



Tansley review

Defining codominance in plant communities




Authors for correspondence:

Jesse E. Gray

Email: jesse.gray@colostate.edu

Melinda D. Smith

Email: melinda.smith@colostate.edu

Jesse E. Gray^{1,2} , **Kimberly J. Komatsu³**  and **Melinda D. Smith^{1,2}** 

¹Department of Biology, Colorado State University, Fort Collins, CO 80521, USA; ²Graduate Degree Program in Ecology, Colorado

State University, Fort Collins CO 80521, USA; ³Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

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Summary

Species dominance and biodiversity in plant communities have received considerable attention and characterisation. However, species codominance, while often alleged, is seldom defined or quantified. Codominance is a common phenomenon and is likely to be an important driver of community structure, ecosystem function and the stability of both. Here we review the use of the term 'codominance' and find inconsistencies in its use, suggesting that the scientific community currently lacks a universal understanding of codominance. We address this issue by: (1) qualitatively defining codominance as mostly shared abundance that is distinctively isolated within a subset of a community, and (2) presenting a novel metric for quantifying the degree to which relative abundances are shared among a codominant subset of plant species, while also accounting for the remaining species within a plant community. Using both simulated and real-world data, we then demonstrate the process of applying the codominance metric to compare communities and to generate a quantitatively defensible subset of species to consider codominant within a community. We show that our metric effectively distinguishes the degree of codominance between four types of grassland ecosystems as well as simulated ecosystems with varying degrees of abundance sharing among community members. Overall, we make the case that increased research focusses on the conditions under which codominance occurs and the consequences for species coexistence, community structure and ecosystem function that would considerably advance the fields of community and ecosystem ecology.

I. Introduction

Conservation research is often focussed on biodiversity and rare species (Gaston, 2010, 2011), but frequently overlooks the common species that drive many ecosystem functions and services

(Grime, 1998; Gaston, 2011; Avolio *et al.*, 2019). Rare species are certainly threatened by human activities (Vitousek *et al.*, 1997; Ohlemüller *et al.*, 2008; Schatz *et al.*, 2014); these species can play important roles in ecosystem function both directly and through their contributions to biodiversity (McCann, 2000; Loreau & de

Mazancourt, 2013; Jain *et al.*, 2014; Gross *et al.*, 2014). Common species largely control ecosystem function, however, often proportional to their greater abundance and biomass in the system (Grime, 1998; Avolio *et al.*, 2019). They also exert a strong influence over community structure, including the potential facilitation of rare species (Smith *et al.*, 2004; Avolio *et al.*, 2019). Moreover, because by definition the plurality, or even majority, of individuals in many ecosystems belong to a common species, the phenotypic plasticity and genetic diversity associated with these highly abundant species can have ecosystem-level effects in excess of those related to species diversity (Whitham *et al.*, 2006; Bangert *et al.*, 2008; Crutsinger *et al.*, 2008; Hughes *et al.*, 2008; Bailey *et al.*, 2009; Crawford & Rudgers, 2012, 2013). Accordingly, long-term ecosystem sensitivity to environmental change may also be principally determined by the population-level responses of common species (Avolio & Smith, 2013). For these reasons, recent reviews have argued in favour of increasing consideration of common species in conservation programmes and research, with recommendations for a shift in focus primarily towards common species over biodiversity for the better understanding and management of ecosystem function (Gaston, 2010, 2011; O'Loughlin *et al.*, 2018; Avolio *et al.*, 2019).

In plant communities, the effect of a common species can clearly be determined when a community is highly uneven, meaning when there is a single common species with the remaining species in low abundance (Fig. 1). In such instances, these plant species are often referred to as dominant or dominating in the community (*sensu* Avolio *et al.*, 2019), and there is ample evidence that the loss of these species can have large consequences for ecosystem function and stability (Smith & Knapp, 2003; Gaston & Fuller, 2008; Sasaki & Lauenroth, 2011; Smith *et al.*, 2020). However, there are instances where there is more than one common species in a plant community (Fig. 1); these are often referred to as *codominant* species (e.g. Danin, 1978; Woods, 1979; Kuebbing *et al.*, 2015). Where they occur, codominant plant species are distinct from uncommon (or subordinate, Grime, 1998) species, in that they also can control a large proportion of ecosystem function (Silletti & Knapp, 2002; Ma *et al.*, 2020; Valencia *et al.*, 2020). The often-observed pattern that ecosystems are frequently characterised by a few abundant and many rare species (e.g. Preston, 1948; MacArthur, 1960; Whittaker, 1965) suggests that codominated ecosystems may be as (or even more) common than communities dominated by a single species (i.e. mono-dominated communities). Even if there is a single regionally common species, such dominant species are likely to be locally codominant with other species within portions of their ranges. As such, studies that focus on the characteristics of only the most abundant plant species may fail to capture important aspects of local ecosystem function and stability (Grime, 1998; Smith & Knapp, 2003; Smith *et al.*, 2020). For instance, the influence of a single common species on ecosystem function will be overestimated if its abundance is correlated with both the measure of that function and the abundance of another common species. Moreover, greater temporal stability in ecosystem function may occur in communities with more than one common species, for example if changing environmental conditions favour one common species one year, and the other common species in another. Collectively, variance in ecosystem function would be

expected to be lower for the codominated community than for a community that is mono-dominated (Wilcox *et al.*, 2017).

Given the potential for plant communities to contain more than one common species and the implications of codominance for community and ecosystem functioning and stability, it is surprising that, to our knowledge, no synthesis of ecological literature on codominance has yet been presented. Moreover, based on our review of the literature, the concept of what qualifies as codominance has depended largely upon the author, with species comprising between 5% and 83% (e.g. Toft & Elliott-Fisk, 2002; Gilbert, Turkington & Srivastava, 2009) of total abundance having been described as codominant. We assert that this overly broad range of abundances has made the term 'codominant' practically meaningless. Additionally, some authors have instead relied on frequencies, rather than abundances in their delineations of codominance (e.g. Lawesson, 2000; Lisa & Renato, 2006; Costa *et al.*, 2009; El-Keblawy, Abdelfattah & Khedr, 2015), which can reflect strong dispersal abilities of species that otherwise bear little ecological influence. To illustrate, a species with low abundance that appears in all samples would appear equivalent in frequency to a species that also appears in all samples but at high abundances. We acknowledge that frequency can be a valuable component of codominance but suggest that it can be misleading when reported in the absence of other abundance metrics. By contrast, others have used the term to refer to indicator species that are unique in their localised abundance and coincident *lack* of frequency across a study

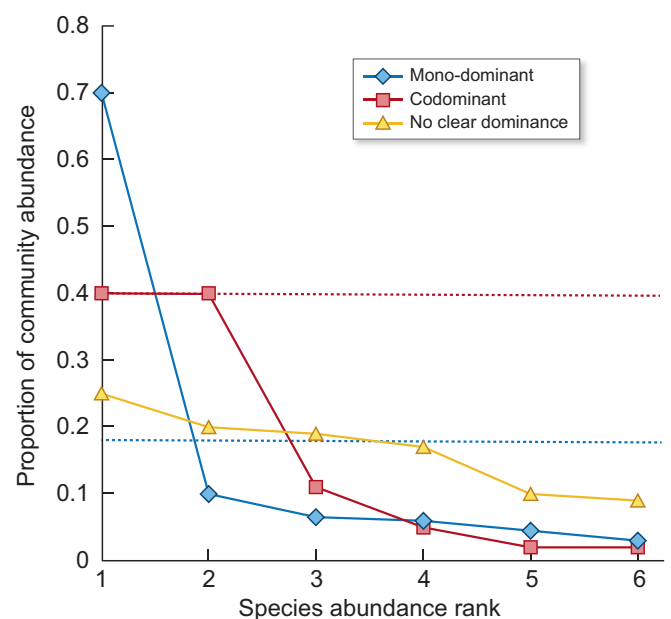


Fig. 1 Rank-abundance curves of hypothetical communities with contrasting species assemblages. Monodominated communities have a single species with a markedly greater abundance than that of any other species in the community. In codominated communities, two or more species share a similar degree of abundance that is distinctly greater than that of any other species in the community. In contrast with these, some communities have much smaller differences in abundance among any of their species (no clear dominance, yellow). Dotted horizontal lines show harmonic means of the two most abundant species of codominated (= 0.4, red) and monodominated (= 0.175, blue) communities. Both have arithmetic means = 0.4.

area (e.g. Dias & Melo, 2010). Such labels are valuable for floristically distinguishing between ecologically dissimilar areas within a region, and we would agree that such species may be codominant within those limited areas. However, this use of the term 'codominant' to refer to a species' distribution throughout an entire region where it is distinctly uncommon is confusing in its incongruity with the more common understanding of the term. Similarly, numerous (especially earlier) papers used the term codominant to classify species with abundances immediately inferior to those of coexisting dominant species (e.g. Bazzaz, 1968; Day & Monk, 1974; Busch, 1995). Lastly, although less problematic, many authors have reported only absolute abundances of their codominant species, without referencing the abundances of the remaining species in their communities for comparison (e.g. Hamerlynck *et al.*, 2002; Kürschner, 2004). Without a consensus in defining codominance, or a standardised method for quantifying codominance (in line with metrics of dominance), progress towards a better understanding of the mechanisms that lead to such relationships and the consequences of codominance for community structure and ecosystem function and stability will be hindered by ambiguity.

Here, we aim to facilitate more clear communication and generate deeper discussion of codominance in three ways. First, we delve deeper into the importance of codominant species. Second, we conduct a literature review to synthesise existing definitions or implied meanings of codominance and characterise the mechanisms that have been used to explain the stability of codominant relationships. Based on this synthesis, we provide a qualitative definition of codominance and summarise the proposed mechanisms underlying codominance included in the reviewed papers. Third, we provide a novel metric of codominance that can be used to identify the occurrence of codominance, and to quantitatively compare ecosystems, experimental treatments and community states in space and time. We then present examples of the utility of this metric using synthetic and real data. Finally, we provide an overview of the implications of codominance and future directions of codominance research. We believe a clear qualitative definition and a metric to quantify codominance will garner greater mutual understanding of this underappreciated community characteristic, fostering a more complete conception of plant communities and the roles that their most important members play in them.

li. Why codominance matters

The usage of the term 'codominance' is common in plant ecology but often not explicitly defined (see next section). As such, we contend that its importance in plant communities has been overlooked and understudied. Below we describe three ecological topics for which the study of codominance may provide important insights.

1. Coexistence theory

The history of community ecology may be said to embody our lengthy endeavour to better understand how species coexist (Loreau, 2010). Current frameworks around this fundamental

question rest on two foundations: niche differences and relative fitness differences among coexisting species. However, the relative importance of the roles that these aspects play are imperfectly understood (Levine & HilleRisLambers, 2009; Carroll *et al.*, 2011; HilleRisLambers *et al.*, 2012; Kraft *et al.*, 2015; Valencia *et al.*, 2020) and are likely to be variable (Chase & Myers, 2011; HilleRisLambers *et al.*, 2012). For instance, sets of codominant species that exhibit similar degrees of shared abundance but contrasting degrees of functional similarity (e.g. Kikvidze *et al.*, 2006; Kuebbing *et al.*, 2015) suggests that the degree of niche partitioning can vary greatly across sets of codominant species. Moreover, while relative fitness differences can cause better competitors to capture greater shares of abundance within their communities, this property must be tempered to enable codominance. As such, species exhibiting stable codominance, particularly in variable environments, present ideal model systems for exploring the relative importance of niche vs fitness differences in determining the outcomes of species interactions.

2. Ecosystem function and stability

When an ecosystem is overwhelmingly dominated by a single species, many of its functions (e.g. annual net primary productivity) will be controlled primarily by the dominant species in direct proportion to its relative abundance (i.e. mass ratio hypothesis; Grime, 1998; Avolio *et al.*, 2019; Smith *et al.*, 2020). In turn, the stability of such functions will be a consequence of the population dynamics of that single dominant species and its responses to changing environmental conditions (Smith & Knapp, 2003; Gaston & Fuller, 2008). By contrast, when an ecosystem is codominated, control over its ecosystem functions will frequently depend on the mechanism(s) underling codominance (Mouquet *et al.*, 2002; Tylianakis *et al.*, 2008) and may be more evenly distributed across the co-dominating species in proportion to their shared abundances (Grime, 1998). In addition to sharing in the control of the magnitude of expression of ecosystem function, codominant species can affect the spatial and temporal variability in ecosystem function when they differ in their responses to changing environmental conditions, (Loreau *et al.*, 2003; Shanafelt *et al.*, 2015). This, in turn, can result in enhanced temporal stability of those functions (Valencia *et al.*, 2020). For instance, if in one year environmental conditions favour biomass production of one species more so than its codominant, and the next year favours the latter over the former, variance in community biomass productivity over those two years will be lower than in an ecosystem that experiences the same environmental variability but is mono-dominated by either one of the two species (Wilcox *et al.*, 2017). Thus, codominance is likely to be an important, yet under-recognised, feature of plant communities that influences ecosystem functioning and stability in ways that differ from the most common (dominant) species or species diversity.

3. Global change

Although common species carry a relatively low probability of extirpation, such events have occurred arising from introduced

invasive plants, species-specific pathogens, and uncontrolled preferential herbivory (e.g. Anagnostakis, 1987; Vinton *et al.*, 1993; Ash *et al.*, 1997; Mal *et al.*, 1997; Nuzzo, 1999; Dilleuth *et al.*, 2009; Condon *et al.*, 2011; White, 2012; Fernandez-Winzer *et al.*, 2020), often with dramatic ecosystem consequences. Future losses of common species are anticipated to occur at a greater rate as a result of changing abiotic conditions such as warming (Llorens *et al.*, 2004; Bokhorst *et al.*, 2008), drought (Visser *et al.*, 2002; Llorens *et al.*, 2004), and altered nutrient availabilities (Cantarel *et al.*, 2013; Isbell *et al.*, 2013). Such issues can be expected to be particularly problematic in cases in which codominance is a direct result of interactions between the traits of codominant species and historic climatic conditions and patterns. Interactions between changing abiotic and biotic factors are also likely (Bale *et al.*, 2002; Theoharides & Dukes, 2007; Kelly & Goulden, 2008). However, if codominant species differ in their responses to environmental change and are redundant in their effects on ecosystem functions, the negative impacts of changing biotic and abiotic factors may be greatly mitigated relative to mono-dominated ecosystems (Mori *et al.*, 2013). This potential should be at the forefront of restoration planning and greater knowledge of the traits of codominant species could be critical for success in these efforts (Laughlin *et al.*, 2018). Similarly, conservation science (*sensu* Kareiva & Marvier, 2012), a field currently oriented towards crisis mitigation (Geldmann *et al.*, 2020), could be well served through increased consideration of codominant species. Because of the visibility of codominant species and their proportionally greater control over ecosystem functions and services (Grime, 1998; Smith *et al.*, 2020), arguments for their conservation may be more persuasive among stakeholders than those made for charismatic, but seldom seen species (O'Loughlin *et al.*, 2018). Moreover, because codominant species can have positive effects on biodiversity and function by facilitating rarer species (Smith & Knapp, 2003), investments in their conservation may be required for long-term success. Conversely, when species are more complementary or mutually facilitative in their effects, or if they respond to certain environmental changes in synchrony, the regions where they co-dominate may be particularly vulnerable to such changes through positive feedbacks (Traveset & Richardson, 2014; Valencia *et al.*, 2020). It will be increasingly important to understand the contributions that various codominant species make to their ecosystems and whether the characteristics of their responses to abiotic and biotic changes will buffer those systems or place them at greater risk of collapse.

III. Defining codominance

1. Literature search

To determine how codominance is used and defined in the literature, we conducted a literature review. We based our literature search on the criteria that: (1) authors mention some form of the terms 'codominance' or 'codominant', (2) the usage of the term references abundance or degree of ecosystem function determined by cohabiting species, and (3) the focal species were plants. To ensure repeatability, our primary literature search, conducted in March 2020, used the Web of Science and the topic terms 'plant',

'ecolog*', and either 'co-domin*' or 'codomin*'. These searches returned 83 and 46 articles, respectively (Table S1). These were further filtered to remove uses of the term that were not compatible, including references to gene interactions, tree canopy structure and nonplant focal species. A second search was performed in Web of Science using only the topic terms 'co-domin*' or 'codomin*'. Results were refined using the Web of Science 'categories' filter set to 'ecology', returning 331 and 315 results, respectively. These returns were then subjected to the same manual filtering described above. In total, 165 research papers were found that matched all our criteria. We performed a supplemental, but less replicable search using Google Scholar and the terms 'codominant', 'ecology', and 'plants'. This resulted in a return of over 17 000 matches. However, as we reviewed these matches in order from best match to worst, we found they had rapidly decreasing relevance (more frequently incompatible uses of the term and fewer focal species that were plants) and more replicate entries. In addition, a lower proportion of papers from the Google Scholar search provided definitions of, relative abundance data related to, and mechanisms explaining codominance. We therefore limited this supplementary inclusion to our core set of literature to the best-matching 100 papers uniquely returned in Google Scholar. In total we reviewed 265 papers (Table S1). Importantly, no review or meta-analysis articles of codominance were returned using any of these methods.

2. A qualitative definition of codominant species

To define codominant species, we sought to inclusively synthesise conceptualisations presented in the literature as much as was feasible. Most (77%) of the reviewed papers did not include an explicit definition of codominance, and species were referred to as codominant only in passing (Table S1). Of those that included definitions, 10 papers defined codominant species in aggregate terms (i.e. sum of relative abundances), without explicitly stating the individual contributions of the component codominant species. Qualitative definitions that explicitly stated the relationship between the codominant species were provided in only nine papers. Quantitative definitions were included in 10 of the papers, but all but one of these was based on an arbitrarily set threshold of abundance with no criteria described for their relationship with subordinate species. Species described as codominant included those with: (1) the highest individual or aggregate measures of abundance, (2) more than a threshold abundance; or (3) were individually or aggregately major components of the vegetation (without reference to relative abundance), (4) had greater than average species importance value, and (5) exerted more control over an aspect of ecosystem function and/or diversity than other species in the community. Some also defined codominant species as those that were subordinate to dominant species, or those that served as indicator species in which dominant species were ubiquitous. Because the latter uses of the term codominance are limited to specialised fields such as phytosociology and contradict the broader usages, they were not considered when formulating our definition. Although referring to their focal species as codominant, 15 of the papers provided definitions for dominance only, most notably in terms of Simpson's D (e.g. Hart, 2001; Taft *et al.*, 2011; Almazán-

Núñez *et al.*, 2016). Because Simpson's D is a description of the community rather than of its component species, we also did not consider these uses of the term in defining codominant species.

Overall, our review suggested that definitions of codominance vary substantially, but most authors have not found it necessary to provide their interpretation of 'codominant' or 'codominated', despite an intuitive impulse to describe species or ecosystems using these terms. This might be acceptable if the intuitions of the authors were dependably similar. However, data gleaned from the reviewed papers revealed a wide range of abundances among the species that were described as codominant, both relative to one another, and relative to the remainder of species in their communities. For example, in some cases the first and second-ranked species had an equal share of relative abundance, while in others the first-ranked species had as much as 19 times more abundance than the second (Quartile 1: 1.13 \times , Q2: 1.33 \times , Q3: 2.20 \times , Fig. 2a). Aggregate relative abundances of the two most abundant species ranged from 0.07 to 1 (Quartile 1: 0.41, Q2: 0.67, Q3: 0.89), indicating that these species collectively accounted for as little as 7% to as much as 100% of their total communities (Fig. 2b). These broad ranges indicated that investigators frequently have very different interpretations of codominance. We therefore sought to qualitatively define codominance to synthesise its various, but compatible, uses to be as general as was reasonable and to set intuitive thresholds for inclusion under the classification. We, accordingly, define *codominance* as species that have a 'shared' abundance that together comprises the majority (i.e. >50%) of the total abundance of a spatially and temporally specified community. In this definition, two species are considered to have a shared abundance when the

maximum ratio between two codominant species is 75% : 25% (i.e. one species has no more than three times the abundance of the other). We chose this cutoff as it is more than halfway between unshared (when species 1 has 100% and species 2 has 0%) and evenly shared (50% : 50%). Of the 167 pairs of first and second-ranked species reported with relative abundance data in our literature review (Fig. 2a), 91 met both of these criteria, while 25 had uneven sharing of abundance and 53 pairs contributed less than a majority (<50%) of their community abundances. Importantly, despite these numerical cut-offs, this definition is still qualitative. A metric for mathematically comparing the degree of codominance between communities is described in a later section.

Our definition is conceptually similar to the definition of dominance in that codominant species have higher relative abundance than others in their community (Avolio *et al.*, 2019), but with caveats that reflect the complications of multispecies dominance, namely that the species must be abundant, but not so abundant that others do not also capture a substantial share of the total community abundance. However, unlike Avolio *et al.* (2019), we do not (yet) include the relative influence of the species on ecosystem function for classification as codominant, not because we do not think this is an unimportant qualification, but because we did not find data of this nature sufficiently reported in the literature we reviewed. Until such data are more readily available (e.g. through multispecies removal experiments), it would be difficult to label any species sets as codominant under this criterium. Some species may be codominant using one type of abundance measurement (e.g. stem density of a bunchgrass), but not in another (e.g. canopy cover of a bunchgrass). As such, the measure

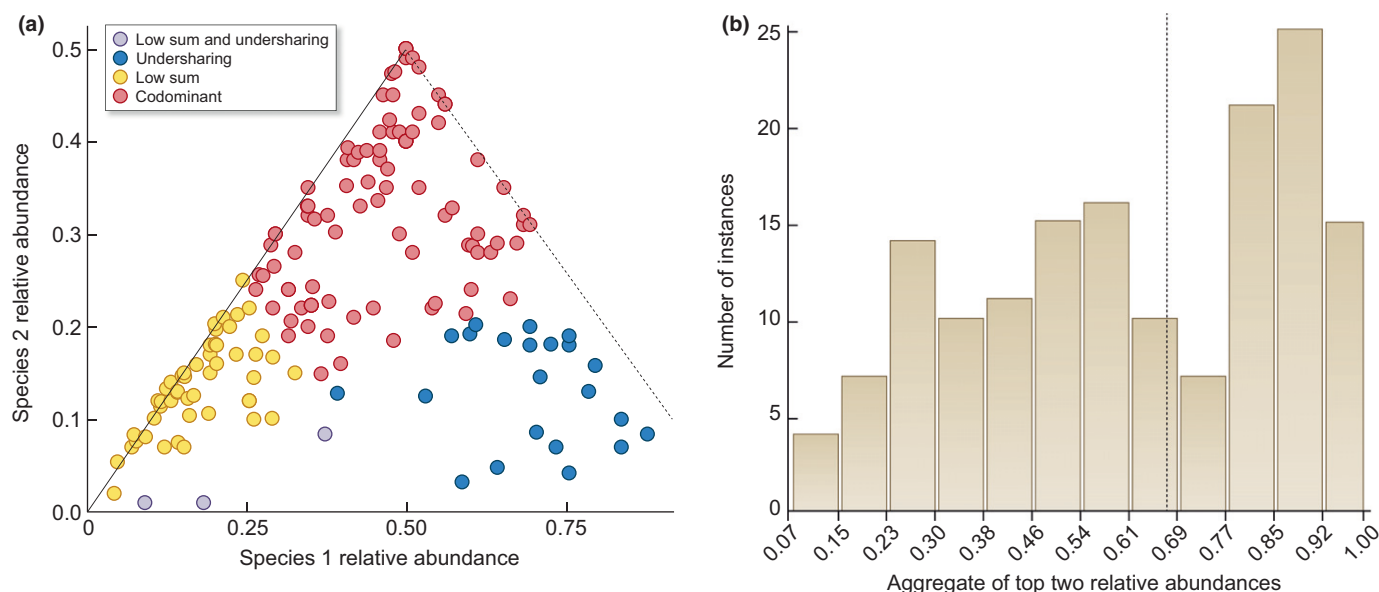


Fig. 2 (a) Relationship between the relative abundances of 167 pairs of first and second-ranked species reported in the literature we reviewed. Solid diagonal line indicates a 1 : 1 relationship between the two most abundant species at a site. Most species pairs lie near the diagonal, but a large portion shows much greater abundance in the first-ranked species than in the second. The degree of abundance sharing reported within the reviewed literature spans a broad range and was not sufficient in 25 of the 167 species pairs to meet our criteria of codominance as outlined in the text (red and violet points). Dotted diagonal line indicates the limit of the relationships (sums cannot exceed 1). (b) The frequency distribution of aggregate relative abundances of 167 pairs of first and second-ranked species are shown as a histogram. The median aggregate relative abundance is indicated by the dashed line, but many species pairs constitute only a small portion of their community total abundances. Here, 53 of the 167 species pairs did not contribute at least 50% of the total community abundance (yellow and violet points in (a)).

by which codominance is determined should always be reported. Moreover, the types of measures of relative abundance should be consistent across the species considered, but may be one of a variety of measures such as densities, biomass productivity, canopy cover or basal area. Combinations of the above (i.e. importance values), can be useful when comparing across plant functional groups. Frequency may also be considered when combined with other measures (see Avolio *et al.*, 2019). Our definition also maintains that for species to be considered codominant, they should be present in the same space and at the same time, within the scale considered. Investigators should be specific about the temporal and spatial scales within which they consider their species to be codominant. Alternatively, dominance should be considered complementary and temporary/isolated rather than shared.

3. Potential mechanisms for codominance

Differences in the degrees of codominance between communities offer opportunities to gain greater understanding of the various factors that determine interaction outcomes between highly abundant species. Of the 265 papers that met our criteria and were accessible, 132 had explicitly stated assumptions or findings regarding the cause(s) of codominance (Table S1). An additional 37 out of the 265 studies lacked explicitly proposed mechanisms but were interpreted as having inferred mechanisms of codominance based on context (Table S1). For example, if a study involved measuring species traits related to drought tolerance in conjunction with a spatial soil moisture gradient, we would assume the authors were testing for spatial niche partitioning. Six of the studies tested for specified mechanisms but did not find evidence for them, and in the remaining 96 studies we could not detect either explicit or inferred mechanisms. In Table 1, we summarise the explanations for codominance found in our literature search and highlight the frequencies of those explanations. These explanations vary widely in their purported driving mechanisms, including bottom-up and top-down controls, abiotic and biotic influences and relatively stable and dynamic environments. In general, however, the explanations share the common thread of interactions between a pervasive environmental driver and unique traits possessed among the codominant species. While our comparison of mechanism frequencies may be a suitable starting point for linking coexistence mechanisms to patterns of codominant species abundance, it should not be interpreted as a reliable reflection of the strength of the factors in determining codominance. Multiple factors may be responsible for biases in the frequency by which particular mechanisms are reported, including the potential inaccuracy of our interpretations of implied mechanisms, the inability to infer mechanisms from many of the reviewed studies, the current under-recognition of the codominance phenomenon within coexistence literature, and the potential for observing only a subset of the types of mechanisms driving codominance within systems in which multiple mechanisms operate concurrently.

Furthermore, our review found no efforts to compare the strengths or relative importance of these mechanisms, nor the conditions under which they are more likely to be detected.

Aside from a universally understood codominance concept, a metric of codominance could further enable comparative research, allowing for the quantification of differences between ecosystems, communities over time and community responses to experimental treatments. In the following sections we describe such a metric and demonstrate its uses and statistical characteristics.

IV. Quantifying codominance

1. A codominance metric – C_{\max}

To enable more systematic, quantitative and unbiased characterisations of codominance among communities, we developed a metric that can be readily used to mathematically compare systems of interest and be included in large data sets for broader analyses. Such a metric also will aid in the search for patterns among the mechanisms of codominance. This metric relies on measures of abundance that are relativised to those from the community aggregate, and as such is adaptable to many types of abundance measurements and to a diversity of ecosystems. However, similarity in measurement types used will facilitate greater confidence in such comparisons.

Our approach begins by selecting the number of species to be considered codominant, hereafter termed the *codominant subset*. The number of codominant species can range from including only the two most abundant species to inclusion of all but the single, most uncommon species. Comparisons can be made between the various calculations that use different putative codominant subsets to make decisions on what number of codominants is the most appropriate to the question and the ecosystem.

The harmonic mean of the relativised measures of abundance (or their relative aggregate measures, e.g. importance values) for each codominant subset was calculated as shown below:

$$\text{shared abundance, } A_n = \frac{n}{\sum_{i=1}^n \frac{1}{x_i}}$$

when n is the number of species in a given codominant subset and has a domain of $\{2, \dots, R-1\}$, when R is the total species richness of the community. The relative abundance of each species i within the codominant subset is given as x_i . A harmonic rather than an arithmetic mean of relative abundance values was used to distinguish between codominant subsets composed of species with disparate abundance values from subsets that have species with more similar abundances. To illustrate, if species a and b had relativised abundance measures of 0.4 and 0.4, both their arithmetic and harmonic means would be 0.4 (Fig. 1). Conversely, if species w and z had values of 0.1 and 0.7, their arithmetic mean would also be 0.4, but their harmonic mean would be 0.175. The bias towards lower values in the harmonic mean can be used to indicate that species w and z share less of their abundance than do a and b .

The value of A_n alone can be useful to investigators interested in only a particular codominant subset, but it is limited in that it does not account for the remaining community. If two species have the same measure of relative importance as a third, there will be no difference in the values of A_n if considering codominant subsets

Table 1 Summary of reviewed codominance forms and mechanisms, with examples of each.

Type of codominance	Specific mechanism	Details	Examples
Fluctuation-dependent niche partitioning (61 instances): recurrent changes in the environment alternately benefit the growth of some species over others. Competition strength varies with the fluctuations of the environment and can be strong. Results in a storage effect when in combination with reduced competition at low population densities and generation of long-lived surplus adults or propagules (Chesson, 2000)	Competition/colonisation trade-off	A rapid coloniser achieves high abundance in disturbed sites, and is gradually replaced by stronger competitors	Zedler & West (2008); Duan <i>et al.</i> (2015)
	Competition or colonisation/tolerance trade-off	Stress-tolerant species remains at relatively constant abundance while competitive/colonising species abundance oscillates with environmental variability	Ribichich & Protomastro (1998); Hartvigsen (2000)
	Life stage mortality differences	Similar to the above, but differences are limited to certain growth stages, allowing broad similarities between species at mature stages	Mori & Komiya (2008); Witwicki <i>et al.</i> (2016)
Spatial niche partitioning (52 instances): environmental heterogeneity over space alternately favouring codominant species. Relaxed interspecific competition between the codominants is typical. Contributes to the storage effect in combination with other factors (Chesson, 2000)	Partial spatial niche partitioning	Sharing of some resources (e.g. light), while others (e.g. nutrients and water) are obtained from different soil depths	Breshears <i>et al.</i> (1997); Ward <i>et al.</i> (2013)
	Complete spatial niche partitioning	Species separated into adjacent areas that are more suited their respective requirements and tolerances	Dias & Melo (2010); Cohn <i>et al.</i> (2011)
Attenuated dominance (55 instances): abundance of a species that would otherwise be monodominant is negatively impacted by a factor resulting in codominance. Interspecific competition may be strong, particularly in cases of successional circumstance, but may be reduced or mitigated by the factors attenuating dominance	Successional circumstance (temporally attenuated dominance)	Codominance circumstantially observed at a midpoint in the decline of one species and rise of another	Simard <i>et al.</i> (1998); Sefidi <i>et al.</i> (2011)
	Spatially attenuated dominance	A factor occurring in region of codominance (e.g. soil toxicity) reduces the growth rate of a highly competitive species	Rebele (2013); Káplová <i>et al.</i> (2011)
	Consumer control	An herbivore or pathogen selectively reduces the growth rate of a highly competitive species	Goheen <i>et al.</i> (2007); Augustine <i>et al.</i> (2017)
	Allelopathy	The growth rate of a competitive species is reduced by secondary compounds released by its codominant partner	Meier <i>et al.</i> (2009)
	Mutualist intervention	Growth rate of an otherwise subordinate species is selectively benefited by a third-party mutualism	Petanidou <i>et al.</i> (1995)
Equalising factors (6 instances): reductions in fitness differentials between the codominant species. Delays competitive exclusion but cannot independently and indefinitely prevent it. Competition may (or may not) be strong, but because fitness differences are minimal, exclusionary outcomes are close to random	Mutual attenuation	Similar to spatially attenuated dominance, but occurring for both species, which may dominate at polar ends of an environmental gradient	Meentemeyer & Moody (2002); Balzotti & Asner (2017)
	Similarity degree of adaptation	Similarity in fitness can operate either through convergent traits and strategies, or through differential traits and strategies that nevertheless are equally successful and do not confer meaningful advantages	Drenovsky & Richards (2006); Bai <i>et al.</i> (2015)
Facilitation (14 instances): presence of one codominant species increases the population growth rate of another. This benefit may be mutual	Direct facilitation	One of the codominant species alters the environment to make it more favourable for the other	Kikvidze <i>et al.</i> (2006); Pueyo <i>et al.</i> (2016)
	Indirect facilitation	One of the codominant species alters the environment to make it less favourable for all other species except the codominant	Souza <i>et al.</i> (2011)

See Supporting Information Table S1 for the complete list of citations.

with two or three species and, therefore, it would be incorrect to say that two of the species were dominant over the third. The remainder of approach proceeds iteratively to consider all possible codominant subsets, while optimising for the subset with largest combination of shared abundance among codominants and disparity between them and their subordinates. The relative abundance of the next most abundant species, j (S_j , when $j = n + 1$, hereafter referred to as the primary subordinate) is subtracted from the

shared abundances of its associated codominant subset to arrive at its codominance index:

$$C_n = A_n - S_j$$

The difference of A_n and S_j is a metric that increases both as a function of similarity between the abundances of species within the codominant subset (A_n) and the degree to which the shared

Box 1 Codominance Index, C_{\max} , Usage Illustration

We created 12 simple communities that specifically differed in relative abundances of seven species and, therefore, the degree of dominance or evenness (Table B1a). We find that lower C_{\max} values occur both in highly *monodominated* communities (such as 1, 3, 4 and 5), in which abundance is not well shared among species in the codominant subset, and in communities, such as 2, in which abundance is overly shared with the whole community (i.e. highly even). As such, C_{\max} appears capable of distinguishing these types of communities from those that are highly codominated (e.g. 11, 12).

However, at intermediate values of C_{\max} , ambiguities can arise. For example, while the C_{\max} values of communities 9 and 10 are identical, the communities are quite dissimilar (Table B1a). Abundance is more equitably shared in the codominant subset of community 10, while the codominant subset of community 9 contains a larger portion of the total abundance of its community. This comparison illustrates the balance that C_{\max} strikes in representing both the disparity between the codominant subset and the most abundant subordinate species (A_n vs S_j , respectively) and the sharing of abundance within the codominant subset, but it also exposes its limitations in distinguishing between highly monodominated and highly even communities. Nevertheless, other well known metrics such as Simpson's D can distinguish between these communities, with community 9 ($D = 0.45$) having a higher dominance value than 10 ($D = 0.33$). As such, we envision C_{\max} as a complement to other diversity metrics.

While any number of species (n) can be included in a community's codominant subset, C_{\max} is only derived from a codominant subset consisting of the optimal number of species for that community's particular species composition. For example, community 8a is identical to community 8, but a different number of species was used in its calculation of C_n (Table B1b). In this case, the subtraction of the relatively high abundance of the primary subordinate species $j (= 4)$ from shared abundance A_3 gives a suboptimal C_n less than C_{\max} . By comparing all the possible calculations of C_n for community 8, we can determine the most appropriate number of species to be included in its codominant subset, and therefore the number of species that may be more important in the functioning of their ecosystems. In this case, because the calculation using $n = 4$ has the highest value of C_n (i.e. C_{\max}), we would conclude that communities with this set of abundances would optimally be considered to have four codominant species.

The inverse issue arises between communities 10 and 10a, which are also identical in composition (Table B1b). In calculating C_n for community 10a ($n = 3$), a low-abundance species is included in the codominant subset, and a relatively low index value is the result. The C_{\max} value is instead found for the C_n formulation of community 10 ($n = 2$), and we therefore conclude that these communities would optimally be considered to have only two codominant species.

While selection of the most appropriate number of species to include in the codominant subset can sometimes be obvious, as in the above examples, it can also be far less so. A comparison of the calculations of C_n for communities 6, 6a, and 6b illustrates a situation in which the appropriate number of codominant species is far less clear (Table B1b). Here species 4 is distinctively more abundant than species 5, but also distinctively less abundant than species 3. Calculation of C_{\max} is a helpful tool in such scenarios, providing a quantitatively defensible number of species to consider codominant.

Table B1 (a) The communities are arranged by increasing C_{\max} . RA1 – RA7 = Relative abundances of the seven most abundant species within each community. Species included in the codominant subset are in bold. (b). Examples of how C_{\max} values vary depending on which species are included in the codominant subset. Bold indicates which species were included in the codominant subset. D = Simpson's dominance.

(a) Community	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	C_{\max}	D
1	0.9	0.05	0.05	0	0	0	0	0.04	0.81
2	0.15	0.15	0.15	0.15	0.15	0.15	0.1	0.05	0.14
3	0.8	0.1	0.1	0	0	0	0	0.08	0.66
4	0.6	0.2	0.2	0	0	0	0	0.10	0.43
5	0.9	0.09	0.01	0	0	0	0	0.15	0.82
6	0.4	0.3	0.2	0.09	0.01	0	0	0.19	0.29
7	0.3	0.3	0.3	0.1	0	0	0	0.20	0.27
8	0.25	0.25	0.24	0.24	0.02	0	0	0.22	0.23
9	0.6	0.3	0.1	0	0	0	0	0.30	0.45
10	0.4	0.4	0.1	0.1	0	0	0	0.30	0.33
11	0.45	0.45	0.1	0	0	0	0	0.35	0.41
12	0.45	0.45	0.02	0.02	0.02	0.02	0.02	0.43	0.40
(b) Community	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	C_{\max}	D
6	0.4	0.3	0.2	0.09	0.01	0	0	0.19	0.29
6a	0.4	0.3	0.2	0.09	0.01	0	0	0.14	0.29
6b	0.4	0.3	0.2	0.09	0.01	0	0	0.17	0.29
8	0.25	0.25	0.24	0.24	0.02	0	0	0.22	0.23
8a	0.25	0.25	0.24	0.24	0.02	0	0	0.01	0.23
11	0.45	0.45	0.1	0	0	0	0	0.35	0.41
11a	0.4	0.4	0.1	0.1	0	0	0	0.10	0.33

abundance within the codominant subset differs from the abundance of the primary subordinate. This index is calculated for all values of n , and the largest of these index values is considered C_{\max} , the community's optimised codominance value:

$$C_{\max} = \text{maximum}(C_2, \dots, C_{R-1})$$

Only species j is considered for each iteration as it represents the most conservative approach to drawing

Box 2 Evaluation of the codominance index, C_{\max} , with simulated data

The distributions of C_{\max} values depended on the community type (determined by the standard deviations used to generate component species abundances; Fig. B2, A) and the number of species in the optimal codominant subset (Fig. B2, B). While most of the distributions were approximately normal, they were increasingly broad and skewed towards lower values of C_{\max} as the number of codominant species decreased suggesting that, although having fewer species in the optimal codominant subset confers the potential for higher C_{\max} , this scenario also can result in some of the lowest C_{\max} values. Nevertheless, the mean C_{\max} was greatest for communities with only two codominant species (Table B2). This codominance index will often yield the highest values (i.e. C_{\max}) when considering only two species to be codominant. Therefore, we recommend that multiple codominant subsets be examined but that the subset with the largest C_{\max} value be reported. This approach allows C_{\max} to serve as a guide in determining how many species should be considered codominant.

Across all codominant subset sizes, C_{\max} was more closely associated with A_i than with S_i , when i and s refer to the values of n and j , respectively, that result in the highest value of C_i ($m = 0.80, r^2 = 0.91$, and $m = 0.14, r^2 = 0.06$, respectively, both $P < 0.001$). However, the relative importance of A_i and S_i in determining C_{\max} depended on the number of species in the C_{\max} -associated codominant subset. Correlations between C_{\max} and A_i were stronger and more positive for smaller codominant subsets and became weaker and more negatively correlated when nine species were included in the subset, ranging from $r^2 = 0.834$ ($m = 0.92, P < 0.001$) with two species to $r^2 \approx 0$ ($m = -0.12, P = 0.31$) with eight species. The opposite behaviour was observed for the associations between S_i and C_{\max} , being weakest in communities with the fewest codominant species ($r^2 = 0.05, m = -0.54, P < 0.001$) and strongest in the most even communities ($r^2 = 0.90, m = -0.80, P < 0.001$). Overall, these results suggest that large A_i values will typically control C_{\max} values in highly codominated communities, rather than small S_i values, especially given that highly codominated communities are likely to have fewer codominant species.

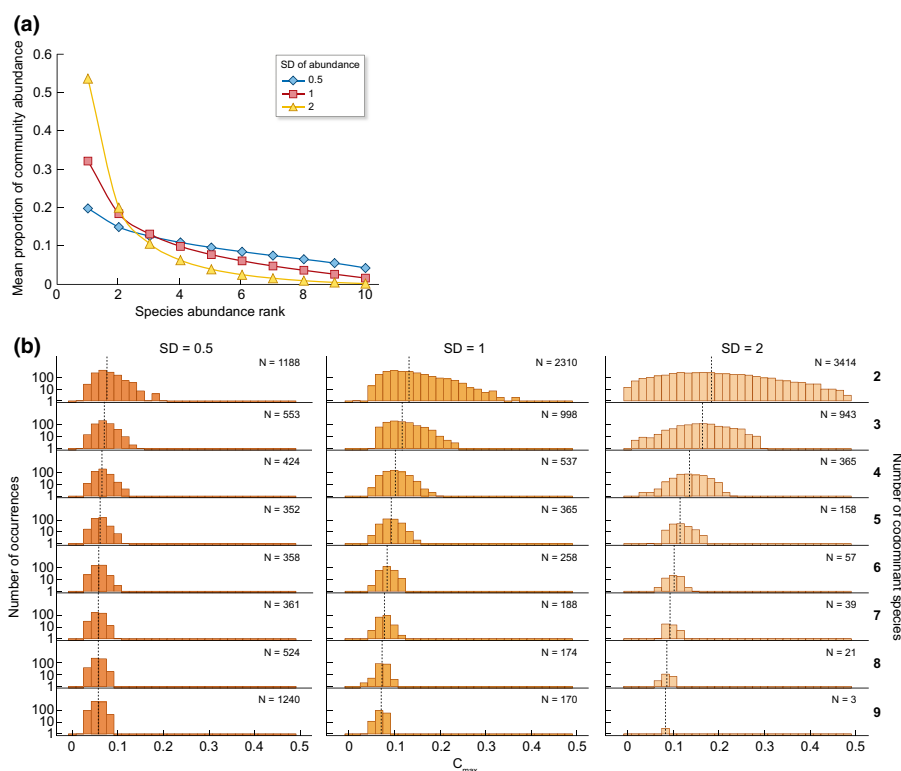


Fig. B2 (a) Rank-abundance curves, averaged across all simulated communities and grouped by the standard deviations used in generating species abundances. (b) Distributions of C_{\max} values grouped by the standard deviations of species abundances used in generating the simulated communities ($sd = 0.5, 1$ or 2), and the number of species in the codominant subset that resulted in the largest codominance (C_{\max}). Mean C_{\max} for each group is given by dashed lines. The number of communities having the indicated number of codominant species for each community type is given by N .

distinctions between the codominants and the subordinates. If instead a mean of the subordinates was subtracted from the shared abundance of the codominants, a larger distinction would necessarily be drawn, but it would reduce the clarity of whether species j (and others) should be also be considered codominant. Moreover, if species j is dominated by the

codominant subset, the remainder of the community is necessarily more so.

To first assess the efficacy of the codominance index, C_{\max} , we simulated 19 different communities that differed in relative abundances of seven species and, therefore, the degree of dominance or evenness. With this set of communities, we found that the

Box 2 Continued

Table B2 ANOVA table and least square means for C_{\max} values grouped by the number of species included in the codominant subset that resulted in that C_{\max} value (i). C_{\max} values varied substantially within each codominant subset size, resulting in a low $\text{adj.}R^2 = 0.242$, but were on average greater when fewer species codominated. Confidence intervals of least square means were adjusted using the Bonferroni method.

	Estimate	SE	t -value	$Pr(> t)$
intercept ($i = 2$)	0.148	0.00073	200.99	<2e-16
$i = 3$	−0.024	0.00143	−16.62	<2e-16
$i = 4$	−0.048	0.00183	−26.08	<2e-16
$i = 5$	−0.063	0.00219	−28.83	<2e-16
$i = 6$	−0.076	0.00247	−30.76	<2e-16
$i = 7$	−0.082	0.00262	−31.14	<2e-16
$i = 8$	−0.086	0.00239	−35.91	<2e-16
$i = 9$	−0.089	0.00178	−50.06	<2e-16

Residual SE: 0.0611 on 14 992 degrees of freedom. Multiple R -squared: 0.242, Adjusted R -squared: 0.242. F -statistic: 685.1 on 7 and 14 992 df, P -value: < 2.2e-16.

Codominant species (i)	LS mean	SE	df	Lower CL	Upper CL
2	0.148	0.0007	14992	0.146	0.149
3	0.124	0.0012	14992	0.121	0.127
4	0.099	0.0017	14992	0.096	0.105
5	0.085	0.0021	14992	0.079	0.091
6	0.072	0.0024	14992	0.065	0.078
7	0.066	0.0025	14992	0.059	0.073
8	0.062	0.0023	14992	0.056	0.068
9	0.058	0.0016	14992	0.054	0.063

codominance index performs well in ranking different communities in both increasing order of average abundance of the codominant subset and decreasing abundance of the primary subordinate (Box 1).

2. Applying C_{\max} to simulated data

To better understand the behaviour of C_{\max} under less extreme contrasts than those included in Box 1, we generated a set of simulated communities, each consisting of 10 species with abundances that were randomly selected from a lognormal distribution with a mean of 2 and standard deviations of either 0.5, 1 or 2. These deviations resulted in different community types: those with similar, disparate and widely disparate abundances among community members, respectively (Box 2, Fig. B2). These artificial communities represent proxies for communities that have either relatively low abundances of all species in the community (e.g. an old-growth rainforest tree community; Villa *et al.*, 2019), codominance among a small set of species (e.g. a temperate forest tree community; Greene *et al.*, 2004), or clear dominance of a single species (e.g. a shortgrass prairie herbaceous community; Munson & Lauenroth, 2009), respectively. The lognormal distribution has frequently been observed for species abundances across a wide variety of ecosystems (Preston, 1948; Sugihara, 1980; Limpert *et al.*, 2001; Avolio *et al.*, 2019). In total, 5000 communities were generated for each of the abundance distributions, giving 15 000 total communities. We first examined the distribution of C_{\max} values to determine how they varied by the numbers of species

within their codominant subsets. As the highest possible shared abundances (A_n) occur when only two species are in the codominant subset, we expected sets of this size to include the highest values of C_{\max} . Then, Pearson's tests of correlations between C_{\max} and its component factors, A_l and S_j , were examined (when l and s refer to the values of n and j , respectively, that result in the highest value of C_n). This was done to determine which factor tends to drive C_{\max} the most: (1) the degree of shared abundance among species in the codominant subset, or (2) the disparity between the codominant subset and the remaining community. Overall, we found that C_{\max} tended to increase and become more strongly correlated with A_l than with smaller codominant subsets across each of the community types (Box 2).

3. Assessment of C_{\max} using real-world data

To assess the applicability of the codominance metric on real-world data, we examined canopy cover from the control plots of an experiment conducted at four North American grassland sites: the Extreme Drought in Grassland Experiment (EDGE; Knapp *et al.*, 2015). These sites included a cold mixed-grass prairie (near Cheyenne, Wyoming, CHY), a warm mixed-grass prairie (near Hays, Kansas, HYS), a warm shortgrass prairie (near Nunn, Colorado, SGS), and a warm tallgrass prairie (near Manhattan, Kansas, KNZ). Canopy cover was measured with 1% to 5% precision as a percentage of 2×2 m plots at the beginning and end of the growing season in 2013 (taking the maximum cover of each species over the growing season), with 10 replicates per treatment.

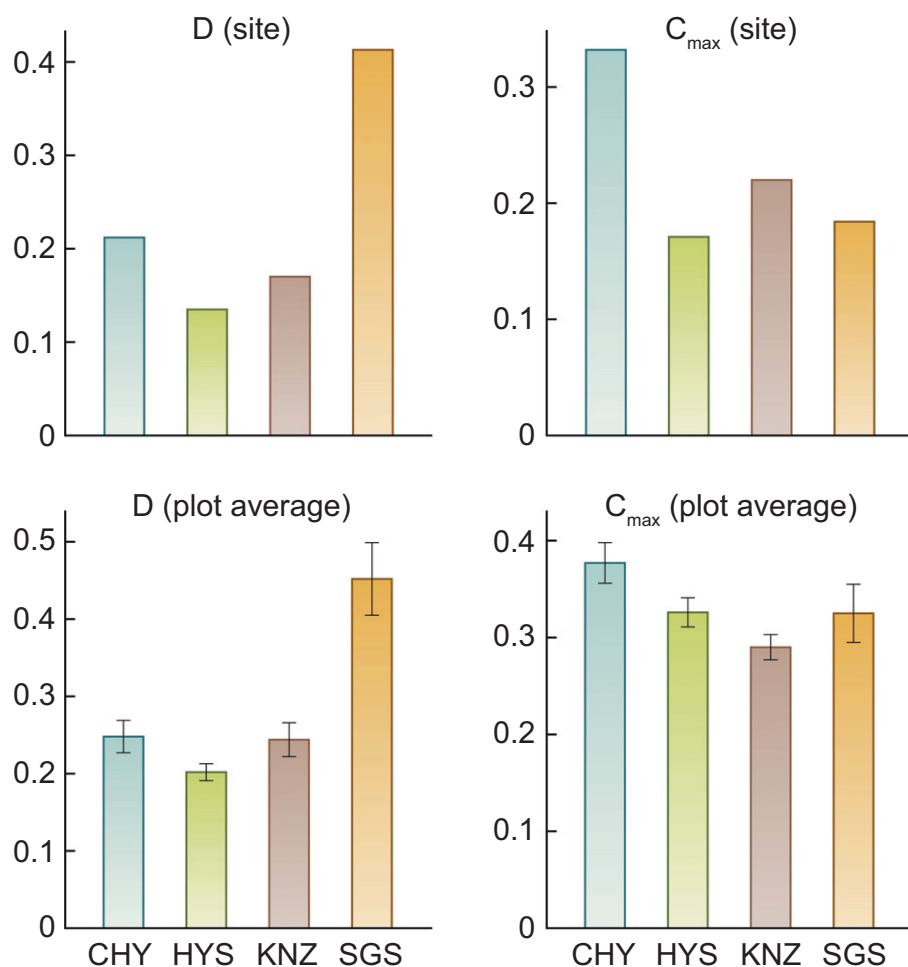


Fig. 3 Measures of average plot-level codominance (C_{max}), Simpson's dominance (D), and plot-level C_{max} and D (\pm confidence intervals at $\alpha = 0.05$) at four Great Plains grasslands sites: a cool mixed-grass prairie near Cheyenne, Wyoming (CHY), a warm mixed-grass prairie near Hays, Kansas (HYS), a tallgrass prairie at Konza Prairie Biological Station near Manhattan Kansas (KNZ), and a shortgrass steppe near Fort Collins, Colorado (SGS). No replication was possible at the site scale, as indicated by the lack of error bars in the upper plots.

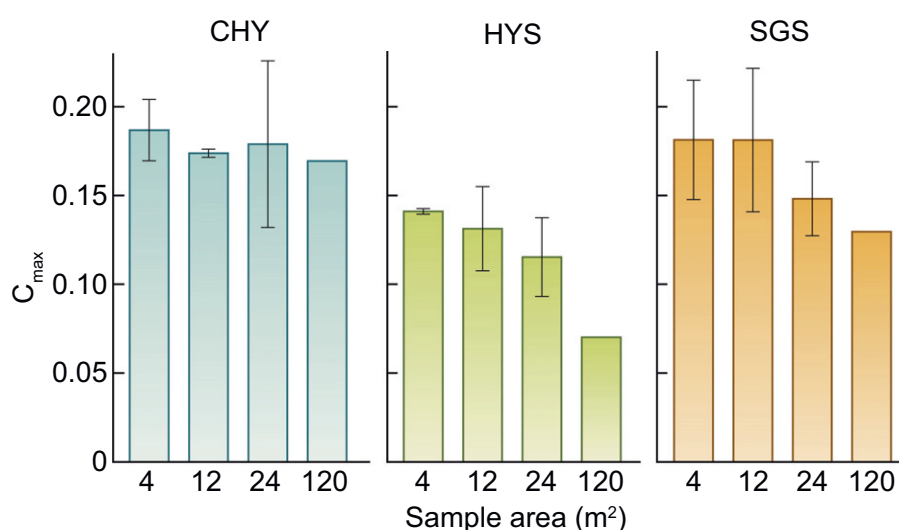


Fig. 4 Average codominance (C_{max}) measured at increasing scales from plot level (4 m²) to block (12 m², cover averaged across three nearby plots before C_{max} calculation), to paired blocks (24 m², averaged across six nearby plots), and site (120 m²). Error bars indicate 5% confidence intervals. No replication was possible at the site scale, indicated by the missing error bars. Data obtained were from a drought experiment at three Great Plains grassland sites (CHY, cool mixed-grass prairie near Cheyenne, Wyoming; HYS, warm mixed-grass prairie near Hays, Kansas; SGS, shortgrass steppe near Fort Collins, Colorado) before treatment. While C_{max} is fairly invariant with increasing scale, it does tend to decline. The rate of decline is characteristic of the site observed, reflecting the rate of turnover of the species that are codominant within those sites. For example, the plots and blocks at HYS were spread further apart than at CHY, and were separated by a drainage, and the turnover of codominant species here was greatest. By contrast, the turnover of codominant species across CHY, a relatively homogenous site, was minimal.

Our objective for this analysis was to determine whether C_{\max} could distinguish between an ecosystem that has often been described as both codominated (KNZ; e.g. Silletti & Knapp, 2001, 2002; Heisler *et al.*, 2004; Swemmer, Knapp & Smith, 2006; Fay *et al.*, 2011; Hoffman & Smith, 2018; Hoffman *et al.*, 2018) and monodominated (Smith & Knapp, 2003; Smith *et al.*, 2004), from one that is more frequently considered monodominated (SGS; Sala *et al.*, 1992; Munson & Lauenroth, 2009; Augustine *et al.*, 2017). We sought further to characterise the codominance of the two mixed-grass prairies (HYS and CHY), which were expected to be codominated, in relation to KNZ and SGS.

As expected, site-level dominance (Simpson's D , calculated from average species abundances across the 10 plots) was greatest at SGS (Fig. 3), with each of the other sites having distinctly lower measures. While we expected C_{\max} to be greatest at KNZ, we were surprised to find that CHY was the most codominated, having the largest C_{\max} despite having an intermediate value of D . While the two most common species at KNZ shared similarly high abundances, there was less of a distinction between their harmonic mean and the abundance of their primary subordinate in comparison with the distribution found at CHY. The lowest degree of dominance resulted for HYS having the lowest value of C_{\max} . A similarly low value of C_{\max} was found at SGS. This was expected, as SGS is typically considered to be highly monodominated (Lauenroth & Burke, 2008).

Our results were similar at the plot level (D and C_{\max} calculated for each plot before averaging), with the pattern of D at the plot-level mirroring that for the site level. Similarly, the highest mean plot C_{\max} was found at CHY, followed by HYS, SGS and KNZ. The mean plot level C_{\max} was higher than the site-scale C_{\max} at all sites, but differed more at HYS and SGS, suggesting that the identities of the species contributing most to codominance at KNZ and CHY were more consistent across plots than they were at the other sites. To further explore the effects of scale on C_{\max} , we used pretreatment data from the same experiment and calculated C_{\max} at four different spatial scales (Fig. 4). This analysis showed that C_{\max} , while fairly scale invariant, tended to decrease in magnitude with increasing scale at a rate that is characteristic of the site investigated (Fig. 4). Overall, we found that site level C_{\max} matched our expectations of the community structure differences between the sites often described as codominated and monodominated, and comparisons with plot-level C_{\max} exposed site-dependent heterogeneities in community structure.

V. Conclusions and future directions

Codominance is an intuitively alluring concept, but it has not been rigorously explored, perhaps due to the lack of a common definition or a common metric for its quantification. The stable codominance of ecologically important species represents a novel inroad to a greater understanding of coexistence and ecosystem functioning and may prove especially important from the perspectives of restoration and conservation under climate change. We provided a qualitative definition of codominance, reviewed the mechanisms commonly invoked to explain codominance, and developed a metric (C_{\max}) to quantify the degree of codominance.

We found that our codominance metric ably facilitated comparisons among ecosystems. Moreover, it is easily interpretable, adaptable to different forms of abundance (e.g. density, productivity, cover, importance values), and can be used for a variety of organisational levels (e.g. species, genus, functional groups). However, comparisons made using different abundance metrics or across organisational levels will be of diminished value. As with other biodiversity metrics, authors must determine which measures of abundance and organisational level are the most appropriate to their questions. For instance, a savanna codominated by a tree species and a grass species would be better represented with C_{\max} calculated in terms of cover than of density in questions relating to contributions to ecosystem function, but may be better represented by measures of density when approaching other topics such as genetic diversity and its relationship to community adaptability under changing environmental conditions. When appropriate measures or combinations of measures are used in its calculation, the codominance metric will be a useful complement to other frequently used metrics of biodiversity and should serve to inspire further development and interest in the codominance concept.

With greater understanding and standardisation of the codominance concept, we can begin addressing new questions. Experiments involving factorial removals of one or more codominant species, or interruptions of the mechanisms purported to determine codominance under a variety of environmental contexts are well warranted. Codominant species have a greater influence over ecosystem function than subordinate species, in proportion to their greater share of abundance, making such experiments increasingly essential as land use and climate change alter the conditions that resulted in their mutual success. Greater understanding of ecosystem stability could also be gained through integrated consideration of codominant species. By virtue of the relatively high availabilities of meristems and propagules associated with their higher abundances, one codominant species potentially represents the most likely driver (or inhibitor) of functional recovery (or compensation; Adler & Bradford, 2002) after the loss of another codominant species (e.g. due to a specialist pathogen or an idiosyncratic sensitivity to climate change). However, such an outcome is likely to depend on multiple factors, including environmental context and rates of dispersal and establishment. A codominant species with a rapid dispersal rate could drive rapid functional compensation, but one that spreads slowly could result in protracted degradation through their competitive effects on less-common species that might alternatively drive compensation. By studying the dispersal properties of all common species, the rate of ecosystem function recovery following extirpation of a codominant partner could be better predicted, while knowing the functional properties of those species could generate a clearer picture of how those ecosystems would behave following recovery.




It is in our interest therefore, to better understand the relationships between the abundance of codominant species and the processes that resulted in those patterns. The degrees of codominance may vary by the type of stabilising mechanisms involved, as well as the characteristics of the ecosystems in which the patterns are observed. For example, the mechanisms resulting in greater codominance in climatically variable systems such as grasslands and deserts may differ

considerably from those in more stable environments, such as forests and peatlands. Similarly, the growth forms, functional groups and functional traits of species may determine the degree to which they are capable of codominance, as well as the mechanisms that facilitate those relationships. Discerning these patterns may prove to be integral for successfully strategising conservation and restoration efforts aimed at stabilising or recreating codominance and affecting associated ecosystem properties.

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ORCID

Jesse E. Gray  <https://orcid.org/0000-0002-9075-5030>
Kimberly J. Komatsu  <https://orcid.org/0000-0001-7056-4547>
Melinda D. Smith  <https://orcid.org/0000-0003-4920-6985>

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