



# Linking local species coexistence to ecosystem functioning: a conceptual framework from ecological first principles in grassland ecosystems

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## Contents

1. Introduction	266
2. Jointly emerging local coexistence and ecosystem functioning from ecological first principles	269
2.1 Abiotic conditions	270
2.2 Biotic conditions	272
3. Population level effects of abiotic and biotic conditions on fecundity, growth, and survival	273
3.1 Abiotic conditions	274
3.2 Biotic conditions	278
4. How ecological first principles influence trade-offs between fecundity, growth, and survival and in turn influence local coexistence and ecosystem functioning	279
4.1 Productivity	281
4.2 Root decomposition	284
5. Conclusion	285
Author contributions	286

Acknowledgements	286
References	286
Further reading	296

## Abstract

One of the unifying goals of ecology is understanding the mechanisms that drive ecological patterns. For any particular observed pattern, ecologists have proposed varied mechanistic models. However, in spite of their differences, all of these mechanistic models rely on either abiotic conditions or biotic conditions, our “ecological first principles”. These major components underlie all of the major mechanistic explanations for patterns of diversity like the latitudinal gradient in diversity, the maintenance of diversity, and the (often positive) biodiversity-ecosystem functioning relationship. These components and their interactions alter the dynamics of plant populations, which ultimately determine local coexistence at the community level, and functioning at the ecosystem level. We present a review, starting from ecological first principles of the ways in which ecosystem functioning may be linked to local coexistence in plant communities via mutual effects on and reactions to the abiotic and biotic conditions in which they are imbedded.



## 1. Introduction

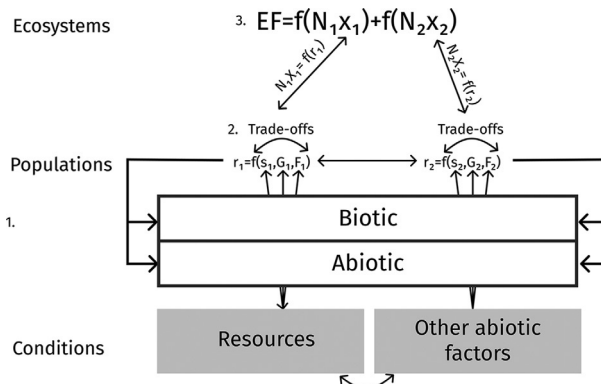
Humans are driving drastic environmental changes including unprecedented global biodiversity loss ([Carneiro da Cunha et al., 2019](#); [Millenium Ecosystem Assessment Ecosystem and human well-being: synthesis, 2005](#); [Newbold et al., 2015](#); [Tittensor et al., 2014](#)). Many studies predict that the rate of biodiversity loss will accelerate in the coming decades (e.g., [Pereira et al., 2010](#); [Pimm et al., 2014](#)). Small-scale biodiversity experiments have shown that certain ecosystem functions typically decline after random species loss in experimental communities (reviewed by [Tilman et al., 2014](#)). This decline of ecosystem functioning at the local community level is often interpreted to mean that regional or global biodiversity loss will also result in declines in ecosystem functioning at global scales (e.g., [Hooper et al., 2012](#)). The effect and extent of diversity loss and compositional change in nature, however, are also thought to be determined by the interplay between local and regional processes that affect local abundance and thereby local ecosystem functioning. Understanding how these processes interact to affect ecosystem functioning is crucial for predicting the consequences of global biodiversity loss and local and regional compositional shifts ([Barry et al., 2019](#)).

At the local scale, coexistence between species arises from population-level interactions with abiotic conditions (including resources and other abiotic factors) and the biotic community (reviewed by Holt, 2013, see also Chase and Leibold, 2003). These interactions are characterized by feedbacks that stabilize local coexistence between populations by preventing dominance and allowing rare species to persist (local stable coexistence, Chesson, 2000, 2018; Ellner et al., 2019; Holt, 2013). These conditions may also allow for long term persistence rather than long term stable coexistence. Two populations of species may coexist because they partition resources, mediate stressful abiotic conditions for each other, or are controlled by species-specific enemies (Bertness and Callaway, 1994; Brooker et al., 2008; Bruno et al., 2003; Holt, 2013; Palmer, 1994; Wright, 2002). Here, we do not differentiate between long term stable coexistence and unstable persistence, rather we refer to both as “local coexistence” throughout. We define this local coexistence as “the state of two or more species being found in the same place at the same time” (Holt, 2013). We exclude, however, coexistence supported by dispersal from outside of the local community; we consider these “meta-community dynamics” to be beyond the scope of this paper.

While local coexistence is a necessary condition for locally diverse communities to exist, it is not a sufficient condition for said biodiversity to enhance ecosystem functioning. Rather, circumstances may result in local coexistence that variably increases or decreases ecosystem functioning with increasing species richness (Becker et al., 2012; Huston, 1997; Loreau, 2004; Tilman et al., 1997). Importantly, the likelihood of a positive or negative relationship between biodiversity and ecosystem functioning depends on the function that is being measured and the coexistence mechanisms at play. Some evidence suggests that negative relationships between ecosystem functioning and species richness may more commonly result from meta-community dynamics which are not examined here (Leibold and Chase, 2018; Mouquet and Loreau, 2003; Vandermeer, 1981). Further, Turnbull et al. (2013) demonstrated that diversity can enhance productivity even when long-term stable local coexistence is not possible because stabilizing resource niche (sensu Chesson, 2000) differences between species were not sufficient to overcome fitness differences between species. That is, biodiversity may enhance productivity when species persist together in the short-term but do not stably coexist.

We propose that local coexistence between species and the effects of species on ecosystem functioning are inherently linked by mutual dependence

and effects on abiotic and biotic conditions operating at the population level. Here, we describe a framework for the link between local coexistence and ecosystem functioning where both jointly emerge from three major population-level life-history variables (fecundity, growth, and survival) that are simultaneously influenced by abiotic and biotic conditions (ecological first principles, Fig. 1). To do so, we first review how abiotic and biotic conditions have traditionally been used to describe local coexistence and enhanced ecosystem functioning in diverse natural communities. Second, we review how abiotic and biotic conditions determine the fecundity, growth, and survival of populations. Finally, we discuss how trade-offs within and between populations may lead to local coexistence between species and how ecosystem functioning may be altered by these population-level dynamic trade-offs.



**Fig. 1** Plant population growth and fitness are regulated by abiotic and biotic conditions. Resources are needed to build and maintain tissues but these processes are influenced by competitors, consumers, mutualists and abiotic factors such as temperature and pH. Different vital rates ( $r$ , e.g., growth—denoted with a “G” in the above figure, fecundity—denoted with an “F” in the above figure, survival—denoted with an “S” in the above figure, or age or stage classes) may be sensitive to different factors, and when population growth is not negative on average, the population will persist (population size = “N” above). Diversity arises if multiple populations differ in their traits and their tradeoffs for various combinations of resources, biotic and abiotic factors. The process of growth also sets up feedbacks between populations and the environment. Local coexistence is characterized by feedbacks that tend to stabilize population growth: preventing dominance and buffering rarity. That is, all populations have positive or at least zero average fitness across the range of resources and conditions they experience. The functioning of individual populations, modified by interactions and environmental factors (“X” above) emerges from the collective population-level processes and how abiotic and biotic conditions affect basic vital demographic rates. The consequence of interacting and coexisting species is the aggregate ecosystem function (“EF” above).

Reviewing the links to the abiotic and biotic conditions as a mutual cause for local coexistence and ecosystem functioning is the major contribution of our review. Formerly, local coexistence mechanisms and mechanisms for biodiversity–ecosystem functioning relationships have been separately discussed in spite of their high overlap. When these links have been made explicit (e.g., [Carroll et al., 2011](#); [Turnbull et al., 2013, 2016](#)), the focus was largely on a single local coexistence mechanism and ecosystem function. Our review provides a general overview for how local coexistence and ecosystem functioning can inform each other and be informed by abiotic and biotic conditions. Thinking of these sets of mechanisms in a more synthetic way allows us to begin to explore how environmental conditions may mutually drive both local coexistence and ecosystem functioning simultaneously, rather than independently. Further, these conditions are one of the key differences between experiments, from which the majority of our understanding of biodiversity–ecosystem functioning relationships come and the natural systems in which nonrandom biodiversity loss is problematic. Finally, understanding how abiotic and biotic conditions influence population level trade-offs that may favour coexistence while simultaneously decreasing ecosystem functioning and vice versa is crucial for predicting the consequences of biodiversity change on ecosystem functioning.



## **2. Jointly emerging local coexistence and ecosystem functioning from ecological first principles**

Various mechanisms have been proposed to explain species coexistence ([Aarssen, 1983](#); [Chesson, 2000](#); [Gause, 1934](#); [Holt, 2013](#); [MacArthur, 1969](#); [MacArthur and Levins, 1967](#); [MacArthur and Wilson, 1963, 2001](#); [Palmer, 1994](#); [Shmida and Wilson, 1985](#); [Tilman, 1982](#); [Wright, 2002](#)). Many of these local coexistence mechanisms are also cited as potential drivers of BEF relationships (reviewed in [Barry et al., 2019](#); [Tilman et al., 2014](#); [Turnbull et al., 2016](#)). While these mechanisms may influence local coexistence and ecosystem functioning independently, these mechanisms are inherently linked by their dependence on their abiotic and biotic conditions. We consider primary effects of the abiotic environment on plant species that occur within a trophic level to fall under the category of “abiotic conditions” while interactions with organisms at other trophic levels to fall under the category of “biotic conditions”. These categories are similar to those proposed by [Chase and Leibold \(2003\)](#) but we believe that our more general categories better capture the diversity of dynamics

within the categories. Further, using these categories we avoid the term “stress” which is difficult to define and does not capture the full spectrum of ways in which nonresource abiotic conditions can affect population dynamics.

## 2.1 Abiotic conditions

### 2.1.1 Resources

Here, we define resources as anything that is needed by a plant and where use by the plant precludes other individuals from using the same unit of resources (Chase and Leibold, 2003). Heterogeneity in resources may stabilize interactions between plant species allowing them to coexist via resource partitioning in space, time, or on different resource types (Chesson, 2000; Tilman, 1982). There is some empirical evidence that this type of resource partitioning may allow for local coexistence between populations. For example, studies have found that the addition of nutrients can reduce limitation of multiple resources and thus reduce the number of coexisting species, indicating that limitation of multiple resources allowed these species to coexist (Harpole and Tilman, 2006; Harpole et al., 2016). Theoretical work allowing populations of interacting species to develop according to Lotka–Volterra models demonstrated that local coexistence resulting from lower inter- than intraspecific competition among species can be related to differentiation between species in their resource use (Loreau, 2004; Vandermeer, 1992).

Partitioning resources in space, time, or by type (resource partitioning sensu Schoener, 1970, 1974, also called resource complementarity) is also hypothesized to drive enhanced ecosystem functioning in more diverse plant mixtures. Using a mechanistic resource–competition model, Tilman et al. (1997) showed that allocation trade-offs that favour local coexistence cause more efficient resource exploitation, leading to higher productivity in more diverse communities. Similarly, Carroll et al. (2011) used a modified version of MacArthur’s consumer–resource model (MacArthur, 1970, 1972) and showed that promoting local coexistence by increasing differences in terms of resource use also increases overyielding in more diverse communities. However, empirical evidence for resource partitioning in biodiversity–ecosystem functioning experiments is limited (reviewed by Barry et al., 2019). Mueller et al. (2013) and Ravenek et al. (2014) found evidence that plants allocate belowground biomass in a way that is consistent with resource partitioning. However, using nitrogen tracers, von Felten et al. (2009) found evidence that species may partition nitrogen across a diversity gradient but

that this resource partitioning was not associated with increases in certain ecosystem functions (notably nitrogen uptake). Finally, [Jesch et al. \(2018\)](#) found that community resource uptake of nitrogen and potassium likely increases with biodiversity but this was not associated with evidence of resource partitioning across a species–richness gradient.

### **2.1.2 Other abiotic factors**

Other abiotic conditions may allow for local coexistence between species, especially if these conditions vary over time and space. If species differ in their performance across environmental conditions like temperature, and if these conditions vary across space or time, then these species can coexist ([Chesson, 2000, 2018](#); [Holt, 2013](#)). In addition to their effect on resources, disturbances over time may also allow for local coexistence between populations via alterations to abiotic conditions that are not traditional resources (but see [Fox, 2013a](#) for a discussion of how such local coexistence might be attributed to changes in average mortality rates and the subsequent responses [Fox, 2013b](#); [Sheil and Burslem, 2013](#)). For instance, in tropical forests, gap formation causes heterogeneity in abiotic conditions, such as light availability, allowing species that may be outcompeted under high shade to recruit and persist ([Connell, 1978](#); [Schnitzer and Carson, 2001](#)). [Denslow \(1995\)](#) provided support for this idea, showing that plant diversity in tropical forests is higher in areas of high stand turnover.

Interactions between populations of plants and their abiotic conditions are also hypothesized to drive enhanced ecosystem functioning in more diverse mixtures. [Yachi and Loreau \(2007\)](#) and [Isbell et al. \(2018\)](#) suggest that species richness can provide a type of temporal or spatial insurance effect against environmental fluctuations and disturbances and that this can result in higher stability over time and an increase in mean functioning. Further, [Loreau et al. \(2003\)](#) suggest that if locally adapted species are able to migrate across an abiotically heterogeneous landscape then local ecosystem functioning may be enhanced. There is some empirical evidence that these types of insurance effects may occur in grasslands ([Isbell et al., 2011](#)) where species redundancy was shown to decrease over time as the production of biomass increased in the face of environmental variability.

In addition to the heterogeneity of abiotic conditions, their spatial and temporal extent can also result in increases in the number of species that can coexist and the ecosystem functioning derived from the increased species richness. For example, longer duration of conditions beneficial for plant growth can lead to more asynchronous phenologies. Additionally,

deeper soils can accommodate more nonoverlapping rooting depths of different plant species by providing vertical space for roots to occupy (Dimitrakopoulos and Schmid, 2004). On a temporal scale, Oehri et al. (2017) found that increases in growing-season length in Switzerland due to global warming was correlated with plant species richness (Oehri et al., 2017).

Within the same trophic level, positive interactions between species (facilitation) promote local coexistence by promoting population growth when rare (Bruno et al., 2003). Empirical examples of this dynamic are common in stressful environments (Bertness and Callaway, 1994). For example, in arid landscapes nurse plant effects whereby one plant ameliorates the microclimate for a whole community are relatively common (reviewed by Brooker et al., 2008). This microclimate amelioration in diverse mixtures also allows mixtures to perform better than lower diversity communities (Barry et al., 2019; Wright et al., 2017b).

## 2.2 Biotic conditions

Biotic interactions between members of different trophic levels, which we refer to here as a plant's "biotic conditions", also allow for coexistence between plant species in a community. For example, mycorrhizae or other beneficial interaction partners of plants may also ameliorate the local microclimate or increase resource availability (Ferlian et al., 2018; Khan and Kim, 2007; Latz et al., 2012; de la Peña et al., 2006; Wagg et al., 2011). Between trophic levels, specialist pests and pathogens may reduce the abundance of common species, while indirectly supporting others. Rare species are less likely to encounter species-specific pests and pathogens than common species (the Janzen–Connell effect, reviewed by Carson et al., 2008; Comita et al., 2014; see also Connell, 1971; Janzen, 1970; Mangan et al., 2010; Mitchell et al., 2002), indirectly promoting population growth for rare species, a necessary condition for local coexistence. Empirical evidence suggests such cross-trophic density-dependent effects drive local coexistence in lakes, deserts, grasslands, marine ecosystems, and temperate and tropical forests (Anderson, 2001; Comita et al., 2010; Goldberg et al., 2001; Johnson et al., 2012, 2014; Ledo and Schnitzer, 2014; Lorenzen and Enberg, 2002; Mangan et al., 2010; Petermann et al., 2008; Schnitzer et al., 2011).

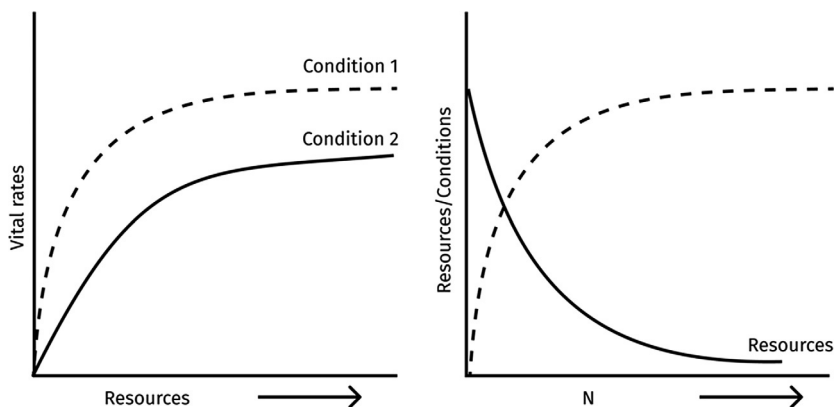
The influence of biotic conditions can also determine enhanced ecosystem functioning. In experimental systems, biotic feedbacks from other trophic levels have been shown to drive enhanced ecosystem functioning



for general belowground biota (Eisenhauer, 2012; Eisenhauer et al., 2012; Maron et al., 2011; Schnitzer et al., 2011; Seabloom et al., 2017), mycorrhizae (Klironomos et al., 2000; Van der Heijden et al., 1998; Wagg et al., 2011), earthworms (Eisenhauer et al., 2009), nematodes (Eisenhauer et al., 2010, 2011), and general aboveground biota (Ebeling et al., 2008; Seabloom et al., 2017).

### 3. Population level effects of abiotic and biotic conditions on fecundity, growth, and survival (Fig. 2)

For many of the above examples of how local coexistence and ecosystem functioning can simultaneously be driven by abiotic and biotic conditions, local coexistence and ecosystem functioning are determined by trade-offs between and within populations in terms of their growth, survival, and fecundity. Because fecundity, growth, and survival are considered to be three fundamental components of plant life-history, we refer to them as plant “vital rates” (Franco and Silvertown, 2004). Their means and variances determine the fitness of individuals and populations. Based on the assumption that plant species must allocate a certain portion of their limited resources to each of them, life-history theory predicts trade-offs among the different components of species life cycles (Obeso, 2002; Roff, 2000; Stearns, 2000). These trade-offs determine local coexistence and ecosystem functioning at the community level. Importantly, all coexistence mechanisms can affect all of these vital rates. The sum total of these effects determines coexistence within and between populations.



**Fig. 2** Abiotic conditions modify population vital rates. As the population size ( $N$ ) increases this will create feedbacks on resources and other abiotic conditions.

### 3.1 Abiotic conditions

#### 3.1.1 Resources

Resource availability may largely influence fecundity through allocation to reproductive tissues (Jongejans et al., 2006; Sugiyama and Bazzaz, 1998; Waite and Hutchings, 1982). Levels and ratios of mineral nutrients, light, and water may have direct physiological effects on plant growth and development (Weiner, 1988). Higher nutrient availability may lead to coupled growth responses involving increases in plant size and therefore higher seed production (Jongejans et al., 2006). Independent of these size-related responses, nutrient availability may also directly affect reproductive allocation or the mode of reproduction (sexual reproduction or clonal growth). Examples in the literature relating resource availability to plant reproduction show mixed results indicating that the effects are species-specific and modified by competition (e.g., Nicholls, 2011; Suter, 2009). The effects of elevated CO<sub>2</sub> on reproductive output have been documented in various studies at the stand level and at the level of individual plants. Further, reproductive allocation (He et al., 2005; Jablonski et al., 2002) and seed production decrease at elevated levels of CO<sub>2</sub>, although these effects vary significantly among species (HilleRisLambers et al., 2009; van Kleunen et al., 2006). Resource availability may also affect the timing of maturity. Biere (1995) showed in a study along a soil fertility gradient, for instance, that plants mature earlier in less fertile sites. Other studies have shown that individuals that postpone reproduction gained an increase in fecundity at first reproduction at fertile sites.

Resource availability is also a clear determinant of plant growth (Clarkson and Hanson, 1980). Plants preferentially allocate biomass to access limiting resources and thus grow more slowly if they have to invest more into roots (low nutrients) or stems (low light) than into assimilating leaves (Müller et al., 2000). Furthermore, the response of different species to resource availability may vary according to their life-history strategy. Species adapted to low resource availability often express a “slow” life-history strategy with low rates of resource uptake, high resource-use efficiency, and slow growth. In contrast, species adapted to high resource availability often exhibit a “fast” life-history strategy with high rates of resource acquisition and fast growth (Reich et al., 2003). Consequently, these “fast” life-history species are more successful in high-resource environments than in low-resource environments. One possible reason promoting the success of fast-growing exploitative species in favourable environments is their greater ability to respond plastically to variation in nutrient availability

(Crick and Grime, 1987). Further, plants may respond to elevated CO<sub>2</sub> by adjusting their photosynthetic processes and therefore leaf production and growth. However, these responses are species-specific due to different growth forms, patterns of resource allocation, different photosynthesis pathways (C<sub>3</sub> vs. C<sub>4</sub> plants) or organ and meristem development (Morison and Lawlor, 1999), all of which may change with time (Reich et al., 2018).

Changes in the pattern of supply and the amount of available resources can accelerate local species extinctions (e.g., Berendse and Elberse, 1990; Harpole et al., 2016; Tilman, 1987). For instance, persistent fertilization has been shown to decrease competition for nutrients belowground, while increasing competition for light by driving the development of denser and taller canopies of more productive plants (Harpole et al., 2017; Hautier et al., 2009). Such changes to plant communities are associated with more asymmetric competition for light and a higher probability that competitive exclusion will drive plant species with smaller statures or slower growth to local extinction (Tilman, 1987). Resource availability may also affect survival under different abiotic stresses, for example, a drought may increase mortality in well-fertilized plants due to low root-shoot ratios whereas increased CO<sub>2</sub> may allow plants to save water and thus reduce mortality risk under dry conditions (Reich et al., 2004; Wei et al., 2017).

Competition between plant species for resources may also indirectly impact fecundity, for example, interference competition for resources from neighbouring individuals. Such competition, if resources are limited, can result in delays in the onset of reproductive activity, alter the mode of reproduction between vegetative and sexual reproduction, or change the proportion of individuals in a population that produce offspring (van Kleunen et al., 2001; Wayne et al., 1999; Weiner, 1988). The effects of competition for resources on reproductive allocation are likely indirect. For example, Aarssen (2005) suggests that competition between plants can reduce growth and therefore reproductive output because plants take longer to reach size thresholds for reproduction.

### **3.1.2 Other abiotic factors**

Apart from resources, other abiotic conditions (e.g., light and temperature) determine together with plant traits (e.g., size, age) the probability of reproduction and thereby fecundity (de Jong et al., 1998). For example, Hansen et al. (2013) showed that dry conditions increased investment in reproductive biomass and that trade-offs between vegetative growth and investment

into reproduction are more pronounced under more stressful dry conditions. A study of the effects of light availability (Jacquemyn et al., 2010) found that the threshold size for initial flowering was three times larger in shaded than sunny environments. Further, some evidence suggests that plants flower more frequently over time and produce more fruits in brighter environments. Similarly, higher temperature has been documented to advance flowering phenology and reproductive allocation (He et al., 2005; Whittington et al., 2015).

Solar radiation, soil and air temperature also may have direct effects on plant growth while also interacting with each other and influencing resource availability. For example, under drought and heat stress, biological processes related to growth, such as rates of photosynthesis and respiration, are reduced. Drought may also reduce plant growth by decreasing soil-nitrogen and -phosphorus uptake (He and Dijkstra, 2014). In spite of the likely effect of these abiotic conditions, a meta-analysis across studies in arid environments showed that the effect of neighbouring plant species on growth of target plants was not dependent on abiotic stress level (in most cases water availability, Maestre et al., 2005).

In experimental plant communities, increased productivity of more diverse plant communities correlates with variable growth responses of individual species in terms of biomass production and plant size (HilleRisLambers et al., 2004; Marquard et al., 2009; Roscher and Schumacher, 2016; Roscher et al., 2007). Several studies in the Jena Experiment demonstrated that grassland species with clearly distinguishable individuals produce fewer shoots per genet in more diverse plant communities (Roscher et al., 2008b, 2011a,b; Thein et al., 2008) resulting in smaller genet sizes. Nevertheless, more shoots are produced per unit area in these diverse communities (Marquard et al., 2009; Thein et al., 2008) suggesting a trade-off between reduced growth and increased survival at the genet level induced by high community diversity. Analyses of foliar nitrate and carbohydrate concentrations as indicators of plant nutritional status indicated that increased light competition at increasing species richness correlated with decreased growth of individual plants in spite of increased productivity at the community level (Roscher et al., 2011a).

Abiotic factors are especially important for plant survival in early stages of the life cycle. For example, it has been shown that water availability is crucial for the survival of seedlings, with additional watering increased seedling survival most in open vegetation (de Jong and Klinkhamer, 1988; Eckstein,

2005). Multiple mechanisms have been suggested to explain the mortality of plants suffering from drought (McDowell et al., 2008) from hydraulic failure due to stomatal closure and subsequent carbon starvation to reduced resistance against biotic “mortality agents” such as pathogens and herbivores. Differential mortality of species in response to drought might have large demographic impacts on populations and shift species composition in response to climate change (Mueller et al., 2005).

For most plant species starting their life cycle from seeds, the risk of mortality is particularly high at the seedling or juvenile stages due to strong competition or abiotic stress (Harper, 1977). In most plant communities, positive (facilitation) and negative (competition) interactions occur simultaneously and their relative impacts on survival probability change with life stage (Eckstein, 2005; Kelemen et al., 2015; Wright et al., 2014). For example, survival of young plants has been shown to be positively influenced by the surrounding vegetation. This positive effect suggests that shading by neighbouring plants may be beneficial for some young plants because the protection against desiccation outweighs the reduction in photosynthesis (Semchenko et al., 2012). This effect may also occur because neighbouring plants reduce soil irradiance and therefore maintain more stable temperatures under severe temperature conditions (Wright et al., 2015). Alternatively, older plants in the same systems experience more negative effects (e.g., in wet meadow vegetation, Kelemen et al., 2015, in a grassland Wright et al., 2014). In experimental grasslands, for instance, it was found that at higher plant diversity where interactions between species of the same trophic level are more intense, grass tussocks were smaller. Furthermore, over a period of 4 years, changes in population sizes (i.e., numbers of individuals per area) indicated a negative population growth rate (i.e., decreasing number of plants) at high plant diversity suggesting that poor performing species were more likely to die and/or new individuals did not establish (Roscher et al., 2011a). It should be noted that in this case the experimental design was not substitutive with regard to the test species and included the test species in all communities at all diversity levels. This experimental design led to higher neighbour diversity being associated with more neighbours with similar resource requirements (Roscher et al., 2008a). In contrast, resident species in substitutive randomized biodiversity experiments on average will have more neighbours with similar resource requirements at lower than at higher diversity where they are planted at reduced density and may increase in size (e.g., Dimitrakopoulos and Schmid, 2004).

### 3.2 Biotic conditions

Interactions between trophic levels, such as herbivory, also influence plant fecundity (Obeso, 1993, 2002). Herbivory pressure can redirect resources to chemical defences from reproductive organs, resulting in decreases in the numbers of flowers and seeds produced (e.g., Louda and Potvin, 1995; Maron, 1998). Further, even when herbivores do not directly feed on reproductive tissue they may reduce seed production. Plant interactions with mycorrhizal fungi may also impact resource availability and allocation. For instance, these associations can reduce limitation for some resources while increasing limitation of others (like carbon). These associations depend on the biotic and abiotic context of the plant and therefore increase fecundity by allowing plants to reach a reproductive size threshold more quickly. However, the effects of mycorrhizal associations on seed production are not consistent, but rather vary with environmental conditions and plant density (Koide and Dickie, 2002).

Different biotic conditions such as plant competition, associations with microorganisms, herbivory, or fungal infestations, do not act in isolation, but exhibit complex interactions affecting plant growth. For example, Nitschke et al. (2010) found that reducing insect herbivory by spraying insecticides increased growth of transplants of *Centaurea jacea* in monocultures but not in plant communities of higher diversity. Plant antagonists such as herbivores or fungal pathogens are thought to promote plant community diversity through negative density-dependence reducing the abundance of dominant species. Faster-growing plant species are expected to be more susceptible to pathogens because of their lower investment in defence (Coley et al., 1985). Parker and Gilbert (2018) demonstrated in an experimental study that faster-growing species experienced greater fungal infestation. However, the impact of fungal infestation on growth was less severe, possibly because these faster-growing species were better able to compensate for fungal damage. Various microbial interactions with plants increase the ability of plants to acquire nutrients in different ways. First, mycorrhizae increase the surface area of roots by extending existing root length. Second, rhizobacteria enhance root growth and branching. Third, phosphate-mobilizing microorganisms (among others) stimulate metabolic processes that mobilize nutrients or nutrient supply. Finally, symbiotic rhizobacteria supply nitrogen via  $N_2$  fixation (Richardson et al., 2009). Further, a number of studies have demonstrated increased mortality under competition due to indirect effects of increased herbivory or diseases (Bell et al., 2006).



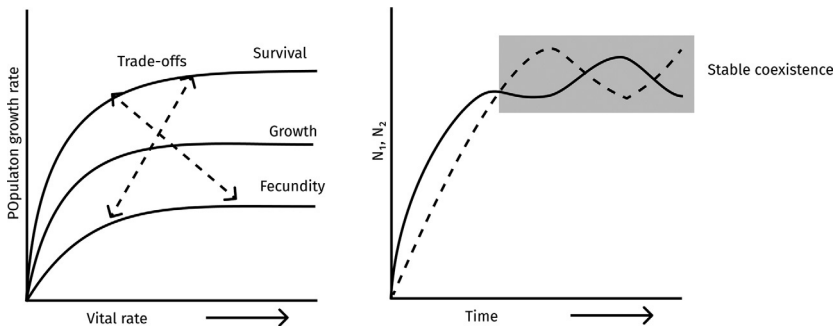
#### **4. How ecological first principles influence trade-offs between fecundity, growth, and survival and in turn influence local coexistence and ecosystem functioning**

Long-term biodiversity–ecosystem function experiments, like the Jena Experiment, provide excellent opportunities to explore the mechanistic links between ecosystem functioning and local coexistence dynamics. Understanding how changes to fecundity, growth, and survival change across diversity gradients at the population level enables us to understand how these factors influence local coexistence and ecosystem functioning simultaneously (see above). While there are many publications that confirm that increasing diversity alters community level biomass production which may be a reasonable proxy for growth, few studies examine population-level growth, survival, and fecundity across diversity gradients. Trade-offs between investment in fecundity, growth, and survival likely alter local coexistence between species in these experiments as well as ecosystem functioning simultaneously.

Community-level growth of resident plants generally increases with diversity via changes to community shoot density and biomass production (e.g., [Marquard et al., 2009](#); [Roscher et al., 2007](#) for grassland biodiversity experiments, [Barrufol et al., 2013](#) for forests, [Roscher and Schumacher, 2016](#) for communities with arable weeds). However, fecundity may decrease as plants grow more slowly, or flower and fruit development are delayed, and plants form fewer inflorescences per shoot in more diverse neighbourhoods. This may result in delayed reproduction as has been shown for transplants, i.e., colonizing plants ([Mwangi et al., 2007](#); [Nitschke et al., 2010](#); [Scherber et al., 2006](#)). In a biodiversity experiment with arable weeds (mostly annual species), the proportion of reproductive individuals decreased with increasing species richness and the associated increase in community density, i.e., a higher proportion of individuals failed to reproduce completely ([Roscher and Schumacher, 2016](#)). Finally, plant diversity and the presence of particular functional groups (i.e., legumes) also decrease the growth and survival of colonizers (but not residents) such as transplants of *Festuca pratensis*, *Plantago lanceolata*, *Knautia arvensis*, *Trifolium pratense* ([Mwangi et al., 2007](#)) or *Centaurea jacea* ([Nitschke et al., 2010](#) in the Jena Experiment). These negative plant diversity effects on colonizers were partly attributed to higher community biomass indicating a negative impact of

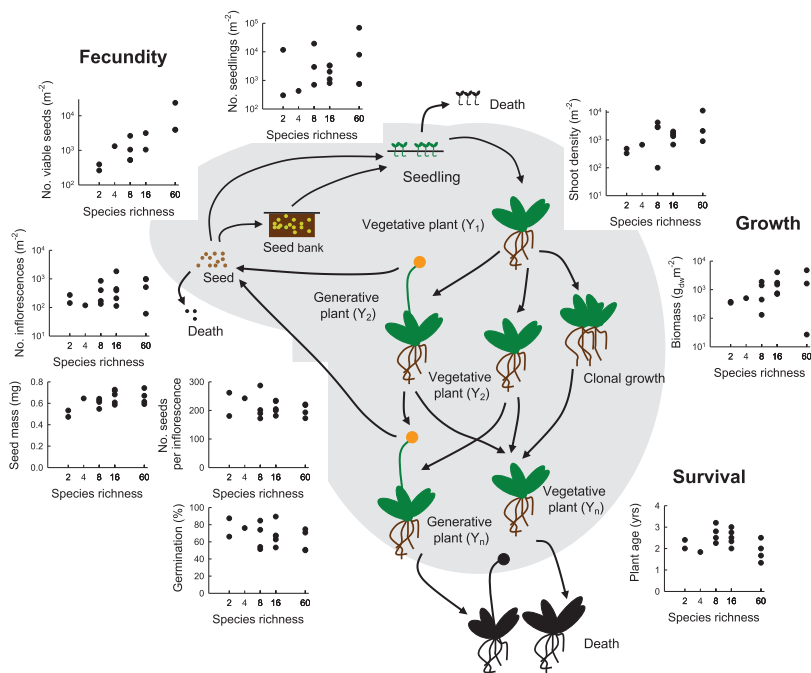
competition by a diverse neighbourhood. As an exception, [Scherber et al. \(2006\)](#) found positive effects of plant diversity on the survival of *Rumex acetosa* transplants in the same biodiversity experiment suggesting that the effect of plant diversity on survival is species-specific.

Trade-offs in investment toward fecundity, growth, and survival may determine species' ability to persist within a community and their potential to enhance ecosystem functioning ([Fig. 3](#)). For example, at the Jena Experiment, *Taraxacum officinale*, sown in 16 plant communities of different plant diversity, does not change shoot density, biomass production and the number of inflorescences per area along the diversity gradient ([Fig. 4](#), [Table 1](#)). Investing heavily in aboveground growth (in terms of shoot density and biomass production) may come at the cost of reduced survival (in terms of lifespan, e.g. because of reduced shoot-root ratios) or fecundity (in terms of the % of seeds that germinate). Although such trade-offs are not evident in this field example, they have previously been found in common garden experiments with offspring of seed families of *T. officinale* collected in plant communities of different diversity in the Jena Experiment. Cuttings of plants originating from resident populations growing at higher diversity produced more leaf and root biomass and had fewer inflorescences, but heavier seeds ([Lipowsky et al., 2012](#)). Consequently, a higher investment in growth rather than in survival and fecundity increased the contribution of *T. officinale* to enhanced biomass production in mixture. These trade-offs likely occur at the population level and, in nature, may cause variation in population contributions to ecosystem functioning ([Wohlgemuth et al., 2017](#)). That is, at the population level, if trade-offs favour investment in reproduction, which may or may not be related to biomass production, then biomass production may not increase with increasing species richness.



**Fig. 3** Trade-offs within populations in investment toward survival growth and fecundity determine whether populations of  $N$  size can coexist.





**Fig. 4** Vital rates of *Taraxacum officinale* change across diversity at the Jena Experiment. Statistics presented in Table 1.

Whether or not these trade-offs between populations result in enhanced ecosystem functioning at the community level may depend on several factors (Fig. 5). First, biomass is a common proxy for ecosystem functioning in biodiversity–ecosystem functioning experiments. Trade-offs between populations that favour investment in growth over investment in fecundity and survival may result in enhanced biomass production in more diverse grasslands. However, the extent to which trade-offs result in enhanced ecosystem functioning at the community level depends on the function(s) of focus. Below, we give two examples of how our framework may inform local coexistence and predict ecosystem functioning between two species positively, for productivity, and negatively for root decomposition.

#### 4.1 Productivity

The positive relationship between species richness and productivity is well documented (Balvanera et al., 2006; Liang et al., 2016; Reich et al., 2012; Tilman et al., 1996). Further, this relationship may be derived from how

**Table 1** Results of analysis of variance on resident *Taraxacum officinale* vital rates across the diversity gradient at the Jena Experiment.

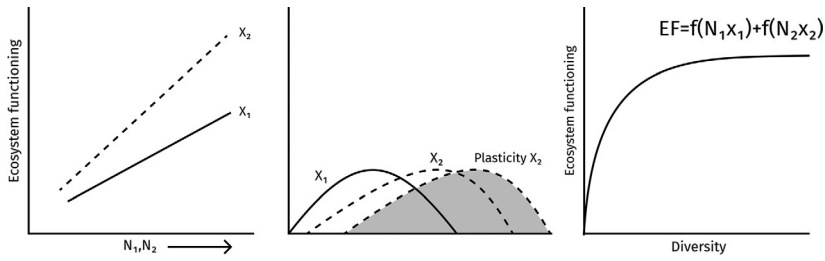
Vital rate	Measure	DF	F	P
Fecundity	# Seedlings	1,11	0.05	0.833
	# Viable seeds	1,11	0.01	0.909
	# Of seeds per inflorescence	1,11	0.24	0.631
	# Of inflorescences	1,11	0.30	0.595
	Seed mass	1,11	3.71	0.080
	% Germination	1,11	0.60	0.455
Growth	Shoot density	1,11	<0.01	0.954
	Population biomass	1,11	0.24	0.636
Survival	Mean age	1,11	1.33	0.274

All models are vital rate  $\sim$  block + species richness. Data were collected in a long-term grassland biodiversity experiment (Jena Experiment; [Roscher et al., 2004](#)). *Taraxacum officinale* belongs to the sown species combinations in 16 plots of the Jena Experiment covering different species-richness levels (2, 4, 8, 16, and 60 species). The biodiversity experiment was established in 2002 by sowing. Sowing density was 1000 germinable seeds per m<sup>2</sup> distributed equally among species in mixture, i.e., for single species 500 seeds per m<sup>2</sup> were sown in a 2-species mixture, and 17 seeds per m<sup>2</sup> were sown in a 60-species mixture.

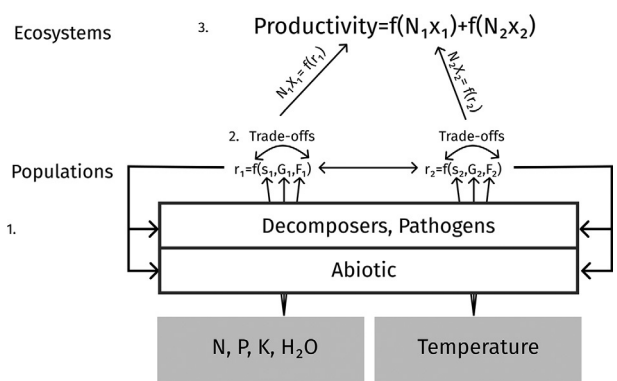
The age of adult plant individuals was determined by analysing growth rings in the root crown of five individuals of *T. officinale* collected in each of the 16 populations in the 12-year old experimental grasslands (for details see [Roeder et al., 2017](#)). Other data shown in [Fig. 4](#) were collected in 2014. The viable seed bank in the topsoil (to 5 cm depth) was determined by taking soil samples, which were sieved and spread on heat-sterilized substrate and cultivated for one growing season to determine the number of germinating *T. officinale* seeds. The number of seedlings emerging on the plots was counted on a permanently marked subplot and summed up from three censuses (spring, summer, autumn). Growth-related variables were determined by harvesting two strips (100  $\times$  10 cm) on each plot at estimated peak biomass before mowing (late May, late August). The number of shoots was counted and averaged between both harvests to get shoot density. Biomass samples of *T. officinale* were dried and weighed; annual biomass production was derived as the sum of both harvests. The number of inflorescences of *T. officinale* was counted on two permanently marked subplots of 1 m<sup>2</sup> size and averaged between both subplots. Three seed heads of *T. officinale* were collected on each plot, when they had ripe seeds. The numbers of seeds per seed head were counted, and 50 seeds were taken to determine seed mass and germination rates under standardized conditions.

To account for the lower number seeds sown for individual species at higher plant diversity, we multiplied all variables, which are related to the sown density (i.e., number of viable seeds in the seedbank, number of seedlings, shoot density, biomass, and number of inflorescences) by species richness for statistical analyses and data presented in [Fig. 4](#).

plant species interact with abiotic and biotic conditions. There is evidence that each of these influences how species richness can enhance productivity. At the Jena Experiment, plants may partition resources ([Ravenek et al., 2014](#) but see [Jesch et al., 2018](#); [Oram et al., 2018](#)) that are likely limiting in this context ([Oelmann et al., 2011](#)). Similarly, abiotic conditions such as stress from flooding alter biodiversity-productivity relationships



**Fig. 5** Trade-offs within and between populations determine how increase species diversity alters ecosystem functioning. Ecosystem functioning is a function of the population sizes ( $N$ ) and the environmental conditions ( $x$ ). Plasticity at the population level determines the effect of  $x$ .



**Fig. 6** Example for how abiotic and biotic conditions may enable local coexistence between two populations of two species and enhance productivity simultaneously. Plant productivity is influenced by the available soil nutrients, temperature and light availability, and the presences of decomposers, pathogens, and other biotic interaction partners. These factors simultaneously allow populations to coexist and result in a positive relationship between species richness and productivity.

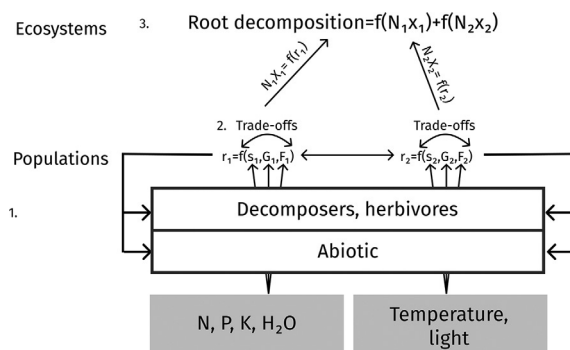
(Fischer et al., 2016; Wright et al., 2017a,b) via their influence on biotic interactions between species at the same trophic level and between species at different trophic levels (Eisenhauer et al., 2009). These interacting factors may enhance productivity by allowing for local coexistence between species (Fig. 6).

In natural systems, this biodiversity-productivity relationship may be reinforced by a positive feedback of productivity on biodiversity (Grace et al., 2016). Further, many other abiotic and biotic conditions may contribute to increased productivity and these factors may not equally influence local coexistence between species (Grace et al., 2016). For example, higher

nutrient availability may decouple local coexistence from biomass production. If nutrient addition reduces the need for plants to partition resources to avoid competition then species richness will decline while biomass production simultaneously increases (as demonstrated by [Harpole et al., 2016](#)).

## 4.2 Root decomposition

Biodiversity can both increase ([Handa et al., 2014](#)) and decrease litter decomposition ([Hättenschwiler and Gasser, 2005](#)). However, for root litter which makes up more than half of plant litter input in grassland ecosystems ([Poorter et al., 2012](#)) the majority of evidence suggests increasing species richness results in slower decomposition ([Chen et al., 2017a,b](#); [Hättenschwiler and Gasser, 2005](#)). Evidence from the Jena Experiment suggests that biodiversity may impact root litter decomposition via three pathways ([Chen et al., 2017a,b](#)): (1) increasing diversity of the litter components may alter the quality of the litter and therefore resource availability (e.g., increasing the carbon to nitrogen ratio, [Chen et al., 2017b](#)), (2) the increased diversity of the environment may alter the abiotic conditions of the community, and (3) the increased diversity of the environment may alter the biotic conditions of the community. Not coincidentally – these categories also enable species local coexistence and alterations to decomposition may arise as an outcome of local coexistence between species ([Fig. 7](#)).



**Fig. 7** Example for how abiotic and biotic conditions may enable local coexistence between two populations of two species and decrease root decomposition simultaneously. Root decomposition depends on the available soil resources, temperature and light availability, as well as the presence of decomposers and herbivores. These factors simultaneously influence local coexistence between populations and root decomposition which decreases with increasing species richness.

Importantly, productivity and root decomposition in a plant community also provide feedbacks on the populations that comprise them and the biotic and abiotic conditions and resources that enable their local coexistence. These feedbacks may reinforce local coexistence by stabilizing population dynamics. For example, higher diversity root litter has a higher K concentration than lower diversity plant litter. This higher K concentration enhances root decomposition, increasing nutrient availability for plants. This enhanced nutrient availability may allow plants to produce more biomass and this increased productivity decreases surface light penetration cooling the soil surface and potentially ameliorating the local microclimate reinforcing local coexistence between species via abiotic facilitation (Milcu et al., 2016). However, while this microclimate amelioration may act to buffer seedlings from harmful abiotic conditions increasing population-level fecundity it may simultaneously decrease the decomposition rate of root litter (Hättenschwiler and Gasser, 2005) and therefore decrease root growth rate and carbon sequestration.



## 5. Conclusion

Abiotic and biotic conditions—ecological first principles—underlie all of the varied mechanisms that may maintain biodiversity and/or enhanced ecosystem functioning in more diverse systems. Starting from these first principles allows us to unify theory and empirical results obtained for originally unconnected reasons. Theory from local coexistence, ecosystem functioning, and plant population biology enables us to understand how abiotic and biotic conditions affect population dynamics and vice versa. Many empirical studies from various contexts in natural environments show how differently the major components of our ecological first principles influence vital rates of populations. Further, although the majority of biodiversity-ecosystem functioning research is conducted at the community level, these effects are species specific. In the context of biodiversity-ecosystem functioning research, such population-level data are often restricted to above-ground biomass. Our review of the literature suggests that deeper mechanistic understanding of the linkage between species coexistence and ecosystem functioning requires more information about population-level trade-offs between growth, survival, and fecundity. This information is especially sparse in terms of their response to varying biotic conditions. Understanding how abiotic and biotic conditions affect population level trade-offs between species across diversity gradients may allow us to combine complementary theories from different field to better

explain how different local coexistence processes can interact to influence ecosystem functioning in grassland ecosystems and how these ecosystem functions provide feedbacks onto local coexistence.

## Author contributions

The idea for this paper was conceptualized during the “BEF-Coexist” workshop organized by C.R. and W.S.H. during discussions among C.R., W.S.H., K.E.B., H.dK., and B.S. These ideas were discussed with many others during the “BEF-Coexist” workshop and this input informed discussion and all drafts of the manuscript. The first draft of the paper was written by K.E.B. and C.R. with contributions from W.S.H., P.D., and B.S. Data on *Taraxacum officinale* presented in Table 1 and Fig. 4 was collected by A.R. and C.R. All authors contributed significantly to the revision of the manuscript prior to submission.

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