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Special feature title

Towards a mechanistic understanding of global change ecology

Title

Towards the general mechanistic prediction of community dynamics

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Abstract

1. “What controls the distribution and abundance of organisms”? This question, at the heart of the dynamics of ecological communities, would have been familiar to the earliest ecologists. Having lain effectively abandoned for many years, community dynamics today is a vibrant research topic of great conceptual interest with practical import for conservation, ecological management, ecosystem services and the responses of ecological communities to climate change.
2. We describe how modern coexistence theory can be applied to predict community dynamics through the use of demography. We explore the challenges that limit the deployment of this demographic framework, and the tools from phylogenetic and functional ecology that have been used to surmount them.
3. Finding existing tools not altogether sufficient, we propose the use of ‘hard’ functional traits and physiological tolerances of environmental conditions and low resource availability to extend the demographic framework so that the dynamics of a broader range of ecological communities can be accurately predicted.
4. We illustrate these new approaches with two case studies. Given the urgent need to accurately forecast the dynamics of ecological communities, we hope that many ecologists will adopt these tools.

Objective

The objective of this contribution is to outline the most promising techniques, as we see them, to predict community dynamics in the medium term. By community dynamics, we mean changes in species composition and relative abundance through time or over environmental gradients. By medium term, we mean 5-10 generations into the future, a timeframe that varies enormously among organisms. It represents an important frontier to advance, however, as it is the scale at which extrapolations from current community structure tend to break down, and yet, given anthropogenic effects on global climate and to environments around the globe, it is relevant to conservation, restoration and ecological management (Agrawal et al., 2007; Clark et al., 2001). Notably, ecologists already have predictive ability over such scales in a few circumstances. Following decades of research, we can make strong, empirically grounded predictions about the dynamics expected, for example, upon the abandonment of agricultural land (Horn, 1974; Norden et al., 2015). Even so, ecologists' ability to accurately predict community dynamics remain frustratingly limited. For example, we currently have little ability to predict changes in tree relative abundance over 200 years in tropical rain forests, or invertebrate species composition over five years in temperate vernal pools.

Improving our predictive ability would be of great conceptual interest, yielding insight into long-standing questions in community ecology. For example, many ecological communities are puzzlingly rich in competing species despite a lack of obvious niche partitioning at the scale of individual patches, resulting in what Hutchinson (1961) famously described as a "paradox of the plankton". Conceptual gaps also remain in understanding how the strength and nature of interspecific interactions vary over space and time and thereby generate variation in community structure (Agrawal et al., 2007; Chamberlain, Bronstein, & Rudgers, 2014; Hairston, Smith, & Slobodkin, 1960). These classic problems deserve general answers.

We begin by outlining the most-promising current approach, based on the estimation of demographic parameters relating to stabilising and equalising coexistence mechanisms (Chesson, 2000b), which has scored notable successes (Adler, Ellner, & Levine, 2010; Kraft, Godoy, & Levine, 2015; Levine & Hille Ris Lambers, 2009). Essential to any accurate prediction is the identification and minimization of uncertainties (Clark et al., 2001), so we next explore the challenges that limit the current approach. We discuss the tools derived from phylogenetic and functional ecology that have been used to surmount these challenges, and their limitations. We conclude by presenting two ongoing investigations that employ complementary techniques, ‘hard’ functional traits and physiological tolerances, to further extend the demographic approach. We see them as offering the most promise to generalise the demographic framework, thus facilitating accurate predictions of community dynamics of a wide variety of ecosystems.

Background

25 years ago, Pianka (1992) declared that “Community ecology… remains a primitive and embryonic science”. He was correct in many ways. Ecologists have debated the controls on population sizes and community structure since the dawn of ecology as a science, and conceptual approaches to community dynamics had proliferated (Fig. 1). Nevertheless, their application stalled because most of the underlying theory, with the exception of limiting similarity (MacArthur & Levins, 1967) was qualitative. The lack of mechanistic quantitative theory precluded accurate predictions of community dynamics (Vellend, 2016).

Two publications re-founded community ecology on a more rigorous basis at the turn of the millennium. The first, Hubbell's 'neutral' theory (2001), set forth a model of community dynamics and biogeography of extreme parsimony. Though its assumptions of species equivalence were derided as unrealistic (McGill, Maurer, & Weiser, 2006), it was simultaneously lauded for its capacity to accurately describe aspects of community structure, such as relative abundance distributions, with a scant handful of parameters (Volkov et al., 2007). As deriving similar predictions for species-rich communities from traditional niche-partitioning theory would require unmanageably many parameters to be estimated (Chase & Leibold, 2003; Silvertown, 2004), neutral theory led ecologists to radically reconsider their approach to community dynamics. The previous year, Chesson (2000b) had synthesised niche theory with an earlier formulation of neutral theory (Hubbell, 1997). He categorised coexistence mechanisms as either equalising, which minimise average fitness differences between species, or as stabilising, which intensify negative relationships between population density and per-capita population growth rate. Chesson's synthesis was highly influential because of its generality. For the first time, the dynamics of any community could be investigated on the basis of the demography of its component populations, so long as the growth rate of each population and the intensities of interactions between them could be estimated.

Chesson's (2000b) synthesis, now referred to as "modern coexistence theory" (Letten, Ke, & Fukami, 2017) is general, in the sense that it applies to all ecological communities. Even so, its relatively abstract mathematical formulation limited its application. Initial attempts to distinguish the relative strength of stabilising and equalising mechanisms were based on the study of macroscopic patterns observed in ecological communities. Niche-based and neutral models can generate very similar relative abundance distributions, however, rendering such pattern-matching exercises uninformative (Chave, Muller-Landau, & Levin, 2002; McGill, Maurer, & Weiser, 2006). A new opportunity for predicting community dynamics was presented when Adler et al*.* (2007) proposed a mechanistic operationalisation of Chesson's synthesis.

To predict community dynamics from demography, first quantify the intrinsic population growth rate of each target species, and the effects of those species' abundances on the population growth rates of the other species of interest (Adler, HilleRisLambers, & Levine, 2007). These are traditionally written as λ_i and α_{ij}, with *i* and *j* representing distinct species. With estimates of population growth rates and interaction coefficients in hand, build a demographic model including stabilisation terms and fitness difference terms for each species (Adler, HilleRisLambers, & Levine, 2007; Chesson, 2000b). Doing so is conceptually interesting, as it gives insight into the mechanisms of coexistence operating in the community. The specific form of the demographic model will depend on the life history of the organisms examined and the nature of the interspecific interactions. Although originally proposed to evaluate the importance of neutral- and niche-based coexistence mechanisms, the Chesson-Adler demographic framework can be applied to predict various aspects of community structure and dynamics. For example, Adler *et al*. (2010) built a spatially explicit individual-based model to predict times to extinction for each of their studied species, as well as a multi-species integral projection model to predict the dynamics of population growth rates and asymptotic population sizes.

Challenges to apply the demographic framework

As Adler et al*.* (2007) note, the demographic framework "…require[s] considerable data on species' performance and interactions across wide ranges of biotic and abiotic variabilities, and also sophisticated quantitative techniques." In this section, we elaborate on this comment, detailing the challenges that most strongly limit the deployment of the demographic framework in the prediction of community dynamics.

First, and most simply, estimating population sizes of organisms that are shy, nocturnal, fossorial, or otherwise difficult to detect is challenging. Moreover, the great majority of species in any community are rare, complicating the estimation of their population sizes (Rabinowitz, 1981).

Second, the life history of some organisms makes it difficult to estimate their population growth rates and the sensitivity of their population growth rates to intra- and interspecific density. Making observations over the complete lifespan of long-lived individuals is often infeasible (Clark et al., 2010). In such cases, it can be profitable to separately assess vital rates such as recruitment, individual growth, survival and fecundity for each target species. Moreover, many species have multiple pathways to fitness. For example, many species reproduce both clonally and sexually, either sequentially, as in aphids (Aphidoidea, Hemiptera**)**, or simultaneously, as in many plants. In the rare systems in which genets are easily tracked, multiple fitness pathways cause little problem, but more often, only data on ramets is easily available. Matrix population models are the traditional technique to integrate vital rates over the lifecycle and estimate population growth rates (Caswell, 2001). They have been widely criticised recently, in favour of integral projection models, which avoid the issue of into how many stages should the lifecycle be divided (Ellner, Childs, & Rees, 2016). Long or complex life histories can be accommodated through careful model construction, but only with detailed knowledge of the target species.

Third, estimating interaction coefficients among co-occurring species can be challenging. To quantify the density dependence of population growth rates rigorously, it is important that the intensity of interactions among species be integrated across life stages, as stabilising processes operating on one life stage can be offset by destabilising effects at others (Adler, HilleRisLambers, & Levine, 2007). For sessile organisms, especially plants, methods for estimating interaction coefficients are well established. The degree to which number, size and distance to neighbouring plants affect plant performance is the subject of a well-established literature (Canham, LePage, & Coates, 2004). These methods have been further refined through the inclusion of functional similarity and phylogenetic relatedness among neighbours (Fortunel, Valencia, et al., 2016; Uriarte et al., 2010). With extensive fieldwork, it is possible to estimate interaction coefficients observationally (Clark et al., 2010; Purves et al., 2008). For mobile organisms, including most animals, on the other hand, it can be challenging to model interactions between individuals. Most mobile species face constraints in reproduction, however, which can lead to breeding aggregations on localised limiting resources, such as flies gathering on dung pats and explosively breeding frogs gathering in temporary pools. Such aggregations offer opportunities to measure the strength of inter- and intra-specific interactions, which may be negligibly weak at other stages of the lifecycle (see *Sepsidae case study*, below).

Moreover, interaction coefficients need to be assessed across the natural range of population density. A challenge in using observational data to do so is that most species tend to be either common or rare throughout a study system

(Rabinowitz, 1981). Thus, regressions of observed population growth rates against observed frequency often lack sufficient statistical power to yield satisfactory estimates of interaction coefficients. An alternative is to generate experimental communities at a range of densities, and to estimate interaction coefficients from them (Levine, Adler, & Hille Ris Lambers, 2008; Levine & Hille Ris Lambers, 2009). In species-rich communities, this approach can be simplified by modelling one target species in competition with the aggregate community, essentially turning a many-species community into a series of two-species systems, and repeating the process for each species in the community (Adler, HilleRisLambers, & Levine, 2007; Kraft, Godoy, & Levine, 2015). Data obtained from artificial communities can be used to parameterise multi-species integral projection models that integrate over the lifecycle, then estimate interaction coefficients and population growth rates for each species (Adler, Ellner, & Levine, 2010).

Finally, incorporating environmental heterogeneity into the demographic framework remains a challenging and open area of research (Agrawal et al., 2007; Maron, Baer, & Angert, 2014). The degree to which population growth rates vary along environmental gradients is little studied, and even less is known about environmental effects on interaction coefficients. Should we expect uncorrelated changes in community interaction coefficients along environment gradients, or can we expect the rank order of interaction coefficients among pairs of species to remain consistent? Although the degree of context dependence in interaction coefficients has begun to be explored (Chamberlain, Bronstein, & Rudgers, 2014), general answers to such questions remain unclear, and to our knowledge, no study has investigated the environmental dependence of population growth rates and interaction coefficients in species-rich communities (but see Griffiths, Warren, &

Childs, 2015). Fortunately, from the perspective of tractability, pairwise interaction coefficients appear to be little affected by the presence of other species (Chamberlain, Bronstein, & Rudgers, 2014). Acquiring data suitable for testing the context dependence of interaction coefficients will require careful experimental design (Levine et al., 2017; Maron, Baer, & Angert, 2014; see Two Ways Forward, below)

Given this list of challenges, it is perhaps unsurprising that relatively few investigators have employed the demographic framework to predict community dynamics. Nor is it surprising that many researchers have turned to tools from phylogenetic and functional ecology to overcome them.

Addressing challenges through shared evolutionary history

With access to phylogenetic data, it is possible to estimate the degree to which shared evolutionary history structures ecological communities (Webb et al., 2002). Access to these data has been facilitated by inexpensive sequencing and tree-building (The Angiosperm Phylogeny Group, 2016; Webb, Ackerly, & Kembel, 2008). Nevertheless, phylogenetic tools are not generally sufficient to generate clear predictions of community dynamics (Gerhold et al., 2015). For example, mortality rates of seedlings in a French Guianan rain forest increased with increased phylogenetic relatedness of neighbours (Paine et al., 2012), even as the opposite pattern was observed in a Panamanian forest (Lebrija-Trejos et al., 2014). More importantly, phylogenetic information is generally the wrong tool to assess interactions between species, as organisms can’t detect each other’s evolutionary history. Rather, they detect only the present-day phenotype (Paine et al., 2012). When ecologists observe phylogenetic community structure, they learn that something is going on, but it is rarely clear what that thing is (Castillo, Verdú, & Valiente-Banuet, 2010). Phylogenetic community structure is particularly difficult to interpret without estimates of trait conservatism over the phylogeny. And if measures of trait conservatism are available, then functional traits must also have been measured. So why not use them directly? Thus, phylogenetic data is unlikely to provide deep insight into community dynamics, unless interspecific interactions are mediated by shared natural enemies. Since the natural enemies may have co-evolved with the plants they consume, it is reasonable to think that they would, to some degree, respond to shared evolutionary history (Paine et al., 2012).

Addressing challenges through functional traits

Functional traits, morphological or physiological attributes of organisms that affect population growth rate through their relationships with vital rates (Violle et al., 2007), hold great promise in the prediction of community dynamics (McGill et al., 2006). Functional traits can be used to reduce the dimensionality inherent to species-rich communities, as one can parameterise models on the basis of functional groups rather than species (Laughlin, 2014). Alternatively, one can assess the degree to which functional traits are associated with vital rates, then use integral projection models to predict population growth rates (Adler et al., 2014). Their use by ecologists has been facilitated by the standardisation of sampling techniques (Pérez-Harguindeguy et al., 2013), and the development of global databases (Kattge et al., 2011). Functional traits frequently vary within, as well as among, species, contributing to variance in vital rates and thus population growth rates (Bolnick et al., 2011). Albert et al. (2011) therefore suggest that intraspecific trait variation should assessed and incorporated in regional- or local-scale studies of community assembly.

Functional traits can be considered to lie along a continuum, from so-called ‘soft’ traits, which are easily measured but distal to vital rates and therefore to population growth rates, to so-called ‘hard’ traits, which are more indicative of physiology and therefore more directly associated with vital rates (Díaz et al., 2004; Lavorel & Garnier, 2002; Weiher et al., 1999; Table 1). Soft traits indicate potential, rather than realised vital rates, whereas ‘hard’ functional traits predict vital rates and population growth rates more accurately, but are often are more time-consuming to measure and require more-expensive equipment (Díaz et al., 2004; Pérez-Harguindeguy et al., 2013). For example, leaf chlorophyll concentration is associated with the potential growth rate of plants, given the ideal availabilities of light, water and nutrients, and can be estimated in less than a second using the difference in optical density at a pair of wavelengths (Coste et al., 2010). Photosynthetic rate, on the other hand, indicates the effective net rate of photosynthate production, but takes longer and requires a much more expensive infrared gas analyser (Table 1). So what are the costs and benefits of ‘soft’ and ‘hard’ functional traits?

Like evolutionary relatedness, ‘soft’ functional traits are generally insufficient to predict community dynamics. Vital rates are only moderately associated with ‘soft’ functional traits (Paine et al., 2015; Wright et al., 2010). These weak relationships occur, in part, because the trait-vital rate relationships are affected by environmental conditions, which are rarely taken into account. For example, chlorophyll concentration may misrepresent a plant’s growth rate when its access to light or soil resources varies. In such cases, photosynthetic rate would be a better indicator of growth rate. Finally, and most damningly, the interpretation of functional traits is complicated by inter-correlations among traits (Díaz et al., 2004, 2015), and their potential for simultaneous associations with stabilising or equalising differences between species (Kraft, Godoy, & Levine, 2015).

Two ways forward

'Hard' functional traits

We see the use of 'hard' functional traits and of physiological tolerances as complementary methods to extend the demographic framework (Craine et al., 2012; Violle et al., 2007). With hard traits, one can predict population growth rates and interaction coefficients among species. They are a useful substitute in the many cases when demographic data are not available or too costly to collect, and they can be parameterised in models to predict community dynamics. The strength of this approach is proportional to the strength of the relationship between the functional trait(s) assessed and vital rates. Thus, we echo the advice of Díaz et al. (2004) for investigators to use functional traits as mechanistically related as possible to vital rates.

The use of hard functional traits come with two caveats. First, as they are associated with actual, rather than potential vital rates, environmental conditions influence their expression more than soft traits. To extend the previous example, the soft functional trait of chlorophyll content is relatively independent of abiotic conditions at the time of measurement, whereas photosynthetic rate is highly context-dependent (Pérez-Harguindeguy et al., 2013). Thus, the signal that 'hard' traits provide can be noisy, and can only be interpreted in the context of environmental data. Thus, using them effectively requires not only their quantification, but also determining the extent of their variation over relevant environmental gradients. Moreover, as they are usually tissue specific, rather than integrating over the entire organism, functional traits may trade off among the tissues of an organism, obscuring their interpretation (Kraft, Godoy, & Levine, 2015).

Physiological tolerances

We further suggest the use of whole-organism physiological tolerances (also referred to as physiological traits; Baltzer et al., 2008) to predict community dynamics. A physiological tolerance is defined as the critical level of a particular resource or environmental condition at which an organism can survive for an extended period (Craine et al., 2012). In other words, it is the whole-organism compensation point for that resource or condition. The relevant tolerances to assess will vary depending on the organisms of interest and the environmental context. They have been intensively investigated for certain taxonomic groups, such as lizards and other ectothermic vertebrates (Buckley & Jetz, 2008; Kearney & Porter, 2009), whereas as other taxa such as plants have received less attention (but see, for example Koehler, Center, & Cavender-Bares, 2012).

Physiological tolerances differ from functional traits in that they integrate the response of the entire organism to their environment, rather than being specific to a particular tissue (Craine et al., 2012). For example, one can measure drought tolerance as the difference in times to death between field capacity and un-watered conditions (Kursar et al., 2009), rather than as the tissue-level functional traits of leaf area, leaf water potential or stem vulnerability to embolism (Pérez-Harguindeguy et al., 2013). Physiological tolerances do not, however, indicate the organ-level mechanism(s) by which low-resource conditions are tolerated. Therefore, it can be useful to measure them in conjunction with functional traits to infer the mechanisms underlying changes in vital rates and therefore population dynamics.

A great advantage of studying physiological tolerances is that they explicitly link vital rates to environmental conditions, making it possible to predict how community dynamics will vary over environmental gradients. The most-relevant environmental gradients over which population growth rates and interaction coefficients vary will generally also be those most relevant for the assessment of physiological tolerances (Kearney & Porter, 2009). One can investigate physiological tolerances to the low availability of resources such as light or nutrients, or to abiotic conditions, such as cold temperatures, flooding duration, or fire intensity. The interpretation of such tolerances differs, in that the former are reduced by competitors, whereas the latter are independent of the presence of competitors. Tolerance can be evaluated as a change in individual performance along a gradient of resource availability, even as interaction coefficients can be inferred as the degree to which an individual reduces the availability of a resource to other individuals. Interaction coefficients measured through the assessment of physiological tolerances thus are closely related to the “effect traits” of Lavorel & Garnier (2002). One can simultaneously estimate physiological tolerances and assess how interaction coefficients vary over environmental gradients by exposing individuals of a focal species to a range of resource availabilities, while simultaneously varying the density of the aggregate community around each focal individual and monitoring the availability of the relevant resource. No such study has been performed, to the best of our knowledge, as the logistical challenges involved in doing so would be substantial. Note that tolerances of abiotic conditions, such as temperature, would be less uninformative in this regard, as they are rarely affected by the presence of competitors. Exceptions could include cases in which competitors limit the access of organisms to refuges or microclimates, for example, safe shelters from elevated temperatures. Physiological tolerances of low resource availability therefore complement the use of multiple functional traits by linking performance of whole organisms to population growth rates and interaction coefficients over environmental gradients.

Physiological tolerances can be assessed observationally or in field-based experiments, for example using common gardens or reciprocal transplantations (Craine et al., 2012). Purely observational studies can be stymied by atypical climatic conditions, however. For example, flood tolerance may be assessed by transplanting tree seedlings into a floodplain, but floods vary in size and duration, potentially clouding the relationship between vital rates and particular environmental conditions (Fortunel, Paine, et al., 2016). Thus, physiological tolerances are more informatively assessed in experimental settings such as laboratories, controlled environment facilities, or glasshouses, depending on the target organisms. Regardless of the setting, the conditions and resources evaluated must be relevant to field conditions, ideally spanning the entire natural range. The assessment of physiological tolerances is hampered by a lack of standard protocols, which has led to much debate about measurement techniques (for shade tolerance, see Valladares & Niinemets, 2008). Establishing a consensus around experimental protocols for estimating physiological tolerances should be a top priority.

A final challenge for the use of both physiological tolerances and hard functional traits is that their measurement is typically labour-intensive, limiting the number of species that can be feasibly studied. This issue can be addressed in three ways. First, the careful selection of study species can yield community-level insight.

In species-rich communities, it is advisable to study relatively common species, as they represent the majority of the individuals present and are the species most likely to interact. Interactions among rare species are by definition rare, outside of specialised host-parasite or mutualistic relationships. It is also advisable to select species with typical functional traits, as these are most representative of the community as a whole. A second way to address this issue is to assess soft functional traits together with hard traits or physiological tolerances. This requires little additional effort and allows the relationships among traits, and between traits and tolerances, to be assessed. Thereby, the enormous amount of soft trait data already available can be leveraged to yield further insight into community dynamics (Kattge et al., 2011). Third, the use of standard measurement protocols would facilitate sharing data among studies (Craine et al., 2012). Additionally, depending upon study design, certain species, for example invasive or endangered ones, may need to be included. Regardless, logistical constraints will rarely permit all co-occurring species to be investigated, imposing an inevitable loss of precision in predictions of community dynamics.

The beginning of the physiological tolerance approach is illustrated by Maynard et al. (2015), who correlated the distributions of three termite species with climatic variables across the eastern United States. They demonstrated dramatic interspecific variation in thermal tolerances, then mined the ecological literature to determine the abiotic and biotic predictors of each species’ distribution. Maynard et al. (2015) identified the primary correlates of termite distribution and abundance, illuminating the gaps in knowledge and setting the stage for experimental studies to predict the dynamics of temperate termite communities. Engelbrecht and colleagues, on the other hand, illustrate an end of the process, by predicting tropical forest community composition on the basis of drought tolerance. As forests on the Isthmus of Panama span a strong rainfall gradient, Engelbrecht et al. (2007) assessed the drought sensitivity of tree seedlings in dry and irrigated plots in a common garden. They coupled these observations with data on species distributions and soil moisture availability. Drought sensitivity predicted species distributions at regional (Engelbrecht et al., 2007) and local scales (Comita & Engelbrecht, 2009), owing to interspecific variation in mortality rates during droughts (Kursar et al., 2009). Thus, changes in soil moisture induced by global climate change are likely to alter tree distributions and community dynamics.

Case studies

Community dynamics on ephemeral patches: a case study of Sepsidae (dung flies)

Although most recent empirical work on community dynamics has focused on plants, there is considerable scope for extending the demographic framework to predict the dynamics of animal communities. Among the most tractable of animal communities are those comprised of short-lived species that complete their life cycles on discrete ephemeral patches of organic matter (Horn & MacArthur, 1972). Ephemeral patch communities encompass a high proportion of global biodiversity and include species that rely on carrion, dung, deadwood, plant tissue, fungi, fruit, flowers, short-lived water bodies, or host organisms to complete their development. Such communities are often highly species-rich despite strong competition and a lack of obvious niche partitioning within patches, making species coexistence especially intriguing (Finn, 2001). They are often highly amenable to experimentation, as the rapid turnover of patch resources facilitates community manipulation, sampling, and replication, and the patch environment itself can typically be controlled and measured during observation. Obtaining population size estimates for ephemeral patch competitors in the field, on the other hand, is often prohibitively difficult.

The coexistence of competitors in ephemeral patch communities is widely assumed to be dominated by the stabilising mechanism of intraspecific versus interspecific aggregation (Chesson, 2000a; Duthie, Abbott, & Nason, 2014, 2015). In general, when conspecifics aggregate within or among patches, intraspecific competition increases relative to interspecific competition, facilitating coexistence. Mechanisms causing conspecific aggregation include the behaviour of females ovipositing onto patches in clutches (Takahashi, 2007), and variation among species in patch attractiveness or accessibility, which generate spatial and temporal heterogeneity in species distributions (Chesson, 2000a; Duthie, Abbott, & Nason, 2014; Heard, 1998). The mechanisms modulating aggregation may be directly linked to hard functional traits, such as individual longevity, wing loading, egg load and larval feeding rate, enabling the prediction of community dynamics (e.g., Duthie, Abbott, & Nason, 2015).

Black scavenger flies are a family of flies (Sepsidae, Diptera) especially amenable to a trait-based approach to predict community dynamics. Sepsids occur worldwide, and 10 species that occur in Scotland form the basis of this case study. Flies are easily located and collected while mating on dung in the field and can be maintained in large numbers under laboratory conditions. We measure traits hypothesised to affect aggregation, and therefore competition, under controlled conditions. The malleability of dung pats and short generation time of flies facilitate the estimation of population growth rates and interaction coefficients through pairwise invasion experiments across a density gradient of resident species (Fig. 2). Unhatched eggs and larvae are collected from dung to measure the sensitivity of each developmental stage to competition (Blanckenhorn et al., 2013). Moreover, we measure dung mass before and after the invasion experiments to estimate decomposition rates, thereby linking species composition and functional traits to a key ecosystem function. Consequently, Sepsids are a promising model system to address fundamental questions in community dynamics and ecosystem functioning.

We use Sepsidae to extend the demographic framework as well. Following the approach of Kraft et al. (2015), the set of functional traits measured on each species is conceptualised as points in multidimensional trait space. Then, competition coefficients are correlated in multidimensional trait space with niche differences and fitness differences between species pairs. This approach can identify the functional traits that are most relevant to coexistence (Table 1), and provides a whole-organism perspective that is critical to consider, because it cannot be assumed that species are simply the sum of univariate traits (Kraft, Godoy, & Levine, 2015). Rather, combined effects of traits might be critical for predicting both niche differences and fitness differences between species. By adopting this whole-organism perspective, it should be possible to predict the recruitment of Sepsidae species from field populations of ephemeral patch competitors.

The manipulability of this system also offers a promising way forward to predict community dynamics under changing environmental conditions using the demographic framework, and for linking demography to functional traits. The short generation time of Sepsids enables multiple invasion experiments to be performed simultaneously under controlled environmental conditions (Fig. 2). Though time-consuming, invasion experiments to estimate all intrinsic population growth rates and interaction coefficients can tractably be replicated across an environmental gradient. For example, temperature strongly affects the functional traits of Sepsids, including body size and development time (Blanckenhorn et al., 2013), and could therefore modulate their population growth rates and interaction coefficients. Measuring these traits and parameters across a range of temperature permits us to estimate the sensitivity of community dynamics to environmental change. Such knowledge would be valuable for better understanding and predicting the resilience of communities to environmental change.

Controls on distribution: a case study of tropical trees

In tropical forests, water and light are two of the most important resources shaping the vital rates of individual trees, and thus their distributions along environmental gradients and community dynamics (Baltzer et al., 2008; Engelbrecht et al., 2007; Valladares & Niinemets, 2008; Wright et al., 2010). As habitat fragmentation, drought frequency and intense rainfall are set to increase in tropical regions, a mechanistic understanding of the degree to which water and light availability interact to control community dynamics will be essential for forest managers to mitigate potential biodiversity loss.

Seeking strong predictors of vital rates and species distributions, we focus on whole-plant tolerances to low resource availability and extreme environmental conditions (Craine et al., 2012). We aim to predict vital rates, and thus community dynamics, in areas for which demographic data is unavailable. More specifically, the aim of this case study is to assess the degree to which physiological tolerances predict observed spatial patterns of vital rates and community compositional turnover. We hypothesise that integrating physiological tolerances with environmental data will explain variation in species distributions at the landscape level, as well as predict changes in species distributions under different climate scenarios.

The rain forests of the Paracou Research Station, French Guiana, provide an ideal situation to assess the influences of light and water availability on the community dynamics of tropical trees. Permanent plots have been established in which all trees > 10 cm diameter at breast height have been censused every 1-2 years since 1984. Hydrology & light availability also have been characterised in these plots (Wagner et al., 2012). The survival and growth of saplings of 25 common tree species have been monitored since 1992 in subplots nested within the tree plots (Fig. 3a, b). This abundance of data allows us to characterise resource availability, species distributions, and the vital rates of individual trees across the landscape. From observation alone, however, the relative importance of these factors in determining the distribution and relative abundance of each species is not evident (Fig. 3b). Stated more precisely, the observed turnover in species composition between floodplain and plateau forests could occur because floodplain-associated species cannot tolerate the intensity of seasonal drought on the plateaux, or plateau-associated species may be intolerant of the flooding regime in the floodplain (Fortunel, Paine, et al., 2016).

We established a shadehouse experiment to assess the physiological tolerances of tree seedlings to drought, flooding and shading (Fig. 3c). We work on seedlings because of their experimental tractability, and also because seedlings are expected to be more sensitive to fluctuations in soil water availability than adult trees. We use shade-cloth to vary light availability over the range found in the forests and impose three levels of water availability: drought (no watering since the commencement of the study), flooding (water maintained above the soil surface) and watering to field capacity, in a factorial split-plot design. For each of 11 species, growth and survival are monitored at least weekly. We generate indices of tolerance to flooding, drought and shading based on the differential survival and growth of individuals in the various experimental treatments (Engelbrecht et al., 2007; Kursar et al., 2009). We also measure a set of functional traits associated with the tolerance of drought, flooding and shade, to assess their associations with the relevant physiological tolerances (Table 1). The location of each individual in the shade houses is mapped, allowing us to assess the effects of neighbourhood composition on individual performance. Even so, our estimates of interaction coefficients between species are weak, because the study does not include variation in neighbourhood density. Including systematic variation in neighbourhood composition and density in the experimental design would be more logistically challenging but would provide stronger estimates of interaction coefficients.

We will predict the vital rates of growth and survival observed in the field as a function of topographic position and physiological tolerance indices. We expect statistical interactions between topographic position and physiological tolerances. For example, if drought is the primary mechanism generating species turnover, then we would expect elevated mortality risk for drought-intolerant species, but only on the plateaux, which are relatively dry (Fig 4d). Once such relationships are characterised for flooding, shading and drought, we will build individual-based and integral projection models to predict the dynamics of our focal species under scenarios of changing precipitation (Adler, Ellner, & Levine, 2010).

Conclusions

Our motivation is to enhance the generality and tractability of predicting community dynamics, especially for species-rich communities, on the basis of the Chesson-Adler demographic framework. Although powerful, this framework is difficult to operationalise in its raw form, and has thus primarily been applied to low-diversity annual plant communities (but see Adler, Ellner, & Levine, 2010). Phylogenetic data and soft functional traits have been useful for the analysis of community structure but are less informative for the prediction of community dynamics. Instead, we advocate the use of hard functional traits and physiological tolerances, as they provide opportunities to predict community dynamics without a complete reliance on demographic data. Moreover, they provide a mechanistic way to incorporate the variation imparted to ecological communities by environmental gradients, over which population growth rates and interaction coefficients vary. Incorporating environmental variation is essential for making predictions in the face of anthropogenic effects, especially over large spatial or temporal scales. Given the urgent need for ecological forecasting (Clark et al., 2001), we hope that ecologists will adopt these approaches, extending the range of ecosystems for which accurate predictions of community dynamics are possible.

Author contributions

CETP conceived the ideas for this review and lead the writing of the manuscript. AD and ABD contributed the case studies. All authors contributed critically to the drafts and gave final approval for publication.

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Table

Table 1. Hard versus soft traits. Examples of ‘hard’ and ‘soft’ functional traits associated with key vital rates for the animals and plants used in the case studies. In general, it is easier to measure hard functional traits and vital rates on animals than on plants. For example, fecundity estimates are relatively easy to measure for many insects (as egg load), but obtaining the equivalent data for long-lived trees may require decades of field observations of seed production and complicated modelling (Clark et al., 2010; Purves et al., 2008).

	Dung flies		**Tropical rain forest trees**	
Vital Rate	**Hard trait**	**Soft trait**	**Hard trait**	**Soft trait**
Survival	Life span	Ovigeny index	Life span	Wood density
Growth	Ingestion rate	Body size	Photosynthetic rate	Foliar chlorophyll concentration Wood density Maximal stature
Fecundity	Egg load	Abdominal mass	Seed production	Above-ground biomass

Figures

Figure 1. Milestones in the prediction of community dynamics. Each milestone is indicated by a key reference in the development of that concept or technique, rather than its first mention in the literature. See also Figure 3.6 in Vellend (2016).

Figure 2. Overview of the dung fly case study. We study 10 species of Sepsidae co-occurring in Scotland to link species functional traits to biodiversity and the ecosystem function of decomposition. Key functional traits are measured for A) fly eggs, B) larvae and C) adults. D) We perform invasion experiments in which a mated female of species i (black) oviposits on dung patches that vary in the density of ovipositing females of species j (red). We repeat this experiment for all combinations of species i and j (including $i = j$) over a temperature gradient. Intrinsic growth rates (λ_i) can be calculated from the number of offspring that eclose from empty patches, and competition coefficients can be calculated by estimating how the eclosion rate is reduced by increasing conspecific (α_{ii}) or heterospecific (α_{ij}) density. Values of λ_i, α_{ii}, and α_{ij} can then be used to calculate niche differences and fitness differences. Dung decomposition can be estimated from the difference in dung mass from oviposition to eclosion. Differences in trait values between all pairwise combinations of species i and j will be calculated. Univariate correlations between each of these trait value differences and stabilising niche and average fitness differences can be estimated, and model selection can be used to identify combinations of traits that best describe niche and fitness differences (Kraft *et al*. 2015). Similarly, trait values and differences can be associated with decomposition rates. Artwork by A. C. Duthie.

Figure 3. Overview of the tropical trees case study. A) The abundance of saplings of 25 common canopy trees has been monitored eight times since 1992 in 960 permanent plots at Paracou Research Station, French Guiana. The sapling plots are distributed in an 8x8 grid in each of 12 6.25 ha permanent tree plots, in which light availability, soil moisture and flooding frequency have also been assessed. Point types and colours indicate the topographic position of each plot. B) The abundance of one species (*Virola michelii*, Myristicaceae), is proportional to the size of the black circles. C) Methods for physiological tolerance testing, in which 11 target species (indicated by varying point types) are factorially exposed to varying water and light availabilities. D) Prediction of field mortality risk from estimated species physiological tolerances. The hypothetical result shown in panel D would indicate that interspecific variation in drought tolerance contributes far more to spatial variation in species composition than does variation in the tolerance of flooding or shading, as drought intolerant species suffer elevated mortality rates, but only on the relatively dry plateaux.