Tansley review

Demystifying dominant species

Authors for correspondence:
Meghan L. Avolio
Tel: +1 410 516 2719
Email: meghan.avolio@jhu.edu

Melinda D. Smith
Tel: +1 970 491 7155
Email: melinda.smith@colostate.edu

Received: *4 May 2018*
Accepted: *17 February 2019*

Meghan L. Avolio[1], Elisabeth J. Forrestel[2], Cynthia C. Chang[3], Kimberly J. La Pierre[4], Karin T. Burghardt[5] and Melinda D. Smith[6]

[1]Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21211, USA; [2]Department of Viticulture and Enology, University of California, Davis, CA 95616, USA; [3]Division of Biology, University of Washington Bothell, 18807 Beardslee Blvd, Bothell, WA 98011, USA; [4]Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037, USA; [5]Department of Entomology, University of Maryland, College Park, MD 20742, USA; [6]Department of Biology, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

Contents

New Phytologist (2019) **223:** 1106–1126
doi: 10.1111/nph.15789

Key words: biodiversity-ecosystem function, common species, dominance, foundation species, species abundance, species identity.

Summary

The pattern of a few abundant species and many rarer species is a defining characteristic of communities worldwide. These abundant species are often referred to as dominant species. Yet, despite their importance, the term dominant species is poorly defined and often used to convey different information by different authors. Based on a review of historical and contemporary definitions we develop a synthetic definition of dominant species. This definition incorporates the relative local abundance of a species, its ubiquity across the landscape, and its impact on community and ecosystem properties. A meta-analysis of removal studies shows that the loss of species identified as dominant by authors can significantly impact ecosystem functioning and community structure. We recommend two metrics that can be used jointly to identify dominant species in a given community and provide a roadmap for future avenues of research on dominant species. In our review, we make the case that the identity and effects of dominant species on their environments are key to linking patterns of diversity to ecosystem function, including predicting impacts of species loss and other aspects of global change on ecosystems.

> The concept of dominance, that is, the idea that certain species so pervade the ecosystem that they exert a powerful control on the occurrence of other species, is one of the oldest concepts in ecology.
>
> McNaughton & Wolf (1970)

I. Introduction

A fundamental pattern in ecology, even in the most diverse communities (e.g. tropical forests, coral reefs), is that ecosystems comprise a few highly abundant species accompanied by many more species that are uncommon or rare – that is, represented by only a few individuals (Whittaker, 1965; Gaston, 2011; Alroy, 2015). This iconic pattern, often depicted as a rank–abundance curve or log-normal distribution (Preston, 1948; Whittaker, 1965), has long fascinated biologists, with Darwin (1859) recognizing its ubiquity, and Hutchinson (1953) acknowledging such uneven species abundance patterns as an 'important but unsolved mystery' – one that continues to puzzle ecologists to this day. As we show below, often the terms 'dominant' and 'common', and to a lesser degree 'foundational', are used interchangeably to describe these highly abundant species (Box 1). Here, we contend that dominant species are a special type of abundant species, those with large local populations *and* impacts on community or ecosystem processes proportional to their abundance.

Intuitively, highly abundant species within communities are often expected to have strong effects on ecological processes, such as food web structure and ecosystem function (Grime, 1998; Gaston, 2011). Grime (1998) formalized this idea as the *mass ratio hypothesis*, which predicts that due to their high biomass and widespread occurrence in communities, abundant plant species should contribute proportionally to production and resource use, and as a consequence, strongly affect energy flow, biogeochemical cycling and degradation processes (Grime, 1998). Grime used the term 'dominant species' to refer to this subset of high-biomass, high-impact species. Perhaps as a result of the assumption implicit to the hypothesis that all highly abundant species have a large impact, dominance and high abundance are often conflated in the literature. However, there are instances where high abundance does not result in concomitant large impacts and these species are termed subordinates (Grime, 1998). Whether a highly abundant species is dominant (large impacts) or subordinate (small impacts) is a key distinction useful for accurate predictions about the role and response of highly abundant species in ecosystems. Here, we argue that the conflation of dominance with abundance can lead to confusion in the literature and impedes progress in understanding the role of dominant species in ecosystems. Despite the ecological importance of dominant species, we still lack fundamental understanding of the causes and consequences of dominant species. This challenge is particularly critical because the loss or reduced abundance of dominant species is often an outcome of anthropogenic global changes, such as habitat loss, land-use change, species invasions and altered biogeochemical cycles (Gaston, 2010, 2011), with the potential for large and cascading effects on biodiversity and ecosystems (Hillebrand *et al.*, 2008; Gaston, 2011).

In order to provide an overview of our understanding of causes and consequences of species dominance, we begin with a historical overview of the dominant species concept. We reviewed nearly 100 yr of literature to ascertain how dominant species have been studied and defined. We also conducted a meta-analysis on a subset of these studies that remove dominant species to study their impacts on community and ecosystem properties and to understand how the term is being used in the ecological literature. The focus of our historical overview and meta-analysis was on plant species, given that the dominant species concept has been applied historically and extensively to plant communities (Whittaker, 1965; McNaughton & Wolf, 1970). However, it is important to note that the dominant species concept cuts across trophic levels and the ideas developed in this review should be more broadly applicable. For example, large-bodied zooplankton have been found to consistently dominate in lakes without fish predators (Goulden *et al.*, 1978) and some genera of nematodes dominate soil environments in the absence of predatory arthropods (Ettema, 1998). Building on historical definitions and the results of the meta-analysis, we develop a synthetic definition of dominant species (Box 1) that formalizes how the term is typically used and clarifies how these species differ from the purely distribution- and abundance-based concept of

Box 1 Definitions: all definitions apply within a trophic level

Common species: Species that are widespread and locally abundant.
Restricted species: Species that are locally abundant, but geographically limited.
Dominant species: Species that have high abundance relative to other species in a community, and have proportionate effects on environmental conditions, community diversity and/or ecosystem function. Dominant species can be common (widespread) or restricted in their range (limited).
Foundation species: Species that have large effects on their surroundings and create conditions (environmental and otherwise) required for the persistence of many other species (see Ellison *et al.*, 2005).These species are a subset of dominant species.
Subordinate species: Species with high abundance that do not have proportionate effects on their surroundings. Subordinate species can be common or restricted in range.
Sparse species: Species that are widespread but maintain small population sizes. Given their low population size they have minimal impacts on their surroundings, unless they are a keystone species.
Rare species: Species that are both geographically limited and have small population sizes. Given their low population size they have minimal impacts on their surroundings, unless they are a keystone species.
Keystone species: Species that have disproportionately large effects on community and/or ecosystem functions relative to their biomass (Power *et al.*, 1996).

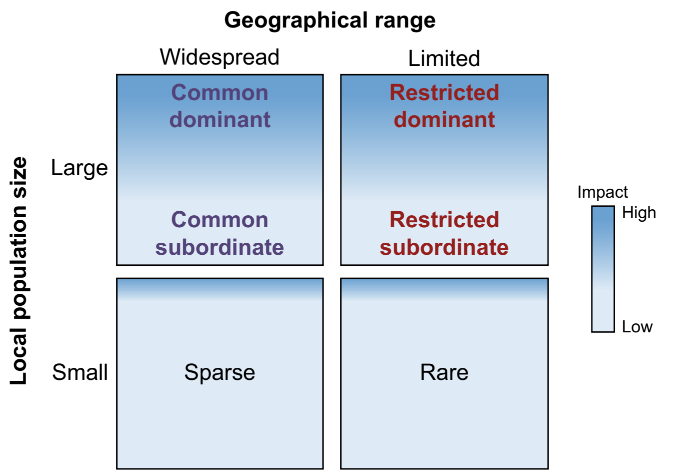

Fig. 1 Categories of species based on their local population size, geographical range and their impact on their surrounding environment, community and ecosystem functioning.

commonality (Gaston, 2011) (Fig. 1; Box 1), or the more narrowly applied term – foundation species (Ellison *et al*., 2005; Box 1). As described in detail below, we define dominant species as having high relative abundance and as having effects on their surrounding environment, community and/or ecosystem that are proportionate to their local relative abundance. Next, based on our definition, we recommend methodological approaches to identify and characterize dominant species, and their impacts on environments, communities and ecosystems. Lastly, we suggest future research directions focused on dominant species.

II. The concept of dominant species

1. A brief history of abundant species in community ecology

The distribution of species abundances across the landscape fascinated scientists even before ecology was formalized as a field of study. As early as the mid-1800s, scientists classified species based on their abundance at a given point in time (number of individuals within a given area), frequency (how often it is encountered across a landscape) and range size (Kenoyer, 1927). It has long been

Table 1 Common themes of historical definitions of dominant species.

	Greatest abundance/ biomass/size		Within a tropic level	Tolerate/ exploit environmental conditions	Evolutionary potential	Modifies environmental conditions	Influences community structure	Controls ecosystem function
	Spatial	Temporal						
Clements (1907, 1916)	X	X					X	
Clements (1936)	X			X			X	
Braun (1950)	X			X			X	
Odum (1959)*	X		X			X	X	
Whittaker (1965)	X			X		X	X	X
McNaughton & Wolf (1970)	X		X	X			X	
Odum (1971)*						X		X
Dayton (1971)						X	X	
Dayton (1972)						X	X	X
Dayton (1975)	X				X		X	
Grime (1977, 2002)	X			X		X	X	
Rabinowitz (1981)	X							
Odum (1993)*	X							X
Power *et al*. (1996)	X					X	X	X
Grime (1998)	X							X
Lincoln *et al*. (1998)*	X						X	
Barbour *et al*. (1998)*	X						X	
Ricklefs & Miller (1999)*	X							
Ricklefs (2001)*	X		X	X				
Gurevitch *et al*. (2002); Gurevitch & Fox (2006)*	X						X	
Odum & Barrett (2005)*	X		X					
Smith & Smith (2006)*	X		X	X			X	
Hillebrand *et al*. (2008)	X					X		
Cain *et al*. (2011)*	X					X	X	X
Mariotte (2014)	X					X	X	X
SYNTHETIC DEFINITION	X	X	X			X	X	X

An 'X' denotes the concept was included in the definition.
*denotes definitions obtained from a textbook.

recognized that in most species assemblages there are a few species that are highly abundant (relative to other species in the community) and many more species that are uncommon or rare (Darwin, 1859; Gleason, 1929; Fisher *et al.*, 1943; Preston, 1948; McIntosh, 1962; Whittaker, 1965; McNaughton & Wolf, 1970). This idea was formalized by Raunkiaer in the early 1900s as the 'law of frequency' (Kenoyer, 1927) and first described statistically by Preston and Fischer in the 1940s (Fisher *et al.*, 1943; Preston, 1948). The influence of these highly abundant species on ecosystem function and community structure has been noted throughout the history of ecology as well (Clements, 1936; Braun, 1950; Quaterman, 1950; Whittaker, 1965; McNaughton & Wolf, 1970; Dayton, 1972; Ellison *et al.*, 2005; Hillebrand *et al.*, 2008; Gaston, 2011), so much so that Clements (1916) defined successional stages and Braun (1947) defined forest regions by their most abundant species and associated traits. Such characterizations of communities based on highly abundant species continue to this day. It was the recognition of these uneven abundance patterns that gave rise to the dominant species concept (Table 1).

A key question that arose from the recognition of the near-universal pattern of uneven species abundance distributions in communities is: what allows species to coexist? Highly abundant species are assumed to be superior competitors (McNaughton & Wolf, 1970; but see Rabinowitz, 1981) at the location where they are most abundant. This assumption underlies a large body of literature on competition (including Gause's competitive exclusion principle; Gause, 1934), as well as the potential mechanisms that maintain diversity and allow for the persistence of rare species. Two important mechanisms of diversity maintenance depend on reducing the abundance of highly abundant species: through predation (keystone predation concept; Paine, 1966, 1969) or disturbances (intermediate disturbance hypothesis, IDH; Connell, 1978). Other concepts of coexistence focus on niche differentiation of species and avoiding direct competition with superior competitors, as well as mechanisms that limit the populations of abundant species (Volterra, 1926; Lotka, 1932; Hutchinson, 1959, 1961; MacArthur, 1964). These concepts that focus on limiting direct competition with abundant species include coexistence theories such as fluctuating and nonlinear effects (Chesson, 2000), negative frequency dependence (Adler *et al.*, 2007), resource-ratio R* theory (Tilman, 1982) and CSR strategies (Grime, 2002), and all incorporate variation among species in their ability to exploit some environments and not others, as well as the criteria of greater intraspecific than interspecific competition. For example, negative density dependence, where intraspecific competition is stronger than interspecific competition, would prohibit any one species from becoming too abundant (Wright, 2002). An additional mechanism that may enable co-existence of species is plant–soil feedbacks (Wardle *et al.*, 2004), which changes the competition dynamics between two species and may affect species abundances (Bever, 2003). Collectively, these concepts demonstrate the influence of abundant species on community ecology and theories of how species co-exist.

Beginning in the mid-1990s a new subfield of community ecology, referred to as biodiversity-ecosystem function (BEF), emerged that shifted focus from the mechanisms that generate or maintain diversity to the consequences of diversity for the functioning of ecosystems. Motivated by the growing recognition of rapid species loss driven by anthropogenic change, early studies showed that more diverse communities were more resistant to drought (Tilman & El Haddi, 1992), more productive (Naeem *et al.*, 1994; Tilman *et al.*, 1996) and retained more nitrogen (Tilman & Downing, 1994). This seminal research inspired numerous subsequent studies that collectively suggest that randomly reducing (or increasing) the number of species in synthetic communities results in the loss (or gain) of multiple ecosystem functions across trophic levels and a range of ecosystem types (Cardinale *et al.*, 2011; Hooper *et al.*, 2012). Importantly, most BEF experiments focus on the number of species alone by randomly assembling communities and initially representing each species with equivalent abundances. This ignores the fact that species vary in their abundance in virtually all natural communities (Wardle, 2016) and obfuscates the role of highly abundant species in determining ecosystem function. In fact, care is often taken in BEF studies to statistically remove selection/sampling effects (i.e. the species-specific influence of the most productive species in polycultures), by contrast to complementarity, which measures the impact of diversity agnostic of identity (Cardinale *et al.*, 2007). Furthermore, because BEF studies traditionally focus on species number, or richness, rather than identity (see Duffy *et al.*, 2017 for a recent synthesis), they do not clarify how the loss of abundant vs rare species would affect ecosystem functioning and community processes (but see Symstad *et al.*, 1998; Smith & Knapp, 2003; O'Connor & Crowe, 2005; Kirwan *et al.*, 2009). As the field of BEF has grown, the idea of functional diversity and functional trait ecology has re-emerged, providing mechanisms for taking into account species identity and effects on ecosystem function (Diaz & Cabido, 2001; Violle *et al.*, 2007; Tobner *et al.*, 2016; Grossman *et al.*, 2017), and methods in trait-based ecology that use community weighted means capture the effect of abundant species on ecosystem processes (Garnier *et al.*, 2004; Diaz *et al.*, 2007).

2. Defining dominant species

Species have long been classified based on their population sizes and, as detailed above, abundant species have long been recognized as ecologically important. However, it is not clear what term is best used to describe highly abundant species, typically called common or dominant. Rabinowitz (1981) defined dominant species as those that have large local population sizes, regardless of geographical range or habitat specificity. Of these dominant species, Rabinowitz notes that some are common (large geographical range and wide habitat specificity), others 'predictable' (large geographical range and narrow habitat specificity), whereas others are 'endemics' (small geographical range and narrow habitat specificity). Gaston (2010) also defines common species as those that are both abundant and widespread. Such common species also are referred to as 'core' species by Hanski (1982), and Mariotte (2014) suggests species whose relative abundance is > 12% should be considered dominant. These descriptions of dominant species, however, are agnostic to the functional roles of species. Indeed, some species may be both abundant and widespread (common), but possess traits (e.g.

diminutive size) with little impact on community or ecosystem processes, which Grime (1998) refers to as subordinate species.

Despite their ecological prevalence and importance, the concept of dominant species does not have an agreed-upon terminology or definition. Instead, we suggest dominant species are currently being used two ways in the literature: (1) to indicate species with high abundance and (2) to denote species that in addition to their high abundance have substantial ecosystem and community effects. We compiled published definitions of dominant species (Table 1) and found considerable variability in how ecologists define this concept. Most of the dominant species definitions which we surveyed consistently include high abundance, and some also mention effects on communities and surrounding environmental conditions, but far fewer include ecosystem-level effects. Perhaps because there is no agreed upon definition, the concept of dominant species is often left out of ecological textbooks. For example, of the ecology textbooks we reviewed, only half included a definition of dominant species (Supporting Information Table S2). Notably, in many of the most common general ecology textbooks (Ricklefs, 1990; Molles, 2005; Begon *et al.*, 2006), and even in community ecology textbooks (Morin, 1999; Mittelbach, 2012) there is no mention of dominant species. Even after Grime (1998) hypothesized that dominant species should have large ecosystem effects, the majority of subsequent definitions do not include this characteristic (Table 1).

In order to provide context for definitions of dominant species and how often the term dominant is used in comparison to other interchangeable terms, we surveyed the ecological literature and conducted a content analysis and a meta-analysis of studies where species identified by the investigator as dominant were removed. Our content analysis of published studies aimed to determine how often 'dominant species' is used in the ecological literature relative to other terms (e.g. most abundant, most common, foundational), and how often each of these terms are explicitly defined (see Box 2 for details). Across aquatic and terrestrial systems, most studies used the word dominant when compared to the three other terms assessed, with the number of published articles using the term 'dominant' increasing through time (Box 2). Most studies that used 'dominant' to describe a species did not include an explicit definition of dominant species. Of those studies that did provide a definition, most defined dominant species in terms of abundance, with far fewer defining it in terms of function or both abundance and function (Box 2). By contrast, the terms abundant, common and foundation were more often defined in terms of abundance, function or both (Box 2). This analysis demonstrates that although the term dominant species is used overwhelmingly in the ecological literature, how dominant species is defined is not always consistent, highlighting the need to clarify its definition.

We next evaluated the mass ratio hypothesis, to understand whether species being described as dominant (whether formally defined in the paper or not) have effects on their surrounding community and ecosystem, as hypothesized by Grime (1998). To do this we conducted a meta-analysis of 57 studies where authors reported removing a dominant species (Box 3). Importantly, we relied on the authors' assessment of whether a species was considered dominant and did not apply our own definition (Box 1) to studies included in the analysis. We assessed the effects of removal of putative dominant species on measures of community diversity and ecosystem function (see Box 3 for details). We selected these two measures of effects as they were the most commonly measured and align with the mass ratio hypothesis. Overall, the effect of removal of putative dominant plant species on ecosystem function was significant and negative (Box 3); most studies found that when the dominant species was removed, all measures of ecosystem function were diminished (Box 3). The effects of dominant species on community diversity was marginally significant (Box 3), with some studies showing that the removal of the dominant species increased measures of diversity whereas others found it decreased diversity. However, when the absolute effect of removal on communities is considered, these effects are significant (Box 3). This finding suggests that although direction of the effect of the removal of dominant species may not always be the same (increasing vs decreasing diversity or function), ecologists are using the term dominant species to describe species that have strong effects on community and ecosystem processes. Further, our meta-analysis is the first of its kind to demonstrate support for the mass ratio hypothesis across over 50 individual studies.

Based on our review of the literature and meta-analysis, we propose a synthetic definition of dominant species (Box 1) that incorporates abundance, distribution, and environmental, community and ecosystem impacts. With respect to abundance and distribution, we modify Rabinowitz's (1981) framework, whereby species are divided into four major categories depending on population size (large or small) and distribution (widespread or limited): common, restricted, sparse and rare (Box 1; Fig. 1). When impact on the community and/or ecosystem processes (large to small) are incorporated, common and restricted species can be further subdivided into those that have a large impact – common and restricted dominants (Fig. 1). To distinguish them from keystone species (following Power *et al.*, 1996), the impact of dominant species should be proportionate to their abundance. If the impact is small, then the species are categorized as common or restricted subordinates (*sensu* Grime, 1998). Sparse and rare species are assumed to have small impacts, with the exception of keystone species (Box 1; *sensu* Power *et al.*, 1996). Although dominant species may turnover in space and time over longer timescales, the concept of dominance persists, and the ecosystem will still have dominant species even as the identity of the dominant(s) changes. An understudied aspect of dominance is the ecological spatial and temporal timescales in which dominant species turnover and the consequences of this turnover on communities and ecosystems.

Our definition of dominant species is a direct contrast to keystone species, which can have disproportionately higher impacts with respect to their abundance (see Fig. 3 in Power *et al.*, 1996). Furthermore, our definition of dominant species includes foundation species, which require that a species controls community and ecosystem processes (Ellison *et al.*, 2005); however, foundation species also must create conditions (environmental and otherwise) required for the persistence of many other species. According to our synthetic definition all foundation species are dominant, but not all dominant species are foundational. This additional requirement may be why this term is used much less often than dominant species

Box 2 Review of terminology and definitions

In order to determine how abundant species were being referred to and defined, we conducted a content analysis of published studies on plants (see Methods below). Overwhelmingly, we found 'dominant' was the most used term; however, the term was not defined in the majority of studies. Of those studies that provided an abundance-based definition and reported data, authors generally defined dominant species as being on average 56 ± 27% abundant (mean ± SD) in terms of cover, frequency or density and ranged from 1% to 100% abundant. For studies that defined dominant species in terms of function, the majority measured ecosystem effects instead of community effects. Most of the studies were in terrestrial systems (90.9%).

Methods

On 23 October 2010 and 22 October 2016, we searched Web of Science using the following search terms: 'most abundant' and 'plant species'; 'high relative abundance' and 'plant* species'; 'relative abundance' and 'plant* species'; 'foundation species' and plant*; 'common species' and plant*, 'dominant species' and plant*. We included only articles published in English within the following categories: environmental sciences and ecology, plant sciences, biodiversity and conservation, forestry, agriculture, zoology, marine and freshwater biology, entomology, evolutionary biology, oceanography and fisheries resulting in a total 12 292 articles from the two searches. We narrowed this to 1350 articles by including only articles that (1) studied plants, (2) mention dominance, most abundant, common or frequent species, or foundation species anywhere in the title, keywords or abstract, (3) were not surveys, and (4) focused specifically on an abundant species. For these 1350 articles, we extracted the following: (1) the term used (dominant, abundant, common, foundation, frequent); (2) how the authors define the term used (abundance, function (invoking species effects on surrounding community or ecosystem processes), both or neither); (3) if the authors defined the term used by abundance: (a) how they qualified abundance (biomass, cover, frequency, density, other or none) and (b) what percentage abundance the species had; (4) if the authors defined the term by function: (a) what measure of function was used (ecosystem, community, neither or both); and (5) what type of ecosystem the study took place in (a) terrestrial: desert, grassland, tundra, temperate forest, tropic forest, wetland, woodland, artificial, agriculture, boreal forest or other/many, or (b) aquatic: marine, stream/river, lake, estuary, artificial, other. Only four papers used the term frequent, thus we do not include the term in our graphs.;

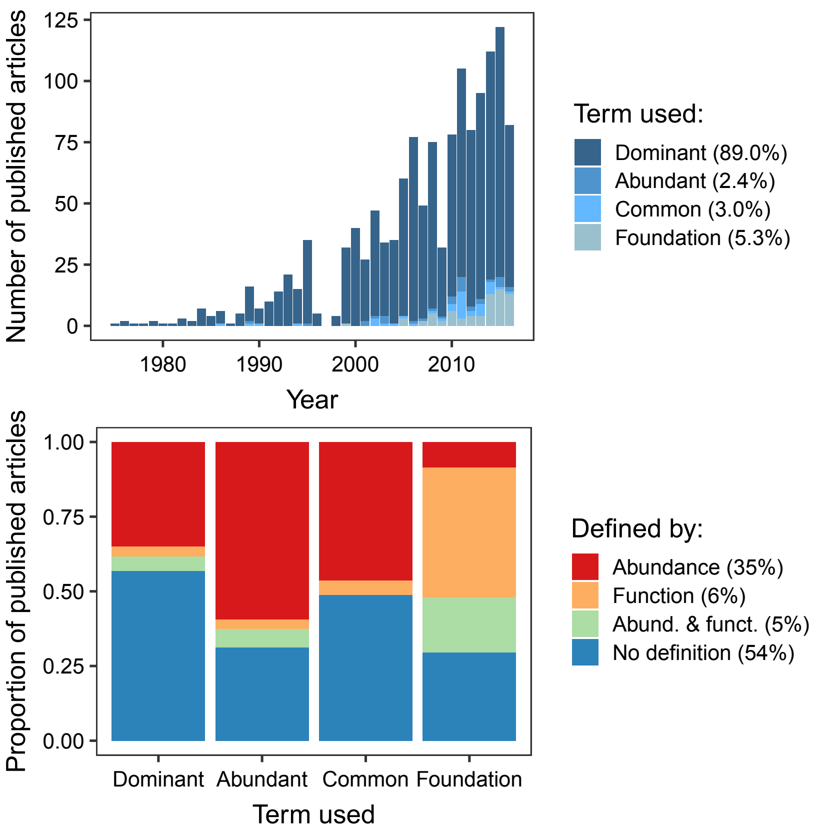

Fig. B2 (upper) Summary of content analysis of terms used to describe abundant species over time. (lower) Summary of how the four main terms used to describe abundant species were defined.

in the literature (Box 2), except in the case of forest and marine studies (Ellison *et al.*, 2005), where a single foundation species often can be easily identified. In summary, our synthetic definition formalizes the mass ratio hypothesis, and goes further to specify that ecosystem effects will be proportionate to abundance, and restricts the use of dominance to only those species with ecosystem effects, leaving other highly abundant species to be called either common or restricted subordinates. Furthermore, our definition clarifies that

Box 3 Meta-analysis of dominant species removal studies

We performed a meta-analysis of dominant plant species removal studies to determine the effect of dominant species on community and ecosystem properties. The magnitude of responses to dominant species removals differed significantly from 0 for ecosystem effects ($t_{48} = -2.28$, $P = 0.03$) and was marginally significant for community effects ($t_{44} = 1.88$, $P = 0.07$; Fig. B3). We found the duration of the experiment did not affect this finding, suggesting that compensation by other species may be lagged or possibly not occur over the timeframe of the study (the average length of a removal study was 40 months). There were stronger effects on ecosystem function for press removals compared with pulse removals, and weaker effects in marine ecosystems. None of the external factors assessed influenced the effect of removals on community properties (see Supporting Information Table S1 for details). We found both community ($t_{44} = 4.12$, $P = 0.0002$) and ecosystem ($t_{48} = 4.03$, $P = 0.0002$) effects were significantly different from zero for the absolute value of $\log_e$RR, demonstrating that although there are large absolute effects of dominant species on communities and ecosystems, the direction of that effect can differ (suppress or enhance community structure and ecosystem function).

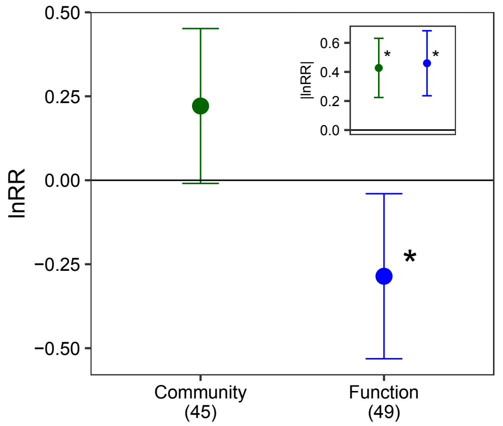

Fig. B3 Mean ± 95% CI of the natural log of community and ecosystem change response ratios ($\log_e$RR) to removal of the dominant species. Inset shows the absolute value of $\log_e$RR. An asterisk indicates the response is significantly different from zero ($P < 0.05$).

Methods

Articles were found by conducting a Web of Science search for dominant plant species (see Box 2 for details) and flagging articles that were removal studies.

There were 94 responses of community diversity (e.g. richness, Shannon's diversity, evenness; $n = 45$) or ecosystem function (e.g. aboveground net primary productivity, total cover (as a proxy for biomass), nutrient availability; $n = 49$) to the removal of a dominant species. From these articles, we recorded the duration of study in months, study system (forest (5), shrubland (8), herbaceous (73), freshwater (1), marine (7)), type of removal (press (62), pulse (32)), treatment and control means, number of replicates and variances (when available) for a variety of response variables. See Appendix A1 for a list of articles included in the meta-analysis. Where multiple metrics within a response category were measured from one study, the response variable most closely related to species diversity (for community responses), or aboveground net primary productivity (for ecosystem function responses) was used. Data were collected using Data Thief III (*Tummers, DataThief III. 2006* http://datathief.org/). Studies were only included from experiments that removed a dominant species without directly manipulating any other variable (e.g. nutrient or water availability, grazer presence).

For all studies, we calculated the *$\log_e$ Response Ratio* ($\log_e$RR) as the natural log of the ratio of the mean of the treatment divided by the mean of the controls. Student's *t*-tests were performed for community and ecosystem responses separately to assess differences from 0. Next, generalized linear models were performed on the $\log_e$RR data for community and ecosystem responses separately to assess how other factors may influence the effect of removal of dominant species. For each model, type of removal, study duration, and study system were included in the model as fixed factors. All analyses were performed in R v.3.2.4 (R Core Development Team); code for the analyses is archived at https://github.com/klapierre/dominance-removal-meta-a.

dominants need not be widespread in order to be impactful enough to dominate local interactions (restricted dominants). Now with this synthetic definition in hand, the next section addresses how these types of species can be identified rigorously and provides metrics for investigators to apply in future studies of putative dominant species.

III. Approaches to identifying dominant species

Although we provide a synthetic definition to help guide future research on dominant species, a significant hurdle that must be overcome in studying dominant species is the consistent use of robust metrics and methodologies to identify these species. Several dominance indices such as Simpson's Dominance (Simpson, 1949; Magurran, 2004) or Berger–Parker (Berger & Parker, 1970) are agnostic over species identity; they convey more about the evenness of the community than dominant species *per se* (Hillebrand *et al.*, 2008) and should not be confused with studying the effect of dominant species. Wohlgemuth *et al.* (2016) found that the effects of particular dominant species were stronger than changes in evenness, and several studies found the abundance of a particular dominant species was more important than richness or species and functional composition in determining community attributes or ecosystem functioning (Smith & Knapp, 2003; Le Roux *et al.*, 2014). Furthermore, Elumeeva *et al.* (2017) found that even after 20 yr of removals, no species were able to compensate for the loss of the dominant species.

Currently, there are several metrics aimed at specifically identifying dominant species. These include the importance value index (IV_i; Curtis & McIntosh, 1951), the competitive index (CI; Grime, 1973) and the community importance index (CI_i; Power *et al.*, 1996). Below, we describe each of these metrics, suggest a modification of the IV_i metric that we refer to as the dominance candidate index (DC_i), and then test the efficacy of combining the DC_i and CI_i metrics for identifying dominant species using observational and experimental data.

1. Metrics for identifying dominant species

The importance value, IV_i metric, identifies species based on three descriptors of abundance: (1) number of individuals per unit area (density), (2) cover and (3) frequency of occurrence. Each value is relativized and multiplied by 100 to become a percentage. Values of IV range from 0 to 300, with values closer to 300 indicating that the species is more likely a dominant species in the community. Although the IV_i metric has been available for some time, it is not used widely, probably because of how difficult it is to measure all three descriptors of relative abundance in any one community. For example, density is rarely measured in herbaceous communities with 1000s of individuals, but cover (basal, aerial or estimated via line intercept) often is measured. The converse is the case for forest communities. Thus, the IV_i often cannot be consistently applied across ecosystem types.

The competitive index (CI) is based on categories of species traits (height, morphology, growth rate and litter production). Although these are likely traits related to the ability of an herbaceous species to dominate, it remains unknown whether the traits proposed by Grime are generalizable across a broad range of species. Because of a lack of overall understanding of traits that promote dominance, we refrained from including traits in our definition of dominant species and do not explore this metric further.

Finally, the community importance index (CI_i; Table 2) assesses the impact of a species on community or ecosystem properties as a function of its abundance and can be calculated using observational or experimental data (Power *et al.*, 1996). CI_i quantifies the impact of a species on community or ecosystem properties by comparing sampling units that differ in abundance (observational data) of the focal species or where the focal species was removed from some sampling units (experimental data). CI_i values are not bounded and can be positive or negative: negative values represent species for which an ecosystem property is lower with the species present, whereas positive values represent cases where a species presence results in an increase in an ecosystem property. It has been hypothesized that dominant species will have ecosystem or community effects that are proportionate to their abundance (Power *et al.*, 1996; Gaston, 2010), or $CI_i \approx 1$, whereas keystone species should have values > 1 and those species that have little impact should have values < 1. Using CI_i alone as a measure of dominance would not include all characteristics in our definition, because this metric does not include measures of species relative abundance compared to other species in the community.

Given the strengths and limitations of the available metrics, we suggest that a modified version of the IV_i metric, hereafter referred to as the dominance candidate index (DC_i), when combined with the community importance index (CI_i) can be used to confirm that a species is dominant based on its ecological impact. The DC_i metric uses only relative abundance (e.g. number of individuals, cover) and relative frequency (Table 2). Both relative abundance and frequency can be easily measured in observational and experimental studies across a range of ecosystem types. It is important to note that the relevant spatial scale to determine abundance and frequency will depend on the processes/functions of interest, biogeographical regions or data limitations (McGill, 2010), and may change depending on the study. DC_i varies between 0 and 1, where values ≈ 1 indicate a species that is in high abundance and is ubiquitous across the surrounding landscape, both requirements to be considered dominant according to our definition. There is no single DC_i value that should be used as a cut-off as the range of DC_i values are system-dependent. As per our definition, a species must have ecological (community and/or ecosystem) impacts proportionate to abundance to be considered dominant. Thus, after a candidate dominant species is identified with the DC_i metric, it is necessary to confirm the effects of this species using the CI_i metric. When combined, both the DC_i and CI_i

Table 2 Metrics to identify dominant species and their impact.

Metric	Formula	Range	Notes
Dominance Candidate Index (DC_i)	DC_i = (average relative abundance + relative frequency)/2 Relative abundance = abundance of a species a in a sampling unit/ total abundance of all species in a sampling unit. Relative frequency = number of sampling units a species occurred/ total number of sampling units	0–1	Relative abundance can be any measure of abundance. *Does not incorporate a measure of impact*
Community Importance Index (CI_i)	$CI_i = (t_A - t_B)/t_A \times 1/(r_A - r_B)$ *t*-trait in sampling unit (A or B). Note that a trait is broadly defined as a community or ecosystem process. *r*-relative abundance of species in sampling unit (A or B). For removal studies plot A would be the controls and B the removal plots	Boundless	Ideal for removal studies. *Does not incorporate a measure of frequency*

Box 4 Examples of proposed metrics to identify dominant species

We tested our proposed metrics (Dominance Candidate Index (DC_i) and Community Importance Index (CI_i); Table 2) to identify dominant species using an observational dataset and an experimental removal study dataset. For the observational data, we found that DC_i was consistent in identifying potentially dominant species, based on prior knowledge of the system. It is important to note that there is not a single DC_i that should be used as a cut-off to determine if a species is dominant. The range of DC_i values are system-specific depending on the evenness of the community. The two North American grasslands are less even (as inferred by the shape of the rank abundance curve) and have higher DC_i values compared with the more even South African grasslands. We then assessed impacts of species using CI_i and compared these values to DC_i values. We found CI_i was consistently ≈ 1 for those species identified as dominant based on their DC_i values (Fig. B4); however, it was highly variable for several species, demonstrating the limitation of calculating CI_i with observational data. For the removal studies (Silletti *et al.*, 2004), *Andropogon gerardii* and *Sorghastrum nutans* were the two most dominant species across the control study plots (mean proportional abundance = 41.1 and 36.7% respectively; mean relative frequency = 1 for both). Reflecting their ubiquity and high abundance, their DC_i values were 0.706 and 0.684, and their CI_i values were 1.217 (SE 0.130) and 0.854 (SE 0.466), respectively.

Methods

Observational data We used data from two North American and two South African xeric and mesic grasslands (Forrestel *et al.*, 2017). Briefly, at each location 20 plots were established from which whole community and annual net primary productivity data, our measure of ecosystem function, were collected. We calculated the DC_i and CI_i metrics for all species at each site separately. Relative abundance was calculated as the mean relative cover across all 20 plots and relative frequency was calculated as the number of plots a species was present in divided by 20. Relative abundance and frequency were utilized to calculate a single DC_i value for each species. CI_i was calculated using plot level relative abundance, and annual net primary productivity as the ecosystem response. Mean CI_i was calculated by taking the average CI_i values of all pairwise comparisons between plots that varied in abundance of a given species.

Removal data We used data from a removal study of dominant species at the Konza Prairie Biological Station (Silletti *et al.*, 2004). In this study, two C_4 grasses, *Andropogon gerardii* and *Sorghastrum nutans*, were independently removed from study plots. Community composition and productivity responses were recorded 2 yr after the initial removal and compared to control plots. For these two species, DC_i was calculated as described above using data from the control plots, and mean CI_i was calculated by taking the average CI_i values of all unique pairwise combinations of the removal plots and control plots.

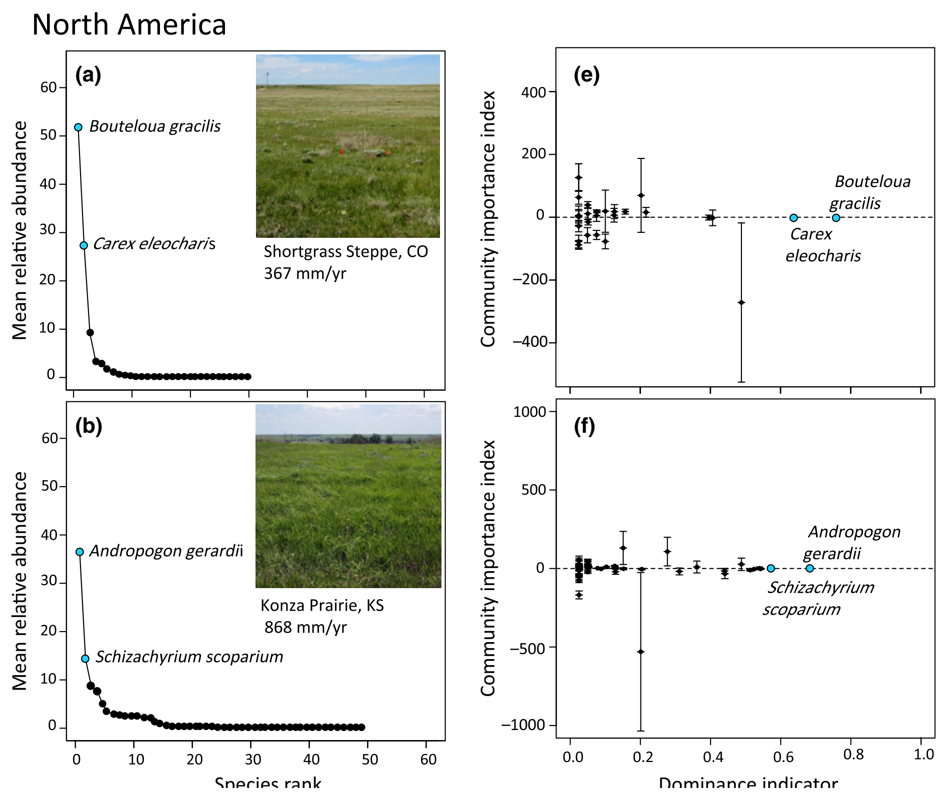

Fig. B4

Box 4 Continued

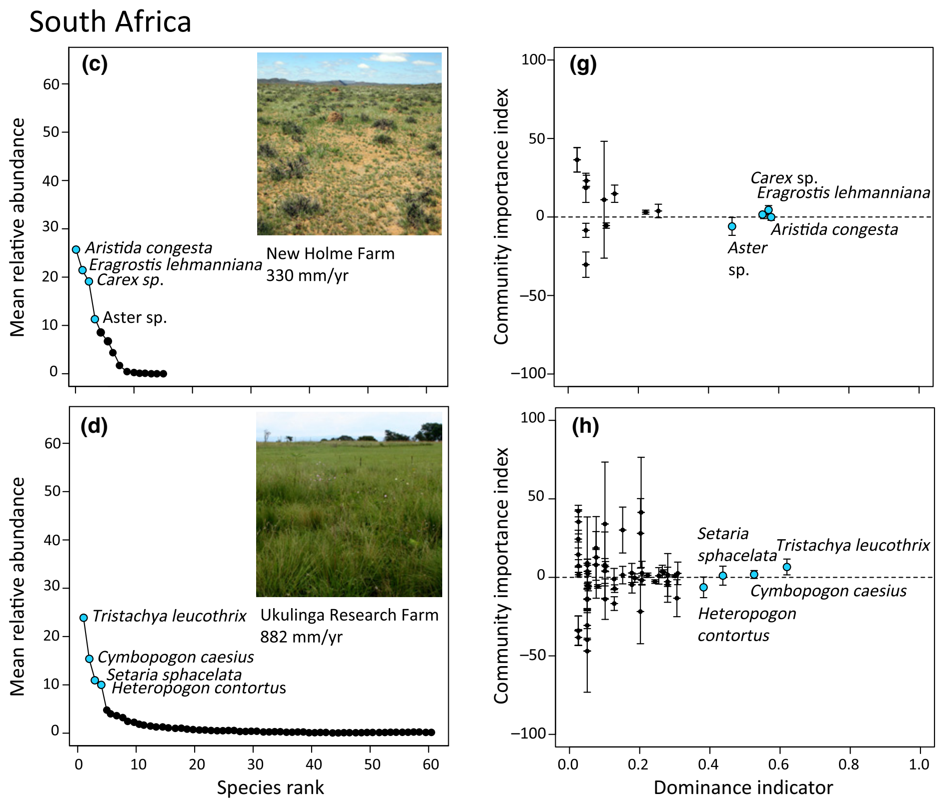

Fig. B4 (a–d) Rank abundance curves for the four grassland sites examined (data from Forrestel *et al.*, 2017). Blue points represent species that are of > 10% mean relative abundance across 20 1-m^2 squared plots in each grassland community. (e–h) Comparison of the Dominance Candidate index (DC_i) vs the Community Importance index (CI_i) of Power *et al.* (1996) for the same grassland communities. Error bars represent standard errors of the mean CI.

metrics consider all characteristics reflected in our synthetic definition of dominant species (Box 1).

In order to test the efficacy of the DC_i and CI_i metrics in identifying dominant species, we utilized observational data from four grassland sites in North America and South Africa (Box 4), as well as data from two removal experiments. We found that the DC_i metric identified those species that are considered dominant based on previous knowledge (Box 4). However, it is important to note that the DC_i metric cannot confirm whether a species is dominant because it does not measure ecological effect, and thus it can only inform on how common a species is or not. Thus, the DC_i metric must be combined with the CI_i metric to confirm whether a species has proportionate ecological effects, and thus is dominant. Using the same observational data from the four grassland sites, we calculated CI_i for all species in the community and found CI_i to be consistently ≈ 1 for species with high DC_i values (Box 4), as expected for dominant species (Power *et al.*, 1996). For the less common species, we found widely variable values of CI_i, often of much greater magnitude than those values of the most abundant species. Most likely, this is an artifact of using observational data, where there could be many drivers of shifts in function unrelated to the presence or absence of a species. Our results highlight the potential danger of using only CI_i to classify dominant species for observational datasets. To further validate their efficacy, we calculated the CI_i metrics for a removal study (Silletti *et al.*, 2004), where two species, *Andropogon gerardii* and *Sorgastrum nutans*, known to be dominant based on a previous removal study (Smith & Knapp, 2003) and the DC_i metric (Box 4), were removed from intact tallgrass prairie (see Box 4 for details). We found $CI_i \approx 1$ for both species (Box 4). Thus, we suggest using DC_i to identify possible dominant species, and then calculating CI_i for those species to see if their effect is proportionate for ecological properties of interest. When both conditions are met, high DC_i values and $CI_i \approx 1$, then a dominant species has been identified.

2. Approaches for determining dominant species impacts

Ideally, experimental work, such as removal studies, would confirm the role that dominant species play in exerting controls over ecological processes under particular conditions. A species impact can be determined, to a limited extent, with observational data of species relative abundance (cover) alone and correlating that to an aspect of community, ecosystem or environmental variables, as was shown with the CI_i metric in Box 4. However, detection of effects will likely be difficult due to an often weak and more variable signal (Power *et al.*, 1996), as we demonstrate in Box 4. By contrast, experimental work could include manipulating species composition to test for the role focal species play in driving or responding to a given change. This can be accomplished using either species removal or species addition studies. Removal studies are a powerful tool for understanding the contributions of species to community and ecosystem properties (see Díaz *et al.*, 2003), and contrast with the more commonly employed species addition studies (Seabloom *et al.*, 2003), which often simulate the addition of a single species. This type of study allows for the examination of the effect of invasion of a focal species. However, we recognize there are time, cost, system-specific and other logistical constraints that make removal studies difficult to conduct in some systems, and thus other approaches (observational, species additions) should be included in the toolbox for identifying and understanding dominant species.

Once dominant species are identified (using the DC_i and CI_i metrics), it is easier to focus on the impacts of these species on ecological processes. We suggest using the relative abundance of particular dominant species to study their effects on additional community and ecosystem processes. By using relative abundance of a dominant species, studies can focus on identified dominant species as an additional potential driver of ecological processes, alongside other diversity measures, such as richness and evenness.

By our definition, dominant species must have an effect on at least one community, ecosystem, or environmental property. Once a species is defined as dominant, it would be inadvisable to then test the effect of the species on the same community, ecosystem or environmental property that was used to define its dominance at the same point in time and space. However, it *is* worthwhile to study the broad effect that the dominant species has on other aspects of the community or ecosystem. For example, several studies demonstrated that *Andropogon gerardii* was a dominant species in tallgrass prairie of Northeastern KS, as its complete removal or reduced abundance affected ecosystem productivity (Smith & Knapp, 2003; Silletti *et al.*, 2004). Since these studies, several additional studies have focused on multiple ecosystem and community effects (e.g. invasion resistance, resistance and resilience to drought) of *A. gerardii* (Chang & Smith, 2012; Hoover *et al.*, 2014), allowing a more complete understanding of the key role of this dominant species in the broader tallgrass prairie ecosystem. Thus, once dominance is demonstrated, it is important to study what environmental conditions strengthen or weaken the effects of dominant species, and whether the dominant species or genotypes affect other community and environmental properties.

IV. Going forward: studying dominant species

Communities comprise interacting species that together determine ecosystem function and services. When all species are considered at once, such complexity makes it difficult (or nearly impossible) to disentangle causal factors. A focus on or manipulation of one (or a few) dominant species within a habitat can allow ecologists to simplify complex systems into those that are experimentally tractable and enable a better understanding of the fundamental community and ecosystem processes within the system (Schmitz *et al.*, 2015). Although there are certainly limitations to this approach – for example, focusing on a single species, one might miss the importance of species interactions – simplifying a community may enable more accurate observation and prediction at larger spatial and/or temporal timescales than would be possible if tracking every community member. We suggest that dominant species, given their high abundance, often widespread distributions, and impacts on community and ecosystem processes, are key to understanding the impacts of global change on ecological processes by serving as proxies (or surrogates; e.g. Lindenmayer *et al.*, 2015) of whole community and ecosystem responses to global change drivers (Fig. 2). We must also increase our basic

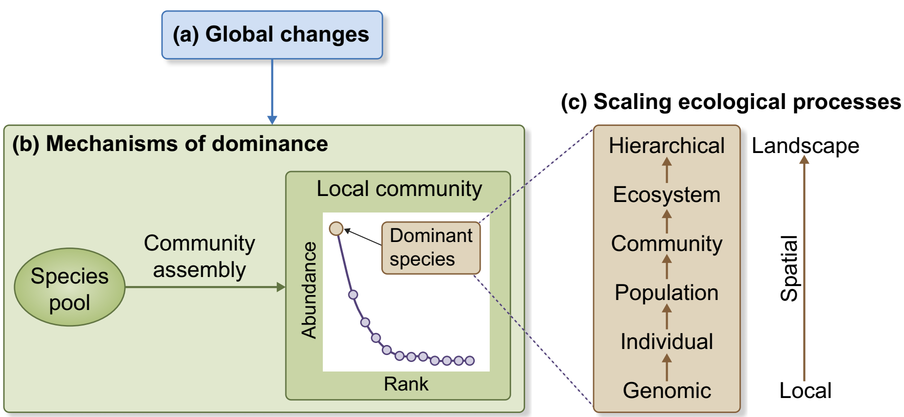

Fig. 2 (a) Future research directions for studying dominant species in the context of global changes. (b) The evolutionary, historical and current community assembly mechanisms that give rise to dominance during community assembly are understudied. (c) Focusing on dominant species responses to global changes creates a more tractable system to then extrapolate how anthropocentric driven change will impact ecological processes across hierarchical scales – from the within individual to ecosystem levels. Moreover, because of their high abundance and widespread distributions, dominant species can be studied to scale local patterns to landscape-level processes.

Table 3 Potential mechanisms of dominance and examples.

Type of dominance	Mechanism underlying dominance	Definition	Example	
Resource acquisition	R* (resource-ratio hypothesis)	Dominant species have the lowest equilibrium resource requirement (Tilman, 1982)	Different species became dominant depending on treatment in the Rothamsted Park Grass Experimental plots (pictured in Hertfordshire, England) where species dominated under resource ratios near their lowest equilibrium resource requirement (Silvertown *et al.*, 2006). Photo by BBC	
	Competitive effect	Dominant species have highest resource uptake capability (Grime, 2002)	*Pteridium aquilinum* (pictured in Hokkaido, Japan) is a rhizomatous fern that dominates a grassland community by producing dense litter accumulation and decreasing available light for other species (Grime, 2002 page 183). Photo by Shiro Tsuyuzaki	
	Stoichiometric homeostasis	Dominant species maintain elemental composition despite variation in the elemental composition of its environment (Sterner & Elser, 2002)	*Leymus chinesis* (pictured in Inner Mongolia Grassland Ecosystem Research Station, Xilinhot, China) has the highest stoichiometric homeostasis (Yu *et al.*, 2010). Photo by S. Reynolds	

Table 3 (Continued)

Type of dominance	Mechanism underlying dominance	Definition	Example	
Niche matching	Niche specialization	Dominant species specialize in using the most abundant resource forms	*Carex bigelowii* (pictured in Toolik Field Station, AK, USA) specializes in using nitrate, the most available form of nitrogen (McKane *et al.*, 2002). Photo by M.K. Raynolds	
	Niche modification	Dominant species have attributes that modify the environment to create a new niche for it to exploit	The leaf litter of *Pinus sylvestris* (pictured in Scotland) species acidifies local soils (Reich *et al.*, 2005). Photo by Bruce McAdam	
Species interactions	Enemy release	Relationships between dominant species with predators and pathogens can dictate abundance of dominant species (Olff & Ritchie, 1998)	Lack of soilborne pathogens and plant-feeding nematodes favors *Festuca rubra* and *Carex arenaria* abundance in grasslands (pictured in the Junner Koeland Nature Preserve, Netherlands) (Olff *et al.*, 2000). Photo by V. Punt	
	Mutualistic relationships	Relationships with mutualistic partners can dictate abundance of dominant species (Bever, 2003)	Arbuscular mycorrhizal fungi promote the dominance of facultatively mycotrophic C_4 tallgrasses such as *Andropogon gerardii* (pictured at Konza Prairie, KS, USA) (Hartnett & Wilson, 1999). Photo by C. Chang	

Table 3 (Continued)

Type of dominance	Mechanism underlying dominance	Definition	Example	
Stochastic processes	Priority effect* *Ecological and evolutionary priority effects interact (De Meester *et al.*, 2016)	Ecological: Dominant species arrive first during community assembly due to stochastic processes (Fukami, 2015)	Priority effects can cause different species to become dominant, as was shown in an old-field succession experiment (pictured in Hutcheson Memorial Forest, NJ, USA) where the order of arrival determined whether *Setaria faberii* or *Erigeron annuus* became dominant (Facelli & Facelli, 1993). Photo by Wikipedia Creative Commons	
		Evolutionary: Early arriving lineages diversify, influence subsequent community assembly, become local dominants (Fukami, 2015)	Evolutionary priority effects cause older lineages to have greater dominance, as shown in New Zealand alpine plant communities across environmental gradients (pictured Murchison Mountains, NZ; Leopold *et al.*, 2015). Photo by New Zealand Department of Conservation	

understanding of the mechanisms that underlie the ability of species to dominate. This is particularly important for understanding how ecosystems will respond to novel environmental conditions in the future, as understanding the mechanisms that lead to dominance may shed light on whether the dominant species will persist or be replaced. Moreover, because of their properties (high abundance and large effects), dominant species are also key for scaling hierarchically from, for example, the individual/population level to the ecosystem level (Fig. 2). It is important to note that we suggest studying dominant species at a given point in space and time where they are abundant and have large impacts, as most species are typically not dominant throughout their entire range (Rabinowitz, 1981). Below we briefly explore these three areas of future research.

1. Dominant species as key to understanding impacts of global change

How dominant species respond to changing environmental conditions will be an important determinant of whether a given habitat will continue to provide expected levels of ecosystem functions and services into the future (Gitlin *et al.*, 2006). Dominant, like rare, species are vulnerable to loss in response to global change (Gaston, 2011). High relative abundances of these species may lure conservation scientists into a false sense of security even though abundance alone does not guarantee a species' persistence (Gaston, 2010), as the fates of the passenger pigeon (Halliday, 1980) or American chestnut (Hepting, 1974) exemplify. Thus, effort should be devoted to monitoring dominant species and assessing how their abundances change over time and across space, particularly given that changes in the abundance of dominants could be an early indicator of future community and ecosystem changes (Pau & Dee, 2016). Such approaches could use remote sensing to track changes in dominant species (Pau & Dee, 2016), plant functional properties at large spatial scales (Jetz *et al.*, 2016) or utilize plant spectral data, which has been found to be a good proxy for plant function, identity, as well as important ecosystem functions (Cavender-Bares *et al.*, 2016b; Schweiger *et al.*, 2018).

Studying the genetic diversity of dominant species also may be important for predicting how populations of these species will respond to global change. The genetic diversity within species (Bailey *et al.*, 2009) has been found to affect ecological processes as much as species diversity effects. In particular, the genetic diversity within dominant species may drive intraspecific trait variation (Albert *et al.*, 2011; Bolnick *et al.*, 2011; Siefert *et al.*, 2015), which can play as large a role as species diversity in driving ecosystem function (Crutsinger *et al.*, 2006; Whitham *et al.*, 2006). As with all species, dominant species will be impacted by global change, and adaptation of the dominant species to global change also will have important implications for whole community and ecosystem dynamics (Avolio & Smith, 2013) and warrants more research.

Given the important role that dominant species play in communities and ecosystems, these species can be used as surrogates (*sensu* Lindenmayer *et al.*, 2015) for assessing changing biodiversity, ecosystem functioning or other aspects of systems that are not easily measured. Before dominant species can be used as surrogates, it will be important to first confirm that a species is indeed dominant (using the measures above) and then establish relationships between a dominant species' abundance and the target measurements of interest (e.g. diversity, aboveground productivity, environmental conditions). It also will be important to ensure that the identity of dominant species is not ephemeral and persists over relevant timescales for the duration of the study. If the dominant species are only dominant for short timescales with rapid seasonal or yearly turnover in identity, it will be necessary to consider limitations in the ability to predict the target measurement or measurements of interest. Finally, the cost-effectiveness of measuring a dominant species vs other more direct measurements needs to be assessed, but the development of remote sensing (Cavender-Bares *et al.*, 2016b; Jetz *et al.*, 2016; Pau & Dee, 2016) will better enable us to monitor and test for the roles that dominant species play in ecosystems at broader spatial scales.

2. Mechanisms and traits that give rise to dominance

Very few species are common (Gaston, 2011) and of those, even fewer are dominant. For example, according to a study on grasses (Poaceae), only *c.* 5% of species within the family are regarded as dominant species (Edwards *et al.*, 2010). Furthermore, it remains unknown whether there are general mechanisms that enable a species to become dominant, such as tall height or rapid growth (Grime, 1973). Certain traits can lead to dominance, such as tolerance of stressful conditions, but there exists a range of other possible mechanisms that promote dominance (see Table 3). It is likely there are multiple evolutionary innovations that enable certain species to dominate, and importantly these innovations or traits are shaped by both their past and current environment (Cavender-Bares *et al.*, 2016a). For example, dominant species within the Poaceae family are not limited to a few lineages, but instead are clustered nonrandomly among diverse clades across the grass phylogeny (Edwards *et al.*, 2010). This result indicates that there is likely not a generalizable set of traits across species that confers dominance, and that dominance is both evolutionarily and environmentally context-dependent. A further complication for identifying general mechanisms or traits of dominance is that the ability to dominate is likely not a static property. Instead, what is a dominant species today may not have been in the distant past under different environmental conditions (Wagner *et al.*, 2006; Jackson & Blois, 2015), especially over evolutionary timescales, as demonstrated by pollen studies (Davis & Shaw, 2001). Studying this temporal turnover may give insight into which mechanisms give rise to dominance. Similarly, the identity of a past dominant species can alter the future successional trajectory of a community (Rundel *et al.*, 2014). For example, in abandoned agricultural fields in Hungary, the identity of the mid-successional dominant species determines whether succession is arrested or rapidly transitions to a woody community (Bartha *et al.*, 2014). In old-field communities in TN, USA, Souza & Weltzin (2011) found that the future invasibility of a plot depended on which of the two co-dominant species were removed.

There is historical context to a species pool at a given point in space and time from which a dominant species will be drawn (Ricklefs *et al.*, 1999), and the characteristics of the regional pool, which is dependent on biogeographical and evolutionary history, is critical to understanding how a species came to be dominant (Fukami, 2015; Leopold *et al.*, 2015; Cavender-Bares *et al.*, 2016a; De Meester *et al.*, 2016). Myriad factors, both ecological and evolutionary, including dispersal ability, the nature of the environment being colonized, the order of arrival time (i.e. priority effects), standing genetic diversity and subsequent diversification dynamics, are critical to determining the outcome of community assembly and abundance distributions (See Table 3). Gaining an improved understanding of the mechanisms, traits and conditions that allow or enable species to dominate will aid in predictions of community assembly and how dominant species will respond to global change (Fig. 2).

3. Using dominant species to scale ecological processes

Dominant species may be informative in the quest for hierarchical (individual to ecosystem) scaling (Felton & Smith, 2017; Fig. 2). A focus on dominant species, because of their important and pervasive role in communities, provides the opportunity to scale from the molecular to whole plant to ecosystem level, without having to quantify these processes in the milieu of species within a community (Whitham *et al.*, 2006; Bangert *et al.*, 2008; Felton & Smith, 2017). Quantifying the molecular and/or physiological/functional responses of all species in a community (most of which are unlikely to be model organisms) is difficult, and a focus on a single dominant species may be equally informative. Additionally, dominant species may be key to spatial scaling, a recognized problem in ecological studies (Wiens, 1989; McGill, 2010), due to their high local abundance and frequency of occurrence. Overall, we contend that dominant species are important focal organisms with which to study ecological processes across hierarchical and spatial scales.

V. Conclusions

In this review, we first provide a synthetic definition of dominant species, which given their ecological importance, was a surprisingly vague term in the literature. We then advocate for a two-step approach to studying dominant species: (1) identify potentially dominant species based on their abundance and frequency of occurrence (DC_i index), and (2) use targeted removal studies to confirm the impact of these potentially dominant species on ecological processes (CI_i index). Athough this review has been focused on plants, future research should study the phenomenon of dominance across trophic levels.

Recently, several papers have called for more nuanced ways of measuring biodiversity change beyond richness (Avolio *et al.*, 2015; McGill *et al.*, 2015; Jetz *et al.*, 2016; Hillebrand *et al.*, 2018). Here, we suggest that studying dominant species is a necessary, key and understudied component of biodiversity, and encourage a focus on identifying dominant species within communities and using these species to scale ecological processes from individuals to ecosystems (Fig. 2). Indeed, several studies have noted the importance of the identity of dominant species in determining ecosystem function (Smith & Knapp, 2003; Sasaki & Lauenroth, 2011; Le Roux *et al.*, 2014; Winfree *et al.*, 2015; Bannar-Martin *et al.*, 2018) and invasion (Crawley *et al.*, 1999; Smith *et al.* 2004; Emery & Gross, 2006, 2007) over species richness or evenness. This research indicates that there is something about particular dominant species, beyond their high abundance, that lead to their strong ecological effects.

Ecology has seen many methodological and theoretical advances linking biodiversity to ecosystem processes from functional ecology (Díaz *et al.*, 1998; Diaz & Cabido, 2001; Violle *et al.*, 2007; Suding *et al.*, 2008; de Bello *et al.*, 2010) to BEF research (Cardinale *et al.*, 2007; Isbell *et al.*, 2011; Reich *et al.*, 2012; Tilman *et al.*, 2012). As ecologists are increasingly tasked with predicting ecosystem responses to global change, we argue for a greater focus on dominant species, particularly their identity and community and ecosystem-level effects. Although trait analyses such as community weighted means (Ackerly & Cornwell, 2007; Garnier *et al.*, 2007) do capture the effect of dominant species relative to others in the community, ecologists are inherently limited in the number of traits that can be measured and it is not always clear which are the most relevant traits to focus on with limited time and funding. Further, it is crucial to recognize that there are not always consistent relationships between functional traits and ecosystem responses in a given environment. For example, Forrestel *et al.* (2017) found that different sets of functional traits underlie similar aboveground productivity–precipitation relationships in South African and North American grasslands, largely due to the representation and relative abundance of different grass lineages within each region. These results emphasize the importance also of considering biogeographical and evolutionary processes as important drivers of the species and traits of a regional species pool, from which dominant species are drawn (Cavendar-Bares *et al.* 2016a). Although the traits of dominant species also may vary over environmental conditions, focus on dominant species and their traits can simplify and focus research in ecosystems characterized by dominance of one or a few species and complement existing methodologies. Mass ratio effects can be used alongside complementarity analyses (Loreau & Hector, 2001) to determine the relative contribution of dominant species vs number of species to ecosystem function. Identifying dominant species and studying how they impact ecosystem functioning results in context-dependency of studies; however, the phenomenon of dominant species is widespread and thus applicable to most ecological systems. Critically, it is unknown how generalizable the effects of dominant species are on community and ecosystem properties, necessitating more research on dominant species.

Given the high abundance and ubiquity of dominant species, their loss from ecosystems is not typically documented as compared with rare species (Gaston, 2010). However, dominant species also are prone to extinction (Gaston, 2011) and are being negatively impacted by anthropogenic changes worldwide (Gaston, 2010). Compared with rarer species, loss of dominant species threatens to have much larger impacts on community and ecosystem processes (Smith & Knapp, 2003; Gaston, 2010, 2011; Winfree *et al.*, 2015). Thus, research on these important species is critical to improving predictions of impacts of global change drivers on ecological systems.

Acknowledgements

We are thankful to Mark Hoover, Shenghua Yuan, Runqi Song, Julia Fogerty and Weihong Wong for their help with the literature review. MLA was supported by the National-Socio Environmental Synthesis Center (SESYNC) NSF DBI-1052875. EJF was supported by an NSF Postdoctoral Research Fellowship in Biology under grant no. 1612237. MDS was supported by the Drought-Net Research Coordination Network funded by the US National Science Foundation (NSF grant no. 1354732) and by the Macrosystems Biology/Emerging Frontiers Programs (NSF grant no. 1239559). Lastly, we thank several anonymous reviewers whose comments have improved the breadth and clarity of this paper.

Author contributions

All authors contributed to the content and writing of the paper, with MLA and MDS conceiving and writing most of the paper.

ORCID

Meghan L. Avolio https://orcid.org/0000-0002-2649-9159
Karin T. Burghardt https://orcid.org/0000-0002-9302-6802
Cynthia C. Chang https://orcid.org/0000-0002-3281-4864
Elisabeth J. Forrestel https://orcid.org/0000-0002-5072-3640
Kimberly J. La Pierre https://orcid.org/0000-0001-7056-4547
Melinda D. Smith https://orcid.org/0000-0003-4920-6985

References

Ackerly DD, Cornwell WK. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* **10**: 135–145.

Adler PB, HilleRislambers J, Levine JM. 2007. A niche for neutrality. *Ecology Letters* **10**: 95–104.

Albert CH, Grassein F, Schurr FM, Vieilledent G, Violle C. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 217–225.

Alroy J. 2015. The shape of terrestrial abundance distributions. *Science Advances* **1**: e1500082.

Avolio ML, La Pierre KJ, Houseman G, Koerner SE, Grman E, Isbell F, Johnson DS, Wilcox KR. 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere* **6**: art280.

Avolio ML, Smith MD. 2013. Mechanisms of selection: phenotypic differences among genotypes explain patterns of selection in a dominant species. *Ecology* **94**: 953–965.

Bailey JK, Schweitzer Ja, Ubeda F, Koricheva J, LeRoy CJ, Madritch MD, Rehill BJ, Bangert RK, Fischer DG, Allan GJ *et al.* 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization.

Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences **364**: 1607–1616.

Bangert RK, Lonsdorf EV, Wimp GM, Shuster SM, Fischer D, Schweitzer JA, Allan GJ, Bailey JK, Whitham TG. 2008. Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. *Heredity* **100**: 121–131.

Bannar-Martin KH, Kremer CT, Ernest M, Leibold MA, Auge H, Chase J, Declerck SAJ, Eisenhauer N, Harpole S, Hillebrand H *et al.* 2018. Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (CAFE) approach. *Ecology Letters* **21**: 167–180.

Barbour MG, Burk JH, Pitts WD, Gilliam FS, Schwartz MW. 1998. *Terrestrial plant ecology, 2nd edn.* Menolo Park, CA, USA: Benjamin Cummings.

Bartha S, Szentes S, Horváth A, Házi J, Zimmermann Z, Molnár C, Dancza I, Margóczi K, Pál RW, Purger D *et al.* 2014. Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands. *Applied Vegetation Science* **17**: 201–213.

Begon M, Townsend CR, Harper JL. 2006. *Ecology: from individuals to ecosystems.* Maldon, MA, USA: Blackwell Publishing.

de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JHC, Bardgett RD, Berg MP, Cipriotti P, Feld CK, Hering D *et al.* 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* **19**: 2873–2893.

Berger WH, Parker F. 1970. Diversity of planktonic roraminifera in deep-sea sediments. *Science* **168**: 1345–1347.

Bever JD. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* **157**: 465–473.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* **26**: 183–192.

Braun EL. 1947. Development of the deciduous forests of eastern North America. *Ecological Monographs* **17**: 211–219.

Braun EL. 1950. *Deciduous forests of eastern North America.* New York, NY, USA: Hafner Publishing Company.

Cain ML, Bowman WD, Hacker SD. 2011. *Ecology.* Sunderland, MA, USA: Sinauer Associates.

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* **98**: 572–592.

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences, USA* **104**: 18123–18128.

Cavender-Bares J, Ackerly DD, Hobbie SH, Townsend PA. 2016a. Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. *Annual Review of Ecology and Systematics* **47**: 433–462.

Cavender-Bares J, Meireles JE, Couture JJ, Kaproth MA, Kingdon CC, Singh A, Serbin SP, Center A, Zuniga E, Pilz G *et al.* 2016b. Associations of leaf spectra with genetic and phylogenetic variation in oaks: prospects for remote detection of biodiversity. *Remote Sensing* **8**: 221.

Chang CC, Smith MD. 2012. Invasion of an intact plant community: the role of population versus community level diversity. *Oecologia* **168**: 1091–1102.

Chesson PL. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**: 343–366.

Clements FE. 1907. *Plant physiology and ecology.* New York, NY, USA: RD Company.

Clements FE. 1916. *Plant succession; an analysis of the development of vegetation.* Washington, DC, USA: Carnigie Institute of Washington.

Clements FE. 1936. Nature and structure of the climax. *Journal of Ecology* **24**: 252–284.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.

Crawley MJ, Brown SL, Heard MS, Edwards GR. 1999. Invasion resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* **2**: 140–148.

Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science (New York, N.Y.)* **313**: 966–968.

Curtis JT, McIntosh RP. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* **32**: 476–496.

Darwin C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* London, UK: J. Murray.

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* **292**: 673–679.

Dayton PK. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**: 351–389.

Dayton PK. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC, ed. *Proceedings of the Colloquium on Conservation Problems in Antartica.* Lawrence, KS, USA: Allen Press, 81–96.

Dayton PK. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* **45**: 137–159.

De Meester L, Vanoverbeke J, Kilsdonk LJ, Urban MC. 2016. Evolving perspectives on monopolization and priority effects. *Trends in Ecology and Evolution* **31**: 136–146.

Diaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* **16**: 646–655.

Díaz S, Cabido M, Casanoves F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**: 113–122.

Diaz S, Lavorel S, de Bello F, Quetier F, Grigulis K, Robson TM. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences, USA* **104**: 20684–20689.

Díaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* **18**: 140–146.

Duffy EJ, Godwin CM, Cardinale BJ. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**: 261–264.

Edwards EJ, Osborne CP, Strömberg CAE, Smith S, Consortium CG. 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science* **328**: 587–590.

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM *et al.* 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**: 479–486.

Elumeeva TG, Onipchenko VG, Werger MJA. 2017. No other species can replace them: evidence for the key role of dominants in an alpine *Festuca varia* grassland. *Journal of Vegetation Science* **28**: 674–683.

Emery SM, Gross KL. 2006. Dominant species identity regulates invasibility of old-field plant communities. *Oikos* **115**: 549–558.

Emery SM, Gross KL. 2007. Dominant species identity, not community eveness, regulates invasion in experimental grassland communities. *Ecology* **88**: 954–964.

Ettema CH. 1998. Soil nematode diversity: species coexistence and ecosystem function. *Journal of Nematology* **30**: 159.

Facelli JM, Facelli E. 1993. Interactions after death: plant litter controls priority effects in a successional plant community. *Oecologia* **95**: 277–282.

Felton AJ, Smith MD. 2017. Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **372**: 20160142.

Fisher RA, Corbet AS, Williams CB. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**: 42–58.

Forrestel EJ, Donoghue MJ, Edwards EJ, Jetz W, du Toit JCO, Smith MD. 2017. Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences, USA* **114**: 705–710.

Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* **46**: 1–23.

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.

Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H, Golodets C *et al.* 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **99**: 967–985.

Gaston KJ. 2010. Valuing common species. *Science* **327**: 154–155.

Gaston KJ. 2011. Common ecology. *BioScience* **61**: 354–362.

Gause GF. 1934. *The struggle for existence.* Baltimore, MD, USA: Williams & Wilkins.

Gitlin AR, Sthultz CM, Bowker MA, Stumpf S, Paxton KL, Kennedy K, Muñoz A, Bailey JK, Whitham TG. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* **20**: 1477–1486.

Gleason H. 1929. The significance of Raunkiaer's law of frequency. *Ecology* **10**: 406–408.

Goulden CE, Hornig L, Wilson C. 1978. Why do large zooplankton species dominate? *Verhandlungen* **20**: 2457–2460.

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**: 344–347.

Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**: 1169–1194.

Grime JP. 1998. Benefits of plant diversity to ecosystems: inmediate, filter and founder effects. *Journal of Ecology* **86**: 902–910.

Grime JP. 2002. *Plant strategies, vegetation processes, and ecosystem properties.* Hoboken, NJ, USA: John Wiley & Sons.

Grossman JJ, Cavender-Bares J, Hobbie SE, Reich PB, Montgomery RA. 2017. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. *Ecology* **98**: 2601–2614.

Gurevitch J, Fox GA. 2006. *The ecology of plants.* Sunderland, MA, USA: Sinauer Associates.

Gurevitch J, Scheiner SM, Fox GA. 2002. *The ecology of plants.* Sunderland, MA, USA: Sinauer Associates.

Halliday TR. 1980. The extinction of the passenger pigeon *ectopistes migratorius* and its relevance to contemporary conservation. *Biological Conservation* **17**: 157–162.

Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**: 210–221.

Hartnett DC, Wilson GWT. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* **80**: 1187–1195.

Hepting GH. 1974. Death of the American Chestnut. *Journal of Forest History* **18**: 60–67.

Hillebrand H, Bennett DM, Cadotte MW. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**: 1510–1520.

Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp D, Larsen S *et al.* 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *Journal of Applied Ecology* **55**: 169–184.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**: 105–108.

Hoover DL, Knapp AK, Smith MD. 2014. Contrasting sensitivities of two dominant C_4 grasses to heat waves and drought. *Plant Ecology* **215**: 721–731.

Hutchinson GE. 1953. The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* **105**: 1–12.

Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**: 145–159.

Hutchinson GE. 1961. The paradox of the plankton. *The American Naturalist* **95**: 137–145.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J *et al.* 2011. High plant diversity is needed to maintain ecosystem services. *Nature* **477**: 199–202.

Jackson ST, Blois JL. 2015. Community ecology in a changing environment: perspectives from the Quaternary. *Proceedings of the National Academy of Sciences, USA* **112**: 4915–4921.

Jetz W, Cavender-Bares J, Pavlick R, Schimel D, Davis FW, Asner GP, Guralnick R, Kattge J, Latimer AM, Moorcroft PR *et al.* 2016. Monitoring plant functional diversity from space. *Nature Plants* **2**: 16024.

Kenoyer LA. 1927. A study of Raunkaier's law of frequence. *Ecology* **8**: 341–349.

Kirwan L, Connolly J, Finn JA, Brophy C, Lüscher A, Nyfeler D, Sebastia M-T. 2009. Diversity-interaction modeling: estimating contributions of speices identities and interactions to ecosystem function. *Ecology* **90**: 2032–2038.

Le Roux PC, Pellissier L, Wisz MS, Luoto M. 2014. Incorporating dominant species as proxies for biotic interactions strengthens plant community models. *Journal of Ecology* **102**: 767–775.

Leopold DR, Tanentzap AJ, Lee WG, Heenan PB, Fukami T. 2015. Evolutionary priority effects in New Zealand alpine plants across environmental gradients. *Journal of Biogeography* **42**: 729–737.

Lincoln RJ, Boxshall GA, Clark FP. 1998. *A dictionary of ecology, evolution and systematics.* Cambridge, UK: Cambridge University Press.

Lindenmayer D, Pierson J, Barton P, Beger M, Branquinho C, Calhoun A, Caro T, Greig H, Gross J, Heino J *et al.* 2015. A new framework for selecting environmental surrogates. *Science of the Total Environment* **538**: 1029–1038.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**: 72–76.

Lotka AJ. 1932. The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* **22**: 481–669.

MacArthur RH. 1964. Environmental factors affecting birst species diversity. *The American Naturalist* **98**: 387–397.

Magurran AE. 2004. *Measuring biological diversity.* Malden, MA, USA: Blackwell Science.

Mariotte P. 2014. Do subordinate species punch above their weight? Evidence from above- and below-ground. *New Phytologist* **203**: 16–21.

McGill BJ. 2010. Matters of scale. *Science* **328**: 575–576.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. 2015. Fifteen forms of biodiversity trend in the anthropocene. *Trends in Ecology and Evolution* **30**: 104.

McIntosh R. 1962. Raunkiaer's 'Law of Frequency'. *Ecology* **43**: 533–535.

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA *et al.* 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* **415**: 68–71.

McNaughton SJ, Wolf LL. 1970. Dominance and the niche in ecological systems. *Science* **167**: 131–139.

Mittelbach GG. 2012. *Community ecology.* Sunderland, MA, USA: Sinauer Associates.

Molles MCJ. 2005. *Ecology: concepts and applications.* New York, NY, USA: McGraw Hill.

Morin PJ. 1999. *Community ecology.* Malden, MA, USA: Wiley-Blackwell.

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734–737.

O'Connor NE, Crowe TP. 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology* **86**: 1783–1796.

Odum EP. 1959. *Fundamentals of ecology.* Philadelphia, PA, USA: W.B. Saunders.

Odum EP. 1971. *Fundamentals of ecology.* Philadelphia, PA, USA: W.B. Saunders.

Odum EP. 1993. *Ecology and our endangered life-support systems.* Sunderland, MA, USA: Sinauer Associates.

Odum EP, Barrett GW. 2005. *Fundamentals of ecology.* Pacific Grove, CA, USA: Thomson Brooks/Cole.

Olff H, Hoorens B, de Goede RGM, van der Putten WH, Gleichman JM. 2000. Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. *Oecologia* **125**: 45–54.

Olff H, Ritchie ME. 1998. Effect of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* **13**: 261–265.

Paine RT. 1966. Food web complexity and species diversity. *The American Naturalist* **100**: 65–75.

Paine RT. 1969. A note on trophic complexity and community stability. *The American Naturalist* **103**: 91–93.

Pau S, Dee LE. 2016. Remote sensing of species dominance and the value for quantifying ecosystem services. *Remote Sensing in Ecology and Conservation* **2**: 141–151.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. *BioScience* **46**: 609–620.

Preston FW. 1948. The commonness, and rarity, of species. *Ecology* **28**: 254–283.

Quaterman E. 1950. Major plant communities of Tennessee cedar glades. *Ecology* **31**: 234–254.

Rabinowitz D. 1981. Seven forms of rarity. In: Synge H, ed. *The biological aspects of rare plant conservation.* New York, NY, USA: John Wiley & Sons, 205–217.

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecology Letters* **8**: 811–818.

Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**: 589–592.

Ricklefs RE. 1990. *Ecology.* New York, NY, USA: W. H. Freeman.

Ricklefs RE. 2001. *The economy of nature.* New York, NY, USA: W. H. Freeman.

Ricklefs RE, Latham RE, Qian H. 1999. Global patterns of tree species richness in moist forests : distinguishing ecological influences and historical contingency. *Oikos* **86**: 369–373.

Ricklefs RE, Miller GL. 1999. *Ecology.* New York, NY, USA: W. H. Freeman.

Rundel PW, Dickie IA, Richardson DM. 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biological Invasions* **16**: 663–675.

Sasaki T, Lauenroth WK. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia* **166**: 761–768.

Schmitz OJ, Buchkowski RW, Burghardt KT, Donihue CM. 2015. Functional traits and trait-mediated interactions. Connecting community-level interactions with ecosystem functioning. *Advances in Ecological Research* **52**: 319–453.

Schweiger AK, Cavender-Bares J, Townsend PA, Hobbie SE, Madritch MD, Wang R, Tilman D, Gamon JA. 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nature Ecology & Evolution* **2**: 976–982.

Seabloom EW, Harpole WS, Reichman OJ, Tilman D. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences, USA* **100**: 13384–13389.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406–1419.

Silletti AM, Knapp AK, Blair JM. 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. *Canadian Journal of Botany* **82**: 450–460.

Silvertown J, Poulton P, Johnston E, Edwards G, Heard M, Biss PM. 2006. The Park Grass Experiment 1856–2006: its contribution to ecology. *Journal of Ecology* **94**: 801–814.

Simpson EH. 1949. Measurement of diversity. *Nature* **163**: 688.

Smith MD, Knapp AK. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* **6**: 509–517.

Smith TM, Smith RL. 2006. *Elements of ecology.* San Franscisco, CA, USA: Benjamin Cummings.

Smith MD, Wilcox JC, Kelly T, Knapp AK. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* **106**: 253–262.

Souza L, Weltzin JF. 2011. Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem. *Journal of Plant Ecology* **4**: 123–131.

Sterner RW, Elser JJ. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere.* Princeton, NJ, USA: Princeton University Press.

Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, Diaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas M-L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125–1140.

Symstad AJ, Tilman D, Willson J, Knops JMH. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* **81**: 389–397.

Tilman D. 1982. *Resource competition and community structure.* Princeton, NJ, USA: Princeton University Press.

Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* **367**: 363–365.

Tilman D, El Haddi A. 1992. Drought and biodiversity in grasslands. *Oecologia* **89**: 257–264.

Tilman D, Reich PB, Isbell F. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences, USA* **109**: 10394–10397.

Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiverstiy in grassland ecosystems. *Nature* **379**: 718–720.

Tobner CM, Paquette A, Gravel D, Reich PB, Williams LJ, Messier C. 2016. Functional identity is the main driver of diversity effects in young tree communities. *Ecology Letters* **19**: 638–647.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional!. *Oikos* **116**: 882–892.

Volterra V. 1926. Variations and fluctuations of the numbers of individuals in anamial species living together (Reprinted in 1931). In: Chapman RN, ed. *Animal ecology.* New York, NY, USA: McGraw Hill, 409–448.

Wagner PJ, Kosnik MA, Lidgard S. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* **314**: 1289–1292.

Wardle DA. 2016. Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science* **27**: 646–653.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–1633.

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, Leroy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM *et al.* 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.

Whittaker RH. 1965. Dominance and diversity in land plant communities. *Science* **147**: 250–260.

Wiens JA. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385–397.

Winfree R, Fox WJ, Williams NM, Reilly JR, Cariveau DP. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* **18**: 626–635.

Wohlgemuth D, Solan M, Godbold JA. 2016. Specific arrangements of species dominance can be more infuential than evenness in maintaining ecosystem process and function. *Scientific Reports* **6**: 39325.

Wright JS. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**: 1–14.

Yu Q, Chen Q, Elser JJ, He N, Wu H, Zhang G, Wu J, Bia Y, Han X. 2010. Linking stoichiometric homoeostatis with ecosystem structure, functioning and stability. *Ecology Letters* **13**: 1390–1399.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Generalized linear models examining the effects of dominant species removals by type of removal (pulse/press), study duration and ecosystem type.

Table S2 Textbooks that either included or did not include a definition of dominant species listed chronologically.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.1

Appendix A1

Citations used in the meta-analyses

Abul-Fatih HA, Bazzaz FA. 1979. The biology of *Ambrosia trifida L.* I. influence of species removal on the organization of the plant community. *New Phytologist* **83**: 813–816.

Akhmetzhanova AA. 2010. Assessment of phytomass changes in an alpine Geranium-Hedysarum meadow after the removal of dominants: the results of a ten-year experiment. *Russian Journal of Ecology* **41**: 38–43.

Altieri AH, Silliman BR, Bertness MD. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *American Naturalist* **169**: 195–206.

Bateman HL, Chung-MacCoubrey A, Snell HL. 2008. Impact of non-native plant removal on lizards in riparian habitats in the Southwestern United States. *Restoration Ecology* **16**: 180–190.

Bechtold HA, Inouye RS. 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *Journal of Arid Environments* **71**: 122–132.

Belsky AJ. 1992. Effects of grazing competition disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* **3**: 187–200.

Boeken B, Shachak M. 2006. Linking community and ecosystem processes: the role of minor species. *Ecosystems* **9**: 119–127.

Borchgrevink MB, Derner JD, Weston TR, Olson RA, Schuman GE, Hess BW. 2010. Small mammal and plant community responses to mechanical disturbance and rest in Wyoming big sagebrush grassland. *Arid Land Research and Management* **24**: 57–67.

Bret-Harte MS, Garcia EA, Sacre VM, Whorley JR, Wagner JL, Lippert SC, Chapin FS. 2004. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* **92**: 635–647.

Bret-Harte MS, Mack MC, Goldsmith GR, Sloan DB, DeMarco J, Shaver GR, Ray PM, Biesinger Z, Chapin FS. 2008. Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* **96**: 713–726.

Brewer JS. 2011. Per capita community-level effects of an invasive grass, *Microstegium vimineum*, on vegetation in mesic forests in northern Mississippi (USA). *Biological Invasions* **13**: 701–715.

Brose U, Tielborger K. 2005. Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. *Plant Ecology* **178**: 51–59.

Buonopane M, Huenneke LF, Remmenga M. 2005. Community response to removals of plant functional groups and species from a Chihuahuan desert shrubland. *Oikos* **110**: 67–80.

Chapin FS, Mcgraw JB, Shaver GR. 1989. Competition causes regular spacing of alder in Alaskan shrub tundra. *Oecologia* **79**: 412–416.

Collins B, Wein G, Philippi T. 2001. Effects of disturbance intensity and frequency on early old-field succession. *Journal of Vegetation Science* **12**: 721–728.

Collins SL, Glenn SM, Briggs JM. 2002. Effect of local and regional processes on plant species richness in tallgrass prairie. *Oikos* **99**: 571–579.

Crow C, van Riper C. 2010. Avian community responses to mechanical thinning of a pinyon-juniper woodland: specialist sensitivity to tree reduction. *Natural Areas Journal* **30**: 191–201.

Curiel D, Guidetti P, Bellemo G, Scattolin M, Marzocchi M. 2002. The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the lagoon of Venice. *Hydrobiologia* **477**: 209–219.

DeMeester JE, Richter DD. 2010. Restoring restoration: removal of the invasive plant *Microstegium vimineum* from a North Carolina wetland. *Biological Invasions* **12**: 781–893.

Duarte CM, Terrados J, Agawin NSR, Fortes MD. 2000. An experimental test of the occurrence of competitive interactions among SE Asian seagrasses. *Marine Ecology-Progress Series* **197**: 231–240.

Ellison AM, Plotkin AAB, Khalid S. 2016. Foundation species loss and biodiversity of the herbaceous layer in New England forests. *Forests* **7**: art9.

Gerdol R, Brancaleoni L, Marchesini R, Bragazza L. 2002. Nutrient and carbon relations in subalpine dwarf shrubs after neighbour removal or fertilization in northern Italy. *Oecologia* **130**: 476–483.

Gilbert B, Turkington R, Srivastava DS. 2009. Dominant species and diversity: linking relative abundance to controls of species establishment. *American Naturalist* **174**: 850–862.

Hils MH, Vankat JL. 1982. Species removals from a first-year old-field plant community. *Ecology* **63**: 705–711.

Honu YAK, Dang QL. 2000. Responses of tree seedlings to the removal of *Chromolaena odorata* Linn. in a degraded forest in Ghana. *Forest Ecology and Management* **137**: 75–82.

Irving AD, Bertness MD. 2009. Trait-dependent modification of facilitation on cobble beaches. *Ecology* **90**: 3042–3050.

Jonasson S. 1992. Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos* **63**: 420–429.

Keddy PA, Smith L, Campbell DR, Clark M, Montz G. 2006. Patterns of herbaceous plant diversity in southeastern Louisiana pine savannas. *Applied Vegetation Science* **9**: 17–26.

Kelemen A, Lazzaro L, Besnyoi V, Albert AJ, Konecna M, Dobay G, Memelink I, Adamec V, Gotzenberger L, de Bello F, Le Bagousse-Pinguet Y, Leps J. 2015. Net outcome of competition and facilitation in a wet meadow changes with plant's life stage and community productivity. *Preslia* **87**: 347–361.

Klanderud K. 2005. Climate change effects on species interactions in an alpine plant community. *Journal of Ecology* **93**: 127–137.

Leps J. 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *Journal of Vegetation Science* **10**: 219–230.

Leps J. 2014. Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. *Journal of Applied Ecology* **58**: 978–987.

Li W, Cheng J, Yu K, Epstein HE, Du G. 2015. Short-term responses of an alpine meadow community to removal of a dominant species along a fertilization gradient. *Journal of Plant Ecology* **8**: 513–522.

Lilley SA, Schiel DR. 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* **148**: 672–681.

MacDougall AS, Turkington R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**: 42–55.

Marchante H, Freitas H, Hoffmann JH. 2011. Post-clearing recovery of coastal dunes invaded by *Acacia longifolia*: is duration of invasion relevant for management success? *Journal of Applied Ecology* **48**: 1295–1304.

Mathis MJ, Middleton BA. 1999. Simulated herbivory and vegetation dynamics in coal slurry ponds reclaimed as wetlands. *Restoration Ecology* **7**: 392–398.

Munson SM, Lauenroth WK. 2009. Plant population and community responses to removal of dominant species in the shortgrass steppe. *Journal of Vegetation Science* **20**: 224–232.

Pinder JE. 1975. Effects of species removal on an old-field plant community. *Ecology* **56**: 747–751.

Pinto SM, Pearson DE, Maron JL. 2014. Seed dispersal is more limiting to native grassland diversity than competition or seed predation. *Journal of Ecology* **102**: 1258–1265.

Platt WJ, Carr SM, Reily M, Fahr J. 2006. Pine savanna overstory influences on ground-cover biodiversity. *Applied Vegetation Science* **9**: 37–50.

Polley HW, Wilsey BJ, Derner JD, Johnson HB, Sanabria J. 2006. Early-successional plants regulate grassland productivity and species composition: a removal experiment. *Oikos* **113**: 287–295.

Prevey JS, Germino MJ, Huntly NJ. 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecological Applications* **20**: 1890–1902.

Raffaele E, Ruggiero A. 1995. Short-term effects of removing the most abundant species on plant-species co-occurrence at a spatial microscale. *Revista Chilena de Historia Natural* **68**: 361–371.

Rixen C, Mulder CPH. 2009. Species removal and experimental warming in a subarctic tundra plant community. *Oecologia* **161**: 173–186.

Roth A-M, Campbell D, Keddy P, Dozier H, Montz G. 2008. How important is competition in a species-rich grassland? A two-year removal experiment in a pine savanna. *Ecoscience* **15**: 94–100.

Sasaki T, Lauenroth WK. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia* **166**: 761–768.
Silletti AM, Knapp AK, Blair JM. 2004. Competition and coexistence in grassland co-dominants: responses to neighbour removal and resource availability. *Canadian Journal of Botany* **82**: 450–460.
Schiel DR. 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. *Journal of Experimental Marine Biology and Ecology* **338**: 233–252.
Smith AP. 1984. Postdispersal parent-offspring conflict in plants – antecedent and hypothesis from the Andes. *American Naturalist* **123**: 354–370.
Smith MD, Hartnett DC, Wilson GWT. 1999. Interacting influence of mycorrhzial symbiosis and competition on plant diversity in tallgrass prairie. *Oecologia* **121**: 574–582.
Smith MD, Knapp AK. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* **6**: 509–517.
Souza L, Weltzin JF, Sanders NJ. 2010. Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem. *Journal of Plant Ecology* **4**: 123–131.
Suding KN, Miller AE, Bechtold H, Bowman WD. 2006. The consequence of species loss on ecosystem nitrogen cycling depends on community compensation. *Oecologia* **149**: 141–149.
Titus JH, Leps J. 2000. The response of arbuscular mycorrhizae to fertilization, mowing, and removal of dominant species in a diverse oligotrophic wet meadow. *American Journal of Botany* **87**: 392–401.
Vila M, Terradas J. 1995. Effects of competition and disturbance on the resprouting performance of the Mediterranean shrub *Erica multiflora* L. (Ericaceae). *American Journal of Botany* **92**: 1241–1248.
Wardle DA, Gundale MJ, Jaderlund A, Nilsson MC. 2013. Decoupled long-term effects of nutrient enrichment on aboveground and belowground properties in subalpine tundra. *Ecology* **94**: 904–919.