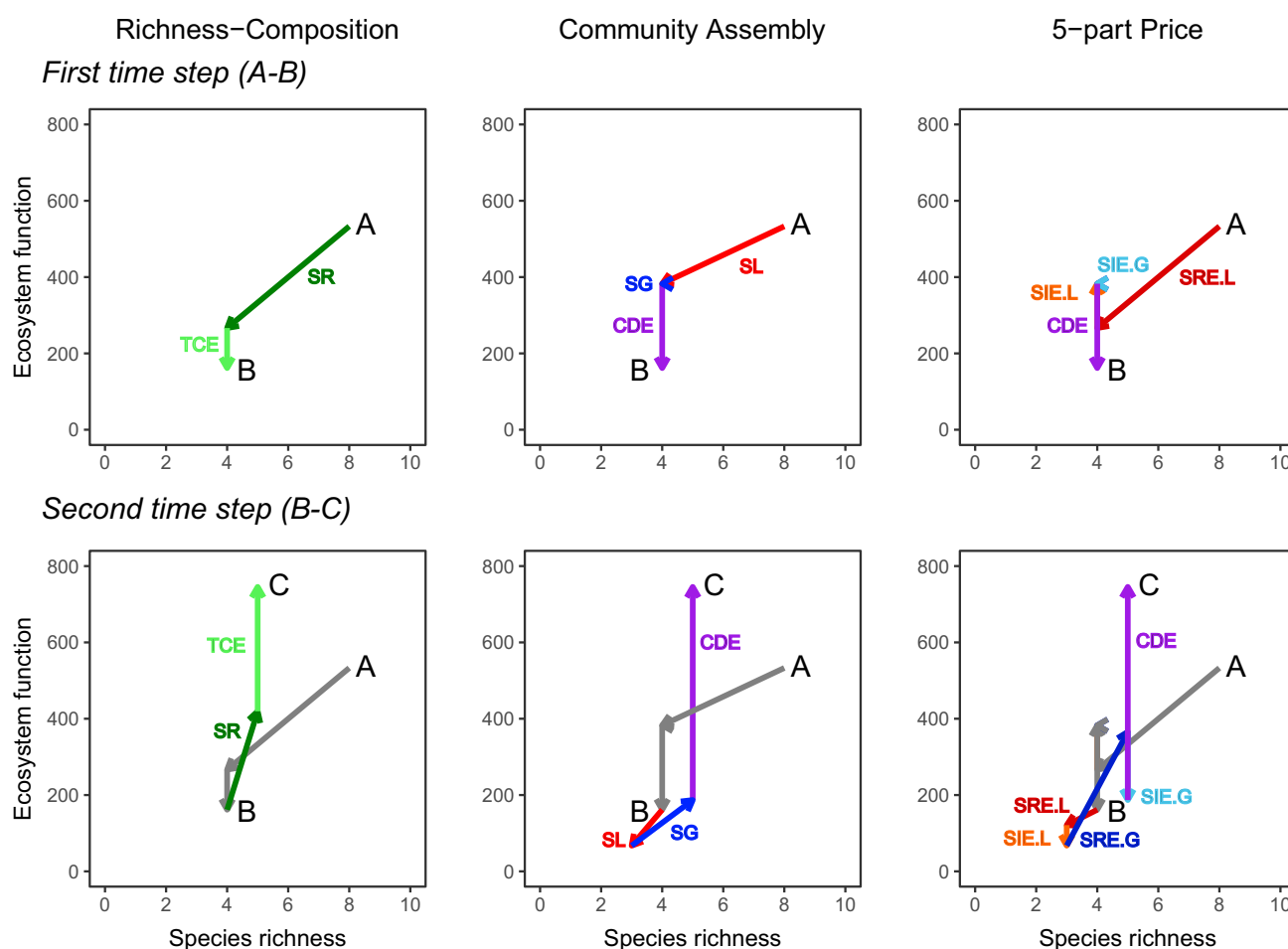


Figure 5 Temporal vector plots comparing the Richness-Composition, Community Assembly and 5-part Price approaches for understanding ecosystem function changes after a pulse disturbance. This example describes the changes in rodent communities from the Portal Project in the Chihuahuan Desert Ecosystem of Arizona after being affected by a flood event in 1999 (Thibault & Brown 2008). The upper plots show changes from the baseline community (A; 1 month prior to flood) to the disturbed community (B; 1 month post-flood), and the lower panel adds changes from the disturbed community (B) to the recovered community (C; 1 year post-flood). Time step A-B is greyed out in the lower panel. The ecosystem function is calculated as the mean energy use per species (watts estimated from the allometry for field metabolic rates and individual weight) and their summed abundances averaged across ten experimental 0.25 hectare plots. Abbreviations: See Fig. 2.

of the Richness-Composition configuration and the CDE in the Community Assembly and 5-part Price configurations.

Temporal recovery from a disturbance

To show how the Price equation can be used temporally, we use data from a long-term ecological study of rodent communities in the Chihuahuan desert where a large flood event caused massive mortality. When the community reassembled, the species composition before and after the flood differed dramatically (Thibault & Brown 2008). Here, we restrict our focus to the plots where rodents had unrestricted access and examine changes in community-level energy use at three distinct time points: prior to a large flooding event (baseline; Fig. 5 point A) on August 14 1999, 1 month post-flood (disturbance impact; Fig. 5 point B) and 1 year post-flood (disturbance recovery; Fig. 5 point C) (Thibault & Brown 2008). We use the Price equation to assess the changes in ecosystem function as the community assembles from disturbance (time points A to B) to recovery (time points B to C). Energy use

was calculated from each species' summed abundances and allometry for field metabolic rates (Thibault *et al.* 2010). As expected, the Richness-Composition configuration shows that immediately post-flood (Fig. 5, top left, point A to B), the decline in ecosystem function was substantial and suggests that it was driven primarily by the loss of species richness (4 species) due to local extinctions (Fig. 5, top middle). The Community Assembly configuration, however, shows that this loss was not solely due to species loss (SL, red vector in Fig. 5, top middle) but even more strongly reduced by the decline in function of resident species (CDE, purple vector). This resident response was obscured in the Richness-Composition configuration because the TCE component combines the CDE, SIE.L and SIE.G. We can use the 5-part Price (Fig. 5, top right) to see that the species lost in the flood were low performers; this generates a large, positive SIE.L which obscured the large negative CDE and created a net weak total composition effect (TCE) in the Richness-Composition configuration. While the flood had dramatic impacts on ecosystem

function through loss of species and reduction in residents, within a year (Fig. 5, points B to C) the recovery of ecosystem function was predominantly due to the positive response of the surviving species (CDE, purple vector, Fig. 5 bottom bottom middle) rather than either species losses (1 species) or gains (2 species) during this time period. Colonisations only weakly contributed to increases in ecosystem function, in part because the number of colonisations (SRE.G dark blue, Fig. 5 bottom right panel) was less than the original number of extinctions (SRE.L red, Fig. 5 bottom right panel) and because the colonising species were weaker than average contributors to ecosystem function (SIE.G light blue, Fig. 5 bottom right panel). Together, these results suggest that the flood disrupted ecosystem function through both extinctions that caused net declines in species richness, and through declines in the surviving (i.e. resident) species' function. Recovery occurred partly through increased richness driven by colonisation of weakly performing species but mainly because of strong increases in the performance and/or abundance of the species that survived the flood event.

DISCUSSION AND CONCLUSIONS

In studying how species impact ecosystem function, we typically focus on only one dimension of the community assembly process: either richness, or colonisation and extinction or resident species responses. Rarely do we use a holistic approach taking multiple aspects of community structure into consideration. Our case studies show that community assembly processes can simultaneously affect many facets of communities, with both synergistic and antagonistic consequences for overall ecosystem function. Rather than considering the ecosystem impacts of changes in richness, or composition, or extinction as separate questions, we should be asking integrative questions about the interaction of these processes. We should also clearly be asking questions not just about the net change in richness, but also about the functional consequences of species gains and how and when they offset the functional consequences of species losses. Our case studies suggest that to predict how ecosystem function will change in response to community change, we need a clearer picture of how richness, functional consequences of extinctions and colonisations and resident species responses change in concert as communities assemble.

Answering integrative questions combining species richness, colonisation/extinction and resident responses is not simple. Here we used the Price equation as a tool for bringing these components together. In particular, the potential for rearranging and aggregating the functional effects of individual species, or groups of species, in different ways made it possible to ask integrative questions linking community assembly with ecosystem function. The Richness-Composition configuration summarises the net effects of species richness changes and composition effects on ecosystem function, whereas the Community Assembly configuration emphasises the roles of colonisation, extinction and resident species responses. Neither adds any information that is not already present in the 5-part Price configuration, but rather focuses this information in useful ways. Like the different magnification levels of a microscope, the Richness-Composition, Community Assembly and 5-part

Price versions allow one to zoom in on details or zoom out to see larger structures of the community assembly process. Indeed, many other vector arrangements in addition to the three we presented are possible; developed in future studies motivated by specific questions, these could offer additional ways to explore the connections between community and ecosystem properties. As such, we see the Price equation as a valuable tool for moving biodiversity science forward in useful ways.

While the Price equation is a useful tool for quantifying how community assembly impacts ecosystem function, it is not without limitations. Like all metrics constrained to pairwise comparisons, non-independence of the pairwise comparisons complicates statistical analysis. We side-stepped the non-independence issue here by only comparing overall treatment averages or sums, but addressing this statistical shortcoming will improve the strength of inferences using this approach (see Appendix S2 for some recommendations). Another weakness of the Price equation in forms presented here is that changes in functional traits cannot be attributed to particular species that are lost or gained – this detail is lost when species-level responses are aggregated. Building on the work by Fox & Harpole (2008) may be one avenue for incorporating a better understanding of how functional traits impact ecosystem function within the Price equation framework. Alternatively, non-Price equation-based approaches already exist that can address this issue (e.g. Kirwan *et al.* 2009; Gotelli *et al.* 2011). The Price equation also does not account for changes in abiotic environmental conditions, which are known to confound the ability of methods such as this one to detect all these effects (e.g. see Loreau 1998). Finally, while the Price equation can quantify contributions of changes in species richness, colonisation/extinction events, resident species responses and loss and gain of productive/unproductive species to changes in ecosystem function, there is a severe theoretical shortage in how these components relate to different community assembly scenarios. Can patterns in Price equation components or configurations be related to neutral *vs.* niche processes, metacommunity dynamics, or complementarity *vs.* selection effects? If they can, then this opens up the possibility of studying community assembly mechanisms in natural conditions. If not, the Price equation remains a useful quantification tool that yields limited mechanistic insight. These statistical and theoretical issues are tractable and will determine whether the Price equation can be used as a central tool in linking communities and ecosystem function, or whether additional approaches will be required.

Even with these current limitations, our application of the Price equation provided important insights into the variety of ways that the community assembly process impacts ecosystem function. One result that emerged consistently across all examples is that, while we often focus on the impacts of extinction, colonisation is an equally strong and prevalent process. Extinctions can be balanced by colonisations, helping to maintain ecosystem function and richness. The loss of many average functioning species may be counterbalanced by the gain of a few very productive species (Fig. 4b). Colonisation is important because most communities are linked by dispersal to other sites of both similar and differing habitats and, thus, species

pools. The impact of colonisation on biodiversity–ecosystem function (BEF) relationships is not unstudied (Gonzalez & Chanton 2002; France & Duffy 2006; Zobel *et al.* 2006), but our results emphasise that whether the species colonising are high functioning, low functioning or average functioning can have profound impacts on ecosystem function. This further helps explain the scatter commonly observed around experimental BEF curves. Thus, the overall ability of any analyses combining BEF and CAFE approaches could ultimately help explain variances (Low-Décarie *et al.* 2014). Better integration of metacommunity mechanisms across large spatiotemporal scales (Cabral *et al.* 2017), including the importance of the structure of the regional species pool (Karger *et al.* 2016), are clearly important avenues to be integrated into future ecosystem function-related research (Leibold *et al.* 2017).

Beyond colonisation and extinction, our case studies suggest that when a community changes, multiple aspects of community structure are impacted at the same time. These different changes in community structure (species identity, number of species, distribution of contributions to function) can impact ecosystem function in similar or different ways. For example all three structural changes can increase (Fig. 5) or decrease (Fig. 4b and Fig. 5) ecosystem function, as well as be antagonistic and cancel each other out (Fig. 4a). Therefore, no single aspect of community structure relating to ecosystem function can be studied in isolation because it is the aggregate of impacts of all aspects of community structure that is important. Studying composition without thinking about richness or richness without thinking about composition will lead to incomplete if not erroneous expectations for how ecosystem function will change. This can be seen most clearly in the example of the invasive grass in a North American forests (Fig. 4a; Flory & Clay 2010). If we focused solely on the importance of species richness, we would predict that ecosystem function should decline in this system. If we focused solely on the compositional changes, we would expect ecosystem function to increase. However, because these impacts are opposite and nearly equal in magnitude, instead ecosystem function was maintained. How general are these contradictory impacts of composition and richness? We suspect that all scenarios will be found in nature. The key challenge of future research should not necessarily be whether those scenarios occur, but to understand and predict what mechanisms regulate their relative importance.

The message that community assembly is an integrated process that impacts multiple aspects of community structure and ecosystem function in non-random ways is the core message of the CAFE framework (Leibold *et al.* 2017). We hope that the CAFE framework will encourage more studies assessing how community structure impacts ecosystem function in a variety of scenarios: unperturbed systems, responses to disturbance, invasions and extinctions to name a few. We believe that the Price equation will be a useful tool for advancing this framework because it can be applied to both observational and experimental data. In this sense, mechanistic models and simulation experiments will also be useful for pushing forward our understanding of the mechanisms regulating how community assembly impacts ecosystem function – for example how do communities assembled by mass effects, selection effects, priority effects or complementarity effects differ in their

community structure–ecosystem function relationship? Analysing emergent results from simulation experiments with the Price equation can help identify the signatures of these different community assembly processes. Moreover, meta-analyses could address whether there are general patterns in natural community assembly–ecosystem function interactions that emerge in response to invasions or disturbances. Only with research using a variety of approaches, synthesising data across systems and taxa and considering how community assembly processes impact all aspects of community structure (species identity, richness and functions), will we truly have a clear picture of how the changes in biodiversity occurring in nature will impact ecosystem functions.

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AUTHORSHIP

ML and SKM secured funding for the two workshops and conceived the original idea. KBM, CK, ML and SKM led the two workshops and designed the study. KBM managed the data; KBM and CK performed analyses. KBM wrote the first draft of the manuscript. All authors attended the two relevant workshops where the ideas for this manuscript were developed and contributed substantially to manuscript revisions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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