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Plant community diversity effect on ecosystem functioning: a functional trait story

Ph.D. Thesis

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Annotation:

This thesis focuses on the effect of different facets of diversity, particularly at the community level, on various aspects of ecosystem functioning. The following sections document novel results and their relevance in the debate revolving around the biodiversity - ecosystem functioning relationship. Primarily, using a common garden experiment specifically designed to disentangle the role of functional and phylogenetic diversity, we study community assembly through the resistance of sown community to surrounding weeds (Chapter I) and their performance on multiple above and below ground ecosystem functions (Chapter II). Next, we compiled a worldwide database of plant communities time series records to identify the drivers of community temporal stability, with a particular focus on synchrony and species diversity patterns (Chapter III). Finally, using parameterized simulations we analysed functional redundancy computation methods and their theoretical relationship with stability through the insurance hypothesis (Chapter IV).

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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Thomas Galland

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The thesis is based on the following papers:

I. **Galland, T**, Adeux, G, Dvořáková, H, E-Vojtkó, A., Orbán, I., Lussu, M., … & Götzenberger, L. (2019) Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology*. 107: 2090– 2104. https://doi.org/10.1111/1365-2745.13246 (IF 5.91)

C.P.C., F.d.B., J.L. and L.G. conceived and designed the experiment; A.E.V., E.V., F.d.B., H.D., J.P., L.G., P.B., T.G and V.L. collected the data; G.A., J.P. and T.G. analysed the data; G.A., H.D, I.O., J.P., M.L. and T.G. drafted the manuscript. All authors contributed to the draft and gave final approval for submission.

II. **Galland T.**, Valencia E., Carmona C.P., Goberna M., Götzenberger L., Lepš J., Verdú M. & de Bello F. Cascading effect from plant community functional structure to above and below ground ecosystem functions. (Manuscript)

C.P.C., F.d.B., J.L. and L.G. conceived and designed the experiment; E.V., F.d.B., L.G, T.G. collected the data; M.G. and M.V. carried the soil sample lab analysis. T.G. analysed the data with the support of F.d.B. and E.V.; T.G. drafted the manuscript. All authors contributed to review and edit the manuscript.

III. Valencia, E., de Bello, F., **Galland, T.**, Adler, P. B., Lepš, J., E-Vojtkó, A., … & Götzenberger, L. (2020) Synchrony matters more than species richness in plant community stability at a global scale. *Proceedings of the National Academy of Sciences*. 117 : 24345-24351. https://doi.org/10.1073/pnas.1920405117 (IF 9.35)

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IV. **Galland, T.**, Carmona, C. P., Götzenberger, L., Valencia, E., & de Bello, F. (2020) Are redundancy indices redundant? An evaluation based on parameterized simulations. *Ecological Indicators*. 116: 106488. https://doi.org/10.1016/j.ecolind.2020.106488 (IF 4.80)

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General introduction

Ecosystems are undergoing environmental changes globally, essentially due to anthropic pressure on land use, dispersion of alien species and changes in atmospheric composition and climate (Chapin *et al.*, 2000; Steffen *et al.*, 2004). As consequence, biodiversity is already being eroded at an unprecedented rate (de Mazancourt *et al.*, 2013) and the delivery of key ecosystem processes and services are subsequently threatened (Chapin *et al.*, 2000; Díaz & Cabido, 2001). Because global change can impact different ecosystem functions simultaneously, it is preferable to assess ecosystem responses by integrating multiple functions and services (Walker, 1992). Moreover, the traditional short-term evaluation should be overcome by a long-term view, where the evaluation of the stability or temporal invariability of the ecosystem must be a priority (McArdle & Gaston, 1995). Understanding the effect of species and communities on ecosystem functions and services is key to answer the growing demand to predict consequences of global-change drivers on biodiversity and the feedback on ecosystem processes.

In the last decades, a shift in paradigm has occurred on the way researchers assess biodiversity effects on multiple ecosystem processes. Specifically, ecologists are increasingly looking at traits, rather than species identity alone, to assess biodiversity effects, in something that has been referred to as ‘the biodiversity revolution’ (Cernansky, 2017). While earlier studies focused on the number of species in a community as the main driver of multiple ecosystem functions, and their stability, it has been demonstrated that the effect of biodiversity on ecosystem functions does not depend on species diversity *per se*, but rather on the functional characteristics of species in an ecosystem (Hooper *et al.*, 2005), i.e. functional traits (Violle *et al.*, 2007). Thus, in order to apprehend the consequences of environmental changes for the stability of ecological communities it is essential to understand how their functional structure relates to ecosystem functioning (Díaz *et al.*, 2007; Valencia *et al.*, 2015).

This thesis is a contribution to this challenge. Combining experimental approaches, simulations and the analysis of a worldwide compilation of long-term time series of vegetation data, we evaluated the relevance of community structure on multiple ecosystem functions. In this introduction, we first set functional and phylogenetic diversity into the wide context of biodiversity, recalling why and how these concepts were developed. Then we move on to community assembly, ecosystem functioning and the role of biodiversity, particularly community functional structure, in those processes.

1. Biodiversity

Biodiversity integrates biological variability across different ecological scales, from the genetic through species and ecosystems, to landscapes (Walker, 1992). Because of the range of scales of biodiversity, it is near to impossible to fully assess it. The relevant level to which biodiversity should be defined often depends on the question studied, although historically species richness has been the most widely used metric of biodiversity (Cadotte, Carscadden, & Mirotchnick, 2011).

Among the different components of biodiversity, functional diversity and phylogenetic diversity are emerging as key components to assess biodiversity effects on the ecosystem (Le Bagousse-Pinguet *et al.*, 2019). Functional diversity, the extent of functional trait differences between species, and phylogenetic diversity, the extent of evolutionary distance between species, are key components of biodiversity that influence how species coexist (Cadotte, Albert, & Walker, 2013) and how ecosystems operate (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Tilman, 2001). One of the ideas behind these concepts is the potential generalization of patterns beyond taxa and locations. In other words, understanding the characteristics that drive species responses to, and effects on, ecosystems could be a key to move from observing biodiversity patterns to understanding the underlying processes. Over the few last decades, the necessity to understand and predict the consequences of biodiversity loss in response to environmental changes has led to a functional approach of biodiversity (Cadotte *et al.*, 2011).

1.1. Functional Diversity

The functional approach of ecology, i.e. the focus on the organisms' strategies and adaptations through their traits rather than on their taxonomical identity alone, has a long tradition in the literature and builds upon several key concepts. Schimper (1903) describes the characteristics of alpine plants with a traits-based approach: *"The characteristic traits of alpine plants can be demonstrated best in species which also occur in the lowlands. The individuals growing in the alpine region have shorter axes, smaller leaves, more strongly developed roots, equally large or somewhat larger, and frequently rather more deeply coloured flowers, and their general structure is xerophilous".* The r/K selection theory from MacArthur & Wilson (1967) and later the competitor, stress tolerant and ruderal adaptive theory developed from Grime (1977) were already based on the link between species characters and their interactions with other species and the environment. However, the leap into the functional ecology as we know it today really took off with landmark papers from Tilman and colleagues, who provided evidence of a positive relation between the functional diversity of plant communities, drought resistance (1994) and productivity (1997).

Violle *et al.* (2007) defines functional traits as *"any morphological, physiological or phenological heritable feature measurable at the individual level, from cell to whole-organism"*. They also describe the hierarchical structure that links functional traits to individual fitness through performance traits (Fig. 1). This framework is the theoretical base for the functional ecology, i.e. inferring/studying ecological interaction and processes from individual functional traits. It also reveals a critical point of this discipline: the choice of a list of key traits that are believed to be important for both understanding and predicting the response and effect of a species (Weiher *et al.*, 1999).

In 1998, Mark Westoby proposed an approach based on a preselection of the most essential traits to differentiate species' strategies, the so called leaf-height-seed (L-H-S) scheme. A minimalist set of three specific traits are proposed to characterize species ability to cope with competition, disturbance and stressful conditions. The L-H-S scheme proposed measuring a leaf trait (L) i.e. specific leaf area (SLA, leaf area divided by dry weight), and the size related traits plant height (H) and seed mass (S). Those three traits have been chosen as representative of fundamental trade-offs in plant strategies. SLA represents the light-capturing area deployed per dry mass allocated, which means that species cannot both invest in a large light-capturing area per mass while also build strong leaves tissues that may serve for a longer period of time. Similarly, a plant can hardly outcompete its neighbours harvesting light in the canopy without investing in a tall stem (H). Finally, the allometric relationship between seed mass and the number of seed produced is a good proxy of the reproductive effort strategy developed by a species. The aim of the approach was certainly not to limit research to only these 3 traits, acknowledging that 3 traits cannot cover all important differences between plants (see also Klimešová *et al.* 2017), but to allow general inferences to be made on the strategies of species from different communities, regions and continents. The L-H-S scheme is also based on the concept of trade-offs, where trade-offs along these 3 traits would indicate adaptations to different competitive, disturbance and stress (C-S-R) conditions. Specifically, SLA would reflect the same type of variation than the C-S axis (responsiveness to opportunities to grow fast, i.e. acquisitive strategy). Height and seed mass reflect different aspects of coping with disturbance – respectively the amount of growth attempted between disturbances (H) and the capacity to colonize growth opportunities at a distance – which was implied in the R strategy of Grime's framework.

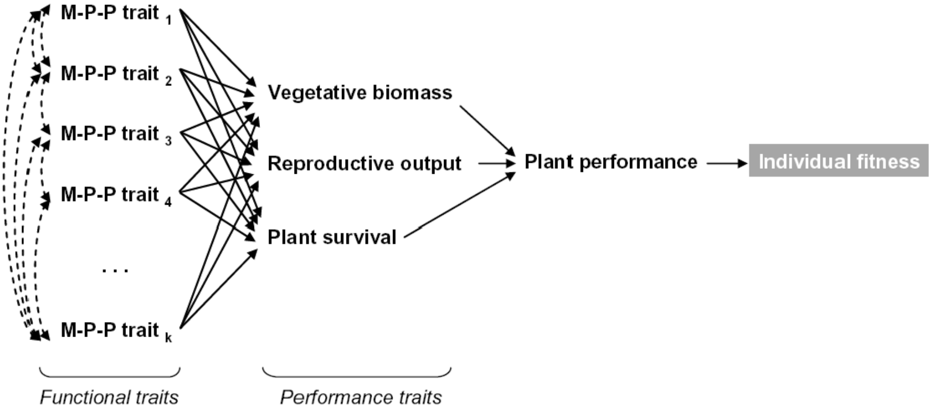

Figure 1: Arnold's (1983) framework revisited in a plant ecology perspective by Violle *et al.* (2007). Morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determines a plant performance and, in turn, its individual fitness. M-P-P traits may be inter-related (dashed double-arrows). For clarity, inter- relations among performance traits and feedbacks between performance and M-P-P traits are not represented.

Detecting fundamental trade-offs between species in terms of traits have required the analysis of large databases where restricted sets of traits were measured on a large number of species across different biomes. Evidences of a ´leaf economic spectrum´ with bundle of traits covarying from rapid acquisition of resources (i.e. live fast and die young) to conservative resource strategies (i.e. grow slowly but steadily) were found by Díaz *et al.* (2004) and Wright *et al.* (2004). Later the economic spectrum was expended to the whole plant strategy (Díaz *et al.*, 2016). Garnier *et al.* (2016) explain well the mechanisms behind such trade-offs echoing the economic concept of resource investment already described in the r/K dualism. The spectrum runs from plants showing a high rate of photosynthesis and a rapid return on investment in terms of mineral nutrients and leaf dry matter (acquisitive syndrome), without a large investment in defence structures, to others characterized by low photosynthetic rates, with a much slower return on investment (conservative syndrome). This conservation strategy is also often associated with well-defended tissues against herbivores and slower afterlife effects on decomposition (Cornelissen *et al.*, 1999; Díaz *et al.*, 2004).

Indubitably, the main trade-offs detected among organisms will depend on which traits data are chosen (or available) and the type of species considered. The research in functional ecology will choose specific traits if they are known to be as tightly as possible linked to the ecological response of interest (Münkemüller *et al.*, 2020; Violle *et al.*, 2007). On the contrary, when general strategies of species are the centre of interest or when the specific traits that would be most adequate are unknown, the researchers tend to choose traits representing the general strategies of the plant. It is hard to know which traits are representative of the general strategies or to measure all the traits relevant to approximate this strategy. One attempt to approach the differences between species as a whole, is to use their difference in terms of evolution, the phylogenetic diversity.

1.2. Phylogenetic Diversity

Species are part of a hierarchically structured phylogeny that represents their evolutionary history. Since traits are an outcome of evolutionary processes, the distribution of traits is not independent across species. For instance, Fig. 2 presents the distribution of specific leaf area among the main clades of vascular plants. This figure shows for example how the divergence between Gymnosperms and Angiosperms strongly contributes to trait variability among currently existing species. In the mid-eighties Felsenstein (1985) exposes his concern regarding the overlooked non-independence of species characters in comparative studies of phenotype across species or phenotype across environmental variables. At the time, precise phylogenies were rare and one of his propositions was to use traits frequency to reconstruct phylogenetic tree, given a set of (non-negligible) conditions: *"If we could find a transformation of the characters to a new set of coordinates that could be modelled as evolving independently by Brownian motion, with equal rate of accumulation of variance, we could apply the maximum likelihood method developed for gene* *frequency data".* The rapid advances of molecular biology over the past thirty years have made relatively accurate phylogenetic trees more available for many organisms. Thus, the same non-independent distribution of characters across taxa is the fundamental argument for the use of evolutionary relationships between members of a community to quantify patterns of trait diversity (Cadotte, Cardinale, & Oakley, 2008).

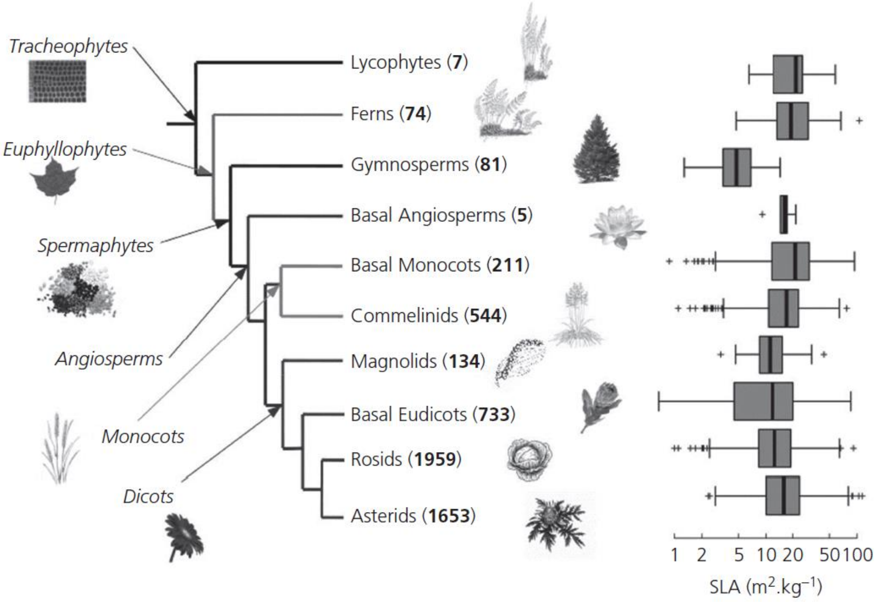

Figure 2: Phylogeny of specific leaf area for the major clades of vascular plants. The numbers shown in parentheses correspond to the number of species considered per clade in the analysis. Taken from Garnier *et al.* (2016).

It is assumed, that within a habitat type, the amount of ecological differentiation among species is proportional to the amount of evolutionary and genetic divergence. In the origin of species, Charles Darwin (1859) already suggested that closely related species will be more ecologically similar, and thus will compete more strongly with each other than they will with more distantly related species. However, in meta analyses (Cahill, Kembel, Lamb, & Keddy, 2008) support for this hypothesis in empirical data was not found. When monocots served as the focal (phytometer) species, the intensity of competition increased with the phylogenetic distance separating species, while competition decreased with phylogenetic distance for eudicot phytometers. There was no relationship between relatedness and competition for eudicots competing with other eudicots, while monocots did compete more intensely with closely related monocots than with distantly related monocots. They conclude that overall, the relationships between competition intensity and relatedness were weak compared to the strong and consistent relationships between competitive ability and functional traits such as plant size that have been reported by other studies. In other words, phylogenetic diversity had less explanatory power than functional diversity. However in several other studies, phylogenetic diversity has been reported to promote ecosystem stability (Cadotte, Dinnage, & Tilman, 2012) and ecosystem functions (Cadotte *et al.*, 2017; Le Bagousse-Pinguet *et al.*, 2019). Experimental work with specific designs is required to disentangle phylogenetic and functional diversity effects on ecosystem functioning. It would help to decide to which extend the phylogenetic diversity can approximate and/or complement functional diversity.

2. Measures and interpretation of community functional structure

A biological community is understood as an assemblage of species coexisting at a given time and place. Any index that attempts to summarize the 'composition' of a community in terms of the traits of the constituent species can be referred as an index of "community functional trait structure" (Garnier *et al.*, 2016), also called "trait distribution" (Carmona, de Bello, Mason, & Lepš, 2016). Authors also refer to a "functional trait space", because most of the indices can be represented in multivariate trait space to represent the extent and distribution of traits in each study unit (e.g. population, community, region etc.). These terms can be employed, basically, as synonyms.

To summarize traits distribution values at any levels (population, community, etc.), ecologists have proposed a plethora of methods and indices. Number of those are inspired by the concept of ecological niche developed by Hutchinson (1959), defined as the volume in multidimensional hyperspace in which species can maintain a viable population. Each of these measures aims at assessing a particular aspect of the community trait structure thought to be relevant in the community functioning, translating either a community response to or effect on ecosystem functioning. The functional structure of communities cannot be assessed by a single measure but rather needs a multi-index approach (Díaz *et al.*, 2007). In the mathematical characterisation of a distribution curve, the four first moments are i) the mean, ii) the variance, iii) the skewness and iv) the kurtosis. The four 'moments' can be useful in characterizing the distribution of traits in a community, or in a region, or on whatever other scale of interest (Le Bagousse-Pinguet *et al.*, 2017). While all four moments are interesting in their own particular way, the first two already provide a considerable amount of information (Ricotta & Moretti, 2011) and potentially present less complicated interpretation in the role they play in the functioning of community. This is why most of the efforts have focused on dominant trait values (Garnier *et al.*, 2004) and the extent of functional differences between organisms (e.g. Villéger *et al.* 2008; Pavoine & Bonsall 2011; Carmona *et al.* 2016).

The dominant traits value in a community are most of the time estimated using the simple yet powerful index, community weighted mean, or CWM (Garnier *et al.*, 2004; Suding *et al.*, 2008). The index corresponds, for each trait (either quantitative or qualitative), to the average trait values in a community weighted by the species relative abundances. In other words, the most abundant species have a bigger 'weight' on the average. The index reflects the trait values of the most abundant species, and specifically it reflects the trait values of an individual that would be randomly selected within a given assemblage.

Estimating the functional differences between species can be more challenging. One of the first measures of functional diversity that has been used in ecology, is the number of functional groups present in a community (Díaz & Cabido 2001). While the functional group approach is appealing by its apparent simplicity, it presents a certain number of practical and theoretical limits. The definition of functional group is rather subjective, and the attribution of a species to one or the other group can be context dependant (Westoby, 1998). Moreover, such classification tends to oversimplify functional differences between species, a species is considered totally similar to the other species of its functional group and completely different from species of other groups (Rosenfeld, 2002). However, in some cases such classification can be adequate, e.g. nitrogen fixing plant species positively affect fertility.

Functional diversity can be measured in many ways with a more continuous approach. Various authors have proposed that functional diversity can be decomposed into three primary components (Fig. 3): namely, functional richness, evenness and divergence (Carmona *et al.*, 2016; Mason, Mouillot, Lee, & Wilson, 2005; Villéger *et al.*, 2008). Functional richness is defined as the amount of functional space occupied by the organisms in an ecological unit, in other word it is a range. It does not account for species abundance. Functional evenness is the regularity in the distribution of the abundance in trait space of the organisms that comprise an ecological unit. Functional divergence is the degree to which the abundance in trait space of the organisms that comprise an ecological unit is distributed toward the extremes of its functional volume, can be then quantified by all indices linked to the weighted mean dissimilarity between species.

In recent years, several other interesting indices describing other aspects of community functional structure have been proposed. A great deal of attention has been devoted to functional redundancy in the literature (Fonseca & Ganade, 2001; Laliberté *et al.*, 2010; Ricotta *et al.*, 2016). Functional redundancy should reflect how stable a community's functional structure is to the potential loss of species. A community with high functional redundancy should be minimally impacted by the loss of one or more species, because there are several species with similar traits (insurance mechanism, Yachi & Loreau 1999). Low functional redundancy should thus imply lower buffering capacities of communities towards potential environmental changes. How to estimate functional redundancy though is not completely clear in the literature as several indices have been proposed (Carmona *et al.*, 2016; de Bello, Lepš, Lavorel, & Moretti, 2007; Laliberté *et al.*, 2010; Ricotta *et al.*, 2016) but not clear comparison had been attempted so far.

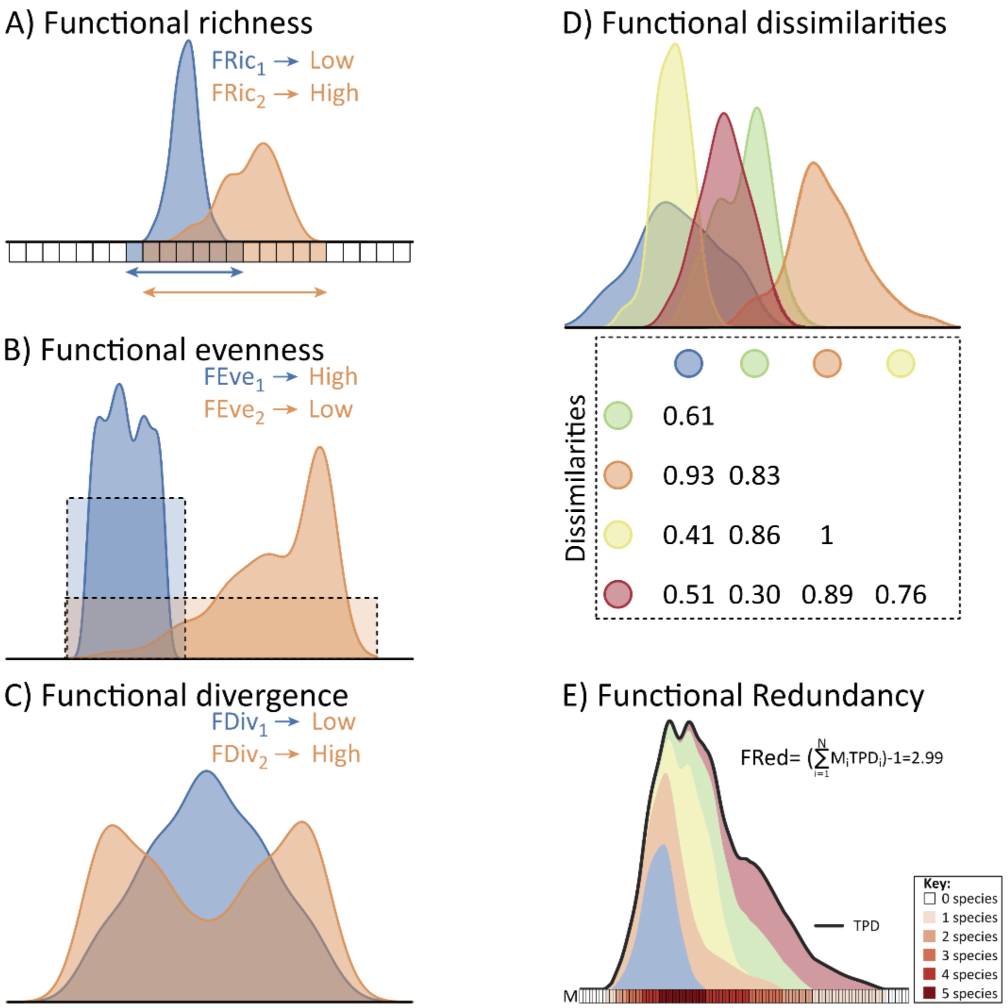

Figure 3: Classical indices describing functional trait distribution using the Trait Probability Density (TPD) Framework. Functional richness (FRic; A) is the amount of functional space occupied by a TPD. Functional evenness (FEve; B) is an indicator of evenness in the distribution of abundance within occupied functional trait space. Functional divergence (FDiv; C) is an indicator of the distribution of abundances within the functional trait volume. The abundance-weighted distance to the center of gravity of the TPD proposed in (Villéger *et al.*, 2008) can be used as an indicator of FDiv, using calculations based on the relative abundance of individual cells within the TPD instead of on species average trait values and species abundances. Dissimilarity between units (D) can be estimated from overlap between their TPD functions. Functional Redundancy (Fred; D), is an indicator of how redundant the species are in their functional traits' values. In other word, the average number of species (taken across cells) that could be removed from the community without reducing its functional volume (i.e., without losing an occupied cell from the grid). Taken from (Carmona *et al.*, 2016).

3. Ecosystem functioning

3.1. Community assembly

The community trait structure is not only important to understand how communities affect ecosystems, but they also reflect the effect of multiple community assembly mechanisms. The filtering framework (Keddy, 1992) builds on the idea that a series of filters decides which species can enter local communities (Fig. 4). Plant community composition is the result of the filtering of species from a regional species pool, that are able to reach to the community (Hubbell, 2001) and that can tolerate the prevailing abiotic environment (Weiher & Keddy, 1999) and the biotic interactions at a given site. The abiotic conditions define the environmental filters selecting species from a, into the local species pool containing all species adapted to the local conditions. Then, biotic interactions influence which species from the local pool can eventually coexist in the community (Chesson, 2000). Beyond species composition it is the functional traits and the community functional structure that result of the assembly process, affecting in turn the ecosystem functioning.

Functional traits are a theoretically important feature of the ecological assembly process as they partially determine the dispersal ability of species, their capacity to cope with abiotic conditions and biotic interaction (Cadotte *et al.*, 2013). Generally, the abiotic conditions would predominantly select the dominant traits values in community functional structure as species close to their optimal ecological niche condition will have more chances to dominate the community in given abiotic condition and tend to reduce the diversity of traits values among species (environmental filtering theory, Macarthur & Levins 1967). Meanwhile, the intensity of biotic interaction is expected to drive more strongly the diversity variable in community functional structure through mechanism like competitive exclusion and limiting similarity.

Studies applied the filtering framework using trait diversity patterns (Violle *et al.*, 2007) and phylogenetic diversity (Webb, Ackerly, Mcpeek, & Donoghue, 2002) to account for species' niche similarities. Such studies assume that measured traits are relevant for assembly processes and that

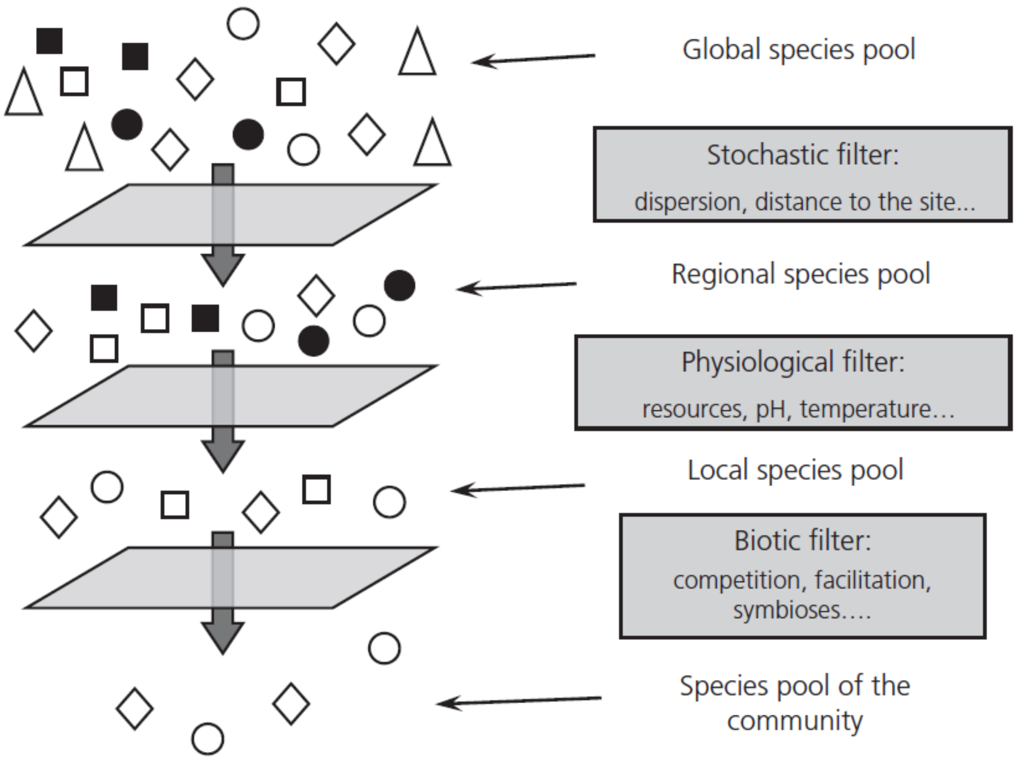

Figure 4: Graphical representation of community assembly rules based on the filtering concept. The different filters are depicted as a hierarchical series of processes that restrict membership in the species pool at the next finer scale, ultimately resulting in the actual observed community. The attributes global, regional, and local refer to the idea that the different processes prevail at different scales. It is important to note that despite the supposed hierarchy, the different processes act simultaneously and can also largely overlap. Taken from (Garnier *et al.*, 2016)

closely related species in the phylogeny are ecologically more similar than distantly related ones. To infer assembly processes, observed patterns of trait and phylogenetic diversity within a community are commonly compared to null expectations (i.e. patterns under random assembly). Low functional or phylogenetic diversity is assumed to indicate a convergence in species ecological niche, such as environmental filtering. Conversely, high functional or phylogenetic diversity can reveal ecological processes that result in limiting similarity, such as competition due to niche overlap. An increasingly large number of studies apply the filtering framework. However, reviews and meta-analyses of empirical (Götzenberger *et al.*, 2012) and simulation experiments

(Gallien, Carboni, & Münkemüller, 2014; T. Münkemüller *et al.*, 2012) tend to show that no simple general conclusion can be drawn from the sole observation of trait and phylogenetic diversity patterns.

3.2. Ecosystem functions

A large body of research has been dedicated to better predict the future distributions of biodiversity and associated functions with the overarching aim of developing management actions and solutions to global change. The idea that biodiversity affects ecosystem functions (BEF) has led researchers to establish a variety of experiments (Hooper *et al.*, 2005). The dominant hypothesis is that higher biodiversity, generally greater species richness, in general leads to higher level of functioning and higher temporal stability of communities and the ecosystems function and services they provide (May, 1972; Tilman, 2001). The main mechanisms that have been proposed to support this hypothesis are complementarity, selection, sampling effect, for effects of biodiversity over short-time scales and compensatory dynamics, dominant species effects and insurance effect over longer time scales.

Complementarity would occur when the performances of species in a community increases above that expected from the summation of the performances of individual species due to niche differentiation and resource partitioning in space and time, for example via differing rooting depths or phenology (e.g. Bazzaz & Catovsky 2001; Berendse 1982), or, facilitation (Loreau, Sapijanskas, Isbell, & Hector, 2012). The selection effect occurs when the performance of the community is due to high dominance of a strong competitor (Loreau & Hector, 2001). The sampling effect hypothesis assumes that under random community assembly process (Hector, Bazeley-White, Loreau, Otway, & Schmid, 2002), all of above mentions mechanisms are stronger (Loreau & Hector, 2001). By increasing the number of species there is higher probability to have species that explore different part of the functional niche having a positive effect on congeneric species, higher probability for a high competitor to be selected from the regional species pool and higher probability to have redundant species supporting similar ecosystem functions.

In terms of stability, compensatory effects occur when the decrease of one species in time is compensated by the increase of another (negative synchrony, see below). Dominant species effects is due to dominant species having conservative traits being more stable in time (Majeková, De Bello, Doležal, & Lepš, 2014). The insurance mechanism supposes that ecosystem functioning is resistant to species loss when several species are supporting similar function, so that one of them can be lost without losing the function.

Since the early 1990's a lot of BEF studies have been published, predominantly focussing on one function and one taxonomic group at a time, most often located aboveground. BEF research interest is growing toward more integrative ecosystem functioning assessment integrating multiple functions simultaneously (Manning *et al.*, 2018), accounting for the interaction between trophic levels and ecosystem compartments. Plant soil feedback is receiving growing attention (Wagg, Bender, Widmer, & van der Heijden, 2014; Zak, Homes, White, Peacock, & Tilman, 2003) as they are subject to strong trophic interactions (Hagedorn, Gavazov, & Alexander, 2019) and respond to similar drivers (Valencia *et al.*, 2018). For example, land-use and climate changes can substantially alter soil communities and therewith the ecosystem functions that they perform (Geisen, Wall, & van der Putten, 2019).

3.3. Tradeoff

The concept of tradeoff underpin most of the research fields in ecology (Garland, 2014). From evolution to conservation, observation shows that the increase of one variable comes generally at the expense of another one. Some examples of trade-off in traits were presented earlier as a core of the L-H-S framework: seed mass *vs.* seed number or light capture efficiency *vs.* deffence structures in leaves. Those particular trade-offs are part of larger set of covariation structures in species traits as describe in the fast-slow plant economic spectrum (Reich, 2014) or the aquisitive-conservative strategies (Díaz *et al.* 2016). An archetypal acquisitive strategy is characterized by faster growing tissues with higher SLA (Specific Leaf Area), shorter lifespan, dissemination of higher number of smaller propagules, but lower investments in defence structure and resource storage. In contrast, conservative strategy translates into trait syndrome requiring higher investment from the plant in its tissues with for example higher Leaf Dry Matter Content (LDMC), longer lifespan and a reproduction based on fewer propagule containing more reserves.

Ecosystem functions, like traits, are not entirely independent from each other but rather covaries into clusters, or bundles (Lamarque, Lavorel, Mouchet, & Quetier, 2014). In fact, because of the effect plants traits have on ecosystem functions, trade-offs among traits can scale up to trade-offs among ecosystem functions (Lavorel & Grigulis, 2012; Wardle *et al.*, 2004). Bundles of ecosystem properties can mirror the conservative-acquisitive continuum in plant traits, where for example plant communities with more conservative species would be associated with ecosystems with lower productivity, slower turnover, higher soil carbon sequestration (Fig. 5).

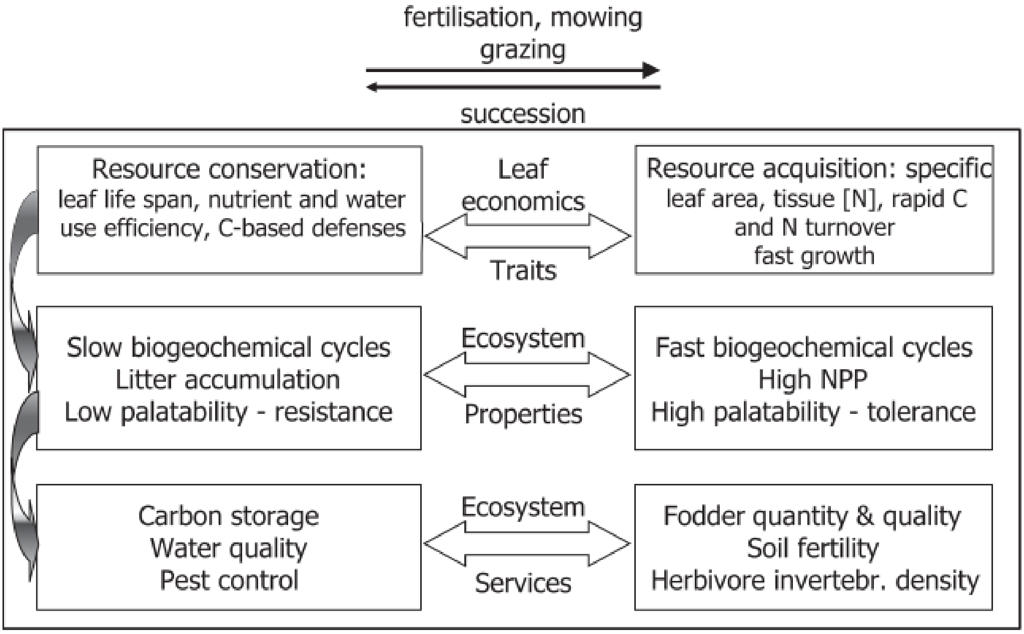

Figure 5: Conceptual model of the scaling of trade-offs between leaf economic spectrum to ecosystem properties and ecosystem services for grasslands along gradients of management intensity, especially fertility, or of secondary succession. Taken from Lavorel & Grigulis (2012).

3.4. Stability (& synchrony)

As seen above, the way by which biodiversity affects the stability of ecosystems deserves specific attention, with specific mechanisms and concepts. Ecosystems are subject to temporal variations in environmental conditions and various stressors. An important aspect of their functioning is their temporal stability in response to these extrinsic factors (de Mazancourt *et al.*, 2013). The stability of ecosystems is a broad concept, which can be interpreted and applied in a variety of ways. Pimm (1984), later revisited by Loreau (2010), identified three principal components: i) temporal stability (low fluctuations over time), ii) resilience (recovery speed after disturbance), and iii) resistance (ability to maintain its original state after disturbance) (Fig. 6).

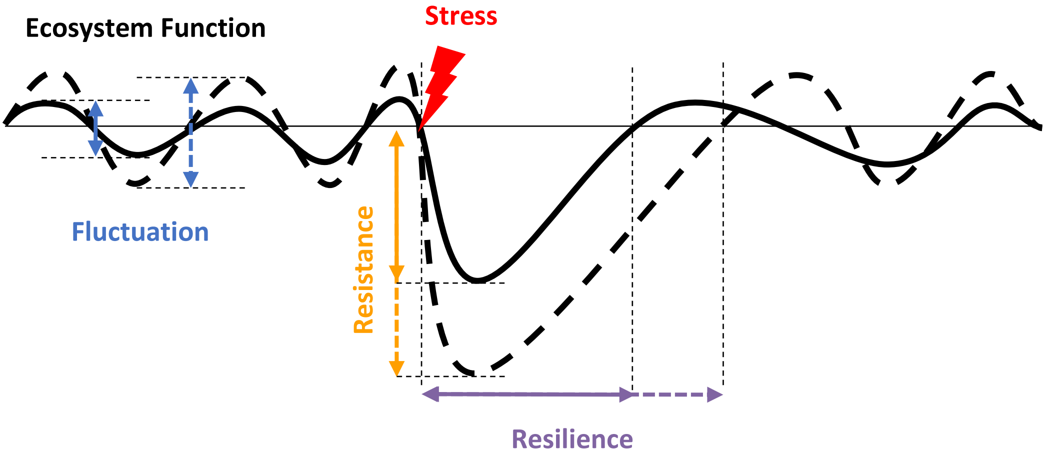

Figure 6: Theoretical representation of the main components of stability. In comparison to the dotted curve, the solid curve represent an ecosystem function (e.g. Net Primary Production) of a community with lower inter-annual fluctuation, higher resistance to stress (i.e. lower displacement during a stress period) and higher resilience after stress period (i.e. faster return to the „normal" level of ecosystem function).

Theoretical and empirical work has already challenged the species richness centred diversity-stability hypothesis, enlightening more complex relationship between diversity and stability (Lepš, 2013) with three main arguments. First, the diversity-stability relationship is highly dependent on the environmental context (Wardle, 2016). Second, the unequal contribution of species to the whole community biomass, e.g. many rare species in a species-rich community have weak impact on ecosystem process compared to the impact of a few dominant species (Lepš, Osbornová-Kosinová, & Rejmánek, 1982), an effect often referred as Mass-Ratio hypothesis (Grime, 1998). Other authors (e.g. Soliveres *et al.* 2016), however, argue that rare species play a crucial role on ecosystem functions by providing a more balanced amount of functions in ecosystems. As they tend to be less redundant than common species in the functional traits they possess, they support communities with more distinct combinations of functional traits. Third, other aspects of diversity can play an important role in the diversity-stability relationship. For example, in a meta-analysis, Cadotte *et al.* (2008) showed that the amount of phylogenetic diversity within communities explained significantly more variability of plant community biomass than other measures of diversity, such as the number of species or functional groups.

However, biodiversity is also expected to support ecosystem stability indirectly via mechanisms such as compensatory dynamics (Loreau & de Mazancourt, 2013), i.e. increases or decreases in the relative abundance of some species that are offset by changes in the relative abundance of others species in the community, varying in an asynchronic way. On the other hand, if species have similar response to environmental factors (synchrony), the community is less stable. Overall, the relative importance of the different drivers of stability is not well established and the analyses of long-term empirical data from natural communities could provide precious insight on this knowledge gap (Hautier *et al.*, 2014).

4. Thesis scope

This thesis focuses on the specific role of community functional structure parameters on diverse aspect of ecosystem functioning. It is composed of four chapters. Chapters I and II are based on a common garden biodiversity experiment specifically designed to disentangle the role of functional and phylogenetic diversity in resisting colonization by surrounding weeds (chapter I) and the simultaneous performances of multiple ecosystem functions, specifically plant-soil interaction (chapter II). Chapter III broaden the scope of the investigation, analysing drivers of community temporal stability, particularly the role of biodiversity and species synchrony, in a compilation of vegetation time series from all around the world. In a simulation experiment, chapter IV open the black box of functional redundancy computation methods and their theoretical relationship with stability through the insurance hypothesis.

Chapter I

Colonisation resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities

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Abstract

1. Functional and phylogenetic diversity (FD and PD respectively) of the resident community are expected to exert a key role in community resistance to colonisation by surrounding species, and their establishment success. However, few studies have explored this topic experimentally or evaluated the interactive effects of these diversity measures.

2. We implemented a diversity experiment to disentangle the role of FD and PD by sowing mixtures of 6 species, drawn from a pool of 19 species naturally coexisting in central European mesic meadows. The mixtures were designed to cover four independent combinations of high and low FD and PD. Species covers were estimated in spring and late summer over 2 growing seasons. We then assessed the establishment success of colonisers as a function of their mean traits and phylogenetic distance to the resident (i.e. sown) communities, as well as the resistance of the resident communities to natural colonisers as a function of their functional and phylogenetic structure.

3. Results generally indicated a temporal shift regarding which trait values made a coloniser successful, from an acquisitive strategy in early stages to a more conservative trait syndrome in later stages.

4. FD decreased community resistance to natural colonisation. However, PD tempered this effect: with high PD, FD was not significant, suggesting complementary information between these two components of biodiversity. On average, colonising species were more functionally distant from the resident species in sown communities with high functional diversity, i.e. those that were more colonised.

5. *Synthesis*. Our results confirm an interplay between FD and PD during community assembly processes, namely resistance to colonisers, suggesting that these two descriptors of biodiversity only partially overlap in their contribution to the overall ecological structure of a community. The hypothesis that higher FD increases resistance through a more complete use of resources was challenged. Results rather suggested that greater FD could

provide an unsaturated functional trait space allowing functionally unique species to occupy it.

1. Introduction

Shifts in species composition resulting from growing human influence and continuous climate change have brought new challenges to community ecology (Pecl *et al.*, 2017). Natural community dynamics are driven by key processes such as the establishment of new species in the local resident communities (Kempel, Chrobock, Fischer, Rohr, & van Kleunen, 2013; Vítová & Lepš, 2011). While colonisation can occur either from a regional species pool or by an invading alien species, the main questions remain roughly the same (Lanta & Lepš, 2008; Shea & Chesson, 2002): what makes a species a successful coloniser? What makes a community more resistant to colonisation? Studies that aim at answering these questions could provide valuable knowledge on the biotic drivers influencing community assembly processes.

Community resistance to colonisation has traditionally been attributed to high species richness. Species-rich communities are expected to resist colonisation through a more complete use of resources (Elton, 1958). Increased resistance due to greater species richness has been repeatedly observed in communities where diversity was experimentally manipulated (Fargione, Brown, & Tilman, 2003; Fargione & Tilman, 2005; Kennedy *et al.*, 2002; Van Ruijven, De Deyn, & Berendse, 2003). However, inconsistent and contradictory results have been shown both within natural (Robinson, Quinn, & Stanton, 1995) and experimental systems (Palmer & Maurer, 1997). Moreover, colonisers diversity can also be positively correlated with resident community diversity, particularly at large scales (e.g. Stohlgren *et al.* 1999; reviewed by Fridley *et al.* 2007). Greater diversity of colonisers in richer regions can be explained by the covariation of biodiversity with extrinsic factors, e.g. resource heterogeneity (Naeem *et al.*, 2000).

At the local scale, inconsistent results on the relationship between resistance to colonisation and species richness, and the recognition that ecosystem processes depend on species' traits rather than species richness (Hooper *et al.*, 2005) has led researchers to study community assembly processes through the lens of species' functional traits and communities' functional structure. Functional structure is often characterised by two components: functional diversity (FD), i.e. the extent of functional trait dissimilarity between species, and traits of dominant species, reflected by community weighted mean (CWM; Violle *et al.* 2007). FD, in studies using a variety of estimators, has been shown to increase colonisation resistance (Finn *et al.*, 2013; Frankow-Lindberg, 2012; Lanta & Lepš, 2008; Schittko, Hawa, & Wurst, 2014; Suter, Hofer, & Lüscher, 2017), suggesting the importance of niche-based processes such as a more complementary use of available resources in functionally diverse communities. Other studies have found no evidence for the importance of processes such as complementarity or limiting similarity in colonisation success (Bennett, Stotz, & Cahill, 2014; Letten, Keith, & Tozer, 2014), leading to inconsistent results among both experimental and observational studies. In this sense, measures of FD which reflect the uniqueness of species in a community (Ricotta *et al.*, 2016) could provide a clearer picture of the relationship between colonisation resistance and saturation of the functional trait space (Gurvich, Tecco, & Díaz, 2009; Loiola *et al.*, 2018). At the same time, dominant species and their trait values could have a greater impact on resistance to colonisation than species richness itself (Smith *et al.* 2004) and could, therefore, be a useful predictor of resistance to colonisation. However, dominant species can either increase or decrease resistance to colonisation in a community. For example high canopy cover can increases competition for light, but also reduce stressful conditions by increasing soil moisture content (M. D. Smith *et al.*, 2004). Assessing the functional structure of a community through both CWM and FD (Ricotta & Moretti, 2011) should allow to disentangle whether trait diversity or dominance (or both) are responsible for resistance to colonisation in homogenous environmental conditions.

Measuring all the relevant functional traits to a given ecosystem function is often materially impossible, therefore, phylogenetic diversity has been proposed as a proxy, or complement, for unmeasured functional diversity (de Bello *et al.*, 2017; Webb *et al.*, 2002). Phylogenetic diversity summarises the evolutionary relationship between species (Faith, 1992). It is commonly used alone or in combination with FD under the hypothesis that closely related species are more similar than distant ones (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Loiola *et al.*, 2018; Mace, Gittleman, & Purvis, 2003).

However, to the best of our knowledge, few studies have measured the effect of PD on the success of individual-species colonisation, with inconsistent results. For example, Whitfeld *et al.* (2014) demonstrated a negative effect of higher PD on invading *Rhamnus cathartica*, whereas Bennett, Stotz & Cahill (2014) showed that invading *Bromus inermis* was not restricted by high PD.

While numerous studies use PD as a proxy for FD, PD and FD are not necessarily correlated (Gerhold *et al.*, 2011; Prinzing *et al.*, 2008). This lack of correlation can be explained by the ability of PD to potentially capture unmeasured functional diversity (de Bello *et al.*, 2017; Webb *et al.*, 2002) and by the limitation of the phylogenetic approach to reflect traits with weak phylogenetic signal, i.e. which are less conserved over the phylogeny (Flynn *et al.*, 2011). Therefore, several studies (Cadotte, 2013; Pavoine & Bonsall, 2011; Prinzing *et al.*, 2008) have highlighted how a combination of phylogenetic and functional measures may paint a more complete picture of ecosystem functioning. Nevertheless, studies that test this approach experimentally are still rare (Feng, Fouqueray, & van Kleunen, 2018; Tan, Pu, Ryberg, & Jiang, 2015).

While resistance to colonisation can be studied through traits and phylogeny of the resident community, it seems equally important to take into account the perspective of the colonising species and the traits that enable them to successfully enter into already established communities (Roscher, Gerighausen, Schmid, & Schulze, 2015). Based on the limiting similarity theory, a successful coloniser should present functional traits that do not completely overlap with those of the resident community (Funk, Cleland, Suding, & Zavaleta, 2008). Several studies have tried to identify traits defining a successful coloniser but a review of these studies has highlighted some contradictions (see Pyšek & Richardson 2007). This lack of consistency can partly be explained by interactions between different traits (Küster, Kühn, Bruelheide, & Klotz, 2008), by trait dissimilarity to resident species being more important for establishment success than specific traits values (Feng *et al.*, 2018; Loiola *et al.*, 2018), and by different traits values being advantageous at different stages of colonisation or in different environments (Crawley, Harvey, & Purvis, 1996; Kempel *et al.*, 2013; Thompson, Hodgson, Grime, &

Burke, 2001; Van Kleunen, Dawson, & Maurel, 2015). Hence, different studies, both experimental and observational, might provide partially contrasting results. The possibility to combine trait and phylogenetic information on species can help to reveal processes underlying community assembly.

In addition to plant properties determining the outcome of colonisation, environmental conditions such as nutrient availability, can modify ecosystem processes by affecting plant-plant interactions and community saturation. For instance, Lepš (2014) showed that 15 years of fertilisation in a central European oligotrophic meadow, led to increased competition between plants and species richness depletion by exclusion of subordinate species. In terms of colonisation, lower nutrient availability was found to reduce establishment of colonisers (Fargione & Tilman, 2005) while higher levels of nitrate in the soil was found to increase the total abundance of colonisers in resident plant communities (Knops *et al.*, 1999; Roscher *et al.*, 2009; Thompson *et al.*, 2001).

In our study, we combine trait-based and phylogeny-based measures, both from a resident community and from a single colonising species perspective, in an attempt to provide a more complete understanding of the colonisation process. We assessed the effects of different levels of FD, PD and fertilisation on spontaneous colonisation in experimental grassland communities with a fixed amount of sown species. The methodological approach leading to these contrasted levels of FD and PD also generated a gradient of saturation of phylogenetic and functional space. We recorded spontaneous colonisation by unsown species and combined this vegetation data with species' traits and phylogeny data in order to address the following questions: i) Which traits promote species colonisation success? ii) Are the colonising species filling empty functional and/or phylogenetic space of the resident community? iii) How does the functional and phylogenetic structure of the resident community affect resistance to colonisation? Furthermore, through a fertilisation treatment we investigate if the relations between traits and colonisation depend on nutrient availability. We argue that such a multi-directional evaluation can help us to understand how ecological differences between species, in particular between colonisers and residents, can shape the colonisation process.

2. Material & Methods

2.1. Experimental design and data collection

A sowing experiment was carried out on a mesic meadow 30 km southeast of Tábor, at an elevation of 660 m (Vysočina region, Czech Republic, 49.331N, 15.003E). The climate is temperate continental with an average annual temperature of 6.7°C and average annual precipitation of 759 mm (data from Černovice meteorological station, ca 4km from the site). The study site is an abandoned crop field, last cultivated in 2001 and ploughed in 2014 prior to the experiment.

Information for five numerical and four categorical traits, related to the competitive ability and niche occupation of the species were obtained from the LEDA trait database (Kleyer *et al.*, 2008) and BiolFlor (Kühn, Durka, & Klotz, 2004) for both the sown species and unsown (i.e. spontaneous colonisers) species. The continuous traits were canopy height (m), seed mass (mg), specific leaf area (SLA, $mm^2\ mg^{-1}$), leaf dry matter content (LDMC, $mg\ g^{-1}$) and length of flowering period (month 1–12). Categorical traits were Raunkiær's life form (T = Therophyte, G = Geophyte, H = Hemicryptophyte, and C = Chamaephyte), lifespan (a = annual, b = biennial and p = perennial), growth form (e = erosulate, leaves are separated by long internodes all along plant growth; h = hemirosette, plants combining a rosette and elongation phase; r = rosette, leaves are exclusively separated by short internodes) and nitrogen-fixing ability (1 = yes, 0 = no; the only nitrogen fixers present on our site were legumes).

The experimental set-up was a fully randomised factorial design with three factors: functional diversity (low and high), phylogenetic diversity (low and high) and fertilisation (yes/no). Following the framework from Dias *et al.* (2013), we simulated all potential combinations of six species from a pool of 19 species (27,132 combinations). From the simulated combinations of species, we removed those with extreme CWM values (highest and lowest 10%) for the continuous traits. We also removed communities with more than 4 legumes or 4 grasses, in order to avoid an over-disproportionate dominance of functional or taxonomic groups in the communities (see Figure S1 for complete flowchart of community selection process). Then, we randomly selected four groups of 10 communities each, covering relatively extreme values of FD and PD with constant species richness (Table S2). In the low FD and low PD group, an additional constraint was set in the random selection of communities: one of the 10 communities had to contain 5 grasses in order to further increase the gradient of PD covered in the experiment.

Each of the 40 communities was sown on two randomly selected plots in the field, one fertilised and one unfertilised, in order to test the effect of nutrient availability. A concentrate of composted cow manure was applied at a rate of 2.2 T/ha (33 N, 55 P_2O_5, 33 K_20) on each fertilised plot at the beginning of the growing season in March 2015, 2016 and 2017.

Each 1.5 × 1.5 m plot, separated by a 0.5 m buffer zone, was sown with a combination of 6 species obtained from a pool of 19 species naturally present in mesic meadows of the area (See Table S1 for sowing densities and trait values). Seeds were obtained from a local commercial provider (Planta Naturalis). In order to maximize the evenness in species abundance and considering that species with heavier seed generally establish better, the sown proportions of seeds from species with bigger seed mass was reduced. Specifically, the number of sown seed decreased linearly with the logarithm of seed mass (see details on the calculation of sown species proportion in Table S1). To ensure a good establishment of the sown communities, sowing took place twice in 2015, once in spring and once in autumn. In summer 2015, the entire field was mainly dominated by *Chenopodium album*; to not restrict the growth of the sown species, we weeded this species from all the plots.

Vegetation sampling was carried out in 2016 and 2017 during May and September. Cover of sown and unsown species was visually estimated on a positively unbounded percentage scale in order to account for the different strata of vegetation. All species that were not sown in a particular plot were considered as colonisers, i.e. species present in the local seedbank and species disseminated from the surrounding area or from the other experimental plots.

Another experiment running at the locality, together with marginal seed admixtures from the seed provider, provided some potential colonisers that do not belong to the local species pool (e.g. *Dianthus superbus*). Nevertheless, the vast majority of colonisers were naturally occurring species in the surrounding area. Species nomenclature follows the key to the flora of the Czech Republic (Kubát *et al.*, 2002).

FD and PD of the sown communities were computed using Rao's index (Rao, 1982). It is important to note that, for a fixed amount of sown species and an expected even distribution of species cover (as in our experimental setup), this index is equivalent to a measure of species uniqueness (Ricotta *et al.*, 2016). This measure of uniqueness (U) is the complement of functional redundancy (R), i.e. R=1-U (Ricotta *et al.*, 2016), where redundancy reflects the saturation of communities in terms of functional or phylogenetic space. In other words, communities with higher sown FD are less saturated in functional trait space because they are less redundant in their traits values.

For FD we considered seven different traits (lifespan and life form were excluded from diversity measures at the community level since all sown species were hemicryptophytes, therefore perennials; these traits were only used to characterise the unsown species and their functional distances from the sown communities; Table S1). The 'trova' function (de Bello, Carmona, Mason, Sebastia, & Lepš, 2013) was used to estimate the Gower dissimilarity between pairs of species. CWMs of the resident species were calculated as average trait values of the 6 sown species. To compute CWM, FD and PD, we considered species weights to be the same, as their initial proportion was intended to be equal (we also computed FD and CWMs for the observed communities, using observed species covers as weights, and generally obtained similar main results, see further below). Height, seed mass and SLA were ln-transformed prior to the calculation of indices to reduce skewness of the distribution. For categorical traits, CWM is equivalent to the proportion of species in each category. To calculate phylogenetic distances between species, we used a dated ultrametric supertree of European plant species, "Daphne" (Durka & Michalski, 2012) and the function 'cophenetic' from the {ape} R package (Paradis, Claude, & Strimmer, 2004).

2.2. Statistical analysis

2.2.1. Functional traits promoting colonisation success

All analyses were carried out with the R software version 3.3.2 (R Core Team, 2017). The colonisation success of each species was estimated as the ln(x+1) transformed sum of its cover over the 80 plots at each sampling time. All continuous traits were scaled around their mean and standardised by their standard deviation. Linear mixed-effect models (LMEM), as implemented in the {nlme} package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018), were used to identify which traits could best predict colonising success with species identity included as a random factor. We first tested the effect of year, season and their interaction. Since only years had a significant effect and it only had two levels, it was included as an *a priori* covariate, i.e. fixed effect, in the models rather than as an additional random variable. Species traits, as well as their interaction with years, were first tested individually and then added sequentially (forward selection) to select the best predictive model through the Akaike information criterion (AIC). A drop of 2 AIC points was considered to significantly improve the model. When categorical variables were identified as significant predictors, post-hoc multiple comparisons were performed using the {multcomp} package (Hothorn, Bretz, & Westfall, 2008) to identify statistically different categories. In total, 110 species occurring in at least one plot within one sampling session were used in the analysis (resulting in 327 data points).

2.2.2. Functional and phylogenetic distances between the colonisers and the resident community

The functional and phylogenetic distances between each of the colonisers and the resident communities were calculated as the mean of the 6 pairwise distances with the 6 sown species of each resident community, using the species pairwise distance matrix previously calculated (Gower distance on seven functional traits or cophenetic phylogenetic distance). Furthermore, for each plot, we averaged the distances obtained above for each of the colonisers in that plot (see below). For each species, LMEM were used to evaluate the relationship between its cover (ln(x+1) transformed) and its mean functional or phylogenetic distance (scaled and standardised) from the sown species in each plot, with plot identity included as a random factor. The strength of the relationship was derived from the estimate and variance explained only by the fixed factors (R^2_M, marginal R^2) using the {MuMIn} R package (Barton, 2018). In total, 79 species (those with at least 10 occurrences across the four sampling sessions) were used in the analysis. Fertilisation, year and season had no significant effect and therefore were not included in the model.

Additionally, in order to compare the functional and phylogenetic distances of the set of colonisers in each plot across the different diversity treatments, we summarised the distance of the colonisers to the resident species as one mean value per plot (and per sampling time). This also provides a greater statistical power, because for several of the colonisers the number of observations was only slightly above 10 plots. These averaged functional and phylogenetic distances of the colonisers to the resident species were treated as response variable in a LMEM with diversity treatments as fixed predictor and plot identity as random factor.

2.2.3. Functional and phylogenetic structure of the resident community and its resistance to colonisation

Finally, we analysed to what extent the functional and phylogenetic structure of the resident community could predict the level of colonisation by unsown species. The level of colonisation was calculated as the ln(x+1) transformed sum of unsown species cover in each plot and sampling session. LMEM were used to assess the effect of different components of functional and phylogenetic structure (PD, FD over all traits, FD and CWM for individual traits), as well as fertilisation, on the total cover of unsown species. Plot identity was included as a random factor and year as an *a priori* covariate. First, each predictor was tested individually, and then, forward selection based on AIC was applied on groups of predictors: i) all individual FD, ii) all CWM and iii) all FD and CWM. This analysis included 320 measures, 80 plots sampled on four different occasions. We also considered the effect of observed FD, PD and CWMs of sown species on the abundance of colonisers, which were generally consistent with the one presented here. We argue that it is preferable to consider the values based on sown densities (i.e. all the sown species in equal proportions) because the realised community composition could already be a consequence of colonisation (Roscher *et al.*, 2013), thus leading to potential circularity in the analyses. Moreover, the sown species successfully established in almost all the plots. Out of the 80 communities, only 2 did not fulfil the sown species richness at least one time during the four sampling sessions. Therefore, the intended diversity levels are relevant a factor in our analyses.

3. Results

Over the 320 samples, 91 colonising species were identified in addition to the 19 sown ones. The four most abundant unsown taxa were *Taraxacum* sect. *Ruderalia*, *Trifolium repens*, *Plantago lanceolata* and *Elytrigia repens* which represented respectively 21, 9, 9 and 8% of the total cover of unsown species. The average total cover occupied by colonising species per plot increased from 18.4% (*SD* = 11.6) in 2016 to 30.9% (*SD* = 17.0) in 2017.

3.1. Functional traits promoting colonisation success

The results show a change in the traits of successful colonisers from 2016 to 2017 driven by a shift in successful species in the two seasons (Figure 1). The interaction effect with year was significant for five of the traits tested individually (Table S3). Perennial colonisers were generally more abundant than annuals and this difference increased in 2017 (F2,214 = 15.27, P < 0.001; Figure 1.A). Similar results were obtained with species lifeforms: hemicryptophytes significantly increased from 2016 to 2017 whereas therophytes decreased (F3,213 = 13.27, P < 0.001; Figure 1.B). In 2016, LDMC, SLA and flowering period length showed no relationship with colonisation success, whereas in 2017 species with higher LDMC, lower SLA and shorter flowering period were more abundant (respectively F1,215 = 13.27, P = 0.005; F1,215 = 6.91, P = 0.010; F1,215 = 25.53, P < 0.001; Figure 1.D-F). Nitrogen fixing colonisers were more abundant than non-nitrogen fixing colonisers and this relationship remained stable across the 2 years of sampling (F1,215 = 1.73, P = 0.189; Figure 1.C).

When all traits were combined into a single model, the only selected predictors in addition to year were nitrogen fixing ability, lifespan and the interaction between lifespan and year. In this final model, 16.2% of the variation in species colonisation success was explained by the fixed predictors (Table 1).

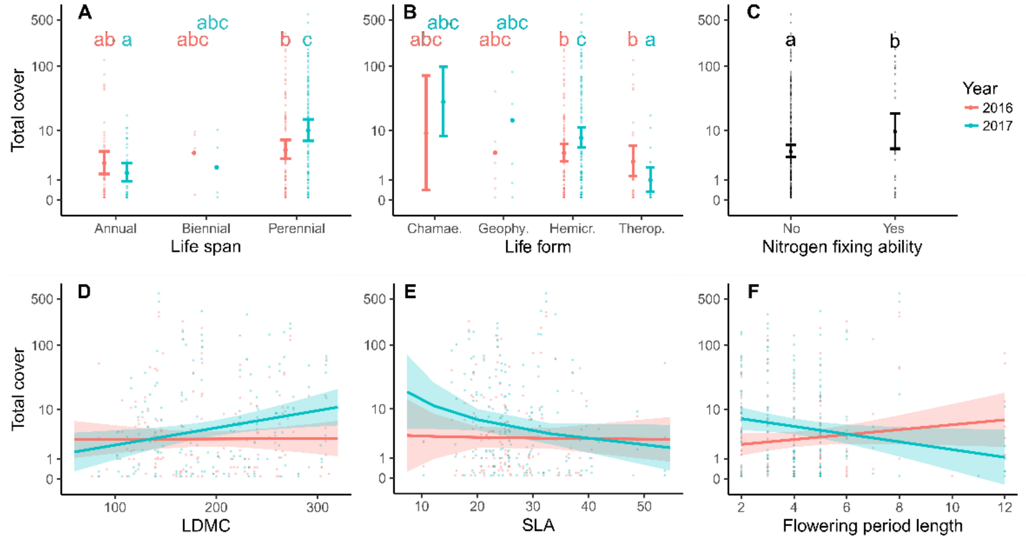

Figure 1: Species' colonisation success as a function of species' traits and sampling year. Each panel presents the relationship between species success (i.e. the sum of cover a species yielded over all the plots on each sampling session) and the species' functional traits in interaction with sampling year. In this figure, we present only the traits that were significant predictors of species colonising success. The interaction between year and functional traits was significant for all but nitrogen fixing ability. The small dots represent partial residual of each data points. Panels A to C, the larger dots with error bars represent the 95% confidence interval (CI) around the mean of each group (except for panel A and B, where the oversized CI due to low number of representing species were not drawn for biennials and geophytes, respectively). The letters represent statistical groups differences ($P<0.05$) according to Tukey HSD test, taking into account the random variable, i.e. species identity. The solid line in panels D, E and F represents the slope estimate surrounded by 95% CI in coloured area.

3.2. Functional and phylogenetic distances between the colonisers and the resident community

Fifteen unsown species presented a significant relationship between their abundance per plot and the mean distance (phylogenetic or functional) from the resident community, 13 of which were positive (Figure 2. A). These species

Table 1: Functional traits affecting species colonisation success. The model presents the functional traits that have been selected to predict the colonisation success of unsown species, (i.e. using the sum of species cover over all the plots on each sampling session). We present the ANOVA (type II) table of the most parsimonious model based on forward selection of predictors (including all species functional traits as well as their interaction with year) by AIC. Species identity was included as a random variable to take into account the non-independence of points (i.e. same species at different sampling sessions). The model used 327 observations from 110 groups (species). The variation explained by fixed and random factors was R2C = 0.69 and the variation explained by fixed factors only was R2M = 0.16.

Variable	***F* value**	***p*(>*F*)**
Intercept	24.08	<0.001
Year	11.65	<0.001
Lifespan	6.66	0.002
Nitrogen fix	4.10	0.045
Year : Lifespan	15.52	<0.001

yielded significantly higher cover in the plots where they were functionally more different from the resident community. The variance explained by fixed factors (R^2_M) ranged from 0.07 to 0.45. When we considered phylogenetic distances, the number of species with a significant relationship was reduced to 11 with 7 positives. R^2_M ranged from 0.04 to 0.43 (Figure 2. B).

When considering the average distance of all colonisers to the residents per plot, communities with high sown FD were on average colonised by species more functionally distant from the residents than communities with low FD (Figure 2. C). Communities with high sown PD tended to be colonised by species on average more phylogenetically similar to the residents than communities with low PD (Figure 2. D). However, the differences in colonisers' phylogenetic distance among diversity treatments were relatively low, and significant only between high PD - low FD and low PD - high FD treatments (Figure 2. D).

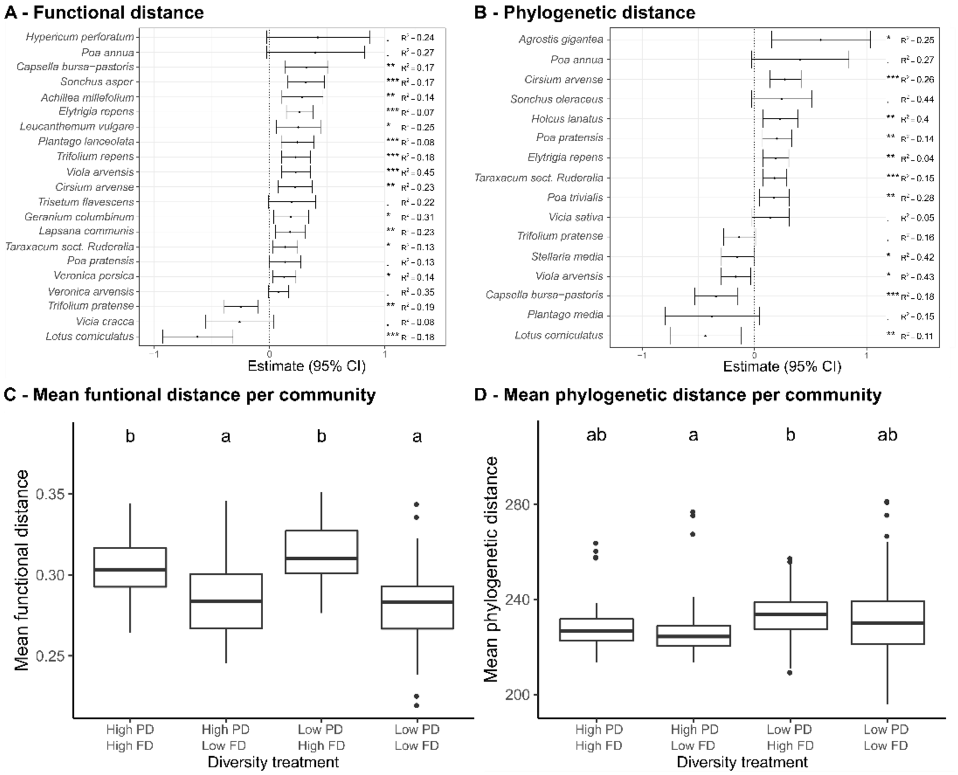

Figure 2. Colonisers' functional (A, C) and phylogenetic (B, D) average distances from the resident species. Panels A and B present the relationships between species cover and their functional (A) or phylogenetic (B) distance from the resident community. For each unsown species with more than 10 occurrences, a linear mixed effect model was fitted to predict the cover of the species by its mean functional (A) or phylogenetic (B) distance from the sown species of the resident community. The distances were scaled, centred around the mean and divided by SD, to standardise the coefficients and allow direct comparisons between species. The estimates of the slopes along with their 95% confidence interval are presented only for the models with $P < 0.1$. P-values are represented by symbols on the right: "." for $P < 0.1$, "*" for $P < 0.05$, "**" for $P < 0.01$, "***" for $P < 0.001$). R^2 is the marginal coefficient of determination of the models representing the variation explained by the fixed factor only (i.e. phylogenetic or functional distance from the resident sown community). Panels C and D present the average of colonisers' functional (C) and phylogenetic (D) distances from the resident species in each community across the four diversity treatments. The letters above each box represent statistical groups differences ($P < 0.05$) according to Tukey HSD test, taking into account the random variable, i.e. plot identity.

3.3. Functional and phylogenetic structure of the resident community and its resistance to colonisation

An important part of the variation in colonisation level per plot, i.e. the sum of colonising species cover within each plot per sampling session, was explained by year alone ($R^2_M = 0.20$, Table S4 model 2). However, adding the diversity treatment in the model substantially improved its fit ($R^2_M = 0.31$, Table 2a). The results show that resident communities with higher FD had a greater cover of colonising species, particularly when PD was low (Figure 3.A). With high PD, the colonisation level in high FD communities was not significantly higher than in low FD communities. The interaction between the effect of year and diversity treatment was not significant ($F_{3,236} = 1.40$, $P = 0.245$; Table 2a), neither was the interaction between the effect of year and any individual traits, FD or CWM tested in the rest of the analysis (Table S4). Fertilisation had no significant effect ($F_{1,72} = 0.59$, ns), nor its interaction with diversity treatment ($F_{3,72} = 0.80$, ns, Table S4).

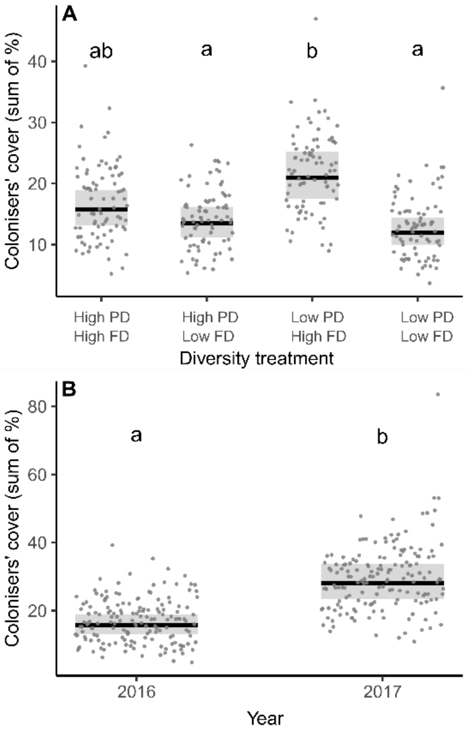

Figure 3: Conditional plots of sown functional (fd) and phylogenetic diversity (pd) treatment (a) and sampling year (b) on the level of colonisation by unsown species (colonisers' cover). Each panel represents the partial effect of a single factor on the response when other variables are held constant, i.e. To their reference level: year 2016 for panel a and high pd high fd for panel b. Although the statistical inferences were made on ln-transformed cover values, the response variable is plotted on the original scale for graphical purposes. The black horizontal lines represent the mean value predicted by the models and the grey area their 95% confidence interval.

Table 2. Effect of the functional and phylogenetic structure of the resident community on resistance to colonisation. For each model, we present the ANOVA (type II) table of the most parsimonious model based on forward selection of predictors by AIC. In model a), diversity treatment, i.e. 4 combinations of high and low FD and PD, is used to predict the amount of cover colonised by unsown species in each plot. In model b), sown community functional attributes have been selected to predict the amount of cover colonised by unsown species in each plot. Forward selection of predictors, including all community functional attributes as well as their interactions with year, was based on AIC. In both models, plot identity was included as a random variable to account for the non-independence of data points (i.e. same plot at different sampling sessions). R^2_M represent the variation explained by the fixed factors only and the conditional R^2 (R^2_C) represent the variation explained by both the fixed and random factors. Both models used 320 observations from 80 groups (plots).

Variable	***F* value**	***p*(>*F*)**
(a) Diversity treatments explain the level of colonisation ($R^2_M = 0.31$,$R^2_C = 0.60$)		
Intercept	4316.14	<0.001
Year	157.33	<0.001
Diversity treatment	7.02	<0.001
Year : diversity treatment	1.40	0.245
(b) Community functional attributes explain the level of colonisation ($R^2_M = 0.42$, $R^2_C = 0.60$)		
Intercept	6340.61	<0.001
Year	154.56	<0.001
$CWM_{NITROGEN\_FIX}$	27.71	<0.001
FD_{SEED_MASS}	9.14	<0.01
FD_{SLA}	11.53	0.001
$CWM_{FLOWERING\_PERIOD}$	5.59	0.020
CWM_{HEIGHT}	8.57	0.005
PD_{SOWN}	5.01	0.028

When considering FD of each individual traits, only functional diversity based on seed mass (FD_{SEED_MASS}) and nitrogen fixing ability ($FD_{NITROGEN\_FIX}$) were significant (Table S4, model 5 to 11), rising the R^2_M to 0.29 and 0.26, respectively. When added in a single additive model, functional diversity based on species SLA (FD_{SLA}) was selected on top of FD_{SEED_MASS} and $FD_{NITROGEN\_FIX}$, and the model's R^2_M reached 0.33 (Table S4, model 12). FD_{SLA} reduced colonisation while FD_{SEED_MASS} and $FD_{NITROGEN\_FIX}$ increased it.

Models using individual CWM traits as predictors yielded comparable performance, with the exception of erosulate growth form and flowering period length, which were also significant predictors of plot colonisation (Table S4 models 13 to 19). However, after forward selection on individual CWM traits, only $\mathrm{CWM}_{\mathrm{NITROGEN\_FIX}}$ and $\mathrm{CWM}_{\mathrm{EROSULATE}}$ were added to the best performing model, and the model's R^2_M reached 0.31 (Table S4, model 20).

Finally, the best predictive model of community colonisation contained both CWM ($\mathrm{CWM}_{\mathrm{NITROGEN\_FIX}}$, $\mathrm{CWM}_{\mathrm{FLOWERING\_PERIOD}}$ and $\mathrm{CWM}_{\mathrm{HEIGHT}}$), FD ($\mathrm{FD}_{\mathrm{SEED\_MASS}}$ and $\mathrm{FD}_{\mathrm{SLA}}$) and sown PD as predictors, and it explained 42% of the variability (Table 2b). The partial effect of $\mathrm{CWM}_{\mathrm{NITROGEN\_FIX}}$ and $\mathrm{FD}_{\mathrm{SEED\_MASS}}$ were positive, i.e. increased colonisation, while the partial effect of $\mathrm{CWM}_{\mathrm{FLOWERING\_PERIOD}}$, $\mathrm{CWM}_{\mathrm{HEIGHT}}$ and $\mathrm{FD}_{\mathrm{SLA}}$ were negative, i.e. decreased colonisation (Figure 4).

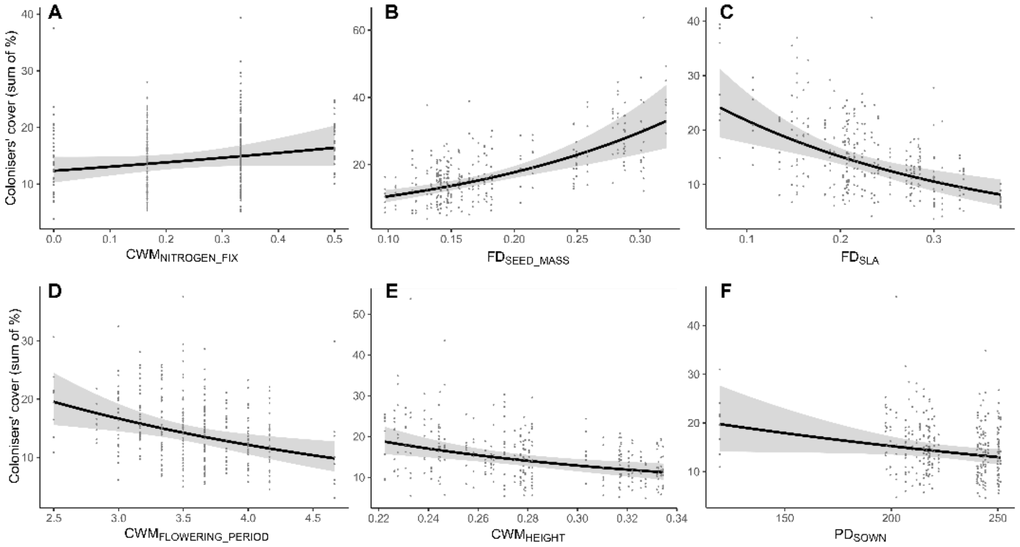

Figure 4. Conditional plots highlighting the effect of each predictor selected in the most parsimonious model (obtained by forward selection on the sown communities' functional attributes) on the level of colonisation. Each plot represents the partial effect of a single component of community functional trait structure on the response when all other variables are held constant, i.e. to their median. Although the statistical inferences were made on ln transformed cover and standardised predictor (centred around the mean and standardised by SD), the response and predictive variable are plotted on their original scale for better interpretability. The black lines represent the mean value predicted by the models and the grey area their 95% confidence interval.

4. Discussion

Our analyses, based on experimental plant communities with contrasted functional and phylogenetic levels, address the complexity of the colonisation process via complementary approaches considering both the colonisers and the resident community perspective. We found support that functional traits help in predicting species colonisation success, but this effect also depended on time and on the dissimilarity between the colonisers and the resident community. The functional and phylogenetic diversity of resident species also presented an interactive effect on the resistance to colonisation, underlying the effect of saturation in functional and phylogenetic space of the resident species.

4.1. Functional traits promoting colonisation success

Our analyses based on colonising species' functional traits support observations made by previous studies, i.e. a shift in traits characterising successful colonisers along successional phases of the colonisation process: initial colonisers are replaced by species with different traits (Catford *et al.*, 2019; Roscher *et al.*, 2015; Thompson *et al.*, 2001). In the first year after establishment, annual colonisers with therophytic life form, high SLA and low LDMC were relatively abundant, although no significant difference in abundance was detected compared to species with contrasting traits (Figure 1). However, only one year later, species with a perennial life cycle, hemicryptophytic life form, low SLA and high LDMC were significantly more successful. This pattern reflects the advantage of fast resource acquisition at the beginning of the colonisation and growing importance of more conservative strategies as succession advances, when interspecific relationships become a stronger driver of the community composition (Catford *et al.*, 2019; Crawley *et al.*, 1996; Garnier *et al.*, 2004; Pyšek & Richardson, 2007).

Furthermore, shorter flowering period was one of the advantageous traits during the second year of sampling. This can be explained by the negative correlation between flowering period length and trait values associated with the afore-mentioned conservative strategy (Figure S5), which requires more investment in vegetative organs. Such a trade-off between investment in sexually reproductive vs. vegetative functions is indicated by several studies associating a long flowering period with traits typical for an annual life cycle (Cadotte & Lovett-Doust, 2001; Crawley *et al.*, 1996; Lake & Leishman, 2004; Roscher *et al.*, 2015).

The last trait promoting successful colonisation of the experimental communities was nitrogen fixing ability. In a 20-year-long field experiment where colonisers were sown into mature resident communities, Catford *et al.* (2019) also showed that the establishment success of colonisers was higher for legumes compared to non-legume species. However, unlike in our study, their result was significant only in terms of occupancy (presence/absence) of colonisers in seeded plots, not in abundance neither in dispersion to the neighbouring unseeded subplots. The importance of nitrogen fixing ability on colonisation success in our results could have been overvalued by the fast vegetative spread and competitive strength of some of the legume colonisers present in our experiment (e.g.: *Trifolium repens, Lotus corniculatus*).

4.2. Functional and phylogenetic distances between the colonisers and the resident community

Besides identifying the particular functional trait values upholding colonisers, another aspect of colonisation success lies in the theories of niche complementarity (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994) and limiting similarity (R. Macarthur & Levins, 1967). According to these theories, species should be more successful colonisers when their functional traits allow them to occupy an empty niche in the community, i.e. when they are more functionally different from the resident species (Thuiller *et al.*, 2010).

Our analysis of colonising species covers in relation to the functional and phylogenetic distances to the resident community revealed a significant advantage of being functionally more different for 16% of the species and phylogenetically more different for 9% of the species, indicating that these species occupied functional and phylogenetic 'gaps' unoccupied by the resident species. Using the measure of mean distance between colonisers and resident species, following the approach proposed by Ricotta *et al.* (2016), allows to evaluate the presence of gaps in functional and phylogenetic space. Similarly, Fargione *et al.* (2003) found that established species suppressed colonising species from the same functional group more strongly than functionally dissimilar ones. Recently, Feng *et al.* (2018) showed that functional distance between the native community and invasive species had a stronger positive effect on the performance of invasive species than phylogenetic distance. On the contrary, Breitschwerdt, Jandt, & Bruelheide (2015) found that colonisers experimentally introduced in semi-natural grassland communities had higher survival rate when they were more similar to the resident community. However, in several other cases, experiments failed to provide evidence for the limiting similarity hypothesis on the effect of phylogenetic and functional distances on the establishment of colonising species (Bennett *et al.*, 2014; Funk & Wolf, 2016). One source of discrepancy in those results, both within and between observational and experimental approaches, could be attributed to different methodological aspects. For instance, different sets of traits, distance metrics or scales at which vegetation is surveyed could affect the results from different studies.

In our study, negative relationships between the coloniser's functional or phylogenetic distance to the resident community and its cover were found in only 2% and 5% of the species, respectively. Similar results were found in a pot experiment on non-native invaders by Conti *et al.* (2018), showing that invaders' growth was less suppressed in functionally similar native communities. Those results are in line with the idea of weaker competitor exclusion (Mayfield & Levine 2010), postulating that competition can sometimes favour species that are similar in their competitive behaviour, leading to trait and phylogenetic similarity between co-existing species. However, with less than 5% of such cases among our species, we cannot conclude that colonisers in our experiment generally follow a pattern that would present strong evidence for weaker competitor exclusion.

Recently, Roscher *et al.* (2018) showed that absolute trait distance between focal species and co-occurring species explained a very limited part of the variation in the productivity of the focal species. In line with our results, most of the variation in species productivity was explained by the actual trait values of the species, rather than their trait distance to the residents. Moreover, in a meta-analysis of experimental studies, Price & Pärtel (2013) suggest that functional group similarity has relatively small impact on biotic resistance.

Only four species showed significant relationships with both functional and phylogenetic distance analysis (*Cirsium arvense*, *Elytrigia repens*, *Taraxacum* sect. *Ruderalia* and *Lotus corniculatus*) and only one species showed significant but contradictory slopes in functional and phylogenetic distance analysis (*Viola arvensis*). The restricted overlap in colonisers' responses to functional or phylogenetic distance from the resident communities, supports the idea that phylogenetic and functional distances are complementary rather than redundant in the information they carry.

It is important to stress that for the majority of species there was no significant relationship between colonizer success and its functional or phylogenetic distance to resident species. The signature of limiting similarity in traits and phylogeny was evident only for a subset of the colonisers when considered individually (see above). Catford *et al.* (2019) found effects of absolute trait difference between coloniser and community on individual colonisers' success only for plant height. For other traits (i.e. SLA, seed mass, LDMC) only the trait hierarchical difference were significant predictors. It is possible that our sown communities with six species might not sufficiently saturate the functional space to trigger niche complementarity consistently. However, during the experiment, we observed 18.5±3.5 species per plot (mean±SD). A nearby experiment with identical habitat condition shows that after 20 years, species richness stabilised around 20 species/m^2, with about 12 species per plots yielding cover higher than 1% (Lepš personal communication).

Despite the signal of limiting similarity being weak when considering individual species, it was consistently stronger when considering the whole set of colonisers in a given plot (average of colonizers distances). This probably because of the limited 'power' of tests on individual species, often based on slightly more than 10 plots colonised per species, while with the averaging approach we maximized the number of observations. The sown communities with high FD were the ones where colonisers yielded the highest cumulated cover percentage (Figure 3. A) and where those colonisers were on average more functionally distant from the residents (Figure 2. C). In other words, in low FD plots the overall colonisation success was restricted by the saturation of the trait space in the resident community.

4.3. Functional and phylogenetic structure of the resident communities and their resistance to colonisation

The analysis between sown FD and PD and resistance to colonisation suggests a non-trivial interaction between the effects of PD and FD. In contradiction with the idea that functional diversity promotes resistance to colonisation through a more complete use of available resources, communities with higher FD were generally more colonised (except in the case of $FD_{SLA,}$ see below). However, this effect was significant only at low levels of PD, suggesting that high PD inhibits colonisation in high FD communities. Our results are in opposition with those obtained by Feng *et al.* (2018), who show that the performance of alien plants decreased with increasing diversity of the native community (for both FD and PD). On the other hand, they are partially in line with the analysis of a large vegetation database by Loiola *et al.* (2018), which revealed that native communities invaded by aliens had both higher FD and PD. These slight differences could be explained by the fact that Loiola *et al.* (2018) used natural communities from different regions of the Czech Republic covering large environmental gradients, but also gradients of FD and PD which were not entirely independent, whereas our localised and experimentally designed communities allowed functional and phylogenetic orthogonal contrasts.

Although the effect of PD was weak, it appeared as an important factor in modulating the expression of FD. Moreover, PD was selected as a significant predictor in the best model along with CWM and FD of individual traits (Table 2b). This could suggest that some important traits were not considered but are nonetheless reflected in the phylogeny of the species. Among potential candidates of unmeasured traits accounted for by phylogeny are clonal traits. There is growing evidence for the importance of clonal traits in interspecific plant competition (Benot, Bittebiere, Ernoult, Clément, & Mony, 2013; Saiz, Bittebiere, Benot, Jung, & Mony, 2016), as well as their phylogenetically conserved character, i.e. related species show similar clonal attributes. For example, Herben, Tackenberg, & Klimešová (2016) found relatively high values of Pagel's lambda (a measure of phylogenetic signal) between 0.8 and 0.95 for clonal traits, where a value of 1 indicates high phylogenetic conservatism.

Statistical models of colonisation level per plot yielded similar performance whether they were based on forward selection of FD or CWM indices per trait (Table S4 models 12 and 20). Both models retained indices of nitrogen fixing ability, which reflects the high correlation between CWM and FD values for traits with only two levels (r=0.95, Figure S4). However, the best model (Table 2b) issued from forward selection on all potential predictive variables integrated both FD and CWM indices, highlighting how the complementarity between the two types can provide a better representation of the community functional structure, as shown in Ricotta & Moretti (2011).

Colonisers were more abundant in communities that presented a higher proportion of legumes ($\text{CWM}_{\text{NITROGEN\_FIX}}$) or greater variation of seed mass ($\text{FD}_{\text{SEED\_MASS}}$). A high percentage of legumes in the community might have made it more receptive to colonisation because nitrogen fixation requires energy (Gutschick, 1981), at the expense of competitiveness, and releases nitrogen in the soil, increasing resource availability for competing species (Vitousek & Howarth, 1991). Seed mass however, is usually associated with high competitive ability at the seedling stage (Bitomský, Mládek, & Cimalová, 2018). This unexpected positive relation might result from a confounding effect because, in this experiment, legume species had higher seed mass and the correlation between $\text{CWM}_{\text{N\_FIX}}$ and $\text{FD}_{\text{SEED\_MASS}}$ was significant (r=0.48, p-value<0.05 Figure S4).

Furthermore, colonisation was negatively associated to $\text{CWM}_{\text{HEIGHT}}$, $\text{CWM}_{\text{FLOWERING\_PERIOD}}$ and FD_{SLA}. These results are expected as plant height is well related to competitive ability of plants, especially in terms of light pre-emption (Y. Hautier, Niklaus, & Hector, 2009). The effect of $\text{CWM}_{\text{FLOWERING\_PERIOD}}$ on colonisation can be interpreted as a reflection of other correlated traits that are indicative of a conservative strategy, rather than an effect of flowering period itself. Among sown species, long flowering period was strongly associated with low SLA and rosette growth form, with the latter two traits potentially leading to a large occupation of the surface of the plot, thus reducing the available space for colonisers. Finally, higher FD_{SLA} values should reflect complementarity between acquisitive and conservative strategies of the sown community, optimising resource pre-emption, mostly regarding water and light (Wright *et al.*, 2004). However, partial effects of FD_{SLA} and FD_{SEED_MASS} essentially compensated each other. The mean sum of colonisers' cover decreased from 24% to 8% along the FD_{SLA} gradient while it increased from 10% to 30% along the FD_{SEED_MASS} gradient (Figure 4, panels B and C). Such interplay between the effects of diversity in different traits can explain the *a priori* contradiction between the results in FD_{SLA} and multidimensional FD. It also emphasises the complex interpretation of FD in multivariate trait space.

4.4. Fertilisation

Fertilisation had no detectable effect, neither on the performance of colonisers nor the resistance of the sown community to colonisers, a result also found in Lanta & Lepš (2008). One possibility could be that colonisation processes and community dynamics are not affected by the level of nutrient availability, though this is in contradiction with studies showing strong competitive exclusion between species under fertilisation treatments (Lepš, 2014). A second plausible explanation could be that both colonisers and resident species established on the plots at the same time and might have equally benefited from fertilisation. Finally, the absence of an effect of fertilisation could result from the already high plot coverage. Burke & Grime (1996) showed that the effect of fertilisation was strengthened by disturbance, which created gaps in the vegetation cover.

Alternatively, we can hypothesise that the effect of fertilisation was down-weighted because nutrient availability was not a strong limiting factor in our site, or because the difference in nutrient availability between fertilised and unfertilised plots was insufficient, due to an already high fertility level of the entire field. This could be the consequence of i) the former exploitation of the site as crop field with a subsequent annual fertilisation until 2001, and ii) the boosting effect of ploughing on mineralisation processes by micro-organisms due to the increased oxygen availability in the soil (P. R. Grace, MacRae, & Myers, 1993). If these two factors are important, then their impacts should decrease in time and we can expect that in the future, the fertilisation treatment will play a more important role in the communities' dynamics. Our results indicate that the effects of abiotic conditions such as increased nutrient availability strongly depend on specific site conditions and time.

5. Conclusion

Our results reinforce the idea that, beyond propagule availability, successful colonisation relies on an interplay between the intrinsic characteristics of the potential coloniser and invasibility of the ecosystem. We brought evidence that successful colonisers were characterised by different combinations of traits along the successive steps of colonisation, adding time as a key factor in characterisation of colonisation as in Thompson *et al.* (2001) and Catford *et al.* (2019). In our study, we found evidence for the limiting similarity theory, stating that colonisers should be more successful in communities from which they differ more, even though the effect was weak, similarly to the conclusions of the meta-analysis conducted by Price & Pärtel (2013).

The interplay between FD and PD in their support of community resistance to colonisers is an important novel finding of this study. It supports the idea that, given the set of traits and the species pool considered in this study, FD and PD only partially overlap in their description of community structure. The widespread hypothesis that higher FD increases resistance by a more complete use of resources is challenged. Greater FD, especially at low species richness and low phylogenetic diversity, could rather provide an unsaturated functional trait space in which colonisers are on average more functionally dissimilar from the residents and yield higher cover.

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Data accessibility:

Vegetation data have been archived on Dryad Digital Repository: doi:10.5061/dryad.5g6254c. Plant traits information can be retrieved from the LEDA database: https://www.uni-oldenburg.de/en/landeco/research/leda/data-files (Kleyer *et al.*, 2008) and the BiolFlor database: http://www.biolflor.de (Kühn *et al.*, 2004). Phylogeny data can be retrieved from the DAPHNE database: https://doi.org/10.6084/m9.figshare.3554421.v1 (Durka & Michalski, 2012).

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Supplementary material

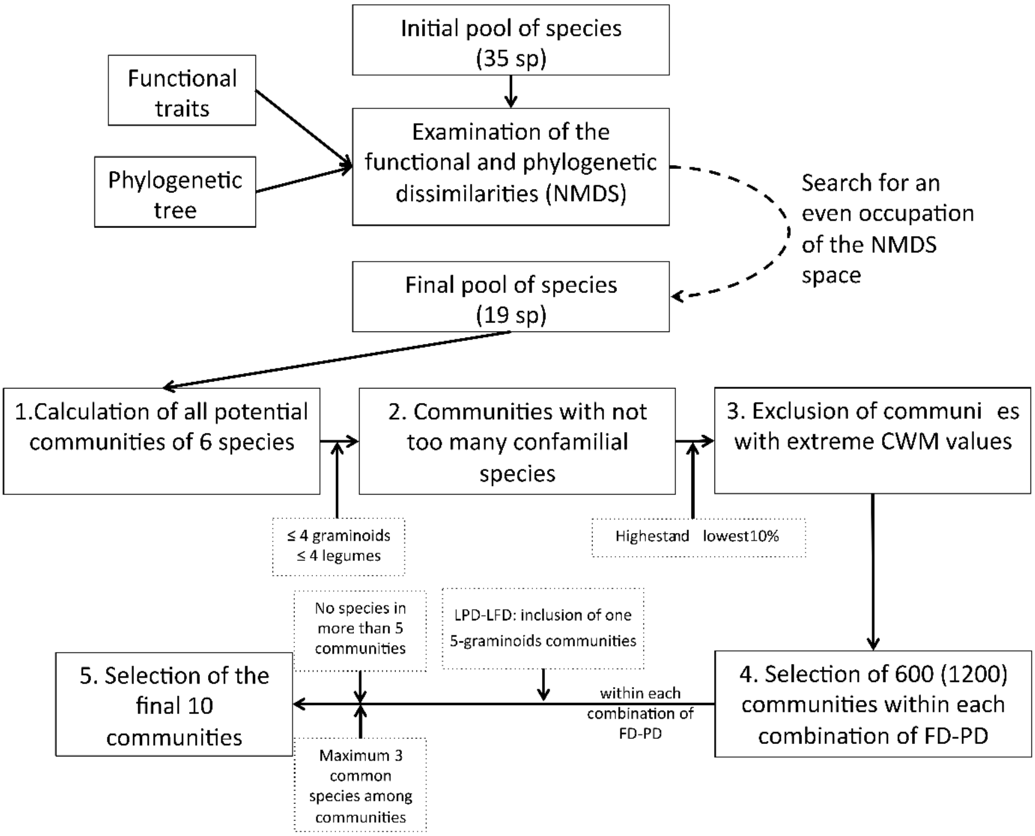


Figure S1: Flowchart of community selection process

Table S1: Information on the sown species. Names, families, functional traits and applied sowing densities of the 19 species used to compose the communities.

Species	Family	Sowing density* (g/plot)	Nitrogen-fixing ability	Canopy height (m)	Seed mass (mg)	SLA ($mm^2.mg^{-1}$)	LDMC ($mg.g^{-1}$)	Begin flowering (month)	End flowering (month)	Rosette type
Achillea millefolium	Asteraceae	0.23	0	0.396	0.132	18.935	185.5	6	10	h
Alopecurus pratensis	Poaceae	0.91	0	0.450	0.658	25.036	308.1	5	6	e
Anthoxanthum odoratum	Poaceae	0.61	0	0.165	0.629	29.767	258.8	5	6	h
Anthyllis vulneraria	Fabaceae	2.20	1	0.200	3.253	16.270	170.0	5	8	h
Dactylis glomerata	Poaceae	1.06	0	0.454	0.911	24.373	262.5	5	7	h
Dianthus deltoides	Caryophyllaceae	0.21	0	0.220	0.203	16.050	262.0	6	9	e
Holcus lanatus	Poaceae	0.34	0	0.325	0.407	34.036	230.2	6	8	h
Hypericum perforatum	Hypericaceae	0.23	0	0.358	0.119	26.064	303.0	7	8	e
Leontodon hispidus	Asteraceae	1.14	0	0.235	1.114	25.801	139.7	6	10	r
Leucanthemum vulgare	Asteraceae	0.47	0	0.364	0.383	19.273	129.7	6	10	h
Lotus corniculatus	Fabaceae	1.11	1	0.429	1.403	23.645	186.0	6	8	e
Lychnis flos-cuculi	Caryophyllaceae	0.24	0	0.413	0.199	24.224	140.0	5	7	h
Plantago lanceolata	Plantaginaceae	1.21	0	0.161	1.617	18.515	166.9	5	10	r
Plantago media	Plantaginaceae	0.41	0	0.172	0.385	19.261	145.3	5	9	r
Poa pratensis	Poaceae	0.28	0	0.300	0.273	21.193	308.6	5	6	h
Prunella vulgaris	Lamiaceae	0.99	0	0.123	0.689	29.545	164.4	6	9	e
Trifolium arvense	Fabaceae	0.45	1	0.147	0.329	18.206	296.1	6	9	h
Trifolium pratense	Fabaceae	1.28	1	0.283	1.581	23.373	223.4	6	9	h
Vicia sepium	Fabaceae	3.20	1	0.467	22.770	38.712	186.0	5	6	e

* In a sowing experiment, it is either possible to use, for each species, a constant number of seeds per plot or constant seed weight per plot. Whereas the first gives some advantage to species with

heavy seeds (because they usually establish better due to their larger amount of reserves), the second gives usually some advantage to species with light seeds, as they are sown with the highest density. We used a log scale in seed weight as a compromise between these two extremes. Specifically, we used the following formula, in which the number of seeds used per species decreased linearly with the logarithm of seed mass: $Nseed = \min(3000, 3000 - \log10(SM + 0.5) * 2000)/6$. Where $Nseed$ is the number of seed sown per m^2 for a given species with a seed mass SM. If the weight of the seed of the species was lower than 0.5 mg, then we would sow 3000 seeds/ m^2, and the number decreased as the weight of the seed increases (log-linearly). 3000 seeds/m2 was the seed density used in a previous studies using similar habitat and species pool (Lanta & Lepš, 2008). 0.5mg is the median seed mass of our species pool (form the 19 species sown). Finally, the number of seed was divided by 6, because 6 species were sown in each community. With this method, species with heaviest seeds are still sown with the highest mass, but with the lowest seed number, and species with lightest seeds is sown with the lowest seed mass but highest seed number, i.e. to obtain a better compromise in density between individuals and biomass (see above). In the table the sowing density is expressed in number of seeds per plot which was obtained by multiplying the $Nseed$ by the SM and the surface of the plot (1.5*1.5 m).

Table S2: Species composition, functional diversity (FD) and phylogenetic diversity (PD) of the 40 sown communities selected. The communities are clustered in 4 groups of 10 communities combining high and low levels of FD and PD.

Diversity treatment	Rep.	FD	PD	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6
High PD High FD	1	2.01	3.49	*D. glomerata*	*H. lanatus*	*L. corniculatus*	*L. flos-cuculi*	*P. vulgaris*	*T. arvense*
	2	2.00	3.16	*A. odoratum*	*L. vulgare*	*P. pratensis*	*T. arvense*	*T. pratense*	*V. sepium*
	3	2.00	3.48	*D. deltoides*	*H. perforatum*	*L. corniculatus*	*P. pratensis*	*P. vulgaris*	*T. arvense*
	4	1.96	3.18	*A. odoratum*	*A. vulneraria*	*D. deltoids*	*L. vulgare*	*P. media*	*V. sepium*
	5	2.06	3.21	*D. glomerata*	*D. deltoids*	*H. lanatus*	*L. corniculatus*	*P. media*	*V. sepium*
	6	1.98	3.46	*A. pratensis*	*A. odoratum*	*H. perforatum*	*L. hispidus*	*L. corniculatus*	*T. arvense*
	7	2.01	3.45	*A. millefolium*	*H. lanatus*	*P. media*	*P. pratensis*	*T. arvense*	*V. sepium*
	8	1.94	3.16	*A. millefolium*	*L. flos-cuculi*	*P. lanceolata*	*P. pratensis*	*P. vulgaris*	*V. sepium*
	9	1.95	3.18	*A. millefolium*	*A. odoratum*	*D. deltoides*	*L. corniculatus*	*P. vulgaris*	*T. pratense*
	10	1.94	3.21	*A. pratensis*	*A. vulneraria*	*D. deltoides*	*H. lanatus*	*P. vulgaris*	*T. pratense*
High PD Low FD	1	1.59	3.25	*A. pratensis*	*D. deltoids*	*H. perforatum*	*P. media*	*P. vulgaris*	*T. pratense*
	2	1.56	3.40	*H. lanatus*	*L. vulgare*	*L. corniculatus*	*L. flos-cuculi*	*P. lanceolata*	*P. pratensis*
	3	1.59	3.41	*A. odoratum*	*D. glomerata*	*L. vulgare*	*L. flos-cuculi*	*P. vulgaris*	*T. pratense*
	4	1.61	3.39	*A. pratensis*	*D. glomerata*	*H. perforatum*	*L. hispidus*	*L. corniculatus*	*P. lanceolata*
	5	1.54	3.43	*D. glomerata*	*H. perforatum*	*L. hispidus*	*L. flos-cuculi*	*P. pratensis*	*T. pratense*
	6	1.55	3.41	*A. millefolium*	*A. odoratum*	*D. deltoides*	*P. lanceolata*	*P. pratensis*	*T. pratense*
	7	1.52	3.38	*A. millefolium*	*D. glomerata*	*H. lanatus*	*H. perforatum*	*P. media*	*T. pratense*
	8	1.55	3.11	*A. millefolium*	*A. odoratum*	*D. glomerata*	*L. hispidus*	*L. corniculatus*	*L. flos-cuculi*
	9	1.51	3.41	*A. odoratum*	*A. vulneraria*	*H. lanatus*	*L. vulgare*	*L. flos-cuculi*	*P. media*
	10	1.57	3.11	*A. pratensis*	*A. odoratum*	*D. deltoides*	*H. perforatum*	*L. hispidus*	*L. vulgare*

Diversity treatment	Rep.	FD	PD	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6
Low PD High FD	1	2.15	2.64	*A. millefolium*	*D. deltoids*	*H. perforatum*	*L. hispidus*	*T. arvense*	*V. sepium*
	2	1.99	2.64	*A. vulneraria*	*H. perforatum*	*P. media*	*P. pratensis*	*T. pratense*	*V. sepium*
	3	1.97	2.68	*A. odoratum*	*A. vulneraria*	*D. deltoides*	*H. lanatus*	*P. pratensis*	*V. sepium*
	4	1.97	2.40	*A. millefolium*	*D. deltoids*	*L. vulgare*	*L. corniculatus*	*P. media*	*V. sepium*
	5	2.01	2.25	*D. deltoides*	*L. hispidus*	*L. vulgare*	*L. flos-cuculi*	*T. pratense*	*V. sepium*
	6	1.95	2.45	*A. millefolium*	*A. vulneraria*	*L. corniculatus*	*L. flos-cuculi*	*P. media*	*P. vulgaris*
	7	2.02	2.59	*A. pratensis*	*A. vulneraria*	*H. lanatus*	*L. corniculatus*	*P. pratensis*	*P. vulgaris*
	8	1.95	2.68	*L. hispidus*	*L. corniculatus*	*L. flos-cuculi*	*P. lanceolata*	*P. vulgaris*	*T. arvense*
	9	1.99	2.67	*A. vulneraria*	*H. perforatum*	*L. flos-cuculi*	*P. vulgaris*	*T. arvense*	*T. pratense*
	10	1.96	2.67	*A. pratensis*	*A. odoratum*	*H. lanatus*	*L. corniculatus*	*T. arvense*	*T. pratense*
Low PD Low FD	1	1.31	1.51	*A. pratensis*	*A. odoratum*	*D. glomerata*	*H. lanatus*	*L. flos-cuculi*	*P. pratensis*
	2	1.52	2.42	*A. millefolium*	*D. glomerata*	*L. hispidus*	*L. vulgare*	*L. flos-cuculi*	*P. vulgaris*
	3	1.57	2.59	*A. odoratum*	*A. vulneraria*	*D. glomerata*	*H. lanatus*	*P. lanceolata*	*P. media*
	4	1.56	2.62	*A. millefolium*	*A. odoratum*	*D. glomerata*	*L. hispidus*	*L. corniculatus*	*P. pratensis*
	5	1.48	2.33	*A. millefolium*	*H. lanatus*	*L. vulgare*	*P. lanceolata*	*P. media*	*P. vulgaris*
	6	1.54	2.57	*A. millefolium*	*A. pratensis*	*H. lanatus*	*L. hispidus*	*L. vulgare*	*T. pratense*
	7	1.57	2.60	*A. vulneraria*	*D. glomerata*	*H. lanatus*	*L. vulgare*	*L. corniculatus*	*P. pratensis*
	8	1.55	2.55	*A. millefolium*	*D. deltoids*	*H. perforatum*	*L. hispidus*	*P. media*	*T. pratense*
	9	1.57	2.55	*D. deltoides*	*H. perforatum*	*L. hispidus*	*L. vulgare*	*L. corniculatus*	*P. lanceolata*
	10	1.44	2.48	*A. pratensis*	*D. deltoids*	*L. flos-cuculi*	*P. lanceolata*	*P. media*	*P. vulgaris*

Table S3: Summary of performances of all the models conducted to predict the colonisation success of species based on their functional traits. The table presents the performance of the LMEM based only on the random factors (null model), each trait separately (individual traits) and all traits together (best model). The best model is the result of forward selection of predictors based on the lowest AIC. For each model, plot identity was included as random variable and, models 3 to 12, year was included as a priori fixed variable. If the interaction between year and the traits tested was not significant, the model was simply additive, and the selected variables are separated by "+" instead of "*" or ":". The marginal R^2 (R^2_M) represents the variation explained by the fixed factors whereas the conditional R^2 (R^2_C) represents the variation explained by both the fixed and random factors.

Analysis n°	**Focus**	**Covariate**	**Candidate Variable(s)**	**Selected variables (in order of selection)**	**AIC**	**Residual degrees of freedom**	**R^2_M**	**R^2_C**
1	Null model: Intercept only	None	None		1044	214	0.000	0.641
2	Sampling session effect		Year*Season	Year	1032	213	0.016	0.658
3	Individual traits	Year	*Growth form	None				
4			*Lifespan	*Lifespan	962	103	0.124	0.707
5			*Life form	*Life form	966	102	0.106	0.714
6			*Flowering length	*Flowering length	972	104	0.0416	0.695
7			*Seed mass	None				
8			*Height	None				
9			*Nitrogen fixing	+Nitrogen fixing	990	104	0.051	0.664
10			*LDMC	*LDMC	983	104	0.039	0.679
11			*SLA	*SLA	984	104	0.042	0.675
12	Best model		*Forward selection	+ Lifespan + Nitrogen fixing +Year : Lifespan	958	102	0.160	0.710

Table S4: Summary of the performances of all the models conducted to predict the level of colonisation in each plot by the functional and phylogenetic attributes of the sown community. The table presents the performance of LMEM based only on the random factors (null model, model 1), sampling session effect (model 2), initial treatment (fertilisation, diversity treatment as factor and as continuous variable (model 3 and 4), FD on individual traits (models 5 to 11) and community weighted mean (analyses 13 to 19). Forward selection based on the lowest AIC were conducted to determine the best models considering the FD on individual traits only (analysis 12), the CWM only (analysis 20) and finally all possible variables together (analyses 21). For each model, plot identity was included as random variable and year as *a priori* fixed variable. The marginal R^2 (R^2_M) represents the variation explained by the fixed factors and the conditional R^2 (R^2_C) represents the variation explained by both the fixed and random factors.

Model n°	**Focus**	**Covariate**	**Candidate Variable(s)**	**Significant/ Selected variables (in order of selection)**	**AIC**	**Residual degrees of freedom**	**R^2m**	**R^2c**
1	Null model: Intercept only	None	None	None	591.8	240	0.000	0.333
2	Sampling session		Year * season	Year	472.1	239	0.200	0.598
3	Initial treatments	Year	+ Fertilisation + diversity treatment	+ Diversity treatment	458.9	235	0.306	0.599
4			+ Fertilisation + FD_{SOWN} + PD_{SOWN}	+ FD_{SOWN} + PD_{SOWN}	456.2	237	0.294	0.599
5	Functional diversity of specific traits	Year	* SLA	+ None				
6			* LDMC	+ None				
7			* Height	+ None				
8			* Seed Mass	+ Seed mass	457.9	238	0.291	0.599
9			* Growth Form	+ None				
10			* Flowering Length	+ None				
11			* Nitrogen Fixing	+ Nitrogen fixing	464.6	238	0.255	0.598
12			*** Forward selection from all FD indices per trait**	+ Seed mass, SLA, Nitrogen fixing	454.5	236	0.327	0.599
13	Community weighted means (CWM)	Year	* SLA	+ None				
14			* LDMC	+ None				
15			* Height	+ None				
16			* Seed Mass	+ Seed Mass	467.3	238	0.215	0.585
17			* Forward selection from all growth forms	+ Erosulate	467.1	238	0.241	0.598
18			* Flowering Length	+ Flowering Length	468.3	238	0.210	0.585
19			* Nitrogen Fixing	+ Nitrogen Fixing	457.2	238	0.294	0.599
20			*** Forward selection from all CWM**	+ Nitrogen Fixing, Erosulate	456.6	232	0.307	0.599
21	Best model	Year	*** Forward selection from all variables**	+ $CWM_{NITROGEN\_FIX}$, FD_{SEED_MASS}, FD_{SLA}, CWM_{FLOWER_PERIOD}, CWM_{HEIGHT}, PD_{SOWN}	437.2	233	0.421	0.599

Figure S4: Correlation between communities' functional attributes. Only significant correlations are presented. In the lower left corner, the numerical Pearson coefficients are displayed, while in the upper right corner the coefficients are represented by coloured ellipses: blue is positive, red is negative, and the intensity of the colour represents the strength of the correlation coefficient.

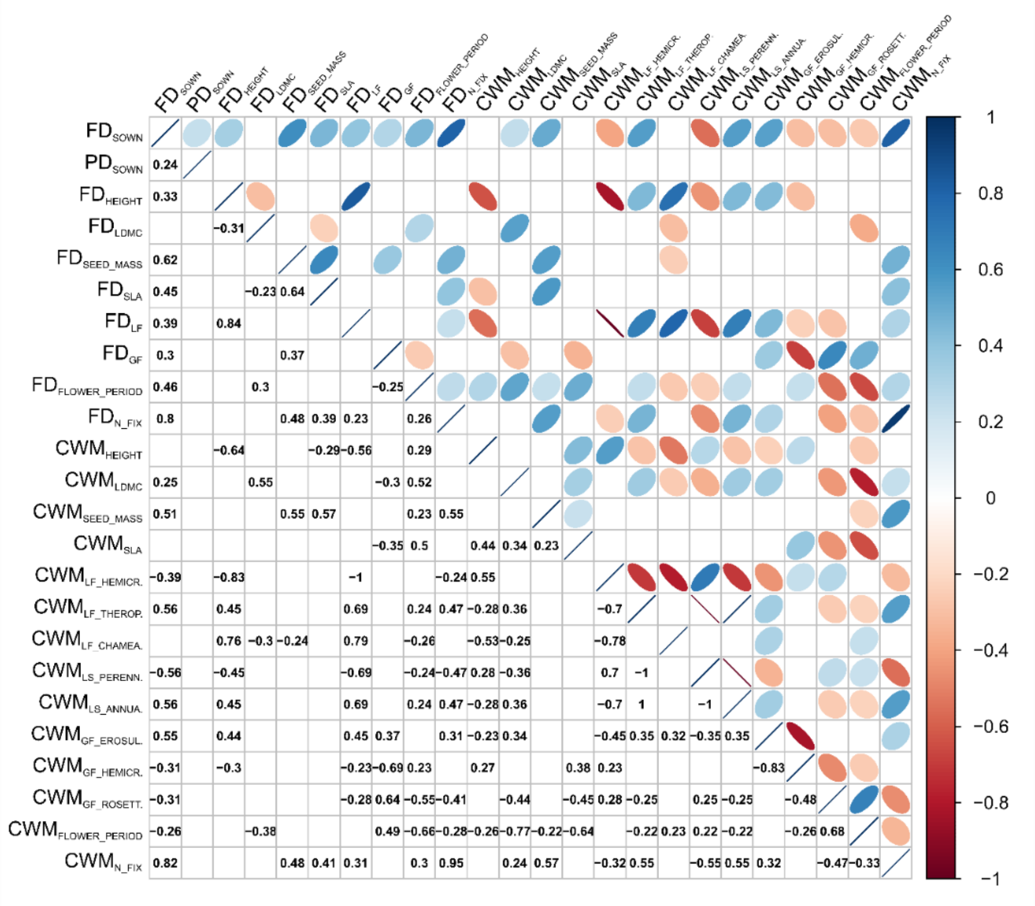
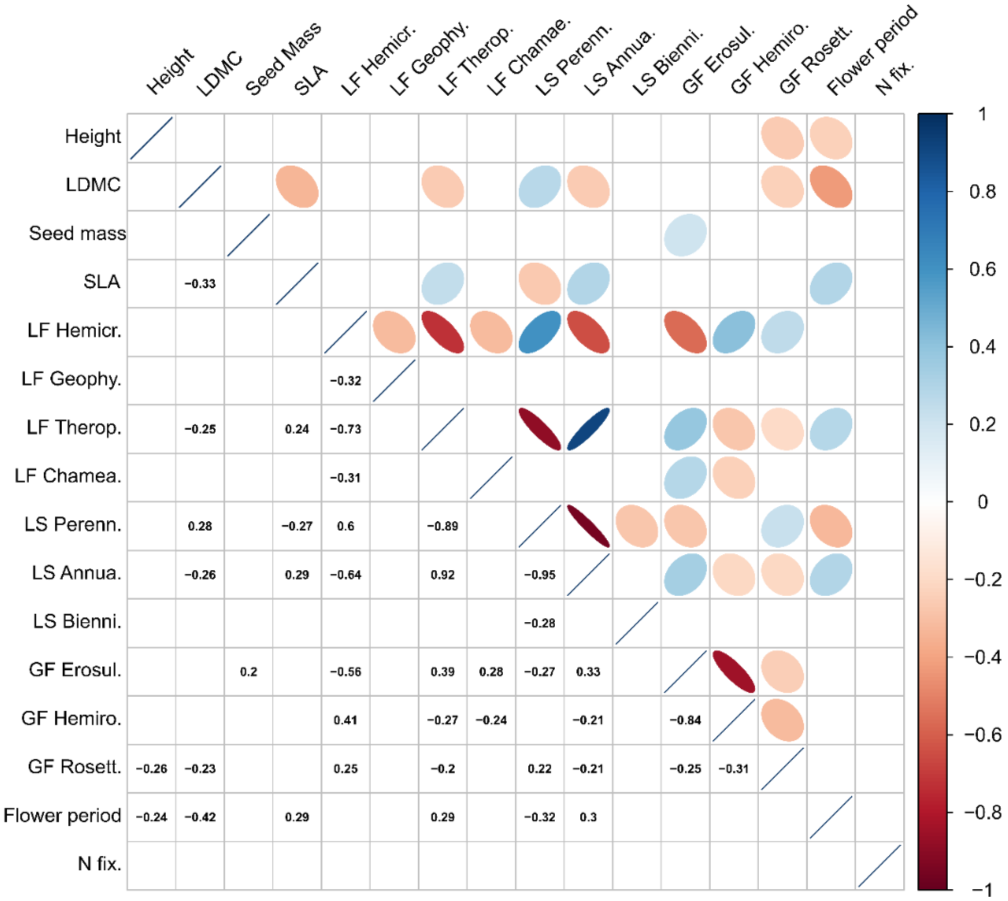


Figure S5: Correlation between functional traits of species (both sown and colonisers). Only significant correlations are presented. In the lower left corner, the numerical Pearson coefficients are displayed, while on the upper right corner the coefficient are represented by coloured ellipses: blue is positive, red is negative, and the intensity of the colour represents the strength of the correlation coefficient.



	Height	LDMC	Seed Mass	SLA	LF Hemicr.	LF Geophy.	LF Therop.	LF Chamae.	LS Perenn.	LS Annua.	LS Bienni.	GF Erosul.	GF Hemiro.	GF Rosett.	Flower period	N fix.
Height																
LDMC																
Seed mass																
SLA		−0.33														
LF Hemicr.																
LF Geophy.					−0.32											
LF Therop.		−0.25		0.24	−0.73											
LF Chamea.					−0.31											
LS Perenn.		0.28		−0.27	0.6		−0.89									
LS Annua.		−0.26		0.29	−0.64		0.92		−0.95							
LS Bienni.									−0.28							
GF Erosul.			0.2		−0.56		0.39	0.28	−0.27	0.33						
GF Hemiro.					0.41		−0.27	−0.24		−0.21		−0.84				
GF Rosett.	−0.26	−0.23			0.25		−0.2		0.22	−0.21		−0.25	−0.31			
Flower period	−0.24	−0.42		0.29			0.29		−0.32	0.3						
N fix.																

Chapter II

Cascading effect from plant community functional structure to above and below ground ecosystem functions

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Abstract

While biodiversity is expected to enhance ecosystem multiple ecosystem functions, the different roles of specific biodiversity components remain difficult to disentangle without carefully designed experiments. We conducted an experiment with plant communities assembled on independent levels of functional and phylogenetic diversity to investigate the direct and indirect role of the ecological differences between species on multiple ecosystems functions (EFs: plant productivity, litter decomposability, soil fertility, respiration and nutrient cycling). The results show strong direct effects of different components of plant functional structure parameters on plant-related EFs, through either dominant plant types or functional diversity, but weak on soil-related EFs and weak effects of PD. However, plant functional structure showed indirect effects on soil EFs mediated by plants EFs and soil abiotic properties. Variations in ecosystem multifunctionality was less predictable than individual groups of EFs. The study shows the importance of considering complementary dimensions of biodiversity for assessing both direct and cascade effects on multiple EFs.

1. Introduction

Understanding the drivers behind the functioning of ecosystems is at the core of both theoretical and applied ecological research. Despite a flourishing research on the role of biodiversity, particularly since seminal experiments in the 1990s by Tilman & Downing (1994) and Naeem *et al.* (1994), the biodiversity-ecosystem functioning (BEF) relationship is still a conundrum due to its huge complexity. BEF relationships are complex, first, because biodiversity can be characterized from multiple perspectives and different dimensions (taxonomical, functional and phylogenetic), often non-independent between them (Dias *et al.*, 2013), where each can play different roles (Cadotte, 2017). Second, ecosystem functions (EFs) are numerous, with both trade-offs, synergies and independent variations among them creating a complex relationship between ecosystem multifunctionality and biodiversity (Lavorel & Grigulis, 2012; Meyer *et al.*, 2018; van der Plas *et al.*, 2019; Zavaleta, Pasari, Hulvey, & Tilman, 2010). Finally, the effect of a given trophic level on certain EFs can be mediated by other trophic levels or other ecosystem properties (Enrique Valencia *et al.*, 2018). Thus, experiments specifically designed to disentangle the effect of different biodiversity components on multiple type of ecosystem functions are needed to improve our understanding of the complex relationship between biodiversity and ecosystem functioning.

Among the different components of biodiversity, awareness is increasing that, rather than taxonomical diversity, the distribution of functional traits values in a community (i.e. functional structure) chiefly control EFs (Cadotte, 2017; Cernansky, 2017; Díaz *et al.*, 2007; Hooper *et al.*, 2005). Recently, results showed that the effect of plant species diversity on ecosystem multifunctionality was mediated by community functional structure (Eisenhauer *et al.*, 2018). However, the relative role of different components of functional structure independently of species richness on ecosystem multifunctionality has not been explicitly tested. The specific role of functional traits on given ecosystem functions depends on the distribution of the trait's values among coexisting species. At the community level, community weighted mean (CWM) and Functional Diversity (FD; Díaz *et al.* 2007a) are the main components of the trait's distribution affecting EFs. Each of these components is generally interpreted as a proxy of different biodiversity effects on EFs: selection effect driven by traits of dominant species (also known as the mass-ratio-hypothesis) for CWM and complementarity effect, or non-additive effects in general, for FD (Cadotte, 2017; Dias *et al.*, 2013). Since trait information is not always available, researchers have used phylogenetic relatedness between species as a proxy of trait differences or as a complement, under the assumption that more closely related species are more likely to have similar trait values (Cadotte *et al.*, 2013). The independence of PD (Phylogenetic Diversity) from FD depends on the identity of traits used to computed FD and the level of conservatism of those traits in the phylogeny (de Bello *et al.*, 2017; Flynn *et al.*, 2011; Webb *et al.*, 2002). While many biodiversity experiments are well designed for evaluating the role of species richness (Fargione & Tilman, 2005; Roscher *et al.*, 2004; Tilman & Downing, 1994), very few are specifically controlling different aspects of the trait's distribution independently from each other or from species richness (Galland *et al.*, 2019; Pichon *et al.*, 2020).

The BEF relationship was primarily studied through individual functions such as biomass productivity (Hector *et al.*, 2002), resistance to weeds invasion (Fargione & Tilman, 2005) or nutrient loss (Scherer-Lorenzen, Palmborg, Prinz, & Schulze, 2003). However, over the past decade, quantitative tests for evaluating multiple functions simultaneously have been developed (see Byrnes *et al.* 2014 for a review). These developments of multifunctionality studies allow the integration of different types of EFs (Delgado-Baquerizo *et al.*, 2019; Maestre, Castillo-Monroy, Bowker, & Ochoa-Hueso, 2012; Enrique Valencia *et al.*, 2018). EFs, like traits, are not entirely independent from each other but rather covaries into clusters, or bundles (Lamarque *et al.*, 2014). In fact, trade-off among different ecosystem functions can be the cause of the absence of effect of biodiversity, or any driver, on multifunctionality (Meyer *et al.*, 2018). In this sense, functional traits are not independent from each other, but covaries in response to trade-offs between, for example in plants, acquisitive-conservative strategies (Díaz *et al.*, 2016; Wright *et al.*, 2004). A typical trait syndrome of acquisitive strategy is characterized by faster growing tissues with higher SLA (Specific Leaf Area), shorter lifespan, dissemination of higher number of smaller propagules, but lower investments in defense structure and resource storage. In contrast, conservative strategy translates into trait syndrome requiring higher investment from the plant in its tissues with, for example, higher LDMC (Leaf Dry Matter Content), longer lifespan and a reproduction based on fewer propagule containing more reserves. Trade-offs among traits can scale up to trade-offs among EFs (Lavorel & Grigulis, 2012; Wardle *et al.*, 2004). Bundles of ecosystem properties could be mirroring the conservative-acquisitive continuum in plant traits, where for example plant communities with more conservative species would be associated with ecosystems with lower productivity, slower turnover, higher soil carbon sequestration (Lavorel & Grigulis, 2012; Wardle *et al.*, 2004).

Finally, plant communities are a strong driver of local environmental conditions, other trophic levels and ecosystem properties. Therefore, they can influence both directly or indirectly, through cascade effects, EFs related to other trophic levels (Lavorel *et al.*, 2013). In this sense Wardle *et al.* (2004) pointed out the complexity of aboveground-belowground interactions with both positive and negative, direct and indirect effects as well as feedback loops. Plant traits related to nutrient content and decomposability of leaves, shoots and roots, as well as root architecture or nutrient uptake efficiency can influence soil microbial community composition and functions by changing resource availability and local abiotic factors (de Vries *et al.* 2012; Moreau *et al.* 2015; Navarro-Cano *et al.* 2018; Colin *et al.* 2019; DeLong *et al.* 2019). The decomposability of litter is strongly related to species´ trait syndromes (Garnier *et al.*, 2004; N. Pérez-Harguindeguy *et al.*, 2013; Pichon *et al.*, 2020) and its position on the acquisitive-conservative strategy continuum, triggering different rates in soil processes such as mineralisation of organic matter and C sequestration (Hättenschwiler, Tiunov, & Scheu, 2005; Hobbie, 2015). Furthermore, experimental work by Valencia *et al.* (2018) showed that plant species richness effect on soil multifunctionality was mediated by changes in plant communities' functional structure and soil microbial communities.

In the present study, we ask three main questions: i) what are the effects of different parameters of plant community's functional and phylogenetic structure on individual ecosystem functions? ii) do most of EFs respond in a similar direction to a gradient of functional and phylogenetic structure components? iii) what is the relative impact of direct and indirect effects of functional and phylogenetic structure parameters on soil ecosystem multifunctionality mediated by plant EFs and soil abiotic parameters? We used a grassland BEF experiment designed with fixed species richness and contrasted levels of FD and PD to investigate the role of ecological differences between species on multiple ecosystems functions considered both individually, simultaneously and in cascade. We used FD, PD and CWM as parameters of plant communities' functional and phylogenetic structure; plant aboveground biomass production, litter decomposability, soil fertility, respiration and enzymatic activity related to carbon and phosphorous cycling as ecosystem functions; and soil abiotic condition (pH, electrical conductivity, gravimetric humidity) as ecosystem properties mediator. Finally, we evaluated the direct and indirect influence of the plant communities' functional and phylogenetic structure of ecosystem functions using predictor selection procedure and structural equation modelling.

2. Material & Methods

2.1. Experimental site & design

A common garden experiment was established in 2015 on a mesic meadow of Czech Republic at an elevation of 660 m (Vysočina region, 49.331N, 15.003E). The climate is temperate continental with an average annual temperature of 6.7°C and average annual precipitation of 759 mm (data from Černovice meteorological station, 4 km from the site). The study site is an abandoned crop field, last cultivated in 2001 and ploughed in 2014 prior to the experiment.

The experimental design is based on plant communities with constant sown species richness (6 species) but contrasted levels (high/low) of FD and PD resulting in four combinations. A species pool of 19 species naturally occurring in similar habitat was selected. Prior to the experimental setup, five quantitative traits and four qualitative (categorical) traits related to the competitive ability and niche occupation of the species were obtained from the LEDA trait database (Kleyer *et al.*, 2008) and BiolFlor (Kühn *et al.*, 2004).

The quantitative traits were canopy height (H, m), seed mass (mg), specific leaf area (SLA, mm^2/mg), leaf dry matter content (LDMC, mg/g) and length of flowering period (month 1–12) and the categorical traits were lifespan (annual/perennial), growth form (erosulate/hemirosette/rosette) and nitrogen-fixing ability.

All potential combinations of 6 species from the pool of 19 species were simulated with their values of FD and PD, using the Rao diversity index (Rao, 1982) based on the trait average differences between species (in the case of a fixed number of species corresponds to the mean pairwise dissimilarity, de Bello *et al.* 2016). Out of the possible mixtures, 10 communities were randomly selected from each of the 4 combinations of high and low values of FD and PD (see Galland *et al.* (2019) for a more detailed description of communities' selection). In addition to the 40 communities, three replicates of monocultures of the 19 species were sown. Finally, the entire setup was replicated on fertilized and unfertilized plots, resulting in a total of 196 plots (two extra monoculture plots were sown, *Lotus corniculatus* unfertilized and *Plantago media* fertilized). Fertilization was applied with dried composted cow manure (2.2 t/ha, 33 N, 55 P_2O_5, 33 K_20) on each fertilized plot every year at the beginning of the growing season (March).

2.2. Plant traits measurements

We measured in-situ traits after the experiment was established, in order to obtain the functional traits information from both the general environmental conditions of our experimental field and intraspecific variability within our experiment. The functional traits were measured following standard protocols (N. Pérez-Harguindeguy *et al.*, 2013). H, SLA and LDMC were measured in June 2016 for each of the 19 species on 2 individuals per plot where the species were sown (22 to 40 samples per species per fertility level). Leaf nutrient concentration (carbon [C], nitrogen [N], phosphorus [P], C:N and N:P ratios) content were measured in September 2016 on 5 samples per species per fertilisation level (1 monoculture and 1 of each of the 4 diversity level). All quantitative traits values (except ratio) were ln-transform to meet normal distribution. For the analysis, all functional structure indices were recomputed with in-situ traits values, intraspecific variability and observed relative abundance from log transformed (ln(x+1)) biomass measurement of July 2017 (see below).

The final functional diversity values used in the analyses were computed using Traits Probability Density (TPD) framework (Carmona *et al.*, 2016) based on in-situ measured traits only. This approach allows for accommodating intraspecific trait variability between species in a multivariate space. To compute TPD, we first selected the traits which had correlation coefficient below 0.7 (see Fig. S1 correlation table between measured traits) in order to avoid some type of traits having a greater effect on the combined functional diversity. The final traits selected to describe the functional differences between species were H, SLA, LDMC, P and C:N ratio. For each fertilization level, using on one hand the mean and standard deviation of each trait per species, on the other hand the correlation structure between the traits, we simulated traits combination for a population of 100 individuals for each species based on multivariate normal distribution (function *mvnorm in* package MASS, Venables & Ripley, 2002)). Then a PCA was computed based on those 5 traits of 19 populations and the scores of individuals on the 2 first axes were used as “traits” values to compute the TPD functions of each species (Fig.1 A). The functional pairwise dissimilarity between species was calculated based on species’ TPD overlap (de Bello *et al.*, 2013) and used to compute RaoQ functional diversity (FD). Moreover, we used PCA axis score of species centroid and species relative abundance in each community to compute CWMs indices. For each community, higher values of CWM_pca1 represent communities dominated by taller species with higher LDMC. Higher values of CWM_pca2 represent communities dominated by species with higher leaf C:N ratio, lower SLA and fewer fabacean (Fig. 1A). In summary, both CWM_pca1 and CWM_pca2 increase with traits syndrome characteristic of more conservative species.

Phylogenetic relationships between species were extracted from ultrametric supertree of European plant species, ‘Daphne’ (Durka & Michalski, 2012). The cophenetic pairwise distances between species and relative abundance from log transformed (ln(x+1)) biomass measurement were used to compute a RaoQ phylogenetic diversity (PD) of each community.

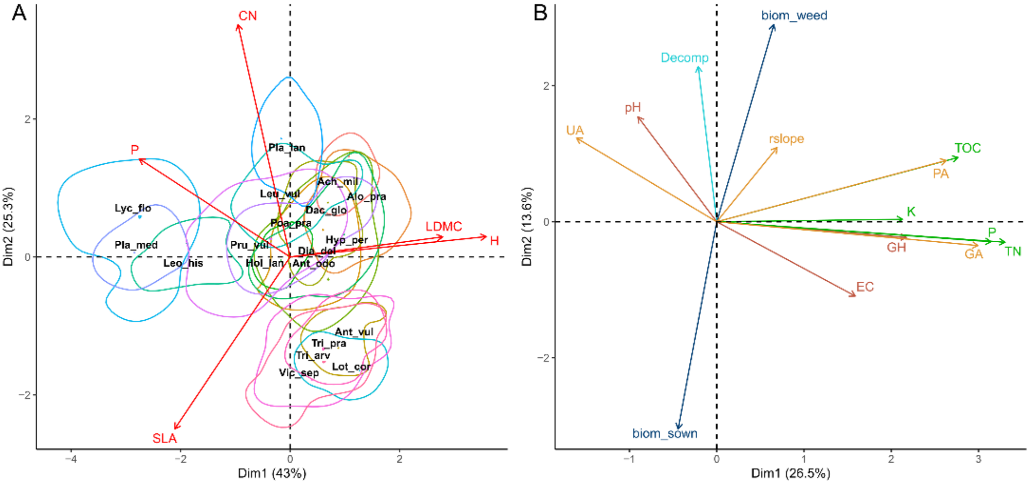

Figure 1: A) PCA on 19 species pool populations in the traits space. Each color represent one species (Ach_mil = *Achillea millefolium*, Alo_pra = *Alopecurus pratensis*, Ant_odo = *Anthoxanthum odoratum*, Ant_vul = *Anthyllis vulneraria*, Dac_glo = *Dactylis glomerata*, Dia_del = *Dianthus deltoides*, Hol_lan = *Holcus lanatus*, Hyp_per = *Hypericum perforatum*, Leo_his = *Leontodon hispidus*, Leu_vul = *Leucanthemum vulgare*, Lot_cor = *Lotus corniculatus*, Lyc_flo = *Lychnis flos-cuculi*, Pla_lan = *Plantago lanceolata*, Pla_med = *Plantago media*, Poa_pra = *Poa pratensis*, Pru_vul = *Prunella vulgaris*, Tri_arv = T*rifolium arvense*, Tri_pra = *Trifolium pratense*, Vic_sep = *Vicia sepium*). Red arrows represent traits: H = plant height, LDMC = leaf dry matter content, SLA = specific leaf area, P = leaf phosphorus content, CN = carbon to nitrogen ratio in leaves. **B)** PCA on the ecosystem properties variables (EPs). The colours represent groups of EPs variables: Navy blue for plant biomass (biom_sown and biom_weed for sown or invasive species respectively), turquoise for litter decomposability, red for soil abiotic properties (pH, EC = Electrical conductivity, GH = Gravimetric Humidity), green for soil fertility (TOC = Total Organic Carbon, TN = Total Nitrogen, P = Phosphorus and K = Potassium) and gold for microbial productivity (rslope = respiration slope (CO2-C accumulation curve), gluco = β-glucosidase, phospha = acid phosphatase)

2.3. Vegetation biomass, diversity effect and weed colonization resistance

In the first week of July 2017, at the peak of vegetative season, the aboveground biomass of each plot was clipped (2cm aboveground) in a 50x50cm quadrat. The biomass was sorted into individual sown species while the colonizing species were pooled into another sample. The samples were dried at 70ºC for 48h before weighing. The colonizing species biomass was used as a proxy of the sown community vulnerability to colonization.

The experimental design with biomass sampling of individual sown species in monocultures and mixtures allows us to evaluate the net diversity effect and its partitioning into complementarity and selection effect as proposed by Loreau & Hector (2001). The net diversity effect is estimated by the difference between the observed and the expected community yield. The expected yield is the weighted (by the initial relative abundance of species in the community) average yield from the monocultures of species that compose the community. In the present experiment the initial sowing density aimed to approximate equal abundance between species by adjusting both sowing density (seed number) and sowing mass (seed mass) (see details in Galland *et al.* 2019), so the expected yield was equivalent to non-weighted averaged. The partitioning of net diversity effect into complementarity and selection effect is based on the following additive formula:

$$\Delta Y = Y_O - Y_E = N\overline{\Delta RY}\overline{M} + Ncov(\Delta RY, M)$$

Where ΔY is the net biodiversity effect, Y_O and Y_E respectively symbolize total observed and expected yield, N is the number of species in the mixture, $\overline{\Delta RY}$ is the average deviation from expected yield, and $\overline{M}$ is the average monoculture yield. $N\overline{\Delta RY}\overline{M}$ measures the complementarity as the product between the average deviation from expected yield and monoculture yield, it is positive if the species yields in a mixture are on average higher than expected based on the weighted average monoculture yield of the component species. $Ncov(\Delta RY, M)$ measures the selection effect as the covariance between the monoculture yield of species and their change in relative yield in the mixture, it is positive if species with higher-than-average monoculture yields dominate the mixtures.

2.4. Litter decomposability

We conducted a litterbag experiment to evaluate the plant community decomposability. On each plot, we collected senescent leaves at the end of 2016 growing season (from the end of September until the end of November) from all species present (sown and colonizing species). With this material collected, we filled three replicate litter bags with 3g of dried material and kept the litterbags on homogenized sand bed for 5 months (see Annex II for methodological details on the decomposition experiment). Finally, for each plot we retained as an estimate of the community decomposability, the averaged complement of the ratio between the final weight and the initial weight (decomposition = 1-[$\text{Weight}_{\text{INITIAL}}$/$\text{Weight}_{\text{FINAL}}$]) from the 3 replicate samples.

2.5. Soil sampling

After the biomass sampling in July 2017, we collected one sample per plot that was composed of three soil cores (3cm in diameter and 10cm in depth) evenly distributed in the central square meter of the plot to account for spatial heterogeneity while avoiding any edge effect. The pooled samples were sieved on a 2mm mesh and split into two: a 20g sample was frozen (give temperature) while the rest was oven dried (60 °C, 48h). Dried samples were used to measure pH and electrical conductivity (EC, µS cm^{-1}). Frozen samples were stored, and subsequently thawed at 5 °C to measure soil gravimetric humidity as the weight loss after oven drying (105 °C) (hum, %). Total organic carbon (TOC, g kg^{-1} dw), total nitrogen (TN, g kg^{-1} dw), total potassium (K, g kg^{-1} dw) and total phosphorus (P, g kg^{-1} dw) were analysed in ground samples following standard protocols as in Navarro-Cano, Verdú, García, & Goberna (2015). In the same root-free sieved samples, we measured microbial CO_2-C production during an aerobic incubation in the dark (ca. 12 g soil, 60% water-holding capacity, 28 °C, 28 days) using a 6700 Headspace CO_2-analyzer (Illinois Instruments). We fitted the curve of cumulative CO_2-C production over time to a sigmoidal equation with three parameters ($R^2 \geq 0.95$, in all cases) in SigmaPlot v10.0. We estimated the kinetic parameters of soil microbial respiration and used the slope of CO_2 production as a proxy for microbial productivity. Enzymatic activities related to C (β-glucosidase, GA) and P (acid phosphatase, PA) cycling were quantified as the amount of p-nitrophenol (PNP) that 0.5 g of soil produced under controlled conditions of temperature (37 °C, 1 h) and pH 6 (Eivazi & Tabatabai, 1988; Tabatabai & Bremner, 1969). Enzymatic activity related to N cycle (urease, UA), which catalyses the conversion of urea into carbon dioxide and ammonia, was quantified colorimetrically as the NH_4^+ produced after incubating (37 °c, 2 h) 1 g of soil in 4 ml borate buffer (pH 10) and 0.5 ml of 0.48 % urea (Kandeler & Gerber, 1988).

We grouped in soil abiotic properties, parameters which are not directly linked to fertility but condition soil microbial community composition, activity or access to organic substances: pH, EC and GH. Soil fertility variables were TOC and macronutrients (total N, P and K). Finally, we used microbial respiration (the slope of the CO_2 accumulation curve of microbial respiration, rslope, and enzymatic activities related to C (GA), P (PA) and N (UA) cycling as indicators of soil microbial productivity (Navarro-Cano *et al.*, 2015).

2.6. Assessing multiple ecosystem properties

The evaluation of multiple ecosystem functions simultaneously has been a central goal of multifunctionality methodological development (see Byrnes *et al.* 2014 for a review of different methodologies). Two of the most popular approaches are the averaging method and the multiple threshold method (Manning *et al.*, 2018), both considered in the present study. The averaged multifunctionality takes the mean of a set of standardized ecosystem functions values per plot. Following Maestre *et al.* (2012), we standardized each function using Z-score transformation (centred on the mean and standardize by standard deviation). We estimated two averaged multifunctionality indices. The first one (MultF_soil) is a soil multifunctionality index and focuses on soil functions (fertility, respiration and nutrient cycling). The second one (MultF_all) also accounts for plant functions (biomass of sown community, resistance to colonization, decomposability). This allows us to evaluate the importance of plant functions as predictors of soil multifunctionality.

Additionally, a multiple threshold approach was used to compare the results among the indices, as this approach performs well even in the presence of trade-offs among EF variables (Byrnes *et al.*, 2014). The multiple threshold approach counts the number of functions that surpass a given threshold, usually given as a percentage of the maximal value observed in the dataset (Manning *et al.*, 2018). Since the strength of the relationship between a predictor and the number of functions that pass a given threshold can vary based on the threshold chosen, it is common to repeat the procedure for a range of thresholds, a method also called multiple threshold approach (Byrnes *et al.*, 2014). We used a threshold range from 5 to 95% of the maximal level of a function. The maximal level of a function was calculated as the average of the 2 highest values of this function in the dataset, this procedure is recommended to avoid potential issues with spuriously high maximal values (Byrnes *et al.*, 2014).

2.7. Analysis

We first explored the relationship between, as dependent variables, individual ecosystem properties and averaged multifunctionality indices, and as independent variables the functional and phylogenetic structure of plant communities together with the fertilization treatment. We used linear models and predictors selection procedure based on Akaike information criterion (AIC) to obtain the best model for each response variable. In addition to fertilisation, the predictors considered were i) FD and PD because they represent the variability in traits and relatedness of species (complementarity effect), ii) CWM_pca1 and CWM_pca2 as proxies of the dominant traits' syndrome in the community (selection effect).

In a second step, in order to investigate if the plant ecosystem functions are better predictors of individual soil ecosystems properties and multifunctionality than plant functional and phylogenetic structure, we included both functional and phylogenetic structure parameters, plant community productivity and decomposability as potential predictors before running the selection procedure. This method allowed to account for the partial effects due to plant EFs after accounting the direct effect of community structure. If a plant EF *m* was well predicted by a functional structure parameter *p*, and this plant EF *m* is selected over the functional structure parameter *p* as predictor of a given soil parameter *r*, this suggests that the effect of functional structure parameter *p* (predictor) on soil parameter *r* (response) is potentially mediated by the plant EF *m* (mediator). Then, we repeated a similar nested model selection including soil abiotic properties as additional potential predictor of soil individual ecosystem functions and multifunctionality indices. Since soil nutrient pool variables were well correlated between them (Fig.1B), and with the aim to reduce the number of mediator variables, we computed a summary variable for nutrient pool using the average multifunctionality method, i.e. MultF_NutPool is the mean of the four Z-transformed nutrient pool variables (rslope, GA, PA, UA).

To explicitly test the direct effect of plant community functional and phylogenetic structure and fertilisation on soil multifunctionality and their indirect effect mediated by the plants EFs and abiotic parameters, we conducted a confirmatory path analysis using a d-sep approach (Shipley, 2013). The total effect of each predictor was calculated as the sum of direct and indirect effect on soil multifunctionality index.

Finally, we also tested i) the full model with fertilization and all functional and phylogenetic structure parameters as predictors and ii) the best model selected for averaged multifunctionality with the multiple thresholds approach (Fig. S2). Since the results were consistent with the averaged multifunctionality method, we present the results of the multiple threshold analysis only in appendix (Fig. S4 and S5).

3. Results

3.1. Direct effects on individual EFs

3.1.1. Plants EFs:

Biomass productivity was the ecosystem function best explained by plant community functional structure (Fig.2, R^2=0.33) while PD was not selected as a significant predictor for any of the plant related response variable. High values of CWM_pca1 (higher H and LDMC), CWM_pca2 (higher C:N and lower SLA) and FD jointly increased the biomass of sown community (Fig. 2). The same predictors have also a positive effect on the net biodiversity effect with respect to the productivity of monocultures. Selection and complementarity effects responded to different parameters of the community functional structure. Selection effect increased with CWM_pca2 while complementarity effect increased under the combined effect of FD and CWM_pca1. The results show an opposite response of weed biomass (community vulnerability to colonisation) compared to biomass of sown species along both CWMs gradients. In other words, the communities with high CWMs values were highly productive and more resistant to weed colonisation. The decomposability of the communities was lower when sown communities had higher values of CWM_pca2 and FD. Interestingly the fertilisation treatment had no impact on plant productivity, although it had a marginally significant positive effect on selection effect.

3.1.2. Soil parameters

Overall, the variables related to abiotic properties of the soil were better predicted by plant community functional structure than the soil EFs (Fig. 2). In particular the pH of the soil decreased along CWM_pca2 and FD. EC tended to decrease along the FD gradient and GH decreased along CWM_pca2, although those relationships were only marginally significant (Fig. 2). The fertilisation treatment had a positive effect on pH and EC.

The soil nutrient pool variables (TOC, TN, K and P) showed no direct relationship to any plant community functional or phylogenetic structure variables. The variables related to microbial activity (rslope, PA and UA) showed a weak but significant relationship to the functional structure of plant community. In particular, soil respiration decreased along CWM_pca2 and FD, phosphatase activity reduced along CWM_pca2 gradient and urease activity tended to increase with PD. The glucosidase activity was the only variable to respond only to fertilisation treatment. Fertilisation had opposite effect on soil abiotic structure than sown community biomass, partially counterbalancing the effect of higher productivity on soil EF (Fig. S2).

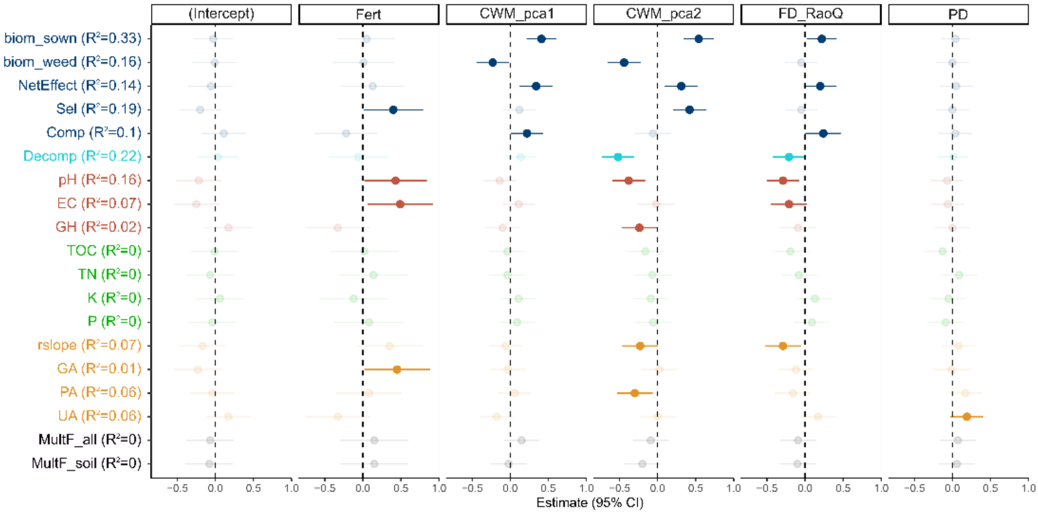

Figure 2: Results from individual response variables models. Each line represents the final model for a given response variable after forward selection of community functional and phylogenetic structure parameters as predictors. The adjusted coefficient of determination of the models are given in between parenthesis next to each response variable. The colours represents groups of EPs variables: Navy blue for plant biomass productivity and its diversity effect decomposition (biom_sown and biom_weed for biomass of sown and invasive species respectively, NetEffect = net biodiversity effect, Sel = Selection effect, Comp = Complementarity effect), turquoise for litter decomposability (Decomp), red for soil abiotic properties (pH, EC = Electro conductivity, GH = Gravimetric Humidity), green for soil nutrient pool (TOC = Total Organic Carbon, TN = Total Nitrogen, P = Phosphorus and K = Potassium), gold for soil microorganism activity (rslope = respiration slope [CO2 accumulation curve], GA = β-glucosidase, PA = alkaline phosphatase), UA = urease and black for averaged multifunctionality indices (MultF_all and MultF_soil).

3.1.3. Direct effect on Multi functionality

Neither functional and phylogenetic community structure nor fertilisation treatment had direct effects on the multifunctionality indices (MultF_all and MultF_soil). The partial effect of plant biomass was selected as predictor improving the model but remain none significant (Fig. S2). The best model selected to predict soil averaged multifunctionality (Fig. S2) was tested on multi-threshold method yielding similar results (Fig. S5).

3.2. Indirect effect of plant communtiy on soil EFs

The results from the path analysis (Fig.3) confirmed the hypothesis that the effect of plants community functional and phylogenetic structure on soil EFs is essentially mediated by plant productivity, decomposability and by soil abiotic variables. The results were consistent with nested selection procedure, i.e. adding plant EFs and soil abiotic parameters (Fig. 2, S2 and S3).

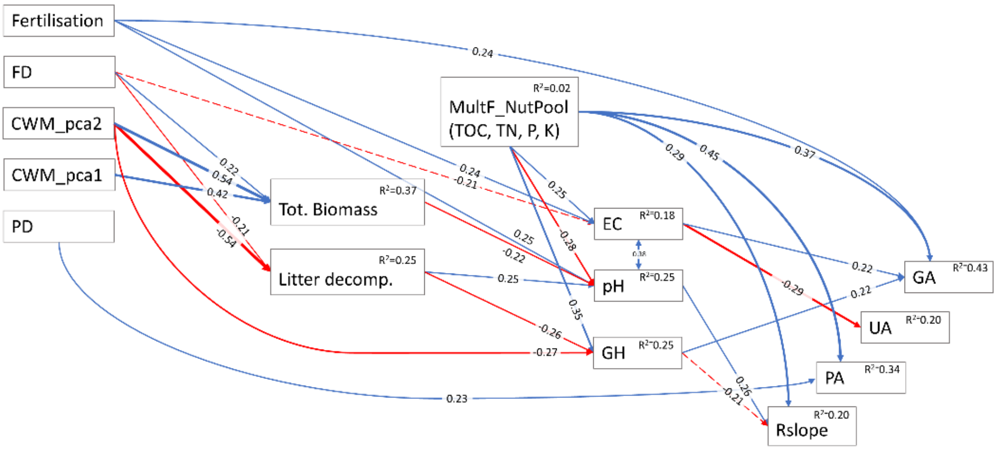

Figure 3: Structural equation models presenting the effect plants community functional and phylogenetic structure and fertilization on soil microbial activity mediated by biomass production, decomposability and soil abiotic properties (there are 4 SEM superposed, one per soil microbial activity variable). The variance explained for each individual model are given in the responses variables boxes. Blue and red arrows describe positive and negative effect respectively, solid lines are significant path (p-value < 0.05) and dashed line are marginally significant path (p-value < 0.1). Non-significant paths are not represented for clarity purpose. The width of the arrows is proportional to the strength of the relationship. See table S1 for all coefficients and global goodness-of-fit measures for individual models. Tot. Biomass = biomass of sown species, Litter decomp. = litter decomposability EC = Electro conductivity, GH = Gravimetric Humidity, TOC = Total Organic Carbon, TN = Total Nitrogen, P = Phosphorus and K = Potassium, rslope = respiration slope [CO2 accumulation curve], GA = β-glucosidase, PA = alkaline phosphatase, UA = urease.

The main driver of soil microbial respiration and activity is nutrient pool (MultF_NutPool) via both direct and indirect effect mediated by the soil abiotic condition (EC, pH and GH ; Fig. 3 and S6). Surpisingly, none of the functional or phylogenetic structure parameters nor the fertilisation treatment was found significant driver of nutrient pools (not as aggregated index Fig. 3, neither on individual variables Fig. 2 & S1).

The effect of CWM_pca1 on soil EFs is essentially mediated through its support of plant biomass. Productivity of sown species lowers pH and rslope (Fig. S2). When considering partial effect of soil nutrient pool (Fig. S3) the effect of biomass on rslope was not significant anymore.

CWM_pca2 and FD partially support plant biomass productivity as well, but additionallythey reduced litter decomposability and impact some abiotic parameters of the soil (Fig. 3). High decomposability was found to increase pH and decrease GH but had no direct effect on any of the soil EFs measured (Fig. S2 and S3). However, the soil EFs were well predicted by the soil abiotic properties and the total effect size (direct+indirect) of total biomass and decomposability were similar (Fig. 4). PD remained significant direct predictor of acid phosphatase activity after the inclusion of nutrient pool and other abiotic soil parameters.

4. Discussion

This study shows the importance of disentangling the diverse roles of ecological differences between species in affecting directly, or indirectly via other trophic levels, a multiplicity of coordinated ecosystem functions. The results show that plant functional structure parameters are good direct predictors of plant community ecosystem functions (biomass of sown community, community resistance to colonisation by weeds and community decomposability) and better than phylogenetic differences between species. In return, these effects have a direct consequence on soil ecosystem properties. On the contrary, the direct effect of plant functional and phylogenetic structure on soil ecosystem properties are limited or null. However, the results (through nested model selection procedure and the path analysis) support also the importance of the indirect effect of plant functional structure on the soil ecosystem functions mediated by i) the plant community EF (biomass production and decomposability) and ii) the modification of soil abiotic properties (pH, EC, GH).

The results also support the idea that some parameters of ecological differences between species are better predictors than others, e.g, PD was least often selected predictor in model prediction of individual EFs (Fig. 2, S2 and S3). CWM_pca2 and FD were the variables most often selected in the models predicting individual ecosystem properties from the plant community functional structure. However, none of those parameters appears to be suficiently good predictor alone: a combination of different parameters of the plant functional structure is necessary to reach a good prediction of EFs.

Finally, the fertilisation treatment had a direct effect on UA and an indirect effect on GA, UA and rslope mediated through the modification of soil abiotic variables (pH and EC) but no significant direct effect on plant EFs nor soil nutrient pool.

4.1. Direct effects on individual EFs and multifunctionality

Theoretical and empirical ecological studies suggest that different dimensions of diversity support different aspects of the BEF relationship. In particular, complementarity is expected to increase with FD and selection effect to increase with CWM (Cadotte, 2017). Our results provide a nuanced support to this idea, FD increased net diversity effect on biomass production via complementarity effect, and CWM_pca2 increased the selection effect. However, CWM_pca1 increased net biodiversity effect via complementarity effect. This seems counter-intuitive but it is not an isolated result in literature, for example Mahaut *et al.* (2020) reported experimental results where complementarity effect was essentially related to CWMs. In light of the relationship between niche differentiation and competitive ability described by Mayfield & Levine (2010), a potential mechanistic explanation of why CWM_pca1 is associated with complementarity effect on biomass production could be its relation to CWM_height (pearson R = 0.7, p-value <0.001). Because CWM value is driven by the dominant species and the dominant species is most of the time the tallest species, the potential for vertical complementarity in the vegetation layers is larger when the dominant species of a community is higher. The first traits' pca axis strongly represent plant height (Fig. 1A). In other words, when the dominant species is short, the subordinates, which are similarly short, are excluded. But when the dominant species is tall the subordinates are still short and can coexiste under the condition that they tolerate partial shading. Of course a tall dominant species can also exclude the subordinates, but a short dominant simply does not leave physical space for vertical complementarity.

The cumulative biomass of species which didn't belong to the 6 sown species on a particular plot represent the vulnerability to colonisation of sown communities, and was negatively associated to high values of CWM_pca1 and CWM_pca2. In other words, the communities composed of bigger and more conservative species were more resistant to colonisation by surrounding weeds, as was generally shown in this system (Galland *et al.*, 2019).

Litter decomposability was strongly related to CWM_pca2 (Fig 2) which can be interpreted as a proxy for litter quality of the community (high CWM_pca2 values represent low quality). Litter quality is particularly associated to low values of C:N ratio in leaves chemical composition (Pérez-Harguindeguy *et al.*, 2000). C:N ratio is a trait well represented on the second axis of trait pca (Fig. 1A) and CWM_C:N is strongly correlated to CWM_pca2 (pearson $R = 0.87$, p-value < 0.001). No complementarity effect between plant species seems to be at play as the litter decomposition was negatively (although weakly) associated to with FD. Theoretically, a negative effect of FD could be interpreted as evidence of selection effect, especially in the light of the hump-shaped relationship between CWM and FD described by Dias *et al.* (2013). Moreover, those results are consistent with the recent findings by Pichon *et al.* (2020) where decomposability increased when communities functional composition was dominated by species with acquisitive traits syndrome. Pichon *et al.* (2020) also reported a positive indirect effect of species richness but no statistically significant effect of functional diversity.

Soil abiotic properties showed a direct response to the experimental treatment. In particular fertilisation increased pH and EC (Fig. 2). It is interesting to note that the rest of soil variables, especially the ones related to nutrient pools (TOC, N, P, K), were apparently not affected by the fertilisation treatment (except for glucosidase activity which was higher in fertilised plot). Two parameters of the experiment could help understanding this seemingly surprising result. First, the nature of the fertiliser used, while in most experiment fertilisers are applied in mineral form, we choose to apply it in an organic form (i.e. dried composted cow manure). Organic fertilisers are known to not only provide mineral nutrients but also affect the physical condition of the soil. The latter effect seems to be larger in the current experiment as shown by the effect of fertilisation treatment on abiotic properties of the soil. Second, there is a possibility that the level of microbial activity and nutrient content in the soil was already high in all the plots, minimizing the effect of fertilisation. Prior to the experiment in 2015, the field was plown for the first time after many years. One frequent effect of the plowing is the stimulation of mineralisation by aeration of underground layers of soil enriched in organic matter, releasing large amount of nutrients. Finally as reviewed by Haynes & Naidu (1998), short-term effects of fertilisation appear to be relatively rare (especially in soil which are already relatively fertile), thus the effect of fertilisation treatment in our experiment could increase with time.

Community functional structure also impacted soil abiotic properties and microbial activity in the soil (i.e. respiration and phosphatase activity). Phosphatase activity responded positively to plant community phylogenetic diversity which is consistent with previous findings (Navarro-Cano *et al.*, 2014) and can result from two mechanisms (Goberna, Navarro-Cano, & Verdú, 2016): i) plant phylogenetic diversity can stimulate soil microbial phylogenetic diversity via niche differences, stimulating microbial activity by complementarity effect; ii) plant phylogenetic diversity can reduce microbial phylogenetic diversity via increased fitness differences, stimulating microbial activity by selection of high competitive clades. As for litter decomposition, CWM_pca2 and FD have a negative effect on those variables and, as discuss below, the effect of community functional structure on soil properties is in fact largely mediated by litter decomposition and biomass productivity.

Multifunctionality indices, neither averaged nor multi-threshold, showed statistically significant direct effect of community functional or phylogenetic structure, nor fertilisation treatment. These results can be explained by the lack of synergy among individual EFs in response to plant community functional structure. Indeed the plants community EFs, biomass production and litter decomposability showed opposite direction in response to CWM_pca2 and FD. Regarding soil functions, none of the four nutrient pool parameters showed a response to treatment, but all four microbial activity measures responded to either fertilisation treatment (GA) or community functional structure (rslope, PA, UA). This observation could be the result of different timelag of response to treatments: while microbial community can respond quickly, changes in nutrient pools can take longer period of time (Haynes & Naidu, 1998). This lack of synergy among individual EFs response could explain the absence of significant response from multifunctionality analysis as suggested by Meyer *et al.* (2018). However, another potential explanation is that the effect can be mediated by other variables or that some of the EFs do not respond to biodiversity (Allan *et al.*, 2013).

Our results point toward the presence of a trade-off between the ecosystem function linked to productivity and the other variables, i.e. while the biomass of the sown communities and their resistance increase along CWM_pca2 and FD, the soil becomes more acidic, litter decomposability and soil microorganism respiration diminished (Fig. 2).

4.2. Indirect effect on soil EFs

The results from model selection procedure in Fig. S2 and S3 are consistent with the results from path analysis (Fig. 3). The soil EFs, are best predicted by combination of plant community EFs (i.e. total biomass and litter decomposition) and soil abiotic properties. Total biomass and litter decomposition seem to mediate most of the effect of plant community functional structure on soil abiotic properties.

The cascading effect of plant community functional structure to soil ecosystem functions was best observed in our dataset regarding microbial respiration. Plant species with the strongest dominance in communities are located in the upper right corner of the pca in Fig.1A, they are characterised by conservative trait syndrome (tall with high LDMC [pca 1st axis], low SLA and high C:N ratio [pca 2^{nd} axis]). Those characteristics explain that communities with high values of CWM_pca1 and CWM_pca2 build up large biomass with slow decomposing material (Pérez-Harguindeguy *et al.*, 2000). High biomass productivity and slow litter decomposition were associated with an acidification of the soil which was in turn associated to slower respiration in the soil. This is an example of top-down control of soil microbial function.

Urease activity unique direct predictor in our experiment was EC. The negative effect of EC on UA could indicate a product inhibition mechanism (Hoare & Laidler, 1950; Pérez-Valera, Goberna, & Verdú, 2019). EC is a proxy of the amount of electrolytes in the soil solution, contrary to parameters like total nitrogen measured as nutrient pool variable, those nutrients should be more directly available to plants and microorganism. The positive effect of fertilisation on EC supports the use of EC as a proxy for nutrient availability. The negative tendency of FD effect on EC could indicate a higher efficiency of plant communities in the caption of nutrients via a complementarity.

5. Conclusion

Our study supports the richness of interaction between plant and soil community and the necessity to include different dimensions of biodiversity on the study of multiple ecosystem functions. We showed that even if the soil nutrient pool was the main driver of soil microbial activity, the indirect effect of plant functional and phylogenetic structure, through plants EFs and soil properties (pH, EC and GH), on soil EFs are not negligible.

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Supplementary material

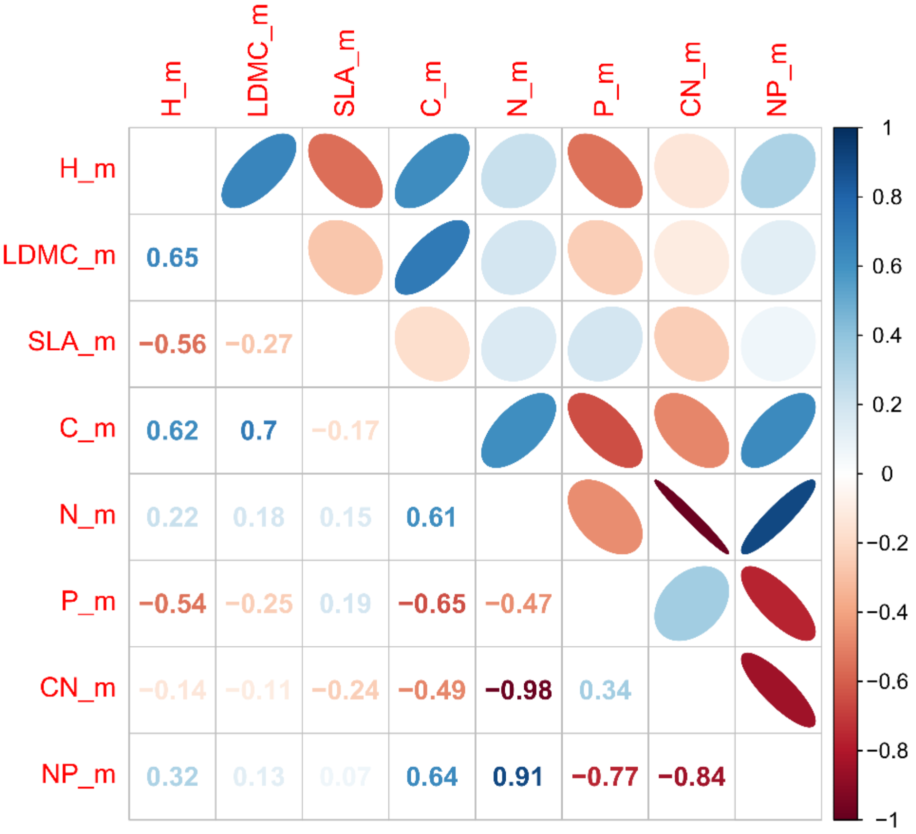

Figure S1: Pearson r correlation coefficient between mean traits values from in situ measurements. H = plant height, LDMC = leaf dry matter content, SLA = specific leaf area, C = leaf carbon concentration, N = leaf nitrogen concentration, P = leaf phosphorus concentration, CN = leaf carbon to nitrogen ratio, NP = leaf nitrogen to phosphorus concentration.

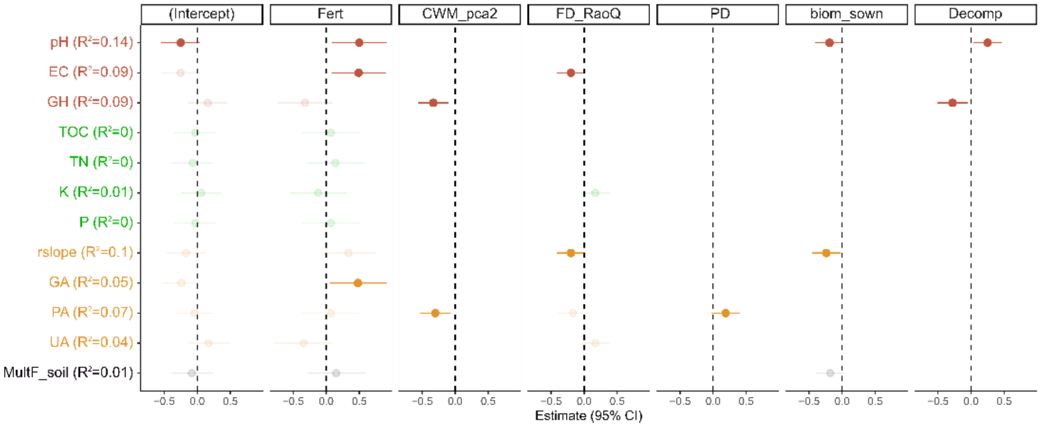

Figure S2: Results from individual response variables nested selection model 1. Each line represents the final model for a given soil EPs (EFs and physico-chemistry) after forward selection of i) community functional and phylogenetic structure (CWMs, FD, PD) and ii) plant community EFs (Biomass & decomposability) as predictors. The adjusted coefficient of determination of the models are given in between parenthesis next to each response variable. The colours represents groups of EPs variables: red for soil abiotic properties (pH, EC = Electro conductivity, GH = Gravimetric Humidity), green for soil nutrient pool (TOC = Total Organic Carbon, TN = Total Nitrogen, P = Phosphorus and K = Potassium), gold for soil microorganism activity (rslope = respiration intercept (CO2 accumulation curve), GA = β-glucosidase, PA = alkaline phosphatase, UA = urease) and black for averaged multifunctionality index (multF_soil).

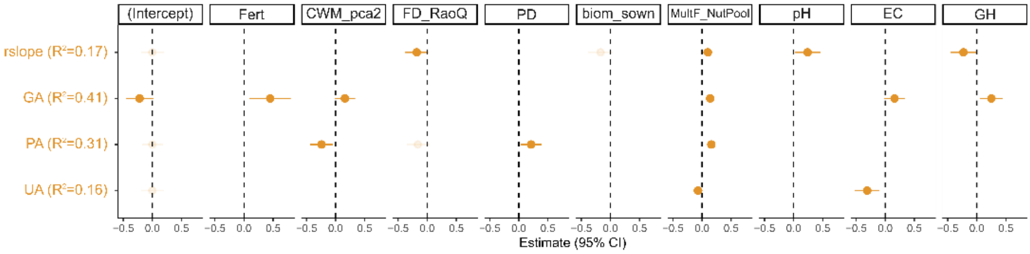

Figure S3: Results from individual response variables nested selection model 2. Each line represents the final model for a given soil EF after forward selection of i) community functional and phylogenetic structure (CWMs, FD, PD), ii) plant community EFs (Biomass & decomposability) and iii) soil abiotic properties (pH, EC = Electro conductivity, GH = Gravimetric Humidity) and iv) agregated soil nutrient pool (MultF_NutPool) as predictors. The adjusted coefficient of determination of the models are given in between parenthesis next to each response variable. Rslope = respiration intercept (CO_2 accumulation curve), GA = β-glucosidase activity, PA = alkaline phosphatase activity, UA = urease activity.

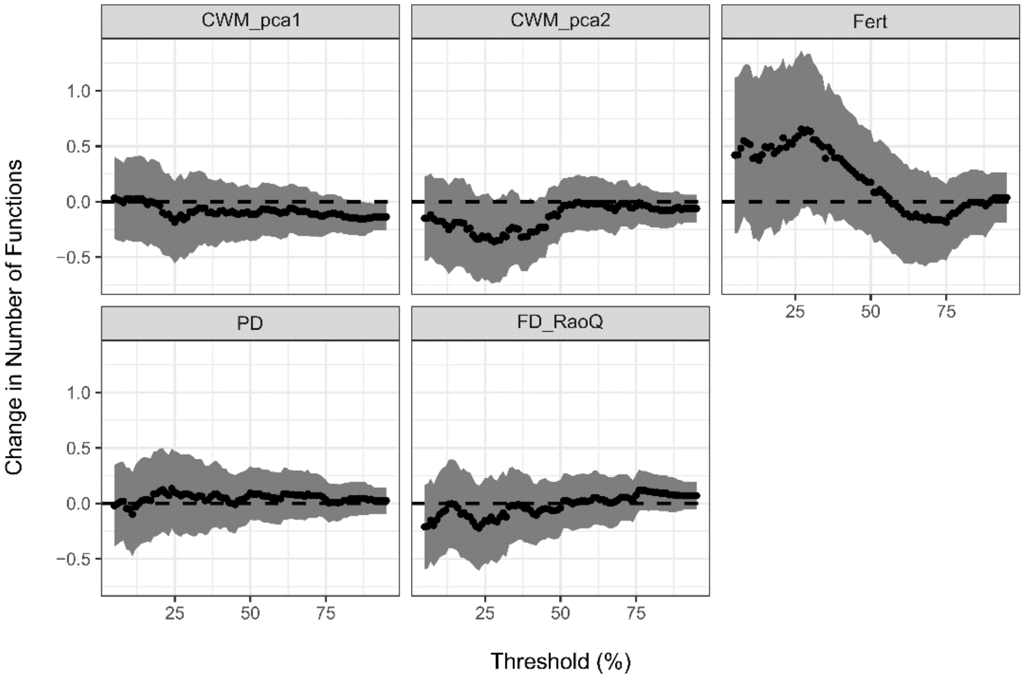

Figure S4: Multiple threshold approach analysis of soil multifunctionality. We fitted models with fertilization and functional and phylogenetic structure parameters as predictor of the number of functions surpassing a given threshold. The graph shows the evolution of predictors' estimates (black dots) and their confidence interval (grey area) along a gradient of threshold values.

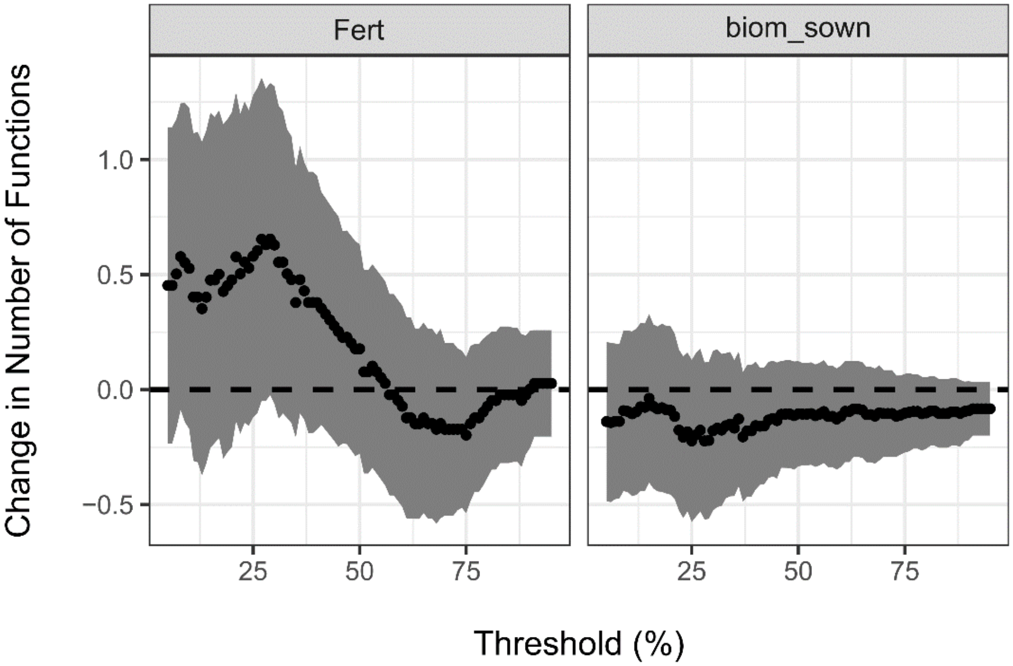

Figure S5: Multiple threshold approach analysis of soil multifunctionality. We fitted models with fertilization (Fert) and sown species biomass (biom_sown) as selected predictor of averaged soil multifunctionality (i.e. Total biomass of sown species and soil physic-chemical properties) as predictor of the number of functions surpassing a given threshold. The graph shows the predictors' estimates (black dots) and their confidence interval (grey area) along a gradient of threshold values.

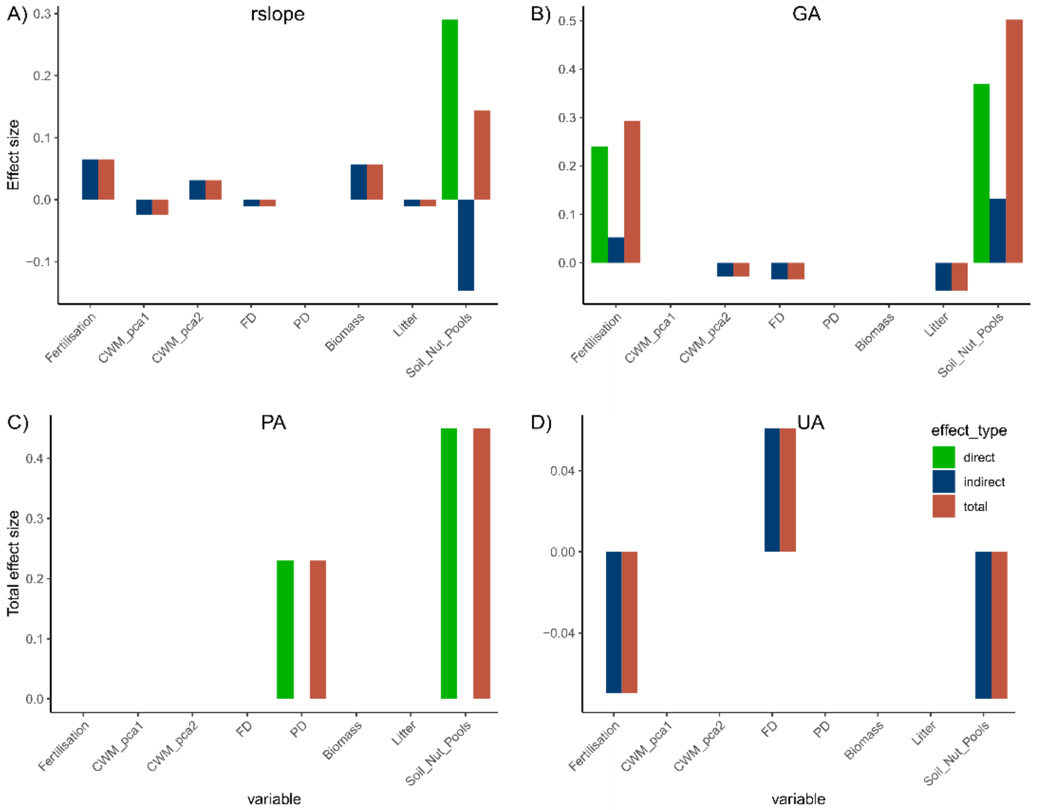

Figure S6: Total standardized effect (sum of direct and indirect effects) from SEMs (Fig. 3) on soil microbial activity (rslope = respiration intercept (CO$_2$ accumulation curve), GA = β-glucosidase activity, PA = alkaline phosphatase activity, UA = urease activity). Biomass = biomass of sown species, Litter = litter decomposability and Soil_Nut_Pools is an agregate variable of TOC = Total Organic Carbon, TN = Total Nitrogen, P = Phosphorus and K = Potassium.

Table S1: Standardized path coefficients of each SEM-model (Fig. 3), using the piecewiseSEM package (Lefcheck, 2016).

Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
SEM 1: Standardized path coefficients of rslope model					36.6	0.44 (36)
tot_biom_sown	Rao_TPD	0.221	0.100	0.03*		
tot_biom_sown	cwm_biom_Dim.1	0.418	0.093	<0.001***		
tot_biom_sown	cwm_biom_Dim.2	0.536	0.100	<0.001***		
tot_biom_sown	fert	-	-	0.782		
tot_biom_sown	fert = U	-0.026	0.130	0.844		
tot_biom_sown	fert = F	0.026	0.130	0.844		
Decomp	Rao_TPD	-0.215	0.108	0.05*		
Decomp	cwm_biom_Dim.2	-0.539	0.107	<0.001***		
Decomp	fert	-	-	0.711		
Decomp	fert = U	0.037	0.140	0.793		
Decomp	fert = F	-0.037	0.140	0.793		
multF_NutPool	Rao_TPD	-0.020	0.133	0.879		
multF_NutPool	cwm_biom_Dim.1	0.062	0.133	0.642		
multF_NutPool	cwm_biom_Dim.2	-0.134	0.166	0.423		
multF_NutPool	tot_biom_sown	-0.063	0.146	0.666		
multF_NutPool	Decomp	-0.078	0.136	0.569		
multF_NutPool	fert	-	-	0.84		
multF_NutPool	fert = U	-0.024	0.163	0.886		
multF_NutPool	fert = F	0.024	0.163	0.886		
pH	tot_biom_sown	-0.219	0.101	0.034*		
pH	Decomp	0.245	0.101	0.018*		
pH	multF_NutPool	-0.287	0.100	0.006**		
pH	fert	-	-	0.012*		
pH	fert = U	-0.257	0.141	0.072		
pH	fert = F	0.257	0.141	0.072		
EC	Rao_TPD	-0.207	0.105	0.052		
EC	multF_NutPool	0.255	0.104	0.017*		
EC	fert	-	-	0.024*		
EC	fert = U	-0.240	0.147	0.106		
EC	fert = F	0.240	0.147	0.106		
GH	cwm_biom_Dim.2	-0.273	0.114	0.019*		
GH	Decomp	-0.261	0.113	0.024*		
GH	multF_NutPool	0.350	0.101	0.001***		
GH	fert	-	-	0.093		

Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
GH	fert = U	0.169	0.141	0.233		
GH	fert = F	-0.169	0.141	0.233		
~~pH	~~EC	0.379	-	<0.001***		
rslope	tot_biom_sown	-0.165	0.113	0.15		
rslope	multF_NutPool	0.289	0.126	0.025*		
rslope	pH	0.258	0.126	0.045*		
rslope	EC	-0.013	0.124	0.915		
rslope	GH	-0.214	0.116	0.068		
rslope	fert	-	-	0.408		
rslope	fert = U	-0.093	0.153	0.544		
rslope	fert = F	0.093	0.153	0.544		
SEM 2: Standardized path coefficients of GA model					38.97	0.34 (36)
tot_biom_sown	Rao_TPD	0.2214	0.0998	0.03*		
tot_biom_sown	cwm_biom_Dim.1	0.4178	0.0927	<0.001***		
tot_biom_sown	cwm_biom_Dim.2	0.5362	0.1001	<0.001***		
tot_biom_sown	fert	-	-	0.782		
tot_biom_sown	fert = U	-0.0255	0.1295	0.844		
tot_biom_sown	fert = F	0.0255	0.1295	0.844		
Decomp	Rao_TPD	-0.2148	0.1077	0.05*		
Decomp	cwm_biom_Dim.2	-0.5391	0.1072	<0.001***		
Decomp	fert	-	-	0.711		
Decomp	fert = U	0.0368	0.1399	0.793		
Decomp	fert = F	-0.0368	0.1399	0.793		
multF_NutPool	Rao_TPD	-0.0203	0.133	0.879		
multF_NutPool	cwm_biom_Dim.1	0.0619	0.1326	0.642		
multF_NutPool	cwm_biom_Dim.2	-0.1337	0.1659	0.423		
multF_NutPool	tot_biom_sown	-0.0631	0.1456	0.666		
multF_NutPool	Decomp	-0.0777	0.1357	0.569		
multF_NutPool	fert	-	-	0.84		
multF_NutPool	fert = U	-0.0235	0.1631	0.886		
multF_NutPool	fert = F	0.0235	0.1631	0.886		
pH	tot_biom_sown	-0.2187	0.1012	0.034*		
pH	Decomp	0.2451	0.1009	0.018*		
pH	multF_NutPool	-0.2868	0.1004	0.006**		
pH	fert	-	-	0.012*		
pH	fert = U	-0.2571	0.1406	0.072		
pH	fert = F	0.2571	0.1406	0.072		

Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
EC	Rao_TPD	-0.2067	0.1047	0.052		
EC	multF_NutPool	0.2552	0.1042	0.017*		
EC	fert	-	-	0.024*		
EC	fert = U	-0.2403	0.1467	0.106		
EC	fert = F	0.2403	0.1467	0.106		
GH	cwm_biom_Dim.2	-0.2729	0.1138	0.019*		
GH	Decomp	-0.2605	0.1129	0.024*		
GH	multF_NutPool	0.3499	0.101	0.001***		
GH	fert	-	-	0.093		
GH	fert = U	0.1692	0.1407	0.233		
GH	fert = F	-0.1692	0.1407	0.233		
~~pH	~~EC	0.3793	-	<0.001***		
gluco	tot_biom_sown	-0.0184	0.0951	0.847		
gluco	multF_NutPool	0.3734	0.1063	0.001***		
gluco	pH	-0.1145	0.1062	0.284		
gluco	EC	0.2176	0.1043	0.04*		
gluco	GH	0.2167	0.0972	0.029*		
gluco	fert	-	-	0.013*		
gluco	fert = U	-0.2393	0.1285	0.067		
gluco	fert = F	0.2393	0.1285	0.067		
SEM 3: Standardized path coefficients of PA model					41.77	0.72 (48)
tot_biom_sown	Rao_TPD	0.2214	0.0998	0.03*		
tot_biom_sown	cwm_biom_Dim.1	0.4178	0.0927	<0.001***		
tot_biom_sown	cwm_biom_Dim.2	0.5362	0.1001	<0.001***		
tot_biom_sown	fert	-	-	0.782		
tot_biom_sown	fert = U	-0.0255	0.1295	0.844		
tot_biom_sown	fert = F	0.0255	0.1295	0.844		
Decomp	Rao_TPD	-0.2148	0.1077	0.05*		
Decomp	cwm_biom_Dim.2	-0.5391	0.1072	<0.001***		
Decomp	fert	-	-	0.711		
Decomp	fert = U	0.0368	0.1399	0.793		
Decomp	fert = F	-0.0368	0.1399	0.793		
multF_NutPool	Rao_TPD	-0.0203	0.133	0.879		
multF_NutPool	cwm_biom_Dim.1	0.0619	0.1326	0.642		
multF_NutPool	cwm_biom_Dim.2	-0.1337	0.1659	0.423		
multF_NutPool	tot_biom_sown	-0.0631	0.1456	0.666		
multF_NutPool	Decomp	-0.0777	0.1357	0.569		

Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
multF_NutPool	fert	-	-	0.84		
multF_NutPool	fert = U	-0.0235	0.1631	0.886		
multF_NutPool	fert = F	0.0235	0.1631	0.886		
pH	tot_biom_sown	-0.2187	0.1012	0.034*		
pH	Decomp	0.2451	0.1009	0.018*		
pH	multF_NutPool	-0.2868	0.1004	0.006**		
pH	fert	-	-	0.012*		
pH	fert = U	-0.2571	0.1406	0.072		
pH	fert = F	0.2571	0.1406	0.072		
EC	Rao_TPD	-0.2067	0.1047	0.052		
EC	multF_NutPool	0.2552	0.1042	0.017*		
EC	fert	-	-	0.024*		
EC	fert = U	-0.2403	0.1467	0.106		
EC	fert = F	0.2403	0.1467	0.106		
GH	cwm_biom_Dim.2	-0.2729	0.1138	0.019*		
GH	Decomp	-0.2605	0.1129	0.024*		
GH	multF_NutPool	0.3499	0.101	0.001***		
GH	fert	-	-	0.093		
GH	fert = U	0.1692	0.1407	0.233		
GH	fert = F	-0.1692	0.1407	0.233		
~~pH	~~EC	0.3793	-	<0.001***		
phospha	tot_biom_sown	-0.1637	0.1041	0.12		
phospha	multF_NutPool	0.4481	0.1157	<0.001***		
phospha	PDbiom	0.234	0.0974	0.019*		
phospha	pH	-0.0056	0.1158	0.962		
phospha	EC	-0.0313	0.1134	0.783		
phospha	GH	0.1434	0.1057	0.179		
phospha	fert	-	-	0.498		
phospha	fert = U	-0.0698	0.1399	0.619		
phospha	fert = F	0.0698	0.1399	0.619		
SEM 4: Standardized path coefficients of UA model					36.9	0.46 (36)
Response	Predictor	Estimate	Std.Error	P.Value		
tot_biom_sown	Rao_TPD	0.2214	0.0998	0.03*		
tot_biom_sown	cwm_biom_Dim.1	0.4178	0.0927	<0.001***		
tot_biom_sown	cwm_biom_Dim.2	0.5362	0.1001	<0.001***		
tot_biom_sown	fert	-	-	0.782		
tot_biom_sown	fert = U	-0.0255	0.1295	0.844		

Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
tot_biom_sown	fert = F	0.0255	0.1295	0.844		
Decomp	Rao_TPD	-0.2148	0.1077	0.05*		
Decomp	cwm_biom_Dim.2	-0.5391	0.1072	<0.001***		
Decomp	fert	-	-	0.711		
Decomp	fert = U	0.0368	0.1399	0.793		
Decomp	fert = F	-0.0368	0.1399	0.793		
multF_NutPool	Rao_TPD	-0.0203	0.133	0.879		
multF_NutPool	cwm_biom_Dim.1	0.0619	0.1326	0.642		
multF_NutPool	cwm_biom_Dim.2	-0.1337	0.1659	0.423		
multF_NutPool	tot_biom_sown	-0.0631	0.1456	0.666		
multF_NutPool	Decomp	-0.0777	0.1357	0.569		
multF_NutPool	fert	-	-	0.84		
multF_NutPool	fert = U	-0.0235	0.1631	0.886		
multF_NutPool	fert = F	0.0235	0.1631	0.886		
pH	tot_biom_sown	-0.2187	0.1012	0.034*		
pH	Decomp	0.2451	0.1009	0.018*		
pH	multF_NutPool	-0.2868	0.1004	0.006**		
pH	fert	-	-	0.012*		
pH	fert = U	-0.2571	0.1406	0.072		
pH	fert = F	0.2571	0.1406	0.072		
EC	Rao_TPD	-0.2067	0.1047	0.052		
EC	multF_NutPool	0.2552	0.1042	0.017*		
EC	fert	-	-	0.024*		
EC	fert = U	-0.2403	0.1467	0.106		
EC	fert = F	0.2403	0.1467	0.106		
GH	cwm_biom_Dim.2	-0.2729	0.1138	0.019*		
GH	Decomp	-0.2605	0.1129	0.024*		
GH	multF_NutPool	0.3499	0.101	0.001***		
GH	fert	-	-	0.093		
GH	fert = U	0.1692	0.1407	0.233		
GH	fert = F	-0.1692	0.1407	0.233		
~~pH	~~EC	0.3793	-	<0.001***		
ure	tot_biom_sown	-0.0692	0.113	0.542		
ure	multF_NutPool	-0.1835	0.1262	0.15		
ure	pH	0.0666	0.1261	0.599		
ure	EC	-0.2898	0.1238	0.022*		
ure	GH	-0.0567	0.1154	0.625		
ure	fert	-	-	0.244		

Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
ure	fert = U	0.1313	0.1526	0.393		
ure	fert = F	-0.1313	0.1526	0.393		

Chapter III

Synchrony matters more than species richness in plant community stability at a global scale

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Abstract

The stability of ecological communities is critical for the stable provisioning of ecosystem services, such as food and forage production, carbon sequestration and soil fertility. Greater biodiversity is expected to enhance stability across years by decreasing synchrony among species, but the drivers of stability in nature remain poorly resolved. Our analysis of time-series from 79 data sets across the world showed that stability was associated more strongly with the degree of synchrony among dominant species than with species richness. The relatively weak influence of species richness is consistent with theory predicting that the effect of richness on stability weakens when synchrony is higher than expected under random fluctuations, which was the case in most communities. Land management, nutrient addition and climate change treatments, had relatively weak and varying effects on stability, modifying how species richness, synchrony and stability interact. Our results demonstrate the prevalence of biotic drivers on ecosystem stability, with the potential for environmental drivers to alter the intricate relationship among richness, synchrony and stability.

Significance statement

The stability of ecological communities under ongoing climate and land-use change is fundamental to the sustainable management of natural resources through its effect on critical ecosystem services. Biodiversity is hypothesized to enhance stability through compensatory effects (decreased synchrony between species). However, the relative importance and interplay between different biotic and abiotic drivers of stability remains controversial. By analyzing long-term data from natural and semi-natural ecosystems across the globe, we found that the degree of synchrony among dominant species was the main driver of stability, rather than species richness *per se*. These biotic effects overrode environmental drivers, which influenced the stability of communities by modulating the effects of richness and synchrony.

1. Introduction

Understanding the mechanisms that maintain ecosystem stability (Thibaut & Connolly, 2013) is essential for the stable provisioning of multiple ecosystem functions and services (Isbell *et al.*, 2018; Tilman & Downing, 1994). Although research on community stability has decades of history in ecology (McNaughton, 1978), with stability often measured as the inverse coefficient of variation across years of community abundance or biomass, the main drivers of stability remain elusive (Hautier *et al.*, 2015). Both abiotic and biotic drivers [e.g., climate, land-use and species diversity (Hallett *et al.*, 2014; Hautier *et al.*, 2014; Isbell *et al.*, 2015)] are expected to govern community stability. Among biotic drivers, the hypothesis that increases in species diversity begets stability in communities and ecosystems [Fig. 1 (de Mazancourt *et al.*, 2013; Gross *et al.*, 2014; Tilman & Downing, 1994; Zhang *et al.*, 2016)] has generated ongoing debate (Blüthgen *et al.*, 2016; McCann, 2000).

The stabilizing effect of biodiversity has been attributed to various mechanisms (McCann, 2000). Most biodiversity-stability mechanisms at single trophic levels involve some form of compensatory dynamics, which occur when year-to-year temporal fluctuations in the abundance of some species are offset by fluctuations of other species (Gonzalez & Loreau, 2009; McNaughton, 1978). Compensatory dynamics are associated with decreased synchrony among species, with synchrony defined as the extent to which species population sizes co-vary positively over time. Decreased synchrony, which is predicted to stabilize communities (Fig. 1a), can result from species-specific responses to environmental fluctuations (Allan *et al.*, 2011; Ives, Gross, & Klug, 1999; Loreau & de Mazancourt, 2013) and from temporal changes in competitive hierarchies (Tilman, 1996), as well as stochastic fluctuations. Importantly, it is expected that species richness can increase stability (Fig. 1c) by decreasing synchrony (Fig. 1e). This positive effect of richness on stability can be, in fact, a result of an increased chance that the community will contain species with differing responses to abiotic drivers or competition, leading to a reduction in synchrony (McCann, 2000). However, the effect of richness on stability should weaken when synchrony is higher than expected if species were fluctuating randomly and independently [*SI Appendix*, see Supplementary text S1 for expanded information (Doak *et al.*, 1998)]. At the same time, other biotic drivers, together with richness and synchrony, have the potential to interact and buffer the effects of on-going climatic and land-use changes. These additional biotic drivers include community evenness, which can both increase or decrease synchrony (Thibaut & Connolly, 2013) or the presence of more stable species, for example, characterized by more conservative resource strategies (Majeková *et al.*, 2014). Long-term empirical data from natural communities can help us reveal the real-world effects of biotic drivers on community stability (Hautier *et al.*, 2014).

Here we explore the generality of biodiversity-synchrony-stability relationships, and their implications in a global change context, across multiple ecosystems and a wide range of environments. We compiled data from 7788 natural and semi-natural vegetation plots that had annual measurements spanning at least six years, sourced from 79 data sets distributed across the World (*SI Appendix*, Fig. S1). Most of the data sets include information about human activities related to global change through the application of experimental treatments, including fertilization, herbivore exclusion, grazing, fire and climate manipulations (hereafter environmental treatments). Biodiversity, synchrony and stability are known to vary in response to climate and land-use, although knowledge of such responses is limited by lack of comparative data across major habitats and geographic extent (8, 13, 21). The compiled data allowed us to compare the relationships between species richness, synchrony [using the *log V* index, (Lepš, Májeková, Vítová, Doležal, & de Bello, 2018)] and stability against theoretical predictions (summarized in Fig. 1), across vegetation types, climates, and land-uses.

2. Results & Discussion

2.1. Interplay between species richness, synchrony and stability

Our results confirmed the general prevalence of negative synchrony-stability relationships: 71% of the data sets exhibited negative and significant relationships ($R^2m = 0.19$, i.e. variance explained by the fixed effects over all individual plots; Fig. 1b). We found similar results for other synchrony indices (*SI Appendix,* Figs. S2a-c). These findings support theoretical predictions (Fig.

1a) and previous empirical evidence (Gross *et al.*, 2014; Hautier *et al.*, 2014; Tilman & Downing, 1994) that lower levels of synchrony in species fluctuations stabilize overall community abundance, despite the large range of vegetation types, environmental treatments, and biogeographic regions we considered.

Our results highlight a second global pattern consistent with theory (Fig. 1c): higher species richness was associated with greater community stability ($R^2m = 0.06$; Fig. 1d). However, this relationship was not nearly as strong: only 29% of the data sets showed a positive and significant relationship. The high proportion of non-significant species richness-stability relationships was unexpected, as species richness is generally considered one of the strongest drivers of stability (de Mazancourt *et al.*, 2013; Hallett *et al.*, 2014; Tilman, Reich, & Knops, 2006; Zhang *et al.*, 2016). Nevertheless, in observational data sets species richness may covary with other factors that influence inter-annual community variability, potentially masking any direct effect of species richness (Tredennick, Adler, & Adler, 2017).

Species richness was positively and significantly associated with synchrony across all studies, and the expected negative relationship predicted by theory was found in only 8% of our data sets (Fig. 1f). Such low frequencies of negative richness-synchrony relationships contradict both theoretical predictions (Fig. 1e) and previous studies. For instance, a recent richness-manipulated experimental study showed a negative relationship between richness and synchrony (Craven *et al.*, 2018), although this could be driven by the low levels of species richness applied in that experiment. We note that in natural or semi-natural communities, such as those analyzed here, richness often exceeds the low levels commonly applied in experimental studies that manipulate richness. Our results showed that while the relationship between synchrony and species richness across data sets depended on the index of synchrony considered (Figs. 1f, *SI Appendix*, S2a-c and see Supplementary Text S1 and S2 for expanded information), in most cases it was relatively weak. Our results thus provide only partial support for the hypothesis that more diverse communities are more stable due to the negative effect of richness on

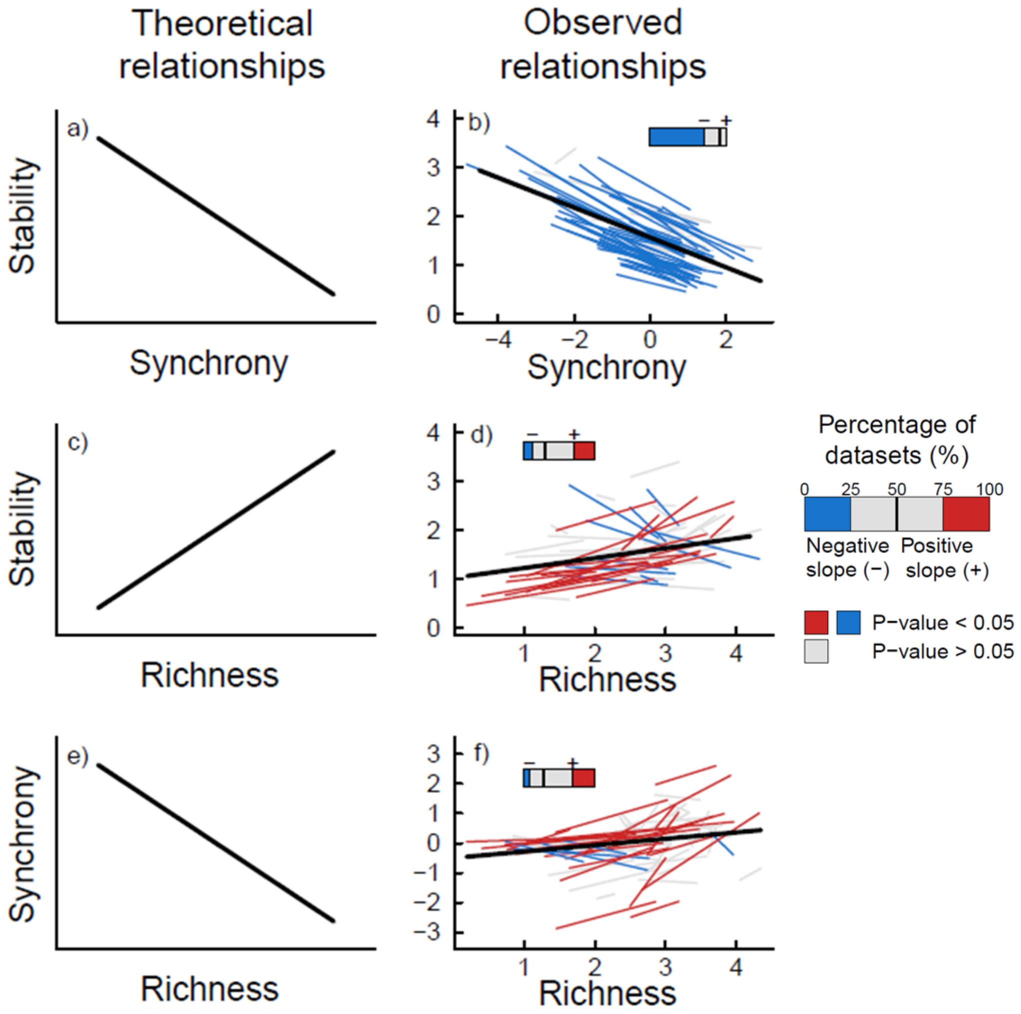

Figure 1: Relationships between synchrony and stability (a, b), richness and stability (c, d), and richness and synchrony (e, f). Richness and stability were ln-transformed. Left panels (a, c, e) are the schematic representation of these relationships following theoretical predictions (Doak *et al.*, 1998; McCann, 2000; Thibaut & Connolly, 2013; Valone & Barber, 2008). Right panels depict these relationships for each data set (b, d, f; n = 79). Red, blue and grey lines respectively represent the statistically significant positive, negative and non-significant slopes. Black lines show each relationship based on all plots (n = 7788), using a linear mixed-effects model with data sets as a random factor; these were all statistically significant. The synchrony index was *log V* (Lepš *et al.*, 2018).

synchrony (Blüthgen *et al.*, 2016; Hautier *et al.*, 2014; Lepš *et al.*, 2018). Indeed, we expected to observe a negative relationship between species richness and synchrony, particularly for those plots and data sets where the relationship between species richness and stability was strong.

To better understand our results, we explored a random fluctuation scenario which we approximated using null models that disrupt synchrony patterns between co-occurring species (see methods and *SI Appendix,* Supplementary Text S2). Specifically, we compared the relationships observed among richness, synchrony and stability against values expected under random species fluctuations. We also considered potential mathematical constraints on these relationships (*SI Appendix,* Supplementary Text S1 and S2). This modelling exercise revealed that the observed relationship between species richness and stability was weaker than expected under random species fluctuations (observed relationship $R^2m = 0.059$; expected relationship $R^2m = 0.157$). However, the relationship between synchrony and stability was greater than expected under the null model (observed relationship $R^2m = 0.191$; expected relationship $R^2m = 0.021$; *SI Appendix,* Supplementary Text S2), particularly for the index of synchrony we focused on the main text. Note, also, that for this index the observed relationship between richness and synchrony was lower than expected by chance (observed relationship $R^2m = 0.024$; expected relationship $R^2m = 0.082$; see Methods) and very weak. Most importantly, synchrony between species was higher than expected under the random fluctuations scenario, regardless of the index used (based on paired t-test, $P < 0.001$; t = 6.38; mean observed synchrony = -0.02 and mean expected synchrony = -0.08). These findings show that, in natural ecosystems, synchrony in species abundances (positive covariances) are more common than random fluctuations or negative covariances (Houlahan *et al.*, 2007), likely because many species-rich communities contain ecologically similar species, with similar responses to weather (Doak *et al.*, 1998; Lepš, 2004). When synchrony is greater than expected under random fluctuations, the effect of richness on synchrony and stability will be reduced [*SI Appendix*, Supplementary Text S1 (Doak *et al.*, 1998; Thibaut & Connolly, 2013)]. Our results provide empirical evidence that, for a wide range of ecosystems, species richness does promote stability, but this effect is not necessarily caused by a direct, negative effect of richness on synchrony.

2.2. Predictors of Ecosystem Stability

We examined whether synchrony and stability are mediated by different drivers, an issue that is gaining momentum in a global change context (Hautier *et al.*, 2014; Isbell *et al.*, 2015; Lepš *et al.*, 2018). We evaluated the effect of climate, vegetation type, environmental treatments and biotic attributes (percentage of woody species, species evenness and richness) on synchrony and community stability (*SI Appendix*, Table S1). Overall, the combined effect of environmental treatments reduced both temporal synchrony and stability (Figs. 2a and 2b). While the effect size of the combined treatments was small compared to biotic factors (*SI Appendix*, Table S1), this mostly reflects opposing effects of different treatment types (SI *Appendix*, see Supplementary text S3 for expanded information).

Using only those data sets with similar treatments and associated control plots (fertilization, herbivore exclusion, grazing intensification, removal plant species, fire and manipulative climate-change drivers), we ran separate analyses to disentangle the effect of the environmental treatments on synchrony and stability. Fertilization and herbivore exclusion significantly decreased synchrony, whereas intensification of grazing significantly increased synchrony (Fig. 2c). These relationships were partially unexpected because previous studies have shown that fertilization could promote synchrony (Zhang *et al.*, 2016) while grazing intensification could decrease it (Blüthgen *et al.*, 2016). However, in agreement with our results, Lepš *et al.* (Lepš *et al.*, 2018) demonstrated in a local study that while nutrient enrichment increases competition among plant species, it also decreases stability by increasing differences in productivity between favourable and unfavourable years. This could override the potential compensatory dynamics due to synchrony. Moreover, herbivore exclusion or a reduction in grazing intensity acted to increase community stability (Fig. 2d). These results suggest that herbivory affects interspecific competition, promoting the species best-adapted to grazing, but reducing the year-to-year stability of the community (Lepš *et* *al.*, 2018). Overall, these results show that changes in environmental drivers, associated to global change scenarios, can disrupt the interplay between diversity, synchrony and stability, even reversing the expected effects of biotic drivers on stability. Thus, the joint consideration of a wide variety of factors provides novel insights into the relationships underlying synchrony and stability, enhancing the future prediction of community stability in the face of global changes.

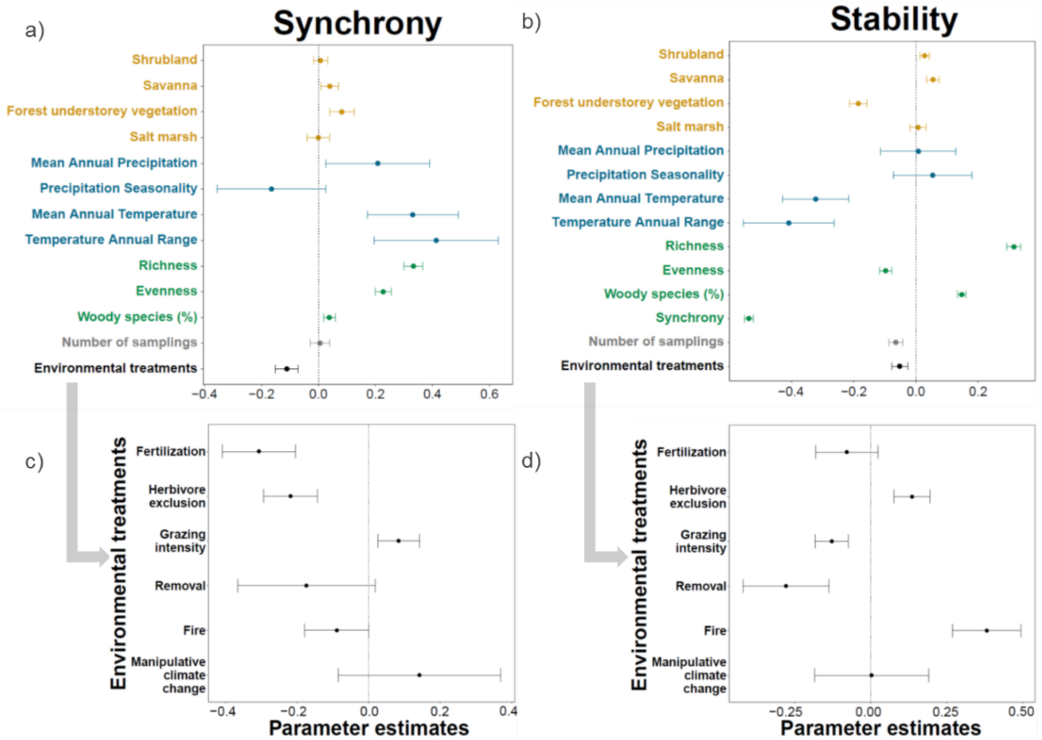

Figure 2. Effects of multiple abiotic and biotic drivers on the synchrony values (a, c) and stability (b, d) of the different communities. We show the averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals. In panels a and b, all the predictors were evaluated together using general linear mixed-effect models (n = 7788). The colours represent the different drivers of vegetation type (orange, grassland is the reference level), climatic data (blue), biotic attributes (green), number of measurements (grey) and global change treatments (black). The effects of each environmental treatment on synchrony values and stability (c, d) were evaluated separately and only for the studies where each driver was measured [fertilization: n = 1058, DS (number of data sets evaluated) = 17; herbivore exclusion: n = 2284, DS = 19; grazing intensity: n = 1920, DS = 24; removal plant species: n = 518, DS = 8; fire: n = 974, DS = 11; manipulative climate change: n = 122, DS = 5].

It should be noted that nutrient addition and/or grazing pressure could promote directional changes in species composition, with some species increasing over the years and others decreasing (Lepš, Götzenberger, Valencia, & de Bello, 2019). This could cause a decrease in synchrony values for indices studied here (Enrique Valencia *et al.*, 2020), with the indices not only reflecting year-to-year fluctuations due to compensatory dynamics but also these long-term trends. More research is certainly needed in the future to account for the effect of directional trends on the interplay of biotic and abiotic effects on stability.

We found that forest understorey vegetation was more synchronous and less stable than grasslands, shrublands and savannas (Fig. 2b), similarly to Blüthgen *et al.* (2016). We suggest that forest understorey vegetation has weaker compensatory effects that lead to destabilization. Also, this result could be related to the fact that we excluded from the analyses the tree layer, i.e. the most stable vegetation layers in these systems. Alternatively, this vegetation might support a greater proportion of rare species, which benefit from shared favourable conditions (P Chesson & Huntly, 1997) increasing the synchrony of the community. Finally, communities with a greater proportion of woody species were more stable. The longer life span of woody species and their structural storage of carbon and nutrients should buffer them against environmental fluctuations and the fluctuations of other species, although we note that longer measurement timescales may be required to accurately capture their dynamics.

Finally, we found evidence of a positive evenness-synchrony association (Fig. 2a) and a negative evenness-stability association (Fig. 2b). In other words, low synchrony is more common in communities with low evenness that are dominated by a few species. These communities appear to fluctuate-less and are therefore more stable (Sasaki & Lauenroth, 2011; Valone & Balaban-Feld, 2018). This finding suggests two potential ecological mechanisms. First, these few species could be the best-adapted species and tend to perform well across years (i.e. have comparatively little fluctuations), thus promoting stability. In some cases, for example, species with slower growth strategies are locally more abundant and stable in time (Majeková *et* *al.*, 2014). Second, a small number of dominant species with different adaptations (Bello *et al.*, 2009; Lepš *et al.*, 2018; Pistón *et al.*, 2019) could lead to decreased synchrony and increased stability at the community level. If synchrony is a common feature of vegetation [as suggested by our study and in Houlahan *et al.* (Houlahan *et al.*, 2007)], evenness can have an effect on stability via synchrony (Fig. 3). Low synchrony among a small number of dominant species could thus represent an important stabilizing effect in ecosystems worldwide.

2.3. Direct and indirect effects of abiotic and biotic attributes on community stability

To clarify the ensemble of directional effects of abiotic and biotic factors on community stability, we generated a piecewise structural equation model (Fig. 3). Our model explained 88% of the variance in community stability and confirmed that the most important determinant of stability was the direct negative effect of synchrony. Analogous results were found when we evaluated either individual habitats or the control plots among habitats (*SI Appendix,* Figs. S3 and S4) or when other synchrony indices were used (*SI Appendix,* Figs. S5a and S5b). Further, mean annual temperature showed a direct, negative effect on stability, as in other studies (Hautier *et al.*, 2014), which was further reinforced via its indirect effects on evenness, species richness and synchrony (Fig. 3). Communities in more variable climates, such as Mediterranean environments, should show large variation in productivity from year to year, increasing synchrony between species and decreasing stability of the whole community. Again, the positive associations between species richness-synchrony and evenness-synchrony suggest that the stabilizing effect of communities originates from lower synchrony among the dominant species (Koerner *et al.*, 2018) rather than by the number of species *per se* (Allan *et al.*, 2011; Sasaki & Lauenroth, 2011), emphasizing the role of evenness in the distribution of abundance over time.

Overall, this study demonstrates the consistent cross-system importance of the interplay among species richness, synchrony and environmental parameters in the prediction of community stability. As expected, low synchrony and high species richness defined the primary stabilizing pattern of

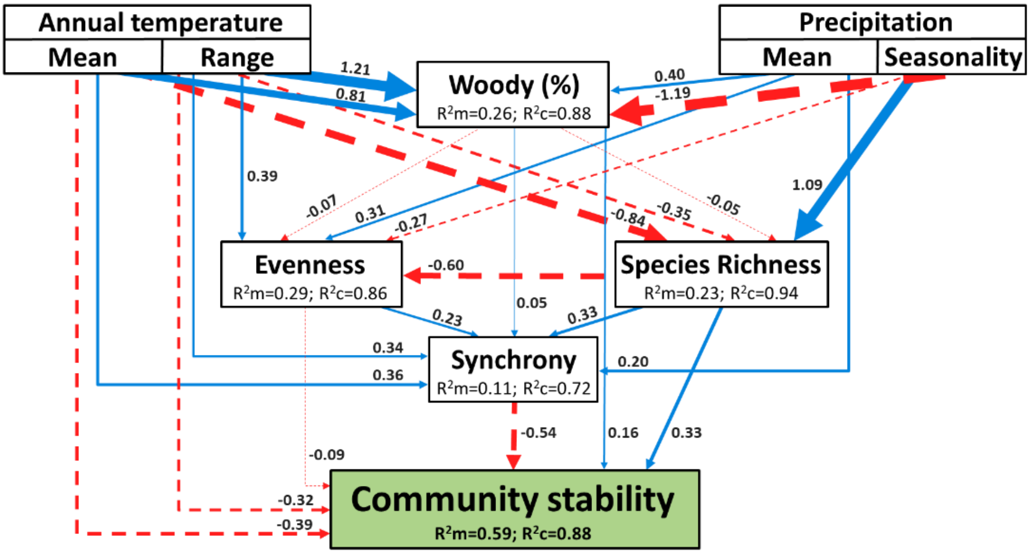

Figure 3: Piecewise structural equation model showing the direct and indirect effects of multiple abiotic and biotic drivers on the stability across the 79 data set (Fisher's C statistic: C = 14.96, p = 0.134, n = 7788). Marginal (R2m) values showing variance explained by the fixed effects, and conditional (R2c) values showing variance explained by the entire model, are provided for each response variable. Solid lines represent positive effects, while dashed lines indicate negative effects. Blue and red lines represent statistically significant effects and grey lines non-significant effects. The width of each arrow is proportional to the standardized path coefficients (more information SI Appendix, Table S5).

communities (de Mazancourt *et al.*, 2013). However, contrary to expectation, the stabilizing effects of species richness via synchrony were relatively weak. Yet, despite a prevalence of synchrony between species found in our communities, richness had a net positive association with stability (direct effect + indirect effects = 0.23; Fig. 3), implying an important effect of richness unrelated with synchrony. Environmental factors associated with different global change drivers also directly or indirectly affect stability, and have the potential to reverse the effects of biodiversity and synchrony on stability, although biotic factors generally had a stronger effect. Our results suggest that interventions aiming to buffer ecosystems against the effects of increasing environmental fluctuations should focus on promoting the maintenance or selection of dominant species with different adaptations or strategies that will result in low synchrony, rather than by focusing on increasing species richness *per se*. Further, the evaluation of the direct effects of evenness and environmental drivers on stability adds new insights on the complex underlying biotic and abiotic relationships. To consider these different drivers of stability in concert is critical for defining the potential of communities to remain stable in a global change context.

3. Methods

We used data from 79 plant community data sets where permanent or semi-permanent plots of natural and semi-natural vegetation have been consistently sampled over a period of 6 to 99 years (*SI Appendix*, Fig. S1 and S6, Table S2 and Supplementary Text S4). We focused our analyses on vascular plants as the main primary producers affecting subsequent trophic levels and ecosystem functioning. These data sets have some differences, such as the method used to quantify *abundance* (*e.g.* aboveground biomass, visual species cover estimates and species individual frequencies), plot size (median = 1 m^2; range = 0.04 to 400 m^2), vegetation type (grassland, shrubland, savanna, forest and salt marsh), and number of sampling dates (median = 11.5; range = 6 to 38). The studies encompassed different localities with different species pools and different types of vegetation responding to different types of treatments. The total number of individual plots was 7788 across the 79 data sets (number of observations ~ 190900).

3.1. Climatic data

We collected climatic information related to temperature and precipitation for each of the 7788 plots using WorldClim (www.worldclim.org) where location coordinates were available. Where these were not available, weather data were derived from the study centroid. We selected four variables: mean annual temperature (ºC) and mean annual precipitation (mm), related to annual trends, and mean annual temperature range and coefficient of variation of precipitation within years as proxies for annual seasonality (Hautier *et al.*, 2014). These variables were selected from the 19 available WorldClim climatic variables because they describe relatively independent climatic features and account for most of the other climatic relationships observed with our data (see climatic variable correlation in *SI Appendix*, Table S3).

3.2. Biotic attributes

In each plot, we calculated stability over time as the inverse of the coefficient of variation (standard deviation/mean) of the year-to-year fluctuations of total *abundance* of that community. This has been widely used as a reliable estimator of temporal invariability (McArdle & Gaston, 1995). Standard deviation was based on *n-1* degrees of freedom. We only included data sets using percentage cover as an estimate of community structure if the summed cover was not constrained.

Although we did not measure ecosystem services directly, multiple studies highlight the importance of a stable vegetation (primary producers) for a stable delivery of multiple key ecosystem processes. For example, *biomass* or *abundance* are often considered to be ecosystem functions in their own right (e.g. forage production and carbon sink), while these can also act as a proxy or driver of other functions, including litter quantity, soil organic matter, evapotranspiration or erosion control. Clearly, the value of stability depends on its relationship to the provision of specific ecosystem services, and temporal invariability does not necessarily imply a positive effect on the ecosystem service of interest. Our study aims at identifying ecological drivers of stability at a global scale.

In each plot, we also calculated various indices that characterize the biotic attributes of the community averaged over all annual observations: average species richness [average number of species (Tilman & Downing, 1994; Tilman, Lehman, & Bristow, 1998)], the average percentage of woody species per year, and evenness (using the E_{var} index ; Smith & Wilson 1996):

$$Evar = 1 - 2/\pi \arctan\left\{\sum_{s=1}^{S}\left(\ln(x_s) - \sum_{t=1}^{S} ln(x_t)\,/S\right)^2 /S\right\}$$

where S is total number of species in the community and x_s is the abundance of the *s-th* species. Finally, we calculated synchrony (log-variance ratio index: *log V* ; Lepš *et al.* 2018) as follows:

$$log\,V = \ln\left(\frac{var(\sum_{i=1}^{S} x_i)}{\sum_{i=1}^{S} var(x_i)}\right)$$

where x_i is the vector of abundances of the *i-th* species over time. The *log V* index ranges from -Inf to +ln(S). For this index, positive values indicate a common response of the species (synchrony, formally positive sum of covariances in the variance-covariance matrix), while values close to zero indicate a predominance of random fluctuations, and negative values indicate negative covariation between species. One theoretical issue of this index is that its upper limit is a function of species richness and evenness, questioning its independence from those parameters. Our results, however, were not affected by this constraint. It is important to note that the observed index value can vary considerably within its theoretical range; in fact the relationship between richness and *log V* index is very weak. The chance of reaching maximum synchrony decreases with the number of species. To reach maximum synchrony, there must always be perfect synchrony between all species pairs, no matter how many species are in the community [i.e. with n species, the correlation of n (n-1)/2 pairs must be perfect (i.e. 1) within each pair]. The values of synchrony that would be close to the maximum 1 were not present in real communities (such as those that are the focus of this manuscript). Thus, the upper limit of *log V*, which represents the caveat to the use of this metric, is not invalidating our results.

To ensure that our results were not biased by the choice of this index, we calculated other commonly used indices, specifically the Gross (Gross *et al.*, 2014), Gross' weighted (Blüthgen *et al.*, 2016) and phi (Loreau & de Mazancourt, 2008) synchrony indices. Following Blüthgen *et al.* (2016), we weighted the abundance of species to decrease the influence of rare species that can vary substantially while having a negligible abundance. Both Gross and Gross' weighted synchrony indices were positively correlated with *log V* index (r = 0.75 and 0.86, respectively, *SI Appendix*, Table S4) and gave concordant results. The phi synchrony index was also positively correlated with the *log V* index but negatively with species richness (r = 0.48 and 0.41, respectively, *SI Appendix,* Table S4), an expected output as this index builds in the decrease in synchrony with increasing species richness expected when species have independent population dynamics (Loreau & de Mazancourt, 2008). We only present the results of *log V* in the main text both for clarity and because the models with this index had the lowest AIC values and explained more variance

(R^2m = 0.59, *SI Appendix,* Table S1) than those using the alternate indices. Similarly, this index showed a greater difference between the observed synchrony-stability relationships and the ones generated by null-models (SI *Appendix,* see Supplementary texts S2 for expanded information).

Previous research has identified the relationship between stability and synchrony, both in biological (McCann, 2000) and mathematical terms (Thibaut & Connolly, 2013). However, it has also been shown that stability is affected by a number of other factors (Craven *et al.*, 2018; Hallett *et al.*, 2014; Lepš *et al.*, 2018; McCann, 2000; Thibaut & Connolly, 2013). Given these multiple influences, the relationship between synchrony and stability would not necessarily be expected to be consistently significant or characterised by a strong correlation. We assessed this relationship for the different indices in comparison with null-models that assume random, independent species fluctuations (SI *Appendix*, see Supplementary texts S1 and S2 for expanded information).

We also considered the vegetation type of each plot based on the characterization of the community by the authors of the study (grassland, shrubland, savanna, forest and salt marsh). Savanna was characterized as a grassland scattered with shrubs and/or trees while maintaining an open canopy. For forest plots, we restricted our analysis to data sets that measured understorey vegetation.

3.3. Analysis

Linear models were used to evaluate the relationships between: i) synchrony and species richness; ii) species richness and stability; and iii) synchrony and stability. In all cases, richness and stability were ln-transformed to improve their normality. We obtained the slope and the significance for these relationships individually for each of the 79 data sets as well as for all the plots together. We used a null model approach to compare the observed values of stability and synchrony and observed richness-synchrony and richness-stability relationships to expected values under a random fluctuation scenario. To do so, we randomized species abundances within a plot across years, by means of torus randomizations (also referred to as cyclic shifts). This approach preserves the temporal sequence of values within a species, but changes the starting year. In each individual plot, the sequence of abundance values of each species was shifted 999 times, using a modification of the ‘cyclic_shift’ function in the *codyn* package for the R statistical software (Hallett *et al.*, 2016). This procedure kept the total (i.e. summed) species abundance constant for each species but varied (and therefore disconnected) the temporal co-incidence of species abundances within years. Based on the 999 randomizations, we calculated values of mean expected synchrony and stability. We used a paired t-test to evaluate the relationship between observed and expected values of synchrony. We then tested the relationship between observed species richness and (i) observed and expected synchrony and (ii) observed and expected stability, using linear mixed-effects models with data set as a random factor. Additionally, we used the same models to test the relationship between observed synchrony and stability, and expected synchrony and stability.

We performed linear mixed-effects models over all individual plots ($n = 7788$) to assess the effects of the abiotic and biotic variables on synchrony (*log V*). We included climatic data, vegetation type, percentage of woody species, evenness, species richness, number of years each plot was sampled and environmental treatments as predictors in the model; data set was a random factor. Environmental treatments constituted a binary variable (0 = control plots *vs* 1 = environmental treatments). The mean and confidence interval of the parameter estimates of the predictors were used to model their effects on synchrony values among all the plots of the 79 studies. Mean annual precipitation, temperature annual range, richness and stability were ln-transformed to improve their normality. All predictors were centred on their mean and standardized by their standard deviation. For vegetation type, the parameter estimates were obtained by fixing grasslands as a reference level for the other habitats. We analyzed the effects of the biotic and abiotic factors and synchrony values on stability, using the same approaches previously described. Although plot size was originally included in our model, this variable was not significant ($\chi^2 < 0.01$; $P = 0.95$) so was removed as predictor. To evaluate the individual effect of each environmental treatment on synchrony values and stability, treatments were grouped into six categories (fertilization, herbivore exclusion, grazing intensity, removal, fire and manipulative climate-change drivers), retaining only data sets where these treatments were applied or assessed.

Finally, we conducted a stepwise selection of a piecewise structural equation model [SEM (J. B. Grace, 2006)] to test direct and indirect pathways of biotic and abiotic factors on stability. A piecewise SEM is a confirmatory path analysis using a d-step approach (Laliberte & Legendre, 2010; Shipley, 2009). This analysis is a flexible framework to incorporate different model structures, distributions and assumptions. This method is based on an acyclic graph that summarizes the hypothetical relationships between variables to be tested using the C statistic (Shipley, 2013). We built an initial SEM containing all possible biotic and abiotic relationships, independent of the vegetation type evaluated. Then, we used the Akaike information criterion (AIC) to select the minimal and best model (Shipley, 2013) based on the initial SEM, using the stepAIC procedure (J. B. Grace, 2006). This process selects the most important paths and removes the majority of non-significant paths. Standardized path coefficients were used to measure the direct and indirect effects of predictors (J. B. Grace & Bollen, 2005). We conducted the SEM analyses across all individual plots (n = 7788), for non-treatment plots across all habitats (n = 4013), and for plots of each vegetation type separately (except in salt marsh). In all the models, data sets were considered as a random factor.

All analyses were carried out with R (R Core Team, 2016) (R Development Core Team, 2011), using packages piecewiseSEM (Lefcheck, 2016), lme4 (Bates, Mächler, Bolker, & Walker, 2014), and modified source code in codyn (Hallett *et al.*, 2016).

Data Availability

The data that support the findings of this study are available at Figshare (E. Valencia *et al.*, 2020).

Acknowledgements

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Supplementary material

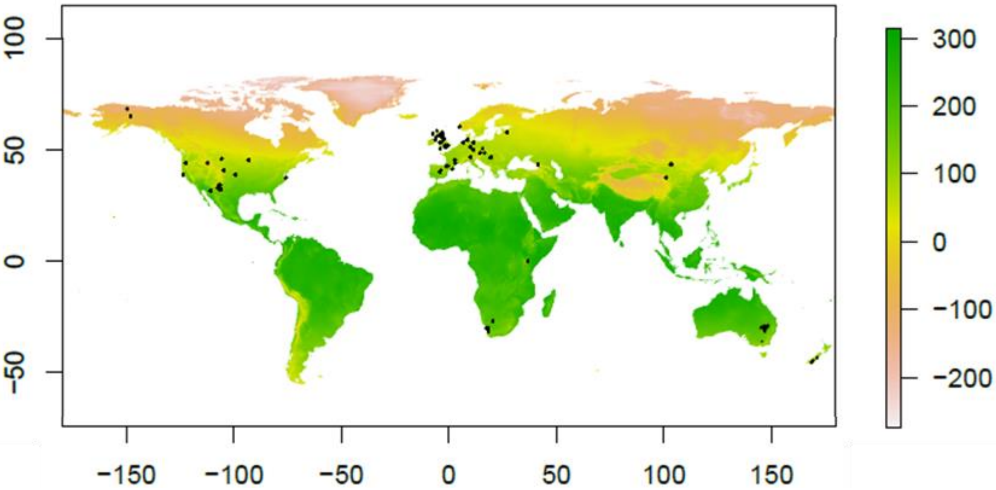
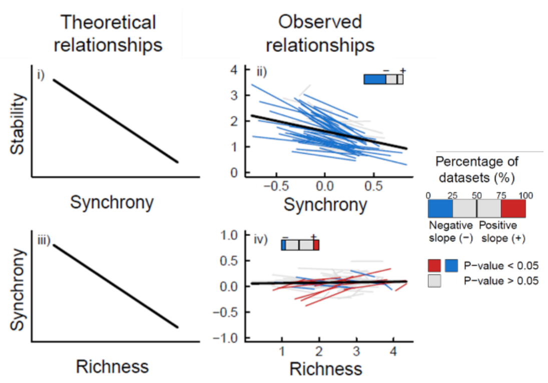
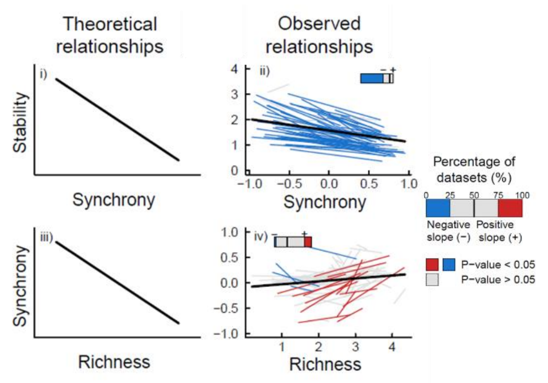


Figure S1: Map with the geographical position of the study sites. The colour indicates mean annual temperature (°C*10).

a) Synchrony index: *Gross* η (Gross *et al.*, 2014)



b) Synchrony index: *Gross weighted* η_w
(Blüthgen *et al.*, 2016)



c) Synchrony index: *phi index* (Loreau & de Mazancourt, 2008)

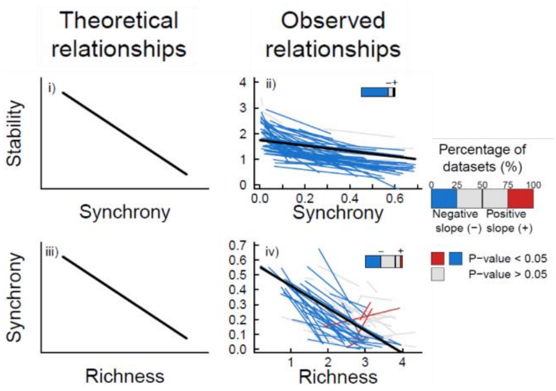
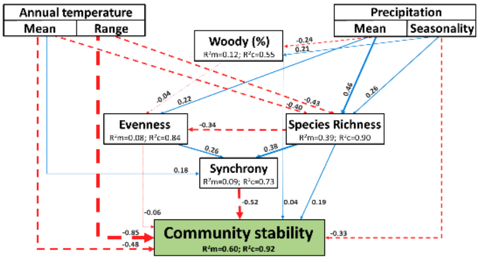
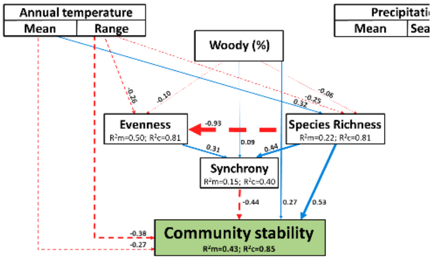


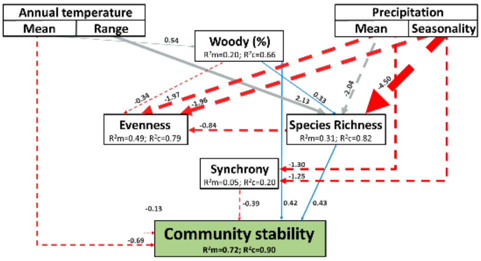
Figure S2: Relationships between synchrony-stability (i, ii) and richness-synchrony (iii, iv), with different synchrony indices: a) *Gross* η (Gross *et al.*, 2014), b) *Gross weighted* η_w (Blüthgen *et al.*, 2016), and c) *phi index* (Loreau & de Mazancourt, 2008). Richness, stability and *phi index* were ln-transformed. Left panels (i, iii) are the schematic representation of these relationships following theoretical predictions (Doak *et al.*, 1998; McCann, 2000; Thibaut & Connolly, 2013; Valone & Barber, 2008). Right panels depict these relationships for each data set (ii, iv; n = 79). Red, blue and grey lines respectively represent the statistically significant positive, negative and non-significant slopes. Black lines show each relationship based on all plots (n = 7788), using a linear mixed-effects model with data sets as a random factor; these were all statistically significant.



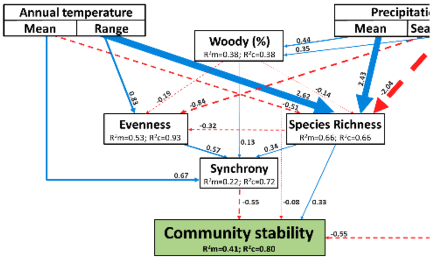
a) Vegetation type: grassland



b) Vegetation type: savanna



c) Vegetation type: shrubland



d) Vegetation type: forest understorey

Figure S3: Piecewise structural equation models (SEMs) showing the direct and indirect effects of multiple abiotic and biotic drivers on stability across the different vegetation types. We used only grassland (Fig. a; Fisher's C statistic: C = 27.08, *P* = 0.208, n = 4708), savanna (Fig. b; Fisher's C statistic: C = 21.66, *P* = 0.916, n = 1751), shrubland (Fig. c; Fisher's C statistic: C = 26.21, *P* = 0.562, n = 770) and forest plots (Fig. d; Fisher's C statistic: C = 19.48, *P* = 0.616, n = 347) to run the different SEMs. Mean annual precipitation, temperature annual range, richness and stability were ln-transformed. Marginal (R^2m) values showing variance explained by the fixed effects, and conditional (R^2c) values showing variance explained by the entire model, are provided for each response variable. Solid lines represent positive effects, while dashed lines indicate negative effects. Blue and red lines represent statistically significant effects and grey lines non-significant effects. The width of each arrow is proportional to the standardized path coefficients (more information Table S5).

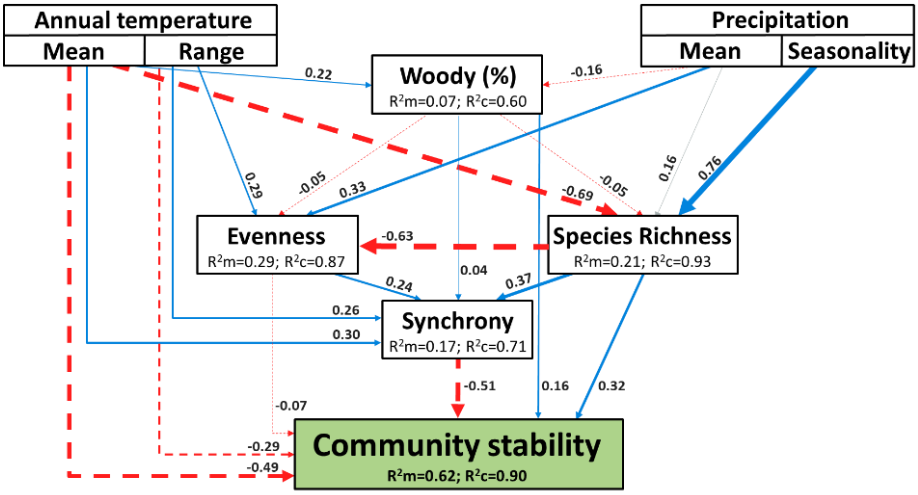
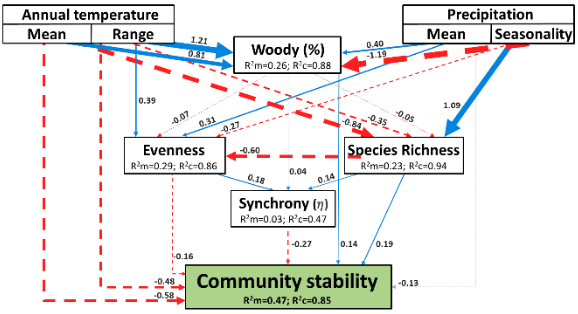
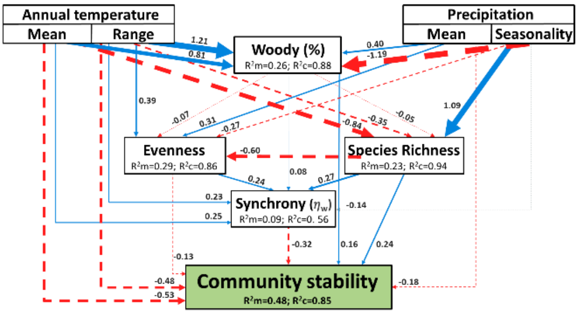


Figure S4: Piecewise structural equation model showing the direct and indirect effects of multiple abiotic and biotic drivers on stability of different ecosystems (Fisher's C statistic: C = 10.61, P = 0.910, n = 4013) using only the control plots of each data set. Mean annual precipitation, temperature annual range, richness and stability were ln-transformed. Marginal (R2m) values showing variance explained by the fixed effects, and conditional (R2c) values showing variance explained by the entire model, are provided for each response variable. Solid lines represent positive effects, while dashed lines indicate negative effects. Blue and red lines represent statistically significant effects and grey lines non-significant effects. The width of each arrow is proportional to the standardized path coefficients (more information Table S5).

a) Synchrony index: *Gross η* (Gross *et al.*, 2014)



b) Synchrony index: *Gross weighted* η_w (Blüthgen *et al.*, 2016)



c) Synchrony index: *phi index* (3)

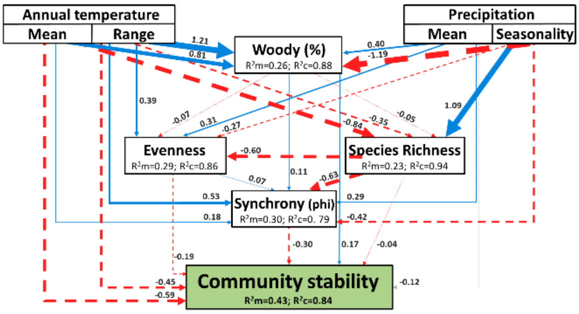


Figure S5: Piecewise structural equation model showing the direct and indirect effects of multiple abiotic and biotic drivers with different synchrony indices: a) *Gross η* (Gross *et al.*, 2014), b) *Gross weighted* η_w (Blüthgen *et al.*, 2016), and c) *phi index* (Loreau & de Mazancourt, 2008) on stability across the 79 data set (a: Fisher's C statistic: C = 12.09, *P* = 0.599, n = 7788; b: Fisher's C statistic: C = 5.97, *P* = 0.650, n = 7788; c: Fisher's C statistic: C = 6.37, *P* = 0.383, n = 7788). Mean annual precipitation, temperature annual range, richness, *phi index* and stability were ln-transformed. Marginal (R^2m) values showing variance explained by the fixed effects, and conditional (R^2c) values showing variance explained by the entire model, are provided for each response variable. Solid lines represent positive effects, while dashed lines indicate negative effects. Blue and red lines represent statistically significant effects and grey lines non-significant effects. The width of each arrow is proportional to the standardized path coefficients (more information Table S5).

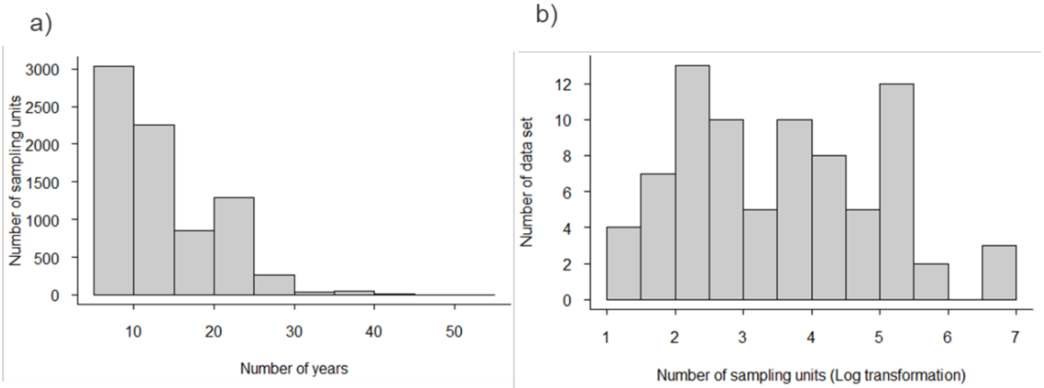


Figure S6: Histograms of the number of plots sampled at different time intervals (a) and number of sampling units (log-transformed) per data set (b).

Table S1: Summary results of the linear mixed-effect models. These models evaluated the effects of vegetation type [dummy variable: grassland (reference level), shrubland, savanna, forest and salt marsh] weather condition variability (mean annual precipitation, precipitation seasonality, mean annual temperature and temperature annual range), species richness, evenness, percentage of woody species, number of samplings and global change treatments on synchrony and stability (ln(1/CV)). Global change treatments had two levels control plots *vs* treatments plots pooled. Data set was considered as a random factor. R^2m: marginal model R^2; R^2c: conditional model R^2; AIC: Akaike information criterion (Akaike, 1998). * variable with ln transformation.

a) Synchrony index: *log V* (Lepš *et al.*, 2018)

		Synchrony (*log V*)			**Stability (ln (1/CV))**		
R^2m, R^2c and AIC		0.10,0.74 and 15023			0.59, 0.88 and 8532		
	DF	Est	Chi^2	*P* value	Est	Chi^2	*P* value
Shrubland	1	0.01	0.42	0.519	0.03	12.21	**<0.001**
Savanna	1	0.04	6.05	**0.014**	0.05	27.72	**<0.001**
Forest understorey vegetation	1	0.08	14.10	**<0.001**	-0.19	166.13	**<0.001**
Salt marsh	1	0.00	0.00	0.975	0.01	0.28	0.598
Mean Annual Precipitation*	1	0.21	5.03	**0.025**	0.01	0.02	0.902
Precipitation Seasonality	1	-0.16	2.84	0.092	0.05	0.70	0.403
Mean Annual Temperature	1	0.33	16.41	**<0.001**	-0.32	35.29	**<0.001**
Temperature Annual Range*	1	0.41	13.68	**<0.001**	-0.41	30.73	**<0.001**
Richness*	1	0.33	381.73	**<0.001**	0.32	750.44	**<0.001**
Evenness	1	0.23	238.28	**<0.001**	-0.10	98.33	**<0.001**
Woody species (%)	1	0.04	13.31	**<0.001**	0.15	464.07	**<0.001**
Number of samplings	1	0.01	0.11	0.737	-0.06	30.96	**<0.001**
Synchrony (*log V*)	1				-0.54	5181.66	**<0.001**
Global change treatments	1	-0.11	29.81	**<0.001**	-0.05	15.30	**<0.001**

b) Synchrony index: *Gross* η (1)

		Synchrony (η)			**Stability (ln (1/CV))**		
R^2m, R^2c and AIC		0.05, 0.49 and 18100			0.44,0.85 and 11255		
	DF	Est	Chi^2	*P* value	Est	Chi^2	*P* value
Shrubland	1	0.07	22.41	**<0.001**	0.04	18.66	**<0.001**
Savanna	1	0.13	44.74	**<0.001**	0.07	30.76	**<0.001**
Forest understorey vegetation	1	0.10	14.54	**<0.001**	-0.20	141.22	**<0.001**
Salt marsh	1	0.02	0.60	0.439	0.01	0.73	0.394
Mean Annual Precipitation*	1	0.11	1.59	0.208	-0.06	0.63	0.429
Precipitation Seasonality	1	0.11	1.50	0.220	0.15	3.72	0.054
Mean Annual Temperature	1	0.05	0.58	0.445	-0.48	52.56	**<0.001**
Temperature Annual Range*	1	0.05	0.27	0.606	-0.59	42.77	**<0.001**
Richness*	1	0.15	55.14	**<0.001**	0.18	170.60	**<0.001**
Evenness	1	0.16	82.06	**<0.001**	-0.18	233.56	**<0.001**
Woody species (%)	1	0.00	0.01	0.903	0.13	244.05	**<0.001**
Number of samplings	1	-0.04	4.33	**0.038**	-0.08	32.02	**<0.001**
Synchrony (η)	1				-0.27	1352.34	**<0.001**
Global change treatments	1	-0.11	20.34	**<0.001**	-0.02	2.09	0.148

c) Synchrony index: *Gross weighted* η_w (2)

		Synchrony (η_w)			**Stability (ln (1/CV))**		
R^2m, R^2c and AIC		0.10, 0.53 and 17940			0.48, 0.86 and 10600		
	DF	Est	Chi^2	*P* value	Est	Chi^2	*P* value
Shrubland	1	0.07	27.89	**<0.001**	0.05	25.25	**<0.001**
Savanna	1	0.11	35.45	**<0.001**	0.07	35.20	**<0.001**
Forest understorey vegetation	1	0.08	9.20	**0.002**	-0.21	157.84	**<0.001**
Salt marsh	1	0.00	0.02	0.880	0.01	0.24	0.626
Mean Annual Precipitation*	1	-0.02	0.07	0.789	-0.11	2.26	0.133
Precipitation Seasonality	1	0.00	0.00	0.956	0.11	2.08	0.149
Mean Annual Temperature	1	0.17	5.73	**0.017**	-0.43	46.88	**<0.001**
Temperature Annual Range*	1	0.10	1.07	0.301	-0.57	44.81	**<0.001**
Richness*	1	0.28	189.32	**<0.001**	0.23	308.87	**<0.001**
Evenness	1	0.22	156.75	**<0.001**	-0.15	172.08	**<0.001**
Woody species (%)	1	0.05	14.22	**<0.001**	0.14	331.26	**<0.001**
Number of samplings	1	-0.07	11.77	**<0.001**	-0.09	45.98	**<0.001**
Synchrony (η_w)	1				-0.33	2155.98	**<0.001**
Global change treatments	1	-0.11	20.75	**<0.001**	-0.03	3.88	**0.049**

d) Synchrony index: *phi index* (3)

		Synchrony (ln *phi*)			**Stability (ln (1/CV))**		
R^2m, R^2c and AIC		0.29, 0.75 and 15855			0.43, 0.85 and 11137		
	DF	Est	Chi^2	*P* value	Est	Chi^2	*P* value
Shrubland	1	0.11	72.96	**<0.001**	0.06	38.22	**<0.001**
Savanna	1	0.09	28.24	**<0.001**	0.06	25.78	**<0.001**
Forest understorey vegetation	1	-0.04	2.89	0.089	-0.24	203.45	**<0.001**
Salt marsh	1	0.00	0.03	0.873	0.01	0.32	0.574
Mean Annual Precipitation*	1	0.20	5.03	**0.025**	-0.03	0.15	0.695
Precipitation Seasonality	1	-0.10	1.18	0.277	0.11	2.00	0.158
Mean Annual Temperature	1	0.11	2.07	0.150	-0.47	50.39	**<0.001**
Temperature Annual Range*	1	0.22	4.32	**0.038**	-0.55	37.23	**<0.001**
Richness*	1	-0.62	1205.81	**<0.001**	-0.07	21.70	**<0.001**
Evenness	1	0.05	11.91	**<0.001**	-0.20	311.38	**<0.001**
Woody species (%)	1	0.07	38.58	**<0.001**	0.15	337.70	**<0.001**
Number of samplings	1	-0.20	113.44	**<0.001**	-0.13	91.00	**<0.001**
Synchrony (*phi*)	1				-0.32	1492.18	**<0.001**
Global change treatments	1	-0.10	20.23	**<0.001**	-0.02	2.29	0.130

Table S2: Main characteristics of the study sites. Climate variables were extracted from the WorldClim global database (www.worldclim.org).

COD	SU	Ns	Ri	AMT	TAR	MAP	PS	Vegetation	LAT	LON	Sa Me
1	42	12.5	10.9	7.6	46.5	329	62	GR	46.32	-105.80	Co
2	51	34.5	6.3	11.9	43.0	583	56	GR	38.80	-99.30	Co
3	24	13.5	8.5	8.4	40.6	365	60	GR	40.85	-104.71	Co
4	160	11.2	4.6	17.9	34.3	403	78	GR	31.83	-110.88	Co
5	23	21.5	16.8	5.8	43.2	253	36	SA	44.20	-112.20	Co
6	222	8.0	12.3	15.5	39.1	252	73	GR	32.83	-107.33	Fe
7	1001	11.5	5.2	14.8	37.8	275	76	GR and SH	32.93	-107.36	Co
8	20	10.7	9.9	20.1	34.5	184	75	GR	-26.76	20.61	Co
9	24	15.8	28.7	17.2	21.7	140	68	SA	-30.19	17.54	Co
10	40	14.7	30.0	15.2	25.5	255	49	SA	-30.40	18.28	Co
11	40	16.0	27.7	18.9	24.9	163	65	SA	-31.28	18.59	Co
12	380	14.5	7.0	10.9	30.9	538	25	SA	46.73	19.54	Co
13	50	7.0	8.0	6.3	45.6	751	51	GR	45.41	-93.16	Co
14	184	6.2	9.6	6.3	45.6	751	51	SA	45.41	-93.19	Fe
15	60	24.8	8.4	6.3	45.6	751	51	GR	45.41	-93.19	Bi
16	234	22.0	7.7	6.3	45.6	751	51	GR	45.40	-93.20	Bi
17	237	14.8	6.9	6.3	45.6	751	51	GR	45.40	-93.20	Bi
18	795	13.5	3.8	8.2	40.2	367	59	GR	40.85	-104.77	Co
19	96	6.0	11.2	8.8	25.1	572	19	GR	53.05	11.41	Co
20	12	6.0	23.2	8.6	18.1	711	18	SH	57.73	-3.10	Fe
21	193	21.4	12.4	7.6	27.1	2140	63	FO	44.35	-122.41	Co
22	47	10.2	27.8	19.7	30.4	446	31	SA	-30.12	147.17	Bi
23	8	8.0	7.5	7.8	18.8	729	15	GR	56.87	-2.60	Fe
24	16	28.0	13.4	10.6	26.3	793	15	GR	43.92	3.10	Fe
25	145	24.3	8.7	1.3	28.7	912	45	GR	43.45	41.69	Co
26	9	12.0	3.6	7.2	18.7	1189	21	SH	53.06	-3.47	Fe
27	400	10.0	12.5	11.5	21.1	1208	85	GR	38.85	-123.50	Co
28	68	27.8	2.6	14.7	39.4	257	72	GR	32.62	-106.67	Co
29	4	16.8	8.8	3.2	24.2	921	27	GR	50.69	15.71	Bi
30	4	29.8	27.5	4.6	26.2	809	32	GR	50.69	15.79	Bi
31	28	18.9	5.2	14.2	31.3	1027	12	GR	37.67	-75.67	Co
32	12	12.0	31.6	10.6	25.8	939	19	GR	42.72	-1.22	Fe
33	8	6.0	20.3	-11.4	51.8	228	61	GR	68.62	-149.61	Co
34	4	6.0	10.5	-11.5	51.8	225	64	GR	68.63	-149.58	Co
35	15	7.7	14.7	8.3	26.3	645	21	GR	49.92	11.59	Co

COD	SU	Ns	Ri	AMT	TAR	MAP	PS	Vegetation	LAT	LON	Sa Me
36	7	8.0	38.4	8.6	29.3	605	35	GR	48.87	16.64	Co
37	10	13.0	19.1	7.4	24.4	877	19	GR	45.64	2.73	Fe
38	48	9.0	2.3	8.3	40.5	366	60	GR	40.85	-104.71	Fe
39	12	16.0	27.5	7.6	28.8	769	33	GR	48.95	14.59	Bi
40	8	8.0	18.5	8.0	24.7	799	24	GR	45.72	3.02	Fe
41	6	14.3	31.7	12.3	39.6	282	64	GR, SH and SA	34.27	-106.68	Fe
42	20	6.2	27.0	5.3	22.7	1262	10	GR	-45.17	169.33	Fe
43	7	6.0	33.8	6.8	20.2	2592	14	GR	-43.12	171.50	Fe
44	48	6.8	19.5	8.1	14.9	1231	27	GR	57.27	-7.40	Co
45	16	6.0	17.7	6.6	19.6	1442	24	GR	56.29	-4.07	Fe
46	8	7.0	14.1	6.6	19.5	962	16	GR	55.80	-2.84	Fe
47	7	6.0	12.1	7.0	19.5	905	16	GR	55.81	-2.86	Fe
48	12	6.0	19.0	6.7	19.6	960	15	SH	55.37	-2.45	Fe
49	17	6.0	18.2	8.9	16.9	1516	27	SA	57.35	-5.55	Fe
50	4	19.0	17.1	0.7	22.1	1430	12	GR	42.67	-0.06	Fe
51	68	11.5	24.7	13.5	29.3	443	37	GR	40.60	-3.63	Fe
52	9	17.0	12.4	15.5	21.6	630	29	SH	41.30	1.82	Fe
53	734	24.0	4.1	14.5	35.6	289	72	GR, SH and SA	32.00	-106.00	Co
54	10	6.0	22.6	6.7	19.6	960	15	SA	55.37	-2.45	Fe
55	216	10.0	6.4	5.6	19.4	1290	20	SH	54.69	-2.41	Fe
56	198	11.1	18.2	7.8	19.5	986	18	GR, SA and FO	53.95	-3.23	Fe
57	5	10.0	15.4	8.5	29.3	1904	64	FO	44.22	-122.25	Co
58	74	9.9	16.6	9.7	21.9	668	11	GR	51.81	-0.37	Bi
59	210	6.0	13.4	13.8	29.9	396	33	SA	40.38	-4.20	Co
60	14	14.9	42.3	7.7	24.7	773	18	GR	51.55	10.07	Co
61	6	38.0	64.5	8.3	24.9	675	22	GR	51.56	9.96	Co
62	41	12.2	32.2	0.2	21.0	1199	26	GR and FO	46.68	10.22	Co
63	95	9.8	2.9	11.2	38.2	339	61	SA	34.31	-106.49	Fe
64	81	9.2	13.3	12.6	40.4	252	62	GR, SH and SA	34.33	-106.74	Co
65	216	7.7	2.9	12.2	39.7	278	62	GR	34.33	-106.63	Co
66	100	13.0	6.5	10.9	38.1	350	59	FO	34.37	-106.54	Co
67	100	16.4	10.4	12.4	40.3	262	64	GR and SA	34.37	-106.58	Co
68	18	8.2	11.3	8.4	40.3	364	59	GR and SH	40.85	-104.77	Co
69	7	18.0	21.7	8.2	24.9	682	20	FO	51.57	10.32	Co
70	40	10.3	21.6	7.6	28.8	765	34	GR	48.99	14.61	Co
71	80	28.9	24.4	8.7	22.5	787	18	GR	53.05	6.66	Co
72	30	9.0	23.1	0.7	37.2	446	95	GR	37.62	101.20	Co

COD	SU	Ns	Ri	AMT	TAR	MAP	PS	Vegetation	LAT	LON	Sa Me
73	212	18.7	8.7	8.2	21.6	822	26	SM	54.49	8.75	Co
74	18	14.7	14.6	17.4	19.9	657	53	SA	0.28	36.87	Fe
75	59	6.0	28.4	7.6	17.4	2086	33	GR	60.70	5.08	Fe
76	180	12.0	5.5	-3.9	47.8	301	62	GR and SA	65.00	-148.00	Co
77	18	7.1	13.1	3.6	48.0	140	102	GR	43.61	104.13	Co
78	9	18.0	34.2	9.7	20.6	627	14	GR	51.78	-1.31	Fe
79	55	8.9	10.5	5.0	31.7	607	33	GR	58.11	27.07	Co

COD: code of the data set, SU: sampling units, Ns: number of years each plot was sampled (yr), Ri: mean richness per year, AMT: annual mean temperature (°C), TAR: temperature annual range, MAP: Mean annual precipitation (mm), PS: precipitation seasonality (coefficient of variation), LAT: latitude (WGS84 datum), LON: longitude (WGS84 datum), vegetation types (GR: grassland, SH: shrubland, SA: savanna, FO: forest, and SM: salt marsh), and Sa Me: Sampling method (Co: cover, Bi: Biomass, and Fe: Frequency).

Table S3: Pearson correlations between climatic variables from WorldClim for Bio1: Annual Mean Temperature; bio2: Mean Diurnal Range [Mean of monthly (max temp - min temp)]; bio3: Isothermality (bio2/ bio7) (* 100); bio4: Temperature Seasonality (standard deviation *100); bio5: Max Temperature of Warmest Month; bio6: Min Temperature of Coldest Month; bio7: Temperature Annual Range (bio5- bio6); bio8: Mean Temperature of Wettest Quarter; bio9: Mean Temperature of Driest Quarter; Bio10: Mean Temperature of Warmest Quarter; Bio11: Mean Temperature of Coldest Quarter; Bio12: Annual Precipitation; Bio13: Precipitation of Wettest Month; Bio14: Precipitation of Driest Month; Bio15: Precipitation Seasonality (Coefficient of Variation); Bio16: Precipitation of Wettest Quarter; Bio17: Precipitation of Driest Quarter; Bio18: Precipitation of Warmest Quarter; Bio19: Precipitation of Coldest Quarter.

	bio1	**bio2**	**bio3**	**bio4**	**bio5**	**bio6**	**bio7**	**bio8**	**bio9**	**bio10**	**bio11**	**bio12**	**bio13**	**bio14**	**bio15**	**bio16**	**bio17**	**bio18**	**bio19**
bio1	1.00	1.00	0.71	-0.38	0.73	0.70	-0.05	0.53	0.78	0.80	0.88	-0.39	-0.27	-0.43	0.39	-0.29	-0.41	-0.54	-0.16
bio2	1.00	1.00	0.71	-0.38	0.73	0.70	-0.05	0.53	0.78	0.80	0.88	-0.39	-0.27	-0.43	0.39	-0.29	-0.41	-0.54	-0.16
bio3	0.71	0.71	1.00	-0.59	0.43	0.63	-0.20	0.16	0.72	0.37	0.80	-0.16	0.06	-0.44	0.62	0.03	-0.42	-0.67	0.17
bio4	-0.38	-0.38	-0.59	1.00	0.30	-0.90	0.89	0.47	-0.70	0.25	-0.77	-0.40	-0.37	-0.32	0.13	-0.36	-0.35	0.29	-0.56
bio5	0.73	0.73	0.43	0.30	1.00	0.05	0.63	0.83	0.31	0.97	0.37	-0.70	-0.50	-0.77	0.62	-0.52	-0.76	-0.47	-0.53
bio6	0.70	0.70	0.63	-0.90	0.05	1.00	-0.74	-0.17	0.87	0.15	0.93	0.15	0.14	0.12	-0.06	0.14	0.15	-0.44	0.37
bio7	-0.05	-0.05	-0.20	0.89	0.63	-0.74	1.00	0.69	-0.47	0.53	-0.48	-0.59	-0.45	-0.61	0.46	-0.46	-0.63	0.02	-0.64
bio8	0.53	0.53	0.16	0.47	0.83	-0.17	0.69	1.00	-0.02	0.85	0.12	-0.74	-0.61	-0.62	0.49	-0.63	-0.65	-0.11	-0.72
bio9	0.78	0.78	0.72	-0.70	0.31	0.87	-0.47	-0.02	1.00	0.37	0.90	0.00	0.08	-0.14	0.23	0.07	-0.08	-0.60	0.29
bio10	0.80	0.80	0.37	0.25	0.97	0.15	0.53	0.85	0.37	1.00	0.43	-0.69	-0.54	-0.67	0.51	-0.55	-0.67	-0.41	-0.54
bio11	0.88	0.88	0.80	-0.77	0.37	0.93	-0.48	0.12	0.90	0.43	1.00	-0.08	-0.01	-0.15	0.22	-0.03	-0.13	-0.55	0.17
bio12	-0.39	-0.39	-0.16	-0.40	-0.70	0.15	-0.59	-0.74	0.00	-0.69	-0.08	1.00	0.93	0.64	-0.33	0.94	0.71	0.39	0.90
bio13	-0.27	-0.27	0.06	-0.37	-0.50	0.14	-0.45	-0.61	0.08	-0.54	-0.01	0.93	1.00	0.32	0.01	1.00	0.41	0.17	0.94
bio14	-0.43	-0.43	-0.44	-0.32	-0.77	0.12	-0.61	-0.62	-0.14	-0.67	-0.15	0.64	0.32	1.00	-0.81	0.35	0.99	0.66	0.36
bio15	0.39	0.39	0.62	0.13	0.62	-0.06	0.46	0.49	0.23	0.51	0.22	-0.33	0.01	-0.81	1.00	-0.02	-0.78	-0.50	-0.08
bio16	-0.29	-0.29	0.03	-0.36	-0.52	0.14	-0.46	-0.63	0.07	-0.55	-0.03	0.94	1.00	0.35	-0.02	1.00	0.44	0.19	0.94
bio17	-0.41	-0.41	-0.42	-0.35	-0.76	0.15	-0.63	-0.65	-0.08	-0.67	-0.13	0.71	0.41	0.99	-0.78	0.44	1.00	0.64	0.45
bio18	-0.54	-0.54	-0.67	0.29	-0.47	-0.44	0.02	-0.11	-0.60	-0.41	-0.55	0.39	0.17	0.66	-0.50	0.19	0.64	1.00	-0.04
bio19	-0.16	-0.16	0.17	-0.56	-0.53	0.37	-0.64	-0.72	0.29	-0.54	0.17	0.90	0.94	0.36	-0.08	0.94	0.45	-0.04	1.00

Table S4. Pearson correlations among biotic attribute factors, synchrony indices and stability.

	Richness (ln)	**Evenness**	**Woody species (%)**	***Gross* index**	***Gross* weighted index**	***Phi* index**	***Log V* index**	**Stability (ln (1/CV))**
Richness (ln)	1							
Evenness	-0.421	1						
Woody species (%)	0.005	-0.113	1					
***Gross* index**	0.118	0.071	0.124	1				
***Gross* weighted index**	0.114	0.05	0.223	0.748	1			
***Phi* index**	-0.410	0.083	0.221	0.463	0.591	1		
***log V* index**	0.151	0.108	0.167	0.749	0.857	0.482	1	
Stability (ln(1/CV))	0.469	-0.133	-0.086	-0.38	-0.449	-0.548	-0.519	1

Table S5. Standardized path coefficients of each SEM-model (Fig. 3, S3, S4 and S5), using the piecewiseSEM package (Lefcheck, 2016). *P* of C: Pvalue is obtained by comparing the value of the C statistic for each hypothesis to a chi-square distribution with the same degrees of freedom. * variable with ln transformation. Synchrony indices: Gross η (Gross *et al.*, 2014), Gross weighted ηw (Blüthgen *et al.*, 2016), phi index (Loreau & de Mazancourt, 2008), and log V (Lepš *et al.*, 2018).

	Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
	SEM 1: Standardized path coefficients of Fig. 3.					14.96	0.134 (10)
1	Woody species (%)	Precipitation Seasonality	-1.19	0.13	<0.001		
2	Woody species (%)	Temperature Annual Range*	1.21	0.15	<0.001		
3	Woody species (%)	Mean Annual Temperature	0.81	0.11	<0.001		
4	Woody species (%)	Mean Annual Precipitation*	0.40	0.13	0.002		
5	Richness*	Woody species (%)	-0.05	0.01	<0.001		
6	Richness*	Mean Annual Temperature	-0.84	0.07	<0.001		
7	Richness*	Temperature Annual Range*	-0.35	0.09	<0.001		
8	Richness*	Precipitation Seasonality	1.09	0.10	<0.001		
9	Evenness	Richness*	-0.60	0.01	<0.001		
10	Evenness	Woody species (%)	-0.07	0.01	<0.001		
11	Evenness	Temperature Annual Range*	0.39	0.09	<0.001		
12	Evenness	Mean Annual Precipitation*	0.31	0.07	<0.001		
13	Evenness	Precipitation Seasonality	-0.27	0.08	<0.001		
14	Synchrony (*log V*)	Richness*	0.33	0.02	<0.001		
15	Synchrony (*log V*)	Evenness	0.23	0.01	<0.001		
16	Synchrony (*log V*)	Woody species (%)	0.05	0.01	<0.001		
17	Synchrony (*log V*)	Mean Annual Temperature	0.36	0.08	<0.001		
18	Synchrony (*log V*)	Temperature Annual Range*	0.34	0.10	<0.001		
19	Synchrony (*log V*)	Mean Annual Precipitation*	0.20	0.09	0.027		
20	Stability (log (1/CV))	Synchrony (*log V*)	-0.54	0.01	<0.001		
21	Stability (log (1/CV))	Richness*	0.33	0.01	<0.001		
22	Stability (log (1/CV))	Woody species (%)	0.16	0.01	<0.001		
23	Stability (log (1/CV))	Evenness	-0.09	0.01	<0.001		
24	Stability (log (1/CV))	Mean Annual Temperature	-0.39	0.05	<0.001		
25	Stability (log (1/CV))	Temperature Annual Range*	-0.32	0.05	<0.001		

	Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
	SEM 1: Standardized path coefficients of Fig. S3a					27.08	0.208 (22)
1	Woody species (%)	Mean Annual Precipitation*	-0.24	0.08	0.002		
2	Woody species (%)	Precipitation Seasonality	0.21	0.09	0.016		
3	Richness*	Mean Annual Precipitation*	0.46	0.09	<0.001		
4	Richness*	Mean Annual Temperature	-0.40	0.09	<0.001		
5	Richness*	Temperature Annual Range*	-0.43	0.15	0.003		
6	Richness*	Precipitation Seasonality	0.26	0.10	0.009		
7	Evenness	Richness*	-0.34	0.01	<0.001		
8	Evenness	Woody species (%)	-0.04	0.01	<0.001		
9	Evenness	Mean Annual Precipitation*	0.22	0.05	<0.001		
10	Synchrony (*log V*)	Richness*	0.38	0.02	<0.001		
11	Synchrony (*log V*)	Evenness	0.26	0.02	<0.001		
12	Synchrony (*log V*)	Mean Annual Temperature	0.18	0.08	0.032		
13	Stability (log (1/CV))	Synchrony (*log V*)	-0.52	0.01	<0.001		
14	Stability (log (1/CV))	Richness*	0.19	0.01	<0.001		
15	Stability (log (1/CV))	Temperature Annual Range*	-0.85	0.09	<0.001		
16	Stability (log (1/CV))	Mean Annual Temperature	-0.48	0.06	<0.001		
17	Stability (log (1/CV))	Woody species (%)	0.04	0.01	<0.001		
18	Stability (log (1/CV))	Evenness	-0.06	0.01	<0.001		
19	Stability (log (1/CV))	Precipitation Seasonality	0.33	0.08	<0.001		

	SEM 1: Standardized path coefficients of Fig. S3b					21.66	0.916 (32)
1	Richness*	Woody species (%)	-0.06	0.02	<0.001		
2	Richness*	Mean Annual Temperature	0.32	0.13	0.014		
3	Richness*	Temperature Annual Range*	-0.25	0.12	0.031		
4	Evenness	Richness*	-0.93	0.03	<0.001		
5	Evenness	Woody species (%)	-0.10	0.02	<0.001		
6	Evenness	Temperature Annual Range*	-0.26	0.10	0.011		
7	Synchrony (*log V*)	Woody species (%)	0.09	0.03	<0.001		
8	Synchrony (*log V*)	Richness*	0.44	0.05	<0.001		
9	Synchrony (*log V*)	Evenness	0.31	0.04	<0.001		
10	Stability (log (1/CV))	Mean Annual Temperature	-0.27	0.13	0.031		

	Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
11	Stability (log (1/CV))	Temperature Annual Range*	-0.38	0.11	<0.001		
12	Stability (log (1/CV))	Woody species (%)	0.27	0.02	<0.001		
13	Stability (log (1/CV))	Richness*	0.53	0.02	<0.001		
14	Stability (log (1/CV))	Synchrony (*log V*)	-0.44	0.01	<0.001		
	SEM 1: Standardized path coefficients of Fig. S3c					26.21	0.562(28)
1	Woody species (%)	Mean Annual Temperature	0.54	0.32	0.088		
2	Richness*	Woody species (%)	0.33	0.03	<0.001		
3	Richness*	Precipitation Seasonality	-4.50	1.42	0.013		
4	Richness*	Mean Annual Precipitation*	-2.04	1.21	0.092		
5	Richness*	Mean Annual Temperature	2.13	1.16	0.066		
6	Evenness	Richness*	-0.84	0.03	<0.001		
7	Evenness	Woody species (%)	-0.34	0.03	<0.001		
8	Evenness	Mean Annual Precipitation*	-1.97	0.69	0.005		
9	Evenness	Precipitation Seasonality	-1.96	0.63	0.015		
10	Synchrony (*log V*)	Mean Annual Precipitation*	-1.30	0.52	0.012		
11	Synchrony (*log V*)	Precipitation Seasonality	-1.25	0.48	0.030		
12	Stability (log (1/CV))	Synchrony (*log V*)	-0.39	0.02	<0.001		
13	Stability (log (1/CV))	Woody species (%)	0.42	0.03	<0.001		
14	Stability (log (1/CV))	Richness*	0.43	0.04	<0.001		
15	Stability (log (1/CV))	Evenness	-0.13	0.03	<0.001		
16	Stability (log (1/CV))	Mean Annual Temperature	-0.69	0.22	0.001		
	SEM 1: Standardized path coefficients of Fig. S3d					19.48	0.616 (22)
1	Woody species (%)	Mean Annual Precipitation*	0.44	0.04	<0.001		
2	Woody species (%)	Precipitation Seasonality	0.35	0.04	<0.001		
3	Richness*	Mean Annual Precipitation*	2.43	0.19	<0.001		
4	Richness*	Temperature Annual Range*	2.62	0.22	<0.001		
5	Richness*	Precipitation Seasonality	-2.04	0.17	<0.001		
6	Richness*	Mean Annual Temperature	-0.51	0.05	<0.001		
7	Richness*	Woody species (%)	-0.14	0.04	0.001		
8	Evenness	Richness*	-0.32	0.03	<0.001		

	Response variable	Predictor	Estimate	Std.error	Pvalue	C statistic	*P* of C (df)
9	Evenness	Woody species (%)	-0.19	0.03	<0.001		
10	Evenness	Temperature Annual Range*	0.83	0.15	<0.001		
11	Evenness	Precipitation Seasonality	-0.84	0.31	0.007		
12	Synchrony (*log V*)	Evenness	0.57	0.11	<0.001		
13	Synchrony (*log V*)	Mean Annual Temperature	0.67	0.14	<0.001		
14	Synchrony (*log V*)	Richness*	0.34	0.08	<0.001		
15	Synchrony (*log V*)	Woody species (%)	0.13	0.06	0.043		
16	Stability (log (1/CV))	Synchrony (*log V*)	-0.55	0.03	<0.001		
17	Stability (log (1/CV))	Richness*	0.33	0.04	<0.001		
18	Stability (log (1/CV))	Precipitation Seasonality	-0.55	0.21	0.009		
19	Stability (log (1/CV))	Woody species (%)	-0.08	0.04	0.033		
	SEM 1: Standardized path coefficients of Fig. S4					10.61	0.910 (18)
1	Woody species (%)	Mean Annual Temperature	0.22	0.09	0.016		
2	Woody species (%)	Mean Annual Precipitation*	-0.16	0.08	0.044		
3	Richness*	Precipitation Seasonality	0.76	0.11	<0.001		
4	Richness*	Mean Annual Temperature	-0.69	0.10	<0.001		
5	Richness*	Woody species (%)	-0.05	0.01	<0.001		
6	Richness*	Mean Annual Precipitation*	0.16	0.09	0.058		
7	Evenness	Richness*	-0.63	0.02	<0.001		
8	Evenness	Woody species (%)	-0.05	0.01	<0.001		
9	Evenness	Mean Annual Precipitation*	0.33	0.07	<0.001		
10	Evenness	Temperature Annual Range*	0.29	0.09	0.002		
11	Synchrony (*log V*)	Richness*	0.37	0.02	<0.001		
12	Synchrony (*log V*)	Evenness	0.24	0.02	<0.001		
13	Synchrony (*log V*)	Mean Annual Temperature	0.30	0.07	<0.001		
14	Synchrony (*log V*)	Temperature Annual Range*	0.26	0.07	<0.001		
15	Synchrony (*log V*)	Woody species (%)	0.04	0.01	0.001		
16	Stability (log (1/CV))	Synchrony (*log V*)	-0.51	0.01	<0.001		
17	Stability (log (1/CV))	Richness*	0.32	0.02	<0.001		
18	Stability (log (1/CV))	Woody species (%)	0.16	0.01	<0.001		
19	Stability (log (1/CV))	Mean Annual Temperature	-0.49	0.05	<0.001		

	Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	**_P_ of C (df)**
20	Stability (log (1/CV))	Evenness	-0.07	0.01	<0.001		
21	Stability (log (1/CV))	Temperature Annual Range*	-0.29	0.06	<0.001		
	SEM 1: Standardized path coefficients of Fig. S5a					12.09	0.599 (14)
1	Woody species (%)	Precipitation Seasonality	-1.19	0.13	<0.001		
2	Woody species (%)	Temperature Annual Range*	1.21	0.15	<0.001		
3	Woody species (%)	Mean Annual Temperature	0.81	0.11	<0.001		
4	Woody species (%)	Mean Annual Precipitation*	0.40	0.13	0.002		
5	Richness*	Woody species (%)	-0.05	0.01	<0.001		
6	Richness*	Mean Annual Temperature	-0.84	0.07	<0.001		
7	Richness*	Temperature Annual Range*	-0.35	0.09	<0.001		
8	Richness*	Precipitation Seasonality	1.09	0.10	<0.001		
9	Evenness	Richness*	-0.60	0.01	<0.001		
10	Evenness	Woody species (%)	-0.07	0.01	<0.001		
11	Evenness	Temperature Annual Range*	0.39	0.09	<0.001		
12	Evenness	Mean Annual Precipitation*	0.31	0.07	<0.001		
13	Evenness	Precipitation Seasonality	-0.27	0.08	<0.001		
14	Synchrony (η)	Evenness	0.18	0.02	<0.001		
15	Synchrony (η)	Richness*	0.14	0.02	<0.001		
16	Synchrony (η)	Woody species (%)	0.04	0.01	0.001		
17	Stability (log (1/CV))	Synchrony (η)	-0.27	0.01	<0.001		
18	Stability (log (1/CV))	Woody species (%)	0.14	0.01	<0.001		
19	Stability (log (1/CV))	Richness*	0.19	0.01	<0.001		
20	Stability (log (1/CV))	Evenness	-0.16	0.01	<0.001		
21	Stability (log (1/CV))	Mean Annual Temperature	-0.58	0.06	<0.001		
22	Stability (log (1/CV))	Temperature Annual Range*	-0.48	0.08	<0.001		
23	Stability (log (1/CV))	Mean Annual Precipitation*	-0.13	0.07	0.074		
	SEM 1: Standardized path coefficients of Fig. S5b					5.97	0.650 (8)
1	Woody species (%)	Precipitation Seasonality	-1.19	0.13	<0.001		
2	Woody species (%)	Temperature Annual Range*	1.21	0.15	<0.001		
3	Woody species (%)	Mean Annual Temperature	0.81	0.11	<0.001		

	Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
4	Woody species (%)	Mean Annual Precipitation*	0.40	0.13	0.002		
5	Richness*	Woody species (%)	-0.05	0.01	<0.001		
6	Richness*	Mean Annual Temperature	-0.84	0.07	<0.001		
7	Richness*	Temperature Annual Range*	-0.35	0.09	<0.001		
8	Richness*	Precipitation Seasonality	1.09	0.10	<0.001		
9	Evenness	Richness*	-0.60	0.01	<0.001		
10	Evenness	Woody species (%)	-0.07	0.01	<0.001		
11	Evenness	Temperature Annual Range*	0.39	0.09	<0.001		
12	Evenness	Mean Annual Precipitation*	0.31	0.07	<0.001		
13	Evenness	Precipitation Seasonality	-0.27	0.08	<0.001		
14	Synchrony (ηw)	Richness*	0.27	0.02	<0.001		
15	Synchrony (ηw)	Evenness	0.24	0.02	<0.001		
16	Synchrony (ηw)	Woody species (%)	0.08	0.01	<0.001		
17	Synchrony (ηw)	Mean Annual Temperature	0.25	0.06	<0.001		
18	Synchrony (ηw)	Temperature Annual Range*	0.23	0.08	0.006		
19	Synchrony (ηw)	Precipitation Seasonality	-0.14	0.09	0.115		
20	Stability (log (1/CV))	Synchrony (ηw)	-0.32	0.01	<0.001		
21	Stability (log (1/CV))	Woody species (%)	0.16	0.01	<0.001		
22	Stability (log (1/CV))	Richness*	0.24	0.01	<0.001		
23	Stability (log (1/CV))	Evenness	-0.13	0.01	<0.001		
24	Stability (log (1/CV))	Mean Annual Temperature	-0.53	0.06	<0.001		
25	Stability (log (1/CV))	Temperature Annual Range*	-0.48	0.08	<0.001		
26	Stability (log (1/CV))	Mean Annual Precipitation*	-0.18	0.07	0.008		
	SEM 1: Standardized path coefficients of Fig. S5c					6.37	0.383 (6)
1	Woody species (%)	Precipitation Seasonality	-1.19	0.13	<0.001		
2	Woody species (%)	Temperature Annual Range*	1.21	0.15	<0.001		
3	Woody species (%)	Mean Annual Temperature	0.81	0.11	<0.001		
4	Woody species (%)	Mean Annual Precipitation*	0.40	0.13	0.002		
5	Richness*	Woody species (%)	-0.05	0.01	<0.001		
6	Richness*	Mean Annual Temperature	-0.84	0.07	<0.001		
7	Richness*	Temperature Annual Range*	-0.35	0.09	<0.001		

	Response variable	**Predictor**	**Estimate**	**Std.error**	**Pvalue**	**C statistic**	***P* of C (df)**
8	Richness*	Precipitation Seasonality	1.09	0.10	<0.001		
9	Evenness	Richness*	-0.60	0.01	<0.001		
10	Evenness	Woody species (%)	-0.07	0.01	<0.001		
11	Evenness	Temperature Annual Range*	0.39	0.09	<0.001		
12	Evenness	Mean Annual Precipitation*	0.31	0.07	<0.001		
13	Evenness	Precipitation Seasonality	-0.27	0.08	<0.001		
14	Synchrony (*phi*)	Richness*	-0.63	0.02	<0.001		
15	Synchrony (*phi*)	Woody species (%)	0.11	0.01	<0.001		
16	Synchrony (*phi*)	Evenness	0.07	0.02	<0.001		
17	Synchrony (*phi*)	Temperature Annual Range*	0.53	0.11	<0.001		
18	Synchrony (*phi*)	Precipitation Seasonality	-0.42	0.10	<0.001		
19	Synchrony (*phi*)	Mean Annual Precipitation*	0.29	0.10	0.003		
20	Synchrony (*phi*)	Mean Annual Temperature	0.18	0.08	0.033		
21	Stability (log (1/CV))	Synchrony (*phi*)	-0.30	0.01	<0.001		
22	Stability (log (1/CV))	Woody species (%)	0.17	0.01	<0.001		
23	Stability (log (1/CV))	Evenness	-0.19	0.01	<0.001		
24	Stability (log (1/CV))	Mean Annual Temperature	-0.59	0.06	<0.001		
25	Stability (log (1/CV))	Temperature Annual Range*	-0.45	0.08	<0.001		
26	Stability (log (1/CV))	Richness*	-0.04	0.01	0.005		
27	Stability (log (1/CV))	Mean Annual Precipitation*	-0.12	0.07	0.095		

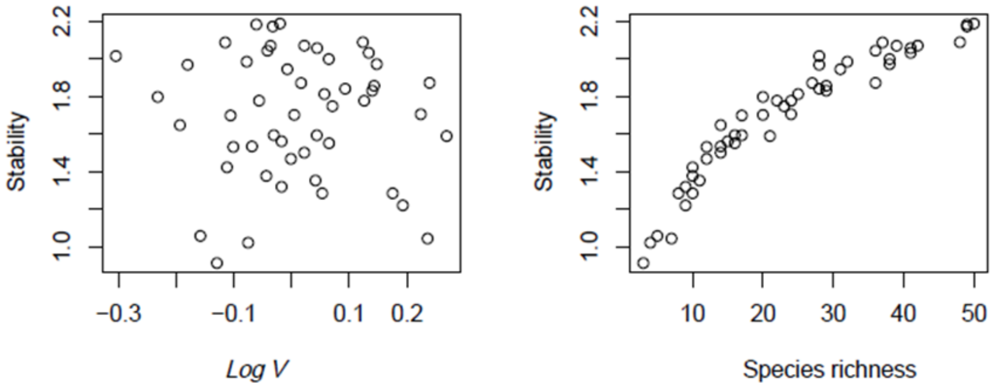
Supplementary Text S1: Effect of richness and synchrony on stability via changes in random fluctuations.

Based on theoretical models, one of the main mechanisms underlying the relationship between species richness and stability is an increase of random fluctuations with increased species richness (Doak *et al.*, 1998). However, this relationship can change depending on the level of synchrony, i.e. when fluctuations deviate from random. In the absence of random species fluctuations, the effect of species richness on stability (Doak *et al.*, 1998) is predicted to be low (Doak *et al.*, 1998; Lepš, 2004). To demonstrate the effect of synchrony vs. random fluctuations, we simulated temporal series of community data under two different scenarios using the "syngenr" function for R (Lepš *et al.*, 2019):

1. Scenario random fluctuations: if species fluctuate independently, the effect of synchrony on stability should be lower when the richness effect is strong.
2. Scenario synchrony: any increase of synchrony should reduce the effect of richness on stability.

The syngenr function offers the possibility to simulate communities with fixed (e.g. length of the time series) and variable (e.g. number of species, synchrony etc.) parameters (SI Appendix, Dataset S1). We simulated 50 communities over a 100 years period with random species fluctuations of different levels of species richness. This first scenario shows a strong relationship between species richness and stability, but a low relationship between synchrony and stability. This is expected in the case of the so called-averaging effect in which synchrony has weak effect, i.e. around zero (Doak *et al.*, 1998). We then simulated 50 communities over a 100 years period with synchrony in species fluctuation and different levels of species richness. This second scenario shows a reduced effects of richness on stability (Thibaut & Connolly, 2013) thus confirming reduced potential stabilizing effects of richness on the whole community when synchrony dominates (Doak *et al.*, 1998). In systems characterized by species synchrony, the averaging-effects should be low, thus increasing the effects of synchrony. For instance, weak effects of species richness on stability in real communities may reflect the fact that many species-rich communities contain large numbers of ecologically similar species, which respond in parallel to yearly conditions (synchronously). In this case, species richness contributes little to stabilizing synchrony. Indeed, it is likely that as species richness increases there is an ever-greater partitioning of existing niche space, with corresponding increases in the probability that species will show similar trait characteristics. This means that in such communities, more species can also increase synchrony, to some degree.

a) scenario random fluctuations



b) scenario synchrony

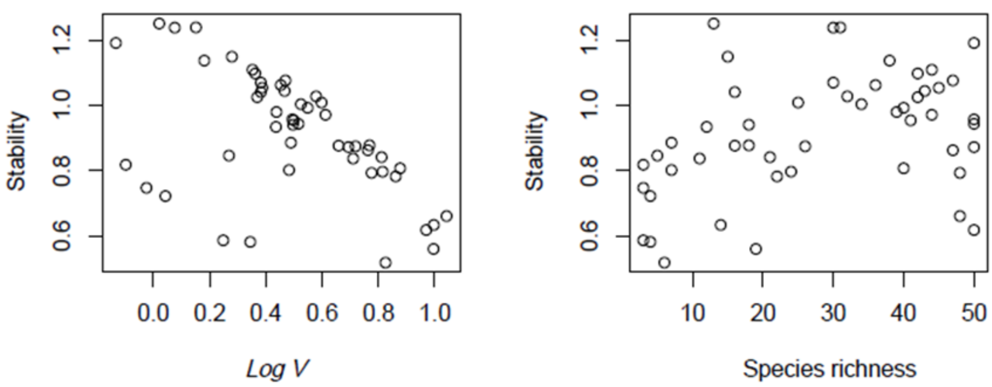


Figure 1 Supplementary Text S1: Relationship between log V (Lepš *et al.*, 2018), species richness and stability in artificial temporal communities using simulations

Supplementary Text S2: Effect of different indices of synchrony on the species richness-synchrony and synchrony-stability relationships.

Species richness was positively related to synchrony for each of three commonly used indices of synchrony [*log V*, (Lepš *et al.*, 2018); *Gross* (1) and *Gross'* weighted (2)]. However, previous studies have described negative species richness-synchrony relationships using the *phi* synchrony index (3). This index incorporates negative dependencies on species richness, particularly in case of any non-perfect synchrony between species (3, 4, 9). Since perfect synchrony is virtually impossible in natural systems, a negative relationship between the *phi* index and richness is expected, and this was verified in our data (Fig. S2c). However, the observed relationship between *phi* and species richness was weaker than expected by species fluctuating randomly (R^2m = 0.293 and R^2m = 0.502, respectively).

To demonstrate the strength of the relationship between synchrony and stability in observed data we compared the results to null-expectations. Using null-models, which simulate random species fluctuations (random fluctuation scenario), we found a relationship between synchrony and stability with R^2m = 0.02 (mixed model with the whole set of data, and data set as random factor). On the contrary, using the observed data, the strength of this relationship increased considerably (R^2m = 0.19). Similar results were found with the other synchrony indices (Table 1 Supplementary Text S2). This shows that the relationship between observed synchrony and stability is stronger than under null-expectations.

Table 1 Supplementary Text S2: Strength (R^2m: variance explained by the fixed effects) of the relationship between synchrony and stability, using the MuMIn package (Barton, 2016).

Synchrony indices	Stability (observed)	Stability (expected)
log V (observed)	0.191	
Gross (observed)	0.056	
Gross' weighted (observed)	0.076	
phi (observed)	0.079	
log V (expected)		0.021
Gross (expected)		< 0.001
Gross' weighted (expected)		< 0.001
phi (expected)		0.026

Supplementary Text S3: Effect of environmental treatments on synchrony and stability.

Environmental treatments related with various global change drivers (when considered together) showed a negative relationship with synchrony. Surprisingly, they also showed a negative relationship with stability. This shows that the effect of these drivers can disrupt the expected effect of biotic stability drivers. Compared to other studied biotic and abiotic drivers considered at the same time, the effects of these environmental treatments were small. We suggest that these results are related to the different effects promoted by multiple treatments evaluated across our data sets. For this reason, we analysed each treatment separately, demonstrating the different effects on synchrony and stability, as well as how these effects can be heterogeneous and context dependent. Our study therefore suggests that to derive generalizations about these drivers, it is necessary to conduct more long-term studies, fully replicated across habitats and treatments.

The drivers that promoted the negative relationships with both synchrony and stability were fertilization and removal. This result was partially counterintuitive, as we expected that high synchrony would be related to low stability (Fig. 1a). We suggest that the study of Lepš *et al.* (2018) offers a good explanation for these unexpected results. They found similar outcomes that could be observed for both treatments, with the exception that the removal treatment had no effect on synchrony. They suggested that the decline in synchrony in fertilized plots may be related to an increase in compensatory dynamics due to greater competition for light among species. However, at the same time, fertilization can increase the differences in productivity between more and less "favourable" years. For example, in a year with favourable weather conditions, the total biomass would be much greater than without fertilization. However, in less favourable years biomass could be more comparable between fertilized and unfertilized plots, decreasing stability in biomass across years in the fertilized conditions. This would occur despite the potential of compensatory dynamics due to decreased synchrony. Additionally, the lower stability in fertilized plots could be related to the lower species richness of these plots (also found in our study). In this sense, fertilization might be a good example of a situation where this treatment decreases both synchrony (suggesting stabilization) and stability, leading to overall destabilization of the community.

Herbivory removal, grazing intensity and fire followed our expectation in the sense that each had an opposite effect on synchrony and stability. Grazing, implemented either as herbivory exclusion treatment by fencing or as an assessment of grazing intensity, increased synchrony and destabilised community productivity. This result could be related to a possible filtering effect of grazing. This treatment may affect interspecific competition among species, promoting a selection of species best adapted to grazing, and consequently, a decrease in total richness. This low number of species is unlikely to support compensation between each other among years, as they have similar traits (strongly filtered by grazing). In other words, this selection effect may increase synchrony among species. Also, the reduction in total biomass promoted by the treatment could have an effect on stability. Some authors expect a decrease in stability with a concomitant decrease in total biomass (e.g. by grazing) as this metric represents the numerator in stability equations (Hector *et al.*, 2010). Fire also involves a decrease in total biomass, although typically in a far more drastically manner than observed by grazing. One might indeed expect a destabilization of the whole community, given the intense disturbance created by fire. However, fire can greatly alter species composition and leads to secondary succession. In a successional series, year-to-year variations in species could be masked by successive replacements among species in time as the community recovers from the fire event. This can lead to year-to-year low synchrony. This negative synchrony over time could in turn result in greater overall stability. Finally, manipulative climate change treatments had neither a significant effect on synchrony nor on stability. However, the number of datasets with this type of treatment was low (n = 5 data sets) and the climate change manipulation category included treatments that were too heterogeneous to allow any strong conclusion for this factor. Ultimately, their effects were highly unpredictable and highly dependent on the environmental conditions considered.

Supplementary Text S4: Data set descriptions. The numbers are related with the code of the data set in Table S2.

1. The data set consists of 42 permanent 1 m^2 quadrats from a northern mixed prairie at a field station in Miles City, Montana, USA. In these quadrats, individual plants were quantified and mapped annually, from 1932 through 1945, to evaluate cattle stocking-rate effects on pastures grazed. Quadrats were distributed in pastures with three levels of cattle grazing intensity: light, moderate, and heavy stocking rates of 1.24, 0.92, and 0.76 (ha/ animal-unit-month). Data set owners: Jed Anderson (Department of Wildland Resources and the Ecology Center, Utah State University), Lance Vermeire (USDA-ARS, Fort Keogh Livestock and Range Research Laboratory), and Peter B. Adler (Department of Wildland Resources and the Ecology Center, Utah State University). More information: http://esapubs.org/archive/ecol/E092/143/#data

2. The data set consists of 51 permanent 1 m^2 quadrats located on a mixed grass prairie in Hays, Kansas, USA. Every year from 1932 to 1972, individual plants were quantified and mapped in each quadrat. Thirty-six permanent quadrats were located inside livestock exclosures and 15 in grazed areas. Data set owners: Peter B. Adler (Department of Wildland Resources and the Ecology Center, Utah State University), William R. Tyburczy (National Center for Ecological Analysis and Synthesis), and William K. Laurenroth (Department of Forest, Range and Watershed, Colorado State University). More information: https://web.archive.org/web/20150128015820/http://esapubs.org:80/archive/ecol/E088/161/default.htm

3. The data set consists of 24 permanent 1 m^2 quadrats located on a shortgrass steppe of North America in Nunn, Colorado, USA. The quadrats were established in six grazed and ungrazed study sites on the Central Plains Experimental Range and individual plants were identified and mapped annually from 1997 to 2010. There were four treatments combining past and present grazing status: ungrazed in the past and at present (ungrazed/ungrazed), grazed by livestock in the past and present (grazed/grazed), grazed in the past and ungrazed during the experiment (grazed/ungrazed), and ungrazed in the past and grazed during the experiment (ungrazed/grazed). Data set owners: Chengjin Chu (Department of Wildland Resources and the Ecology Center, Utah State University), John Norman (USDA-NRCS MLRA Soils Project, Colorado State University), Robert Flynn (Shortgrass Steppe-LTER, Colorado State University), Nicole Kaplan (Shortgrass Steppe-LTER, Colorado State University), William K. Lauenroth (Department of Botany, University of Wyoming), and Peter B. Adler (Department of Wildland Resources and the Ecology Center, Utah State University). More information: https://web.archive.org/web/20150502183659/http:/www.esapubs.org/archive/ecol/E094/128/

4. The data set consists of 160 permanent 1 m^2 quadrats located on semi-desert grasslands at the Santa Rita Experimental Range, Arizona, USA. Every year from 1915 to 1933, individual plants were identified and mapped in these quadrats. Quadrats were located in exclosures (ungrazed) and in pastures grazed by livestock (grazed). Data set owners: Jed Anderson (Department of Wildland Resources and the Ecology Center, Utah State University), Mitchel P. McClaran (School of Natural Resources and the Environment, University of Arizona), and Peter B. Adler (Department of Wildland Resources and the Ecology Center, Utah State University). More information: https://web.archive.org/web/20150502183207/http://esapubs.org:80/archive/ecol/E093/132/default.htm

5. The data set consists of 23 permanent 1 m^2 quadrats located in sagebrush steppe in eastern Idaho, USA. Individual plants in these quadrats were identified and mapped annually from 1926 to 1957. These permanent quadrats were located in both grazed (4 quadrats) and ungrazed units (18 quadrats), and one quadrat was grazed in the past and ungrazed during the experiment. Data set owners: Luke Zachmann (Department of Wildland Resources and the Ecology Center, Utah State University), Corey Moffet (USDA ARS, U.S. Sheep Experiment Station), and Peter B. Adler (Department of Wildland Resources and the Ecology Center, Utah State University). More information: https://web.archive.org/web/20150128015825/http:/esapubs.org/archive/ecol/E091/243/default.htm.

6. The data set consists of 222 stations or plots established in a 135 ha area in southern New Mexico, USA. Previously grazing domestic livestock was excluded from the area where three permanent transects (2.7 km) were established. One of the transects received fertilization of 10 g/m^2 of nitrogen. One of the two control transects (not fertilized), was sampled at 40 stations, the other two transects had 91 stations each. At each station abundance of each species was estimated by point-intercept method along a 30 m transect perpendicular to the each of the three permanent transects. Sampling was carried out every year from 1982 to 1988 and every 5 years until 2003. The data set is based on the Jornada Long-Term Ecological Research site. More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-jrn.2100119001.50.

7. The data set consists of 1001 plots located on one grassland site and one creosote (shrubland) site of the Chihuahuan desert, New Mexico, USA. On the grassland site, three exclusion treatment levels were set in addition to the control treatment left open to all grazers. The first level excluded only domestic animals (cattle), the second excluded lagomorphs, and the third excluded rodents. In the shrubland site, only lagomorph- and rodent-exclusion treatments were set in addition to the control. In each treatment of each sites, 4 grids of 36 permanent plots (1 m^2) were sampled (visual estimated cover) every year from 1995 to 2005 for creosote sites and 2010 for grassland sites. The data belong to a data set on a grazers exclusion experiment in Jornada Basin Long-Term Ecological Research Program (LTER) project. More information: https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.2100086002.39.

8. The data set consists of 20 plots located in an open grassland of the South African Kalahari near Askham, South Africa. The cover values (%) of all individual plant species were estimated annually in each plot (10 m x 10 m) from 2005 to 2016. Data owners: Ute Schmiedel and Norbert Jürgens (Biodiversity, Evolution & Ecology of Plants (BEE) at the Institute for Plant Science and Microbiology, University of Hamburg). More information: (Jürgens, Schmiedel, & Hoffman, 2010).

9. The data set consists of 24 plots located in a leaf-succulent shrub community, consisting of annuals and geophytes in the Succulent Karoo in Soebatsfontein, South Africa. The cover values (%) of all individual plant species were estimated annually in each plot (10 m x 10 m) from 2002 to 2017. Data owners: Ute Schmiedel and Norbert Jürgens (Biodiversity, Evolution & Ecology of Plants (BEE) at the Institute for Plant Science and Microbiology, University of Hamburg). More information: (Jürgens *et al.*, 2010).

10. The data set consists of 40 plots located in a dwarf shrub community in the Succulent Karoo, near Leliefontein, South Africa. The cover values (%) of all individual plant species were estimated annually in each plot (10 m x 10 m) from 2002 to 2017. Data owners: Ute Schmiedel and Norbert Jürgens (Biodiversity, Evolution & Ecology of Plants (BEE) at the Institute for Plant Science and Microbiology, University of Hamburg). More information: (Jürgens *et al.*, 2010).

11. The data set consists of 40 plots located in a succulent dwarf-shrub community in the Succulent Karoo, Knersvlakte near Vanrhynsdorp, South

Africa. The cover values (%) of all individual plant species were estimated annually in each plot (10 m x 10 m) from 2002 to 2017. Data owners: Ute Schmiedel and Norbert Jürgens (Biodiversity, Evolution & Ecology of Plants (BEE) at the Institute for Plant Science and Microbiology, University of Hamburg). More information: (Jürgens *et al.*, 2010).

12. The data set consists of 380 permanent plots of Kiskun LTER, located in Bugac and Orgovány sites of Kiskunság National Park, Hungary. Bugac and Orgovány sites were burnt in 1976 and 2000, respectively, and the vegetation recorded since 1997 and 2002, respectively. Half of the plots were fenced to control grazing pressure. In each plot (1 m^2), the percentage cover per species was visually estimated annually from 1997 to 2011 in Bugac, and from 2002 to 2015 in Orgovány. Data set owners: Miklós Kertész and Gábor Ónodi (Institute of Ecology and Botany, Centre for Ecological Research, Hungarian Academy of Sciences). More information: (Kertész, Aszalós, Lengyel, & Ónodi, 2017).

13. The data set consists of 50 permanent plots located on a grassland in Cedar Creek Ecosystem Science Reserve, Minnesota, USA. The plots were divided in 10 treatments of fertilization and grazing exclusion (Control=no treatment, K=potassium, P=phosphate, N=nitrogen, PK=phosphate and potassium, NK=nitrogen and potassium, NP=nitrogen and phosphate, NPK=nitrogen, phosphate and potassium, Fence=Fence, NPK+Fence=nitrogen, phosphate and potassium + fence). Plant species composition and percentage cover were visually estimated on 1 m^2 permanent plots from 2007 to 2013. This data set was provided from Cedar Creek Long-Term Ecological Research Program (LTER). More information: http://cedarcreek.umn.edu/research/data/dataset?acze247.

14. The data set consists of 184 permanent plots located in Cedar Creek Ecosystem Science Reserve, Minnesota, USA. The experiment was designed to evaluate the effect of burning patterns on vegetation, using the burning program as a restoration method for oak savanna. Plots were distributed across 6 treatments with increasing burning Fe: i) no burning – control – (48 plots), ii) 1 per 10 years (16 plots), iii) 1 per 3 years (32 plots), iv) 1 per 2 years (32 plots), v) 2 per 3 years (8 plots) and vi) 4 per 5 years (48 plots). Plots are located on 12 management areas ranging in size from 2.4 to 30 ha. Plant species composition and percentage cover were visually estimated every 5 or 6 years on 1 m^2 permanent plots from 1984 to 2010. The data belong to the Cedar Creek Long-Term Ecological Research Program (LTER). More information: http://cedarcreek.umn.edu/research/data/dataset?herbe133.

15. The data set consists of 60 permanent plots located in Cedar Creek Ecosystem Science Reserve, Minnesota, USA. The experiment was designed to evaluate the natural colonization and succession of crop field after different length of ploughing abandonment. The experiment started in 1987 on 13 fields that had been ploughed for the last time in 1927, 1941, 1943, 1947, 1952, 1955, 1957, 1961, 1968, 1971, 1975, 1982 or 1987. Two additional fields were added in 1989 and 1998, that were ploughed the same year. Every year from 1987 (or later for the two additional fields) the biomass of individual plants was recorded from 4 plots (0.3 m^2) per field until 2013. In 2006 a prescribed burning treatment was introduced in half of the plots. For those plots, we kept only the records until 2006 (to avoid confounding treatments within single plots). The data belong to the Cedar Creek Long-Term Ecological Research Program (LTER). More information: http://cedarcreek.umn.edu/research/data/dataset?ple054.

16. The data set consists of 234 permanent plots located in Cedar Creek Ecosystem Science Reserve, Minnesota, USA. The experiment combines different levels of fertilization on 4 fields that were abandoned for different periods (14, 25, 48 years and never ploughed before the experiment started in 1982) and where mammal grazers were excluded. Individual plant biomass was recorded on 5 to 6 replicate plots of the fertilizer treatments (from 0 to 40 g/m^2

of nitrogen) per field every year until 2004 or 2011 (depending on the plots). For 3 out of every 5 replicates in field C, the grazing exclusion fences were removed in 2004, but sampled until 2011. To maintain continuity of the treatment within plots the 2004-2011 period of those plots were entered in the database as separate plots of the same data set. The data belong to the Cedar Creek Long-Term Ecological Research Program (LTER). More information: http://cedarcreek.umn.edu/research/data/dataset?ple001.

17. The data set consists of 237 permanent plots located in Cedar Creek Ecosystem Science Reserve, Minnesota, USA. The experiment combines 9 levels of fertilization (from 0 to 40 g/m^2 of nitrogen) and prescribed burning on three fields that were abandoned since 14, 25 and 48 years, and where mammal grazers where excluded. All 3 fields had 6 replicate plots of the 9 fertility treatments from 1982. From 1992 half of the plots in field B were burned every spring, and half of the plots in field A and C stopped receiving the fertilization treatment. To maintain continuity of the treatments within plots the 1992-2011 period of those plots were entered in the database as separate plots of the same data set. Individual plant biomass was measured. The data belong to the Cedar Creek Long-Term Ecological Research Program (LTER). More information: http://cedarcreek.umn.edu/research/data/dataset?ple002.

18. The data set consists of 795 permanent plots (1 m^2) on six sites in the Central Plains Experimental Range, Colorado, USA. On each site, prior to the experiment, the land was managed under two conditions: grazed for more than 20 years and ungrazed (fences against large mammals) for 50 years. In 1992, part of the fenced area was open to grazing and part of the grazed area was fenced. From 1992 to 2008, plots were distributed across the four combinations of past/current management: grazed/grazed, ungrazed/ungrazed, grazed/ungrazed and ungrazed/grazed. In 1998, additional plots were added in a fifth treatment with fences excluding both large and small grazers (rodent exclusion). The data belong to the Shortgrass Steppe Long-Term Ecological Research Program (SGS-LTER). More information:

https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-sgs.527.1.

19. The data set consists of 96 plots located on sandy xeric and meso-xeric, semi-natural grasslands of the Elbe valley in Höhbeck, Germany. The plots had no special treatment (i.e. low-intensity sheep grazing as was the case with all dry grasslands of the area). From 2007 to 2012, the vegetation was surveyed once a year in a 1 m^2 plot using Londo scale (Londo, 1976). Data set owners: Jürgen Dengler (Vegetation Ecology Group, Zurich University of Applied Sciences (ZHAW) and Oliver Schuhmacher (Naturschutzbund Deutschland). More information: (Schuhmacher & Dengler, 2013).

20. The data set consists of 12 plots located on a *Calluna vulgaris*-dominated moorland in a degraded state near Dufftown, Morayshire, United Kingdom. Six treatments were imposed: 1) sheep grazed in winter (0.82 animals ha^{-1} yr^{-1}) and fenced against rabbits, 2) sheep grazed in winter (1.64 animals ha^{-1} yr^{-1}) and fenced against rabbits, 3) sheep grazed in summer (0.93 animals ha^{-1} yr^{-1}) and fenced against rabbits, 4) sheep grazed in summer (1.86 animals ha^{-1} yr^{-1}) and fenced against rabbits, 5) ungrazed (fenced against sheep, but open to rabbits), and 6) ungrazed (fenced against sheep and rabbits). Every year from 1990 to 1995, each species was measured in a transect, using the inclined-point quadrat method (Tinney, Aamodt, & Journal, 1937) (32·5° to the horizontal). All contacts with 5 pins were recorded in 20 quadrat positions per plot. More information: (R. J. Pakeman, Hulme, Torvell, & Fisher, 2003).

21. The data set consists of 193 permanent plots (4 m^2) on 10 sites in Andrew Experimental forest, Oregon (USA). The study had different levels of logging and broadcast burning treatments with the aim of evaluate plant secondary succession and biomass dynamics under these treatments. On each site in 1962, permanent plots were established in i) undisturbed, ii) logged, iii) logged and lightly burned and iv) logged and severely burned areas. Individual species cover was recorded from 1962 to 2013 (23 times). The data belong to the

Andrews Forest Long-Term Ecological Research Program (AND-LTER). More information: https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-and.3217.11.

22. The data set consists of 47 plots located in eastern Australia. In each plot, the biomass of the vegetation was measured annually, from 1991 to 2002, in four 300 m long transects each containing 13 quadrats of 0.72 m x 0.72 m. The sites are in woodlands, grasslands, and shrublands. Data set owners: James Val and David Eldridge (Office of Environment & Heritage, University of New South Wales).

23. The data set consists of eight plots located on a *Lolium perenne* pasture in Fasque, United Kingdom. Four treatment combinations of grazing and fertilization were used from 1991 to 2000: 1) ungrazed and unfertilized, 2) sheep grazing monitored to maintain a sward height of 4 cm and unfertilized, 3) sheep grazing monitored to maintain a sward height of 8 cm and unfertilized, and 4) sheep grazing monitored to maintain a sward height of 4 cm and fertilized. Each species was measured in a transect, using the inclined-point quadrat method (32·5° to the horizontal). A minimum of 20 point contacts were recorded at 18 locations per plot (i.e. a minimum of 360 contacts per plot). More information: (Marriott, Bolton, Barthram, Fisher, & Hood, 2002).

24. The data set consists of 16 plots located on La Fage French National Institute for Agricultural Research (INRA) experimental station, close to Millau, France. Every year from 1978 to 2005, individual plants were identified using the point intercept method on 5 m permanent lines (1 point/10 cm, i.e. 50 points/line). Since 1978, the experimental rangeland was grazed by sheep, with a proportion of biomass removed annually by grazing relative to the total biomass produced of 0.61 kg/ha and fertilized with mineral nitrogen (6.5 g/m^2 each year) and phosphorus (4 g/m^2 every three years). Data set owner: Eric

Garnier (Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), CNRS, Université de Montpellier). More information: (Chollet *et al.*, 2014) and (Garnier *et al.*, 2018).

25. The data set consists of 145 plots situated in Teberda State Reserve, a part of the Karachaevo-Cherkessian Republic in the northwestern Caucasus, Russia. Of these 145 plots, 25 were located in the low-lying snowbed vegetation, 20 plots in the *Geranium gymnocaulon-Hedysarum caucasicum* vegetation, 20 plots in the *Festuca varia* vegetation, and 80 plots in the lichen heath vegetation. The lower plots (snowbed and *Geranium* vegetation) were monitored from 1986-2009, and the higher plots (*Festuca* and lichen heath) were monitored 1981-2009. In each plot, the cover of individual plant species was recorded as number of shoots per m^2. The data sourced from BioTIME (Dornelas *et al.*, 2018), Study_ID 483 and 497- ITEX Dataset 5 - Teberda (Malaya Alpine-Snowbed and Geranium Hedysarum Meadow) and ITEX Dataset 19 - Teberda (Festuca Varia Grassland, Malaya Alpine Lichen-Heath). More information: (Onipchenko, Semenova, & Maarel, 1998).

26. The data set consists of 9 plots located on an upland west-Atlantic moorland in the Clocaenog Forest, United Kingdom. The experiment was designed with three treatments: control, drought (~20% reduction in total annual rainfall) and warming (~64% reduction in heat loss during night and 14% reduction in total annual rainfall). Each treatment had three replicate plots. Every year from 1998 to 2012, the vegetation survey was done by pin-point methodology. Three quadrats per plot were chosen, and in each quadrat, vegetation was quantified using a grid of 100 pins. Pin hits were then converted to biomass (g m^{-2}) data using a biomass calibration-conversion. Data set owners: Reinsch, S. (Centre for Ecology & Hydrology), Sowerby, A. (Former Centre for Ecology & Hydrology member of staff), and Emmett, B.A. (Centre for Ecology & Hydrology). More information: https://catalogue.ceh.ac.uk/documents/5b39a644-d614-4f2b-8df6-

202ed440b4ab. Doi: https://doi.org/10.5285/5b39a644-d614-4f2b-8df6-202ed440b4ab.

27. The data set consists of 400 plots located along 38 serpentine and 42 non-serpentine meadows of California, USA. In each plot (1 m^2), the % cover per species was visually estimated annually from 2006 to 2015. Data set owner: Susan Harrison (Department of Environmental Science and Policy, University of California at Davis). More information: (Fernandez-Going, Anacker, & Harrison, 2015) and (Harrison, 1999).

28. The data set consists of 68 permanent plots (1 m^2) established in 1915 in the Chihuahuan desert, Jornada Basin Experimental Range, New Mexico, USA. Density of individuals per species and per plot were recorded on 7 to 53 occasions over the time period, with the last record being in 2001. The data belong to the Jornada Long-Term Ecological Research Program (JRN-LTER). More information: https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.210351002.75.

29. The data set consists of four plots located on a semi-natural montane grassland in Krkonose Mountains, Czech Republic. From 1984 to 2001, standing biomass was sampled annually in each plot (0.5 m x 0.5 m). Data set owners: Tomas Herben (Department of Botany, Faculty of Science, Charles University and Institute of Botany, Academy of Sciences of the Czech Republic), Frantisek Krahulec, Hana Skalova and Vera Hadincova (Institute of Botany, Academy of Sciences of the Czech Republic). More information: (Herben, Krahulec, Hadincová, Pecháčková, & Kováčiová, 1997).

30. The data set consists of four plots located on a semi-natural montane grassland in Krkonose Mountains, Czech Republic. From 1986 to 2015, standing biomass was sampled annually in each plot (0.5 m x 0.5 m). Data set owners: Tomas Herben (Department of Botany, Faculty of Science, Charles University and Institute of Botany, Academy of Sciences of the Czech Republic), Frantisek Krahulec, Hana Skalova and Vera Hadincova (Institute of Botany, Academy of Sciences of the Czech Republic). More information: (Herben *et al.*, 2017).

31. The data set consists of 28 permanent plots in the coastal sand dunes of Hog island, Virginia, USA. In 1992, plots of 5 m x 5 m were established on the tops of coastal sand dunes, along a chronosequence (three stations). Half of the plots received nitrogen fertilization each year in the form of urea nitrogen (30% uncoated (46-0-0) and 70% (40-0-0) coated for slow release). The fertilizer was applied evenly in a dry form (15 g/m^2 of nitrogen). In each of the 28 plots, species cover (%) was visually estimated in five 0.25 m^2 plots (1.25 m^2 total) each July from 1992 to 2014. The data sourced from BioTIME (Dornelas *et al.*, 2018), Study_ID 243 - Virginia Coast Reserve Long-Term Ecological Research. Data owner: F. Day. More information: (F. Day, 2016).

32. The data set consists of 12 permanent plots located on a calcareous grassland close to Napal, Spain. The experimental area was fenced and shrubs were removed. Six plots were fertilized (sewage sludge to the soil surface with 5000 g/m^2) and six plots were used as controls. From 2004 to 2015, all vascular plant species were measured annually using frequencies. Each plot (1 m^2) was divided into 100 subplots, and the presence/absence of each species was recorded. Data set owner: Ricardo Ibáñez (Department of Environmental Biology, University of Navarra). More information: (Gazol, Uria-Diez, Elustondo, Garrigó, & Ibáñez, 2016).

33. The data set consists of eight plots located on tundra vegetation near Toolik, Alaska, USA. The plots are divided between dry and moist tundra in control and warming experiment with open-top chambers: three control plots in the dry tundra, three open top chambers in the dry tundra, and two control plots in the moist tundra. Biomass estimates were obtained using a fixed 75 cm^2 point frame, with 100 measurements spaced 7 cm apart, from 1994 to 2008. At each of 100 points per plot, the following information was recorded in a spatially explicit format: species hit, condition and woodiness. The data were sourced from BioTIME (Dornelas *et al.*, 2018), Study_ID 491 - ITEX Dataset 13 - Toolik (Dry, Moist).

34. The data set consists of four plots located in Toolik, Alaska, USA. Biomass was assessed by clipping of four or five 0.25 m x 0.25 m plots, and sorting to species level. The experiment had six years of data. The data was sourced from BioTIME (Dornelas *et al.*, 2018), Study_ID 492 - ITEX Dataset 14 - Toolik (LTER Heath, LTER Moist acidic tussock, LTER non-acidic tussock, LTER wet sedge, SAG wet sedge2, Tussock 1981 plots).

35. The data set consists of 15 plots located on a mesic grassland in Bayreuth, Germany. Three treatments were applied from 2008 to 2015: 1) ambient control, 2) winter warming (October–March) starting in October 2009, and 3) summer warming (April–September) since April 2010. To achieve this temperature increase, overhead infrared heaters equipped with reflector domes were used at a height of 0.8 m. Species cover (%) was visually estimated annually in each plot (1 m^2). Data set owners: Anke Jentsch (Department of Disturbance Ecology, University of Bayreuth), Carl Beierkuhnlein (Biogeography, University of Bayreuth), Jürgen Kreyling (Biogeography, University of Bayreuth and Experimental Plant Ecology, University of Greifswald), Mohammed Abu Sayed Arfin Khan. More information: (K. Grant, Kreyling, Beierkuhnlein, & Jentsch, 2017).

36. The data set consists of seven plots located on a dry grassland natural reserve in Czech Republic. The species cover (%) was visually estimated annually from 1993 to 2001 in each plot (1 m^2). Data set owner: Jiří Danihelka (Department of Botany and Zoology, Masaryk University and Department of Vegetation Ecology, Institute of Botany, The Czech Academy of Sciences).

37. The data set consists of 10 permanent 40 m transects located on an upland permanent grassland in Laqueuille, France. The experiment is part of the SOERE-ACBB long term experiment. Five transects were located in intensively managed grassland (10-15 animals ha^{-1} yr^{-1} and 20 g/m^2 of nitrogen), and other five were located in a neighbouring grassland under extensive management (5-8 animals ha^{-1} yr^{-1} and no fertilization). Every year from 2002 to 2016, pin-point methodology was used to measure vegetation. In each transect, presence/absence of species was recorded in 40 pin-points regularly spaced. Data set owner: Katja Klumpp (INRAE, Grassland Ecosystem Research Unit).

38. The data set consists of 48 plots on shortgrass steppe sites in the Central Plains Experimental Range Nunn, Colorado, USA. The experiment evaluated four treatments (12 replicates per treatment): control inside exclosure, control outside exclosures, *Bouteloua gracilis* removal inside exclosure and *Bouteloua gracilis* removal outside exclosure. Treatments were applied on 9 m^2 plots and species density was measured in a central 1 m^2 quadrat from 1997 to 2005 using vegetation point intercept method. A 10 point frame intercept was used in four locations within each 1 m^2 quadrat (in total, 40 points of contact was recorded for each quadrat). This data set was provided from Shortgrass Steppe Long Term Ecological Research (SGS-LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sgs.703.1.

39. The data set consists of 12 permanent 0.25 m^2 quadrats located on a wet meadow in Ohrazeni, Czech Republic. The experiment evaluated four treatments (3 quadrats each): control, fertilization (65 g/m^2 of commercial NPK fertilizer), and dominant removal (*Molinia caerulea* plants were manually removed annually) and fertilization and dominant removal together. Each year in the second half of June a mowing treatment was applied. In each plot, the biomass of each species was measured annually from 1999 to 2015. Data set owner: Jan Lepš (Department of Botany, Faculty of Sciences, University of South Bohemia). More information: (Lepš, 2014).

40. The data set consists of eight plots located on a permanent grassland on the Long Term Experiment SOERE-ACBB in Theix, France. The experiment evaluated, on one hand, the effect of the intensity of grazing with two treatments with cattle rotational grazing at high (Ca+) or low (Ca-) level of herbage utilisation; these two treatments do not received any mineral fertilisation. It also evaluated, on the other hand, the effect of nutrient availability, comparing two treatments conducted under fixed cutting regime (three cut/per year), one with fertilization (NPK fertilizer) and the other without fertilization. Each treatment had two replicate plots. Every year from 2004 to 2013, the presence/absence of species was measured using 40 pin-points regularly spaced along fixed transects. Complementarily, at each pin-point, 6 points are distributed to species according to visual estimation of their volume. Data set owner: Frédérique Louault (INRAE-UREP). More information: (Louault *et al.*, 2017).

41. The data set consists of six permanent plots located on Chihuahuan desert grassland/shrubland in Sevilleta National Wildlife Refuge, New Mexico, USA. In these plots, permanent transects (400 m) were established in 1989 until 2014 (number of years recorded varies from 8 to 26 depending on the plots). The experiment was designed to evaluate natural vegetation, so no management or treatment was applied. The data belong to the Sevilleta Long-Term Ecological Research Program (LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.200.174699.

42. The data set consists of 20 plots located on montane grasslands at three study areas in New Zealand, which were established under a monitoring scheme of the former Crown Leasehold Lands Monitoring Unit. Transects in the different sites were established in different years, but all were remeasured 6 or 7 times. All selected transects were burned either before or soon after the transects were established. The Fe of each species was recorded using fifty 0.25 m^2 quadrats centred at 2 m intervals along a 100 m transect. Data set owner: Caroline Mason (Darroch Limited, Christchurch New Zealand) and Hannah Buckley (Auckland University of Technology, Auckland, New Zealand). Data retrieved from the New Zealand National Vegetation Survey Databank. More information: (N. J. Day & Buckley, 2013).

43. The data set consists of 7 plots located on montane grasslands within the Harper and Avoca catchments, Canterbury, New Zealand. There were no specific treatments, but plots were burned either prior to or after the transects were established. From 1959 to 1991, the Fe of species was recorded using fifty 0.07 m^2 circular subplots centred at 40 cm intervals along a 20 m transect. Data set owner: Alan Rose (Upland Research, New Zealand) and Manaaki Whenua – Landcare Research. Data retrieved from the New Zealand National Vegetation Survey Databank. More information: (Evans, 1969) and (Rose, Platt, & Framptom, 1995).

44. The data set consists of 48 quadrats (1 m^2) located on two adjacent hyper-oceanic coastal grasslands in United Kingdom (one wet, one dry). The experiment was designed as a randomized block design, with six treatments: 1) vertebrate grazing exclusion, 2) burial box with no sand added, 3) buried to 10 cm, 4) buried to 20 cm, 5) windbreak - shelter from prevailing SW winds, 6) no treatment. Each treatment had four replicates on each grassland type. Percentage of vegetation cover was visually estimated annually in each quadrat from 2004 to 2010. Data owners: Robin Pakeman (James Hutton Institute, Aberdeen) and Jack J. Lennon (School of Biological Sciences, Queen's University Belfast).

45. The data set consists of 16 plots located on an *Agrostis capillaris – Festuca ovina* grassland in Cleish and Kirkton, United Kingdom. Four treatments were imposed from 1989 to 1995: 1) ungrazed, 2) sheep grazed to maintain a sward height of 3-4 cm, 3) sheep grazed to maintain a sward height of 4-5 cm, and 4) sheep grazed to maintain a sward height of 6-7 cm. Each species was measured in a transect, using the inclined-point quadrat method (32·5° to the horizontal) at 20 locations per plot with a minimum of 25 contacts per location. More information: (Hulme, Pakeman, Torvell, Fisher, & Gordon, 1999).

46. The data set consists of eight plots located on a *Molinia caerulea* grassland in Bell Hill and Cleish, United Kingdom. Three treatments were used from 1985 to 1991: 1) cattle grazed 33% utilization of *Molinia*, 2) cattle grazed 66% utilization of *Molinia*, and 3) ungrazed. Each species was sampled using the inclined-point quadrat method (32·5° to the horizontal) at twenty locations per plot with a minimum of 25 contacts per location. More information: (S. A. Grant, Torvell, Common, Sim, & Small, 1996).

47. The data set consists of seven plots located on a *Nardus stricta* grassland in Cleish and Sourhope, United Kingdom. There were different treatments where cattle or sheep density was adjusted twice a week to maintain the vegetation height between tussocks, (i) 6-7 cm (cattle, two replicates), ii) 4–5 cm (cattle, three replicates), (iii) 4–5 cm (sheep, one replicate) and (iv) 3–4 cm (sheep, one replicate). Every year from 1984 to 1989 (3 replicates), and from 1988 to 1993 (4 replicates), each species was measured using inclined-point quadrat method (32·5° to the horizontal) at 20 locations per plot with a minimum of 25 contacts per location. More information: (S. A. Grant, Torvell, Sim, Small, & Armstrong, 1996) and (Common, Wright, & Grant, 1998).

48. The data set consists of 12 plots located on a degraded moorland previously dominated by *Calluna vulgaris* on the Burnhead heft at the Redesdale Experimental Farm in Northumberland, United Kingdom. The 12 plots were divided in three areas (mature heath, pioneer phase heather regenerating primarily by vegetative means after burning of young stands of heather in 1987, and pioneer phase heather regenerating from seed after burning older stands of heather in 1987) with four treatments per area. The four treatments were: 1) ungrazed, 2) sheep grazed (0.4 ha^{-1} yr^{-1}), 3) sheep grazed (0.8 ha^{-1} yr^{-1}), and 4) sheep grazed (1.2 ha^{-1} yr^{-1}). Every year from 1989 to 1994, each species was measured in a transect, using the inclined-point quadrat method (32·5° to the horizontal). A minimum of 25 points contacts were recorded, and the procedure was repeated in 20 permanent quadrat locations per plot, giving a minimum total of 500 contacts per plot. More information: (Pakeman & Nolan, 2009).

49. The data set consists of 17 plots located on a heather moorland at Dundonnell (five plots) near Ullapool and at Claonaig (12 plots), near Tarbert Loch Fyne, Argyll and Bute, United Kingdom. The experiment had different sheep grazing and exclusion treatments: 1) low at 0.4 sheep ha^{-1} yr^{-1}, 2) moderate at 0.8 sheep ha^{-1} yr^{-1}, 3) high at 1.2 sheep ha^{-1} yr^{-1}, 4) fenced against both cattle and sheep, and 5) fenced against cattle (only in Claonaig, two plots), also 6) sheep and cattle (variable stocking) recorded from the open hill. Every year from 1992 to 1997 (Claonaig), and from 1993 to 1998 (Dundonell), each species was measured using the inclined-point quadrat method (32·5° to the horizontal) at twenty locations per plot. More information: (Pakeman & Nolan, 2009).

50. The data set consists of four plots located on a high elevation grassland in the Ordesa-Monte Perdido National Park, Spain. Two treatments were used from 1993 to 2012: 1) herbivore exclusion, and 2) No herbivore exclusion. The point intercept method was used annually to measure vegetation along two perpendicular transects (10 m long each) at each plot. This yielded a total of 400 sample points per plot. More information: (Pardo, Doak, García-González, Gómez, & García, 2015).

51. The data set consists of 68 plots located along five sites in Soto de Viñuelas, Spain. In each plot of 8 m^2, vegetation was recorded using presence/absence data (frequencies) of all species in five quadrats of 400 cm^2 each from 1980 to 1995. Data set owner: Begoña Peco (Ecology Department Autonomous, University of Madrid).

52. The data set consists of nine plots located on a shrubland in Garraf, Spain. Three treatments were imposed from 1998 to 2014: 1) control, 2) warming (metallic curtain covering the plots during the night), and 3) drought (transparent curtain covering the plots during rainfall). Number of contacts per plot was used to quantify each species. Data set owners: Josep Penuelas, Marc Estiarte and Romà Ogaya (Global Ecology Unit CREAF-CSIC-UAB).

53. The data set consists of 734 permanent plots (1 m^2) in Chihuahuan desert, Jornada Basin Experimental Range, New Mexico, USA. The study is distributed among 5 habitat types (black grama grassland, creosote bush, grassy playa, tarbush and mesquite). From 1989 to 2012, the biomass of each species per plot was calculated from field measurement of individual species cover and height. The data belong to the Jornada Long-Term Ecological Research Program (JRN-LTER). More information: https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-jrn.2100011001.49.

54. The data set consists of 10 plots located on a degraded moorland previously dominated by *Calluna vulgaris* on the Burnhead heft at the Redesdale Experimental Farm in Northumberland, United Kingdom. The experiment had different grazing treatments: 1) summer grazing (0.7 sheep ha^{-1} yr^{-1}), 2) winter grazing (0.7 sheep ha^{-1} yr^{-1}), 3) year-round grazing (0.7 sheep ha^{-1} yr^{-1}), 4) year-round grazing (1.4 sheep ha^{-1} yr^{-1}), and 5) no grazing. Every year from 1989 to 1994, each species was measured using the inclined-point quadrat method (32·5° to the horizontal) at 20 locations per plot with a minimum of 25 contacts per location. More information: (Hulme *et al.*, 2002) and (Pakeman & Nolan, 2009).

55. The data set consists of 216 plots located on moorlands previously dominated mainly by *Calluna vulgaris* but now invaded by *Pteridium aquilinum* in Derbyshire, United Kingdom. The treatments were: no treatment; cut once per year; cut twice per year; herbicide sprayed; herbicide sprayed in first year, cut in second; and cut in first year, sprayed in second. Within each of these main plot treatments there were two sub-plot grazing treatments - sheep grazing and no sheep grazing. Finally, there were three restoration treatments applied at the sub-sub-plot level: untreated, *Calluna* moorland litter applied as litter, and *Calluna* vegetation applied as cut brash. All these 36 treatments had 6 replicates. From 1994 to 2003, the species composition was recorded using point-quadrats (1 m-long frame with 10 pin positions at 10 cm intervals, pin diameter = 2 mm). Data set owner: Rob Marrs (University of Liverpool).

56. The data set consists of 198 plots located on 12 sites in the United Kingdom (Environmental Change Network, ECN). In each plot (100 m^2), ten quadrats of 0.16 m^2 were selected and the vegetation was surveyed using the inclined-point quadrat method annually from 1994 to 2012. The data belong to UK Environmental Change Network (ECN) database. More information: Rennie *et al.* (Rennie *et al.*, 2016) and https://catalogue.ceh.ac.uk/documents/b98efec8-6de0-4e0c-85dc-fe4cdf01f086 and https://catalogue.ceh.ac.uk/documents/d349babc-329a-4d6e-9eca-92e630e1be3f.

57. The data set consists of 5 plots located in an old-growth Douglas-fir forest in the Oregon Cascade Range, USA. This study evaluated the effects of patch clearcut logging and slash burning (1962-63). From 1964 to 1983, percentage of vegetation cover was visually estimated 10 times in a quadrat of 4 m^2 for trees (vegetation > 60 cm tall) and 9 quadrats (0.1 m^2) for herb and low shrub (< 60 cm tall). The data belong to Andrews Forest Long-Term Ecological Research Program (AND-LTER). More information: Rothacher (Rothacher, 2013) and https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-and.3190.7.

58. The data set consists of 74 of the plots on the Park Grass permanent grassland experiment in Rothamsted, United Kingdom. The purpose of the experiment (begun in 1856) was to evaluate ways of improving the yield of hay by the application of inorganic fertilizers and organic manure. The different fertility and lime treatments have resulted in very different species composition. Herbage was taken from six randomly located quadrats measuring 0.5 m x 0.25 m within each plot, resulting in a total sampling area of 0.75 m^2 within each plot. From 1991 to 2000, the biomass of each species was measured annually for each plot. More information: Crawley *et al.* (Crawley *et al.*, 2005) and http://www.era.rothamsted.ac.uk/Park.

59. The data set consists of 210 plots located on a *dehesa* (savannah-like ecosystems) dominated by evergreen oak trees (*Quercus ilex*) scattered in a pasture in central Spain. The experiment was designed in two different areas, the first in lowlands with higher-productivity pastures composed mainly of taller annual plants and some perennial species and the second in uplands with low-productivity pastures composed mainly of short and sparse annual plants. Three treatments were used on both types of pastures between 2002 and 2007: 1) ungrazed, 2) grazed by small herbivores, and 3) grazed by large and small herbivores. The species cover (%) was visually estimated in each plot (0.20 m x 0.20 m quadrats). Data set holder: Marta Rueda (Department of Conservation Biology, Estación Biológica de Doñana (EBD-CSIC). More information: (Rueda, Rebollo, & García-Salgado, 2013).

60. The data set consists of 14 plots (400 m^2) of a mesophilic meadow in Central Germany after cessation of the former high fertilization. Since 2001 the now unfertilized grassland is mowed by a farmer two to three times a year. From 2001/2002 to 2015, percentage of vegetation and species cover (%) was visually estimated in each plot (20 m x 20 m) three times a year. Data set owner: Wolfgang Schmidt (Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany). More information: (Schmidt, 2007).

61. The data set consists of six plots (125 m^2) of a succession experiment on a former arable field in the Experimental Botanical Garden of the University of Göttingen, Germany. Within this experiment, three mowing and two fertilization treatments were used in this data analysis. Mowing treatments: a) mowing once per year in spring, b) mowing once per year in autumn, c) mowing twice per year. Fertilization treatments: a) unfertilized since 1969 b) twice per year adding mineral fertilizer to replace N, P, and K removed by mowing the previous year. From 1969 to 2015, percentage of vegetation and species cover (%) was visually estimated in each plot (5 m x 25 m) twice per year. Data set owner: Wolfgang Schmidt (Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany). More information: (Schmidt, 2006) and (Bernhardt-Römermann, Römermann, Sperlich, & Schmidt, 2011).

62. The data set consists of 41 plots which were set up from 1917 in various vegetation types after the foundation of the Swiss National Park (IUCN Ia reserve) to monitor the succession after cessation of human activities. The plots vary in size from 1 to 3000 m^2 and are differently shaped: triangles, quadrats or polygons all occur. Vegetation was constantly surveyed until today but in irregular intervals (average time step = 7 years). Percentage of plant species cover was visually estimated. Data set owner: Martin Schütz. More information: (Braun-Blanquet *et al.*, 1931), (Schütz, Krüsi, & Edwards, 2000).

63. The data set consists of 95 permanent plots located in Sevilleta National Wildlife Refuge, New Mexico, USA. The experiment was designed to evaluate the effect of prescribed burning and grazing exclusion. The experiment had 16 sites with half of them fenced against grazers and half unfenced. Among these sites, two areas were left unburned as control treatments, and the other plots were burned in different dates. Six plots (12 m^2) were sampled in each site by recording the individuals present in 36 quadrats (0.1 m^2) plots over 10 years (2004-2013). The data belong to the Sevilleta Long-Term Ecological Research Program (SEV-LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.148.131885.

64. The data set consists of 81 permanent plots located on grassland, grassland/shrubland and shrubland in Sevilleta National Wildlife Refuge, New Mexico, USA. The experiment had a rainfall manipulation treatment. Drought was induced by rainfall shelters reducing the annual rainfall, watering was applied by redirecting the water from the nearby rainfall shelters and control plots were left under natural rainfall regime. On grassland and shrubland sites there was 6, 12 and 9 plots in control, drought and watered treatments, respectively. In the grassland/shrubland site there were 9 plots in each treatment. Percent cover was estimated every spring in 1 m^2 quadrats from 2002 to 2010 or 2011 (depending on the plot). The data belong to the Sevilleta Long-Term Ecological Research Program (SEV-LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.147.167839.

65. The data set consists of 216 permanent plots located on grassland in Sevilleta National Wildlife Refuge, New Mexico, USA. The experiment evaluated the impact of prairie dog reintroduction on vegetation. Plots were divided in six sites: 3 plots in an area grazed by prairie dogs and 3 plots in ungrazed areas. In each site, 36 quadrats (0.25 m^2) were dispersed 20 m apart in a 100 m x 100 m grid. Individual plant species cover was recorded every year from 2005 to 2013. The data belong to the Sevilleta Long-Term Ecological Research Program (SEV-LTER). More information: https://portal.lternet.edu/nis/metadataviewer?packageid=knb-lter-sev.212.4.

66. The data set consists of 100 permanent plots (1 m^2) located on piñon-juniper woodland in Sevilleta National Wildlife Refuge, New Mexico, USA. In all plots, vegetation cover was estimated visually every year from 2003 to 2015. In two sites contained 40 plots and in the other site 20 plots. The data belong to the Sevilleta Long-Term Ecological Research Program (SEV-LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.278.245672.

67. The data set consists of 100 plots located in Sevilleta National Wildlife Refuge, New Mexico, USA. The experiment was designed as a removal experiment with six areas established in 1995 (one of them in 1998). In each area, the experimental consisted of five replicates on each of the three treatments: 1) control plots (untouched vegetation), 2) removal of all three dominant species (*Larrea tridentata*, *Bouteloua eriopoda*, *Bouteloua gracilis*), and 3) removal of one dominant species. However, 10 replicates were established in two sites in the last treatment (removal of one dominant species). Removal and visual estimation of species cover was carried out every year until 2015. The data belong to the Sevilleta Long-Term Ecological Research Program (SEV-LTER). More information: https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.168.192543.

68. The data set consists of 18 permanent plots located on three grassland and three shrubland in Central Plains Experimental Range, Colorado, USA. The vegetation structure was recorded as a driver of small mammal community dynamics. In each of the six areas, species cover was recorded on three permanent transects (1 m^2: sum of plots along the transect), from 1999 until 2006. The data belong to the Shortgrass Steppe Long Term Ecological Research Program (SGS-LTER). More information: Stapp (Stapp, 2013) and https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sgs.140.17.

69. The data set consists of seven plots of a fertilization and litter-removal experiment in a beech forest on limestone near Göttingen, Central Germany. Only the control variants of both experiments (i.e. no experimental impact) were used in this data analysis. From 1998 to 2015, percentage of herb- and shrub-layer vegetation and species cover (%) were visually estimated in each plot (5 m x 5 m) in spring and summer. Data set owner: Wolfgang Schmidt (Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany). More information: (Schmidt, 2009).

70. The data set consists of 40 plots located on an oligotrophic, traditionally managed meadow near Zvíkov, Czech Republic. The experimental design consisted of 10 replicates in each of four treatments: 1) no removals (an intact vegetation), 2) mycorrhizal grasses and forbs left, non-mycorrhizal species weeded out, 3) mycorrhizal *forbs* remaining, everything else weeded out, and 4) mycorrhizal *grasses* remaining, everything else weeded out. In all plots (1 m^2), the percentage cover of all vascular species was estimated visually every year from 2005 to 2016. Data set owners: Petr Šmilauer and Marie Šmilauerová (Department of Ecosystem Biology, Faculty of Science, University of South Bohemia). More information: (Šmilauer & Šmilauerová, 2013).

71. The data set consists of 80 plots (2 m^2) located on a floodplain grassland in Anloo and Taarlo, The Netherlands. Every year a mowing treatment was applied in all the plots. Individual plant species cover was recorded almost every year from 1973 to 2008. Data set owners: Christian Smit and Jan P.

Bakker (Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences).

72. The data set consists of 30 plots located on an alpine meadow in the north-eastern Tibetan Plateau in Qinghai Province, China. From 2005 to 2016, a fertilization experiment was designed with 10 nitrogen treatments. The treatments were control (no N added) and 9 combinations of three N forms and three N rates. The study site was grazed in winter from November 2011 to April 2015 to remove the excessive accumulated plant litter. Percentage cover was visually estimated in a quadrat (1 m^2) established at the centre of each plot. Data set owners: Ming-Hua Song (Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing) and Fei-Hai Yu (School of Nature Conservation, Beijing Forestry University). More information: (Song *et al.*, 2012).

73. The data set consists of 212 plots located on salt marshes of the Schleswig-Holstein Wadden Sea National Park in Hamburger Hallig and Westerhever, Germany. There were two treatments in Westerhever: natural condition and intensive grazing, and only natural conditions in Hamburger Hallig. Annually vegetation cover was measured using Londo scale (percentage of vegetation cover) from 1997 to 2015 in Hamburger Hallig and from 1995 to 2012 in Westerhever. Data set owner: Martin Stock (Wadden Sea National Park of Schleswig-Holstein).

74. The data set consists of 18 plots located on a wooded savanna (black cotton savanna) in Laikipia, Kenya. The treatments were six combinations (3 replicates) of cattle, wildlife, and mega-herbivore grazing. These treatments either allowed (1) the entry of all large mammalian herbivores, (2) the entry of all large mammalian herbivores, less cattle, 3) entry of all large mammalian herbivores except megaherbivores (elephants *Loxodonta africana* and giraffe

Giraffa camelopardalis), 4) entry of all large mammalian herbivores except megaherbivores and cattle, 5) entry of no large herbivores, or 6) entry of no large herbivores except cattle. A permanent 100 m × 100 m grid of 20 sampling stations was established in each plot. Every year from 2000 to 2015, vegetation was assessed by counting the number of pins hit by each species over a ten-point pin frame at each station. Data owner: Truman P. Young (Mpala Research Centre, and Department of Plant Sciences, University of California, Davis). More information: (Veblen, Porensky, Riginos, & Young, 2016).

75. The data set consists of 59 permanent 1 m^2 quadrats located on a coastal heathland in Lurekalven, Norway. Two treatments (grazed vs. ungrazed) were established across three contrasting habitats. All the plots were burnt in April 1994, and the grazing pressure has been c.1 sheep ha^{-1} yr^{-1}. From 1994 to 2005, all vascular plants, bryophytes and lichens were recorded annually using frequencies (1 m x 1 m metal frame divided into 16 subplots). Data set owner: Vigdis Vandvik (Department of Biological Sciences, University of Bergen, Norway). More information: (Vandvik, Heegaard, Maren, & Aarrestad, 2005).

76. The data set consists of 180 permanent plots on nine sites in Bonanza Creek LTER, Alaska, USA. The purpose of the study was evaluated in a succession sequence whether changes in ecosystem structure are accompanied by functional changes. As the experiment was focusing on changes during natural succession, there were no treatments. Percentage cover was visually estimated in each plot between 1983 and 2007 every 1-5 years depending on the plot. The data belong to Bonanza Creek Long Term Ecological Research Program (LTER). More information: (Viereck L.A., Van Cleve, Chapin, Hollingsworth, & Ruess, 2010) and https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-bnz.174.19.

77. The data set consists of 18 plots located on montane desert steppes in Gobi Gurvan Saykhan National Park, Mongolia. Two treatments were applied from

2000 to 2005: 1) exclusion of large ungulates, and 2) no exclusion of large ungulates. The species cover (%) was visually estimated in each permanent plot inside and outside the exclosures. Data set owner: Karsten Wesche (Botany Department, Senckenberg, Natural History Museum Goerlitz). More information: (Wesche, Ronnenberg, Retzer, & Miehe, 2010).

78. The data set consists of 9 permanent plots at a single-site attempting to recreate an *Alopecurus pratensis- Sanguisorba officinalis* floodplain grassland on formerly arable land. In 1986 the study site (3.6 ha) was re-sown with green hay collected from an example of the target community and monitored at the scale of the whole site, using plant quadrats from 1987-1989. From 1989 the site was divided into nine plots of c. 0.4 ha over which three contrasting grazing management practices (control, cattle and sheep) were randomly superimposed. These nine plots were monitored in June of each year from 1991-2009. More information: (Woodcock, McDonald, & Pywell, 2011).

79. The data set consists of 55 plots located on a mesophytic grassland community in southeast Estonia. The treatments were: fertilizer (24 replicates), sucrose (24 replicates) and control (seven replicates). Every year from 2002 to 2015, the species cover (%) was visually estimated in each permanent plot (0.5 m x 0.5 m). Data set holders: Martin Zobel, Kersti Püssa, Rein Kalamees and Meelis Pärtel (Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia). More information: (Liira *et al.*, 2012).

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Chapter IV

Are redundancy indices redundant?
An evaluation based on parameterized simulations

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Abstract

Functional redundancy is considered a major component of the insurance mechanism, which theoretically maintains ecosystem stability by preventing the loss of ecosystem functions with species loss. Over the past decades, examination of functional trait patterns to elucidate processes of community stability and ecosystem functioning have stimulated considerable amount of research in ecology. As a result, a multitude of indices have been developed, describing community functional structure with various levels of overlap in their methodology. Here, we review the set of indices that have been suggested to measure the level of redundancy in traits among species in ecological communities.

We first evaluate the correlations among redundancy indices and classical indices of community taxonomic and functional structure (species richness, Simpson diversity, functional richness, evenness and divergence). Second, we estimate the predictive power of these indices in terms of community vulnerability to species loss. Finally, we assess the sensitivity of the results to scenarios with different species loss orders.

We simulated communities with different levels of taxonomic and functional structure (richness, evenness and divergence). Then, we simulated four scenarios of species loss order (abundance, functional uniqueness, environmental sensibility and random). The vulnerability of communities was estimated by the changes in community structural parameters (functional richness, functional divergence and biomass) as species were progressively removed from the initial communities.

Our results showed that four out of the five redundancy indices tested were strongly correlated (Pearson R>□0.6□) with at least one of the classical indices of community structure. Those correlations partly explained why the redundancy indices did not outperform classical indices in predicting community vulnerability to species loss. The fifth redundancy index (FredD) was the least correlated with classical indices of community structure (Pearson R<□0.24□), however it also reached the lowest performance in predicting community vulnerability to species loss (R2 < 0.07). The order in which

species - and their functional traits - are lost, and the community parameters assessed had a strong impact on communities’ vulnerability to species loss. In contradiction to theoretical predictions of the insurance hypothesis, the current redundancy indices might not be good indicators of vulnerability to species loss.

1. Introduction

Biodiversity loss impairs ecosystem processes and services, as it is generally associated with loss, or modification, of ecosystem functions (Cardinale *et al.*, 2012). In the last decades evidence has been accumulating that ecosystem processes and services depend on the functional traits of species composing biological communities (de Bello, Lavorel, Gerhold, Reier, & Pärtel, 2010; Díaz *et al.*, 2007; Hooper *et al.*, 2005). The maintenance of the functional trait structure of communities even under changes in species composition can therefore ensure the ability of ecosystems to withstand the effects of global change drivers and maintain the provision of ecosystem functions and services. Stressful events, occasional disturbances, or even simple random fluctuations can cause species loss in communities. The functional role of lost species can be maintained by the presence of 'redundant' species that have similar effects on the ecosystems (Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010; Walker, 1992). In this sense, several authors have placed functional redundancy at the core of the theory relating the resistance and resilience of ecosystem functioning to species loss (Lawton & Brown, 1993; McCann, 2000; Rosenfeld, 2002) via the insurance hypothesis (McCann 2000). This hypothesis states that a community needs multiple species with a similar function (effect redundancy), but with different responses to environmental fluctuations (response diversity), so that they can buffer each other when facing environmental changes. In this direction, Mouillot *et al.* (2014) showed, in fish fauna, that low functional redundancy could increase ecosystem vulnerability to environmental changes.

Assessing the insurance effect has proven complicated because of the multiple aspects involved (species richness, functional effect trait redundancy, and functional response diversity). So far, the insurance effect has mostly been assessed through species richness, assuming that it is positively correlated with functional redundancy and response diversity. However, functional redundancy is increasingly recognized as a key parameter of ecosystems' resistance and resilience to species loss (McCann, 2000; McWilliam *et al.*, 2018; Naeem, 1998; Oliver *et al.*, 2015; Walker, 1992). Suitable indices of functional redundancy are essential to quantify the importance of redundancy in ecosystem dynamics. Over the past decade, ecologists have developed multiple methods to evaluate the functional structure of communities (Carmona *et al.*, 2016; Kondratyeva, Grandcolas, & Pavoine, 2019; Mouchet, Villéger, Mason, & Mouillot, 2010; Pavoine & Bonsall, 2011; Schleuter, Daufresne, Massol, & Argillier, 2010) and in particular to quantify functional redundancy (Carmona *et al.*, 2016; de Bello *et al.*, 2007; Laliberté *et al.*, 2010; Ricotta *et al.*, 2016). However, a comparative evaluation of the different functional redundancy methods and how they relate to other components of taxonomical and functional structure is missing. Such an evaluation will improve understanding and interpretation, facilitate comparison across methods, and gauge the value added by new methods with respect to already existing ones (Moriarty *et al.*, 2018).

Although the concept of redundancy seems very promising, there is no consensus on the mathematical definition of functional redundancy in a community. One popular approach is to average the number of species per functional group. As such, most of the existing approaches depend on a subjective a priori definition of functional groups in a community (Fonseca & Ganade, 2001; Laliberté *et al.*, 2010; McWilliam *et al.*, 2018; Mouillot *et al.*, 2014). While in some cases such a definition of functional groups is rather straightforward (e.g. nitrogen fixing plant species), assigning species to separate groups is often unfeasible and context-dependent (Westoby 1998). Alternatively, measures of functional redundancy based on the saturation of the functional space relatively to species richness, without considering functional groups, have been developed (de Bello *et al.*, 2007; Ricotta *et al.*, 2016). Recently, Carmona *et al.* (2016) proposed a measure of redundancy within the traits probability distribution (TPD) framework. The mathematical formulation of redundancy in TPD resembles the concept of an average number of species per group. However, two aspects of the TPD framework make it different and completely independent from the definition of functional groups. First, instead of defining rather broad functional groups, the functional space is divided into a high number of small multidimensional bins. Second, each species does not exclusively belong to one bin but has a probability to belong to each bin. While it has rarely been recognized in the literature, we expected that none of the above-mentioned indices of functional redundancy are completely independent from the classical indices describing either species diversity or community functional structure (see below). However, they are expected to be complementary and to provide an added predictive value, particularly in the characterisation of community resistance or vulnerability to species loss.

In a mathematical framework Fonseca & Ganade (2001) emphasized three characteristics of community structure that influence functional redundancy under the assumption that species loss from the community is random. First, species richness should increase functional redundancy, i.e. more species increase the probability that a lost species and its function can be replaced by another species in the community. Second, functional richness, which can be measured as the number of functional groups in an ecosystem (Laliberté *et al.*, 2010) or as the extent of the functional space occupied by the community (Mason *et al.*, 2005; Villéger *et al.*, 2008), is expected to reduce functional redundancy. Third, unevenness of species affiliation to different functional groups produces some functional groups with very little redundancy and therefore increases the risk of losing ecosystem function with species loss. Besides these characteristics, we can also expect that in the case of the indices proposed by de Bello *et al.* (2007) and Ricotta *et al.* (2016), redundancy will be related to the average dissimilarity between species, which can be estimated using Rao quadratic entropy (RaoQ , Rao 1982). These indices express redundancy in relative terms (i.e. for a given level of species richness and evenness) by taking advantage of the fact that Simpson species diversity represents the upper limit that RaoQ can reach in a community when all species are functionally unique.

Although the properties of several indices of functional structure have been studied (Mouchet *et al.*, 2010; Schleuter *et al.*, 2010), we are not aware of any controlled tests of the predictive power of different functional redundancy indices. Ideally such tests can be based on direct assessments of community vulnerability to species loss (Carmona, Guerrero, Morales, Oñate, & Peco, 2017; Leitão *et al.*, 2016; Sasaki *et al.*, 2014). The principle of these assessments is to evaluate the change in various functional attributes of a community while removing species one by one, following different criteria (for example species rarity, with rare species removed first, or random species loss). After that, vulnerability to species loss can be assessed either using attributes of these “extinction curves” or comparing the trajectories of an informed scenario (i.e. with hypothesis on the order of species loss) and a “null” scenario based on the average of repeated random orders extinctions. In this study we followed this approach, using parameterized simulations based on experimental data of environmental responses of individual plant species and their traits. We simulated four scenarios of species loss in each community and evaluated community vulnerability in terms of total abundance (as a surrogate of productivity), functional richness and functional divergence following (Carmona *et al.*, 2017). Finally, we evaluated and compared models predicting community vulnerability based on the initial characteristics of community functional structure, for classical indices of taxonomic and functional diversity, and for redundancy indices. Our study aims to answer three questions. First, how do the functional redundancy indices relate to classical indices (i.e. taxonomic diversity, functional richness, functional evenness and functional divergence)? Second, are functional redundancy indices good predictors of community vulnerability to species loss and how do they complement the information already contained in classical functional structure indices? Finally, how sensitive are the results to different species loss orders and to the community parameters used to assess vulnerability? We believe this simulation-based study is a timely necessity to help users to select the right tools in a period where indices are flourishing at an unprecedented rate.

2. Material & Methods

2.1. Indices

2.1.1. Redundancy based on functional groups

Most attempts to quantify functional redundancy have considered, in different ways, the number of species per functional group (Walker 1992; Fonseca & Ganade 2001; Wellnitz & Poff 2001; Laliberte & Legendre 2010). Functional groups are usually statistically constructed through cluster analysis, by minimizing the variation in traits within a group compared to the variation between groups (Rosenfeld 2002). One variant on the definition of functional groups is the concept of functional entities, i.e. unique combinations of functional trait values (Mouillot *et al.* 2014), where initial functional traits need to be expressed as discrete variables. In order to test only comparable indices, we selected the ones that are defined on continuous variables and therefore the functional entities method was not included in this study.

Laliberté *et al.* (2010) proposed two indices related to community resistance to species loss, which are based on functional groups and rooted in the concept of response and effect traits. Response traits are those that confer species different adaptations to environmental conditions, and effect traits are those that determine the effect of the species on ecosystem processes or functions (Lavorel & Garnier 2002). Functional effect groups are defined at the (regional) species pool level using Ward’s minimum variance clustering on the Gower dissimilarity matrix computed from effect traits (for details on Ward's clustering method see Legendre & Legendre, 2012). It should be noticed that the actual number of effect groups for each dataset is determined by visual inspection of the clustering dendrogram (Laliberté *et al.* 2010), by a rather subjective decision on which distance from the tips of the dendrogram produce a priori pertinent sets of functional groups. The first index proposed by Laliberté *et al.* (2010) is the average number of species present in each functional group (FRedN, Table 1). The second is the average functional response diversity (FRedD, Table 1). Response diversity is calculated as the dispersion in functional response traits space of species from the same functional effect group, assuming it is possible to clearly separate response and effect traits, which might not always be the case.

FRedD was not designed as functional redundancy index stricto sensu, because it quantifies response traits dispersion rather than effect traits redundancy. However, we considered it interesting to include FRedD in this study because it serves the same purpose as redundancy indices, i.e. predicting community resistance to species loss. In theory, if species within a functional group have different responses to stress events, i.e. high FRedD, the functional group is less likely to disappear after such events. A contrario, if all species from a given functional group have similar responses, e.g. they are all sensitive to drought, this functional group is likely to disappear in the event of a stressor, characterizing the community as less resistant.

2.1.2. Redundancy as the complement of uniqueness

Another approach to estimate functional redundancy represents the saturation of taxonomic diversity by functional diversity (de Bello *et al.* 2007). In this method, functional redundancy is calculated as a function of the relationship between species diversity (calculated using Simpson $= 1 - \sum_i p_i^2$ where p_i is the relative abundance of species i) and functional divergence, estimated by RaoQ index based on species pairwise traits dissimilarity ranging from 0 to 1 (e.g. Gower distance or overlap dissimilarity [de Bello *et al.* 2013] varying from 0, when two species are perfectly similar in their trait values, to 1 when they are maximally different). RaoQ is calculated as the sum of pairwise distances between species weighted by their relative abundance. The index uses the mathematical relationship between RaoQ and Simpson, since they are equivalent in the case that all species are functionally completely dissimilar; on the other hand, RaoQ tends to 0 when all the species are functionally similar. The ratio between RaoQ and Simpson gives an estimate of the functional uniqueness (U) of species in the community and its complement (Ur = 1-U, Table 1) is an estimate of functional redundancy (Ricotta *et al.*, 2016). It should be noticed that U is equal to the index called MPD, main pairwise dissimilarity (de Bello *et al.*, 2016).

2.1.3. Redundancy in the Trait Probability Density framework

The Trait Probability Density (TPD) framework proposed by Carmona *et al.* (2016) uses properties of probability density functions (i.e. the integral of the trait probability at each scale equals to 1) to express the functional trait structure at any ecological organization level. Briefly, the principle is to divide the trait functional space into bins representing all possible combination of unique (semi continuous) traits values and attribute a probability value to each of these bins. The probability value of the community in any given bin equals the sum of the species' probabilities in that bin weighed by their relative abundance in the community. TPD-based redundancy (TPDr, Table 1) is calculated as the number of species per bin, minus one, weighed by the value of the community probability density function at that bin (Carmona, Bello, Mason, & Lepš, 2019). Thus, it expresses the average number of species that could be removed without reducing the functional richness of the community (i.e. creating an empty bin). The index is bounded between 0, when the community is composed of only one species or when all species are completely unique in their traits, and species richness minus 1, when all the species completely overlap in their traits.

TPD relative redundancy (TPDrr, Table 1) is an attempt to decouple redundancy from its potential trivial relationship with species richness by dividing TPDr by the n-1 upper bound (Carmona *et al.*, 2019). After that correction, the index no longer expresses the average number of species, but the average proportion of the species present in the community that could be lost without losing functional richness.

Table 1: Summary table of the functional redundancy indices

Indices	Formula		Ref.
Functional Redundancy (FredN)	$FredN = \sum_{k=1}^{E} \frac{n_k}{e_k}$	- E is the number of functional group based on effect traits of species at the regional level - e_k is the total number of species in the k^{th} functional group at the regional pool level - n_k is the number of species from the k^{th} functional group present in the community levels	(Laliberté *et al.*, 2010)
Functional Dispersion (FredD)	$FredD = \sum_{k=1}^{E} \frac{\sum_{i=1}^{e_k} p_i dG_i}{\sum_{i=1}^{e_k} p_i}$	- p_i is the relative abundance of species *i* - dG_i is the distance between species *i* and the center of gravity of the functional group *k* in the response traits functional space	(Laliberté *et al.*, 2010)
Uniqueness Functional Redundancy (Ur)	$Ur = 1 - U$	- $U = \frac{FDrao}{1-D}$ = Uniqueness - *D* is Simpson dominance index ($D = \sum_i p_i^2$)	(Ricotta *et al.*, 2016)
TPD Functional Redundancy (TPDr)	$TPDr = \left(\sum_{i=1}^{n=FR} M_i \, TPD_i\right) - 1$	- M_i is the number of species present in the i^{th} bin. - TPD_i is the community Traits Probability Density function value of the i^{th} bin	(Carmona *et al.*, 2018)
TPD Relative Redundancy (TPDrr)	$TPDrr = TPDr/(N-1)$	- $TPDr$ is TPD Functional Redundancy - N is the Species Richness of the community	(Carmona *et al.*, 2019)

2.2. Simulations

2.2.1. Plant functional traits and response to environmental condition.

The simulations were parameterized with experimental data of species exposed to different environmental conditions, as published by Dostál *et al.* (2016). In this experiment, 103 species were grown in individual pots under 4 environmental conditions: control, fertilized, shaded and waterlogged. Five traits were measured (Height, SLA [Specific Leaf Area], Greenness [defined as the chlorophyll content of the leave], LDMC [Leaf Dry Matter Content] and leaf thickness) as well as the aboveground biomass of each individual, harvested after exposing the individuals to the treatments for 10 weeks. Data (available in Dostál *et al.* 2016) were reported as mean and standard deviation per species for each treatment. In this study, we used the stress treatment with the overall largest difference from the control treatment, i.e. shading, although other treatments generally provide consistent results. The 3 traits that best explained the difference in biomass between shading and control, i.e. Height, SLA and Greenness, were considered as effect traits, representing the effect on biomass production.

The individual species' response to environmental conditions was calculated using the relative interaction index (RII, Armas *et al.* 2004):

$$RII = \frac{(Biomass_{Control} - Biomass_{Stress})}{(Biomass_{Control} + Biomass_{Stress})}$$

The species environmental response, estimated with RII, was used as a parameter in two independent components of the methodological approach. First, the computation of the FredD index from Laliberté *et al.* (2010) requires estimating the responses the species to given environmental factors, within functional effect groups. We used RII as proxy of this response. Second, the species environmental response was used as ordering factor for the species loss scenario number 3 (see section below on species loss scenario).

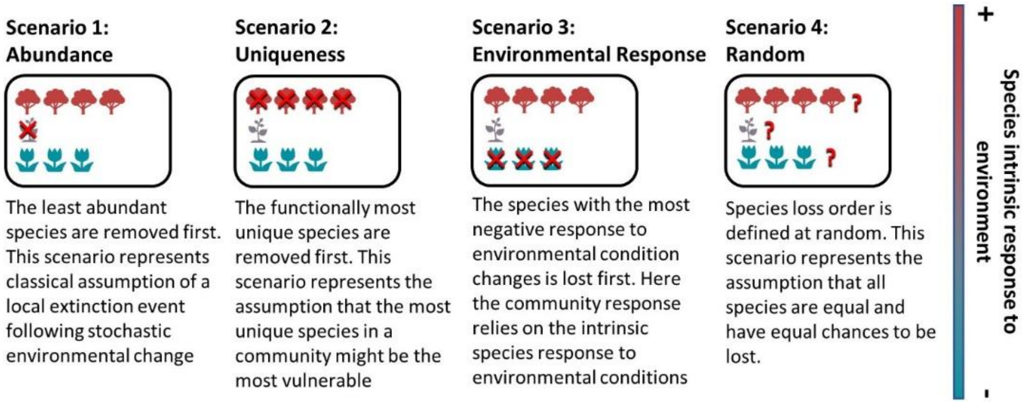
2.2.2. Communities

We simulated 1000 communities varying in species composition, species richness and dominance. To simulate each community, we randomly selected 8 to 50 species out of 103 from the above-mentioned species pool. The abundance of the dominant species was randomly set between 0.3 and 0.6, and the distribution of the rest of the species relative abundance followed a geometric series. This method allows simulating communities with gradients of species richness and dominance, two parameters with expected effect on resistance to species loss (Fonseca & Ganade, 2001). Species richness increases the potential number of species per functional group in a given regional species pool. The level of dominance in the community affects the evenness of the abundance distribution among functional groups; lower evenness of species distribution among functional groups is expected to reduce the resistance of the community to species loss (Fonseca & Ganade, 2001).

Each community was then characterized by five classical indices of taxonomic and functional structure: species richness, Simpson diversity, functional Richness (FRich), functional Evenness (FEve) and functional divergence (RaoQ); as well as by the five redundancy indices of interest presented above and in Table 1. FRich and FEve were calculated using the TPD framework (Carmona *et al.*, 2016). TPD-based indices (FRich, FEve, TPDr and TPDrr) require information on intraspecific variability (ITV) which was obtained from the standard deviation values provided in Dostál *et al.* (2016). Each dimension of the TPD space was divided in 30 bins. The other functional structure indices (RaoQ, FRedN, FRedD and Ur) are typically based on pairwise distances between mean traits values of species therefore this is the version of those indices presented in the main text. However, it is possible to account for ITV with those indices by constructing a pairwise distance matrix based on traits overlap (de Bello *et al.*, 2013). In the supplementary material Fig. S2 and Fig. S3 we show that, for this study, the mean and overlap version of the indices are well correlated and that the results of the models are very consistent with those presented in the main text (Fig. S5). For the indices based on functional groups, the number of functional groups was set to five after visual inspection of the clustering dendrogram. Prior to the computation of all the indices, the traits values were normalized using ln-transformation.

2.2.3. Species loss scenarios

Community vulnerability, or its inverse, resistance to species loss, can be assessed through the change in community functional structure following species attrition. Several authors have used species loss scenarios, both random and informed (i.e. with hypothesis on the order in which species would disappear in natural communities) to evaluate communities' vulnerability to species loss (Carmona *et al.*, 2017; Leitão *et al.*, 2016; Sasaki *et al.*, 2014; Schläpfer, Pfisterer, & Schmid, 2005).



The least abundant species are removed first. This scenario represents classical assumption of a local extinction event following stochastic environmental change

The functionally most unique species are removed first. This scenario represents the assumption that the most unique species in a community might be the most vulnerable

The species with the most negative response to environmental condition changes is lost first. Here the community response relies on the intrinsic species response to environmental conditions

Species loss order is defined at random. This scenario represents the assumption that all species are equal and have equal chances to be lost.

Figure 1: Schematic representation of the four scenarios of species loss. The rectangles represent a community, the forms represent species, and species abundance is represented by the number of occurrences of the forms in the community. The colours of the forms represent the species' intrinsic response to a given environmental factor. The red cross symbolises the removal of a species from the community.

We applied four species loss scenarios (illustrated in Fig. 1) to each of the 1000 simulated communities. In Scenario 1, the least abundant species are removed first. This scenario represents the classical assumption of local extinction events following stochastic environmental change, affecting the rarest species first (Sasaki *et al.*, 2017). In Scenario 2, the functionally most unique species are removed first. In this scenario, the assumption is that the most unique (or, in other words, functionally rare) species in a community are the most vulnerable (Losapio & Schöb, 2017; Mouillot *et al.*, 2013; Violle *et* *al.*, 2017). The uniqueness of a species in each community was calculated as its average distance from all other species present in the community (following the same approach proposed by both Ricotta *et al.* 2016 and Violle *et al*. 2017). In Scenario 3, the species with the most unfavorable response to changes in environmental conditions is lost first (Schläpfer *et al.* 2005, Losapio & Schöb 2017). Here the order of species loss in the community relies on the intrinsic species response to environmental conditions, with the most susceptible species being lost first. Finally, in Scenario 4, species are removed in a random order. It represents a case where no particular driver ordering the vulnerability of species can be established, either because those drivers do not exist or because they are unknown. In this scenario, for each community, results were averaged over 100 draws of random orders of species loss simulations (Leitão *et al.*, 2016).

2.2.4. Stability of community parameters

Following existing studies (Carmona *et al.*, 2017; Leitão *et al.*, 2016; Sasaki *et al.*, 2014) we measured the vulnerability of communities to species loss by quantifying the changes in community functional structure. We selected three community attributes that represent three complementary aspects of the community functional structure and that have been considered by authors in previous studies evaluating community vulnerability to species loss. The sum of species abundances (Biom) of the community, often taken as proxy for above-ground net primary productivity, is a common ecosystem function to consider. Functional richness (FRich) represents the total ‘volume’ of functional trait space occupied by the community and was computed with *TPD* package (Carmona, 2019). The loss of functional richness was used by Fonseca & Ganade (2001) to evaluate community vulnerability to species loss. Functional divergence (RaoQ) represents the average functional dissimilarity between the species present in the community (de Bello *et al.*, 2016). Changes in functional diversity were used to evaluate vulnerability of communities to species loss both by Sasaki *et al.* (2014) and Carmona *et al.* (2017).

Community vulnerability to species loss was then represented by the shape of the extinction curve of a community characteristic (e.g. Functional Richness) as species are successively removed from the community (Fig. 2), similarly to Sasaki *et al.* (2014), Leitão *et al.* (2016) and Carmona *et al.* (2017). There are several options to summarize the shape of the extinction curve and thereby of the resistance of the community to species loss. One of the options is to calculate the integral of the extinction curve, i.e. the area below the curve. In order to evaluate the variation of the shape of the curve but not on the initial value (origin) of the community attribute considered, it is convenient to standardize the integral by its initial functional attribute value and by the initial species richness of the community, bonding the integral between 0 and 1. A community with absolute resistance to species loss would maintain its functional attribute value while species are removed and the integral of the extinction curve would be close to 1 (Fig. 2, community type A). On the contrary, a community that would lose the essence of its functional attribute when losing the first species would have an extinction curve integral close to 0 (Fig. 2, community type C).

The integral solution is ideal for functional attributes that cannot increase with species loss (i.e. monotonic extinction curve, e.g. functional richness, biomass); however, some functional attributes can also increase with species loss (e.g. RaoQ). For a non-monotonic extinction curve (RaoQ) the integral approach is spurious, as it is not possible to standardize the maximum value. Subsequently, integral values superior to 1 are possible but do not necessarily represent higher resistance to species loss (because any deviation, positive or negative, with RaoQ for example, represents a deviation from the initial status and therefore a deviation from resistance to species loss). Therefore, we evaluated the vulnerability of the community functional feature along the extinction curve by a coefficient of variance to the origin CV_{org}:

$$CV_{org} = \frac{\sqrt{\left(\sum_{x=1}^{N}(i_x - i_o)^2\right)/N}}{i_o}$$

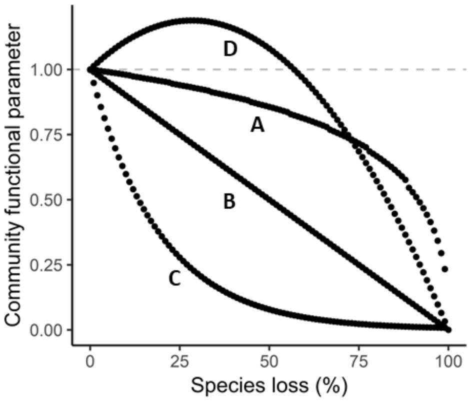
Where i_o is the functional attribute value of the full community and i_x is the functional attribute after x species were removed. N is the total number of species lost in order to compute CV_{org}.

CV_{org} is a measure of the community vulnerability (the opposite of resistance) to species loss in terms of functional attributes. It calculates the variation of a community functional attribute (e.g. FRich, RaoQ, Biomass, etc.) as species are sequentially removed from the community, in comparison to the original functional attribute value of the community. Higher CV_{org} means higher vulnerability, and thus lower resistance, of community functional structure to species loss. It is calculated in the same manner as CV but replacing the mean with the original value of the community attribute. Therefore, it presents similar advantages as the coefficient of variation as a measure of stability: it is standardised by the community attribute value, so that variation is independent of the mean or original value (making it possible to compare communities with high and low initial functional richness for example).

CV_{org} accounts for species richness, in the sense that if two communities have a similar shape of the functional extinction curve but different species richness, the community with higher species richness will have lower CV_{org}. However, the effect of species richness is smaller than the shape of the functional structure parameter extinction curve. This is illustrated in Fig. 2: while species richness reduces CV_{org}, we can observe that a stable community (type A) with 10 or 100 species will have lower CV_{org} than less stable communities (type B or C) regardless of their species richness. For parameters with monotonic extinction curves the integral and CV_{org} solutions are very well correlated and produce models with very similar fits as shown in supplementary material Fig. S2.

2.3. Analysis

First, we examined the responses variables, given that CV_{org} is a standardized measure, it allows comparison of community vulnerability across scenarios and across community parameters on which CV_{org} is calculated (i.e. FRich, RaoQ and Biomass). This can reveal which parameter is more vulnerable under a given scenario and to which scenario a given community parameter is more vulnerable. We used pairwise t-tests, first between CV_{org} measures computed on different community parameters within each scenario, second, between



	(A) Stable	(B) Random	(C) Unstable	(D) Non-monotonic
i) CVorg				
N10	0.384	0.667	0.885	0.426
N20	0.327	0.617	0.860	0.390
N50	0.292	0.586	0.847	0.369
N100	0.280	0.582	0.844	0.362
ii) Integral				
N10	0.761	0.459	0.211	0.848
N20	0.782	0.485	0.207	0.868
N50	0.794	0.500	0.201	0.879
N100	0.798	0.500	0.198	0.883

Figure 2: Theoretical representation of the evaluation of functional structure vulnerability to species loss. The A, B and C series represents monotonic extinction curves of respectively stable, random and unstable community structures. The series D represents a non-monotonic extinction curve, where a community parameter can initially increase compared to its original values while species are removed. The table on the right gives the vulnerability values for theoretical communities with different species richness levels (N10 = 10 species, N20 = 20 species, N50 = 50 species and N100 = 100 species) following the 4 theoretical extinction curves represented on the graph. Vulnerability is estimated with the CVorg method (average deviation from the initial community functional parameter value) and with the integral method (area under the curve).

scenarios within each of the CV_{org} measure (see Fig. S1). Evaluating how communities' vulnerability varies depending on CV_{org} measures and scenarios is helpful to interpret the results on models' prediction of vulnerability presented below.

We then assessed how the functional redundancy indices relate to the classical indices of communities' taxonomic and functional structure (Species Richness, Simpson Diversity, Functional richness, Functional Evenness and RaoQ). For this purpose, we performed Pearson correlations between pairs of indices computed for the 1000 simulated communities.

Then, we evaluated how well the community functional attributes, both classical indices and functional redundancy indices, explain the variability in community vulnerability to species loss (CV_{org}). We fitted linear models for each of the 4 scenarios of species loss and for each of the 3 community metrics considered for stability (CV_{org} for FRich, RaoQ and Biomass). In the models, we first used as single predictors each of the classical indices of taxonomical and functional structure and each of the functional redundancy indices. We then extracted and compared the coefficient of determination (R^2) of each model based on each unique predictor.

Finally, we assessed how much the functional redundancy indices increased the amount of explained variation compared to the classical community structure indices. We thus fitted different linear models with 2 predictors for each scenario and response variable, the first being the classical index producing the highest model R^2 as unique predictor (from the previous analysis), the second being one of the other classical and redundancy indices available. Once again, we extracted and compared the coefficient of determination of the linear models, now with two predictors.

3. Results

3.1. Comparing vulnerability across response variables and scenarios

Communities were not equally vulnerable according to i) the functional attribute considered and ii) the scenario of species loss order (Fig. S1). For example, the values of CV_{org} calculated on RaoQ and biomass were significantly lower in scenario 1 (abundance) than in all other scenarios. Moreover, the ranking of the three CV_{org} differed within the scenarios. In scenario 1 the communities were more vulnerable in terms of functional richness than in terms of biomass or functional divergence. On the contrary, in the second scenario, functional richness was the most resistant to species loss of the three community attributes tested (lowest CV_{org} values).

As mentioned in the characterization of the CV_{org} index, functional attributes such as RaoQ can both increase or decrease following the removal of a species from the community. These properties can result in values higher than 1 of CV_{org} which occurred in scenario 3 and 4.

3.2. Correlations between redundancy indices and classic indices of taxonomic and functional community structure

Redundancy indices correlated, in some cases very tightly, with at least one of the classical indices (Fig. 3). For example, FredN and TPDr were highly correlated with species richness (r=0.99 and r=0.95, respectively). Uniqueness based redundancy (Ur) was highly correlated with functional divergence (RaoQ, r=-0.91) but not with Simpson diversity (r=-0.02), although both parameters are included in uniqueness calculation.

Interestingly, when TPD based redundancy is expressed as proportion of the community (TPDrr) rather than absolute number of species (TPDr), the index was best correlated to the functional divergence (RaoQ) and evenness of the trait distribution in the community (r=-0.6 and r=-0.45, respectively). Functional Richness most strongly correlated with TPDr and FredN (r=0.74 and r = 0.77 respectively).

FredD was the redundancy index most independent from the classical community structural indices. Its highest coefficient of correlation was with species richness and Simpson index and only reached 0.23. The other redundancy index that seems free of trivial mathematical relations with the classical community structural indices is TPDrr, although its coefficient of correlation with RaoQ reached -0.6.

3.3. Model predictions of community vulnerability to species loss

3.3.1. Single predictor models

The results of models using a single predictor of community vulnerability generally showed that functional redundancy indices often do not explain more than the classical indices (Fig. 4). Under the abundance scenario (scenario 1), species richness was the best predictor of community vulnerability both in terms of functional divergence (R^2=0.70) and biomass (R^2=0.40). As expected from their strong correlation to species richness, FredN and TPDr yielded close performances in both cases. The vulnerability of communities' functional richness to species loss was best predicted by functional evenness (R^2 = 0.18).

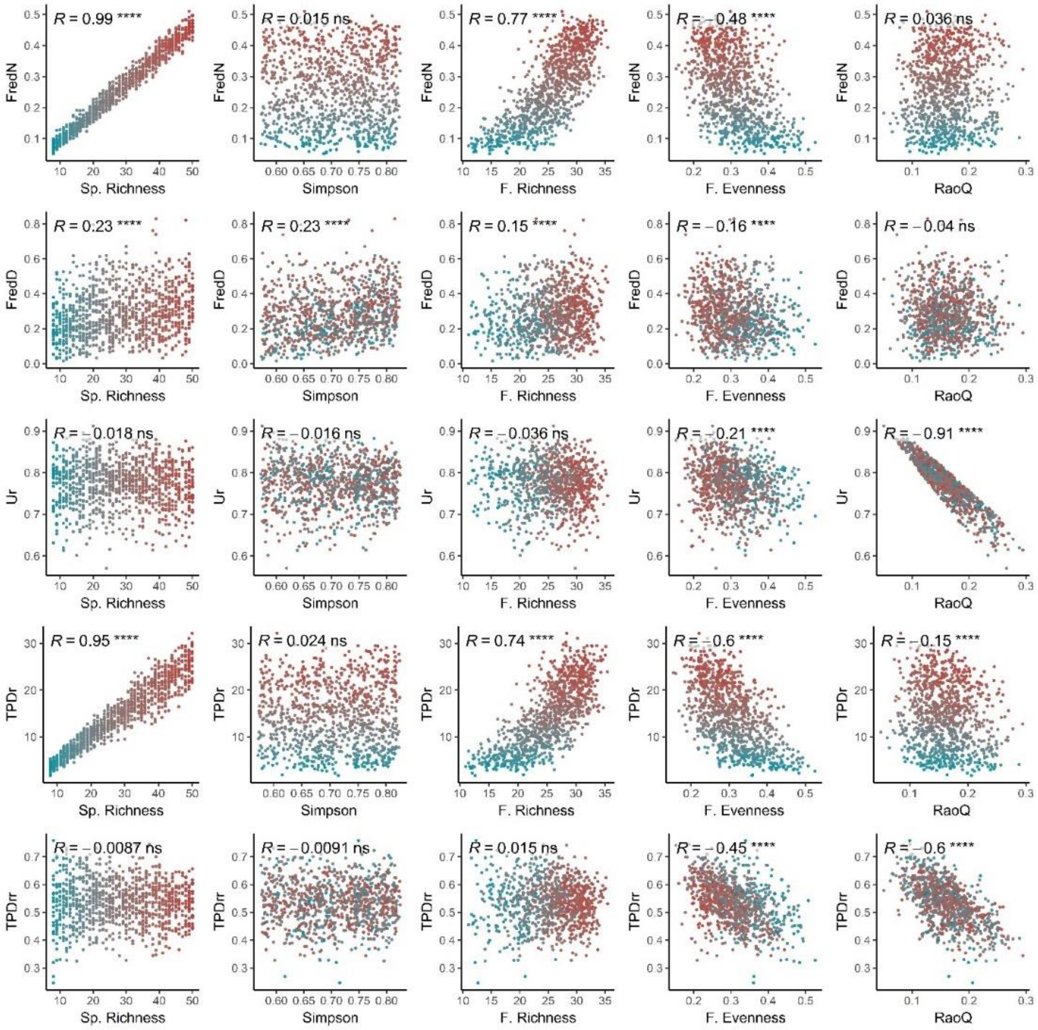


Figure 3: Correlation between functional redundancy indices and classical community functional attributes. Each panel presents the correlation between the functional redundancy indices and the classical taxonomical and functional structure indices of 1000 simulated communities. The colour gradient represents the species richness, the scale can be read on the left graph of each row with species richness on the x axis. Pearson correlation coefficient and the significance of the correlation test are displayed on each panel (“ns” for non-significant, “.” for P <0.1, “*” for P <0.05, “**” for P <0.01, “***” for P <0.001, “****” for P <0.0001).

Under the second scenario, based on the loss of functionally more unique species, the vulnerability of the communities' functional divergence and biomass was best predicted by uniqueness-based redundancy index (Ur, R^2=0.28) and by RaoQ (R^2=0.21). None of the classical or redundancy indices yielded a substantial model fit when predicting functional richness vulnerability.

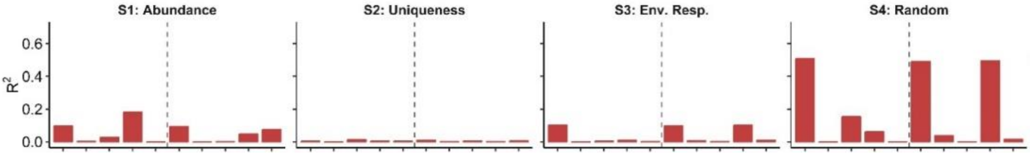
In the third scenario, where species loss order was based on species intrinsic environmental response, community vulnerability was not well predicted by any of the classical or redundancy indices. Even the FredD index, i.e. the only index directly integrating the species' intrinsic response to environment, did not predict vulnerability to species loss in this scenario.

Finally, in the last scenario, based on random species loss order, vulnerability of community functional richness was best predicted by species richness. Similarly to vulnerability of RaoQ and biomass in scenario 1, FRedN and TPDr yielded similar model fit than species richness. Vulnerability of community functional divergence (CV_{org} RaoQ) was best predicted by Simpson and RaoQ. Although it integrates both RaoQ and Simpson in its calculation, uniqueness-based redundancy did not yield similar results.

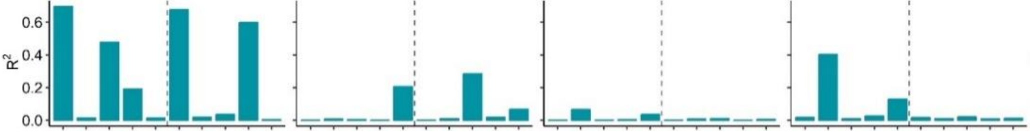
3.3.2. Models with two predictors: the additional value of redundancy indices

When added as second predictor, the redundancy indices did not considerably improve the model fit more than the classical community structure indices. Moreover, when redundancy indices do improve the prediction of the model, it often reflects the classical index it was most correlated with. For example, focusing on the vulnerability of community functional richness to species loss (red bars, Fig. 5), we observed that in first and second scenario species richness was the parameter that improved the model most and that in both cases, FredN and TPDr yield similar results. Similar results were obtained when predicting biomass vulnerability in scenario 4. In the majority of models tested, none of the parameters improved the model fit in a substantial manner.

A) CV_{org} functional richness



B) CV_{org} functional divergence (RaoQ)



C) CV_{org} biomass

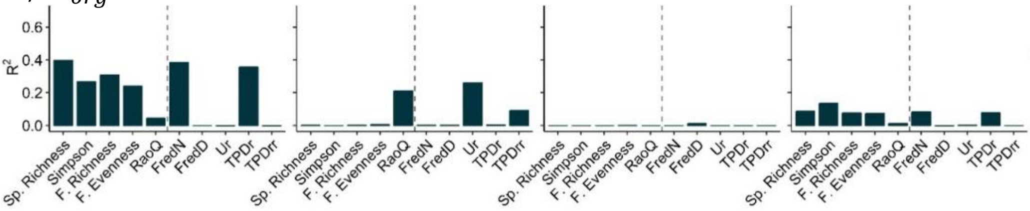
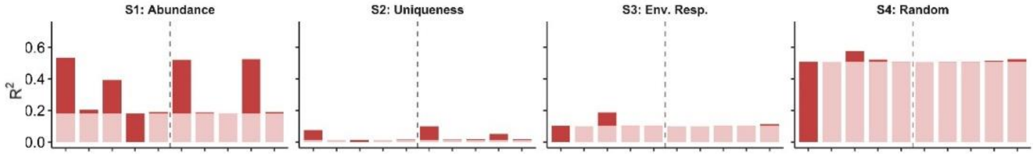
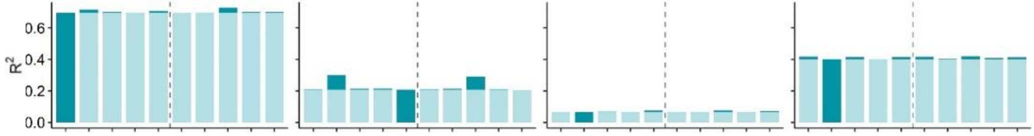


Figure 4: R-square of linear models using one community functional attribute to predict community vulnerability to species loss (CVorg) in functional richness (A), RaoQ (B) and biomass (C) under the 4 scenario of species loss. In each panel, the vertical dashed grey line separates the classical taxonomic and functional community structure indices (left-hand side) from the functional redundancy indices (right-hand side).

A) CV_{org} functional richness



B) CV_{org} functional divergence (RaoQ)



C) CV_{org} biomass

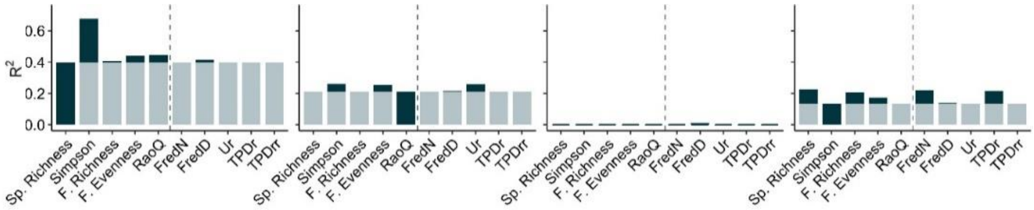


Figure 5: R-square of linear models using one community functional attribute in addition to the best predictor (highest r-square in models of Fig. 4) to predict community resistance to species loss (CVorg) in functional richness (F. Richness), functional divergence (RaoQ) and biomass under the 4 scenario of species loss. The lighter area of the bars represents the part of the variability explained by the best single predictor (including the variation explained by both predictor). The darker area of the bars represents the additional variation explained by the second predictor only. The best single predictor for each scenario per response variable condition can be identified as the only bar without lighter area. In each panel, the vertical dashed grey line separates the classical taxonomic and functional community structure indices (left-hand side) from the functional redundancy indices (right-hand side).

4. Discussion

This study shows that existing functional redundancy indices might not improve predictions of community vulnerability compared to already established indices of community taxonomic and functional structure. Redundancy indices correlate strongly with the classical indices of community structure and considering them did not strongly improve models predicting community changes to different species loss scenarios. While functional redundancy has been repeatedly mentioned as an important component of community resistance to environmental change (McWilliam *et al.*, 2018; Naeem, 1998; Oliver *et al.*, 2015; Walker, 1992), our study highlights that classical indices, namely species richness, Simpson, FRic, FEve and RaoQ, already describe well the functional structure of communities, including the property that can be associated with redundancy.

4.1. Comparing vulnerability across response variables and scenarios

In this study, and we expect also in many types of natural communities, functional attributes are not equally vulnerable among species loss scenarios. As expected, in the second scenario, where the most unique species were removed first, CV_{org} was higher in terms of RaoQ (Fig. S1 B). On the contrary in scenario 1, because the first species removed had the lowest abundance, the total biomass of the community was very resistant. Further, since functional richness is not weighed by abundance, the vulnerability of functional richness was not different between scenarios 1 and 4. The fact that CV_{org} between scenarios 3 and 4 was very similar for the three response variables suggests that species sensitive to environmental stress were not very different from the non-sensitive species in terms of occupation of the trait space. Those differences between scenarios and indices confirm the importance of considering different types of scenarios and the appropriate types of response variables when assessing the vulnerability of community to species loss.

4.2. Correlations between redundancy indices and classic indices of taxonomic and functional community structure

All redundancy indices tested were correlated with at least one classical index of community functional structure. The high correlation of FredN and TPDr with species richness could be explained by the fact that, for a given pool of species, the number of redundant species is mathematically constrained by species richness. In both cases, the dimensions of the functional space, i.e. the maximal functional richness, are fixed by the species pool considered in a given study. For FredN, it is the number of functional groups (5 in our case) defined at the species pool level. In the TPD framework, it is the range of values in each trait considered, again at the species pool level. Therefore, the maximal number of species per functional group (i.e. max FredN) or per unit of functional space (i.e. max TPDr) is directly limited by the species richness of a community. This is especially true under the random assembly process of the simulation. However, even under biotic and abiotic constraints of natural community assembly processes, the maximal redundancy that a community can reach will remain directly related to the species richness of the community. In fact, in a global scale study using large scale natural species assemblages of birds and mammals, Cooke *et al.* (2019) reported a very high coefficient of correlation between functional redundancy (using an index similar to FredN with functional groups based on unique traits combination) and species richness (r=0.94).

The high correlation between Ur and RaoQ can also be explained by the mathematical relation between the two indices. Indeed, uniqueness is calculated as the ratio between RaoQ and Simpson diversity (Table 1). In our dataset, RaoQ ranged from 0.05 to 0.30 while Simpson ranged from 0.58 to 0.82 (due to simulation parameters of relative abundance, *i.e.* geometric series with dominant species relative abundance of 0.3 to 0.6). These are values which are typically found across studies using large species pools and Gower distance as a measure of trait dissimilarity (e.g. Pillar *et al.* 2013; Ricotta *et al.* 2016). Since the maximal value of RaoQ is Simpson and the abundance distribution in the community affects both RaoQ and Simpson in a similar way, it is expected that the uniqueness will always be strongly related to RaoQ.

The negative sign of the correlation between TPDrr and functional evenness suggests that the theoretical consideration of Fonseca & Ganade (2001) on the importance of evenness for community resistance to species loss will be central in the interpretation of the effect of TPDrr redundancy on community resistance. The higher evenness of less redundant communities could compensate the effect on community resistance to species loss.

The positive sign of the correlation between functional richness and TPDr or FredN is in contradiction with theoretical assumption of Fonseca & Ganade (2001): higher functional richness reduces functional redundancy. This is probably an artifact due to the correlation between functional richness and species richness (r=0.78, Fig. S4) and the very strong correlation of TPDr or FredN with species richness. The same can be said for functional evenness, which is negatively correlated with species richness (r=-0.49), FredN (r= -0.48) and TPDr (r=-0.60).

The strong correlation between the redundancy indices and classical indices of community functional structure suggest that they do not necessarily improve the understanding of communities' characteristics, but rather illustrate the other side of the same coin. The remaining task is to assess if this alternative picture of community structure helps in predicting or understanding its properties, in particular regarding vulnerability to species loss.

4.3. Model prediction of community vulnerability to species loss

In the two series of models, with either one or two predictors (Fig. 4 and Fig. 5), we found that redundancy indices never explained much more of the variability in community vulnerability to species loss than the classical indices they are the most correlated with. Thus, the simple correlations we present in Fig. 3 do not only exemplify mathematical relationships between indices but are also the basis of the lack of additional value that redundancy indices bring to the understanding of community functional structure and the ecological properties we try to infer from it.

Parsimonious principle suggests that if no additional value in terms of results is obtained by increasing complexity, one should prefer the simplest methods. Nevertheless, even if they do not increase model performance, some indices like TPDrr present the advantage of an intelligible metric that could allowed easier interpretation and comparison of results. For example, it might be easier to discuss that the functional space of a community is occupied on average by 60% of the species present in that community rather than to say that the functional evenness is 0.3.

The rationale behind the FredD index is appealing, i.e. communities where functionally redundant species (i.e. from the same effect traits functional group) have different responses to an environmental cue (i.e. high dispersion in response traits functional space) should be less vulnerable to species loss under that particular environmental cue (Laliberté *et al.*, 2010; Mori, Furukawa, & Sasaki, 2013). Scenario 3, where species loss order was defined by species intrinsic response, seemed a good tool to test this particular hypothesis. Although the species intrinsic response was explicitly set as response “trait” in FredD calculation, the index did not perform well as a predictor of community’s vulnerability to species loss. This result highlights that tight relationships between effect traits and ecosystem function, and response traits and environmental cues are crucial for response diversity to be a good predictor of functional vulnerability of community to species loss. Cowling *et al.* (1994) provide an example of a simpler system. In a fynbos community, different growth forms and different regeneration traits within each growth form ensure stable diversity of growth forms despite disturbances by fire.

Our simulations are consistent with the main expectations proposed by Fonseca & Ganade (2001) where species richness, functional richness and evenness are expected to be the main determinants of community vulnerability to species loss in terms of functional richness. Focusing on the model fit predicting vulnerability of functional richness (Fig. 5, CV_{org} F. Richness in red), in the four scenarios the pairs of predictors with highest R^2 are systematically composed of those three parameters (species richness, functional richness and evenness). Moreover, the partial effects of predictors in those models always show a negative effect of the species richness and functional evenness on the vulnerability index and a positive effect of functional richness. Overall, communities that are resistant to species loss are characterized by high species richness with relatively low functional richness and high evenness. However, none of the five redundancy indices does estimate redundancy in this way, neither on their own, nor in combination with classical indices. Ideally, a capable index would capture these different aspects of redundancy in one measure.

4.4. Theoretical and practical shortcomings in functional redundancy computation methodologies

A general problem in the definition of some of the functional redundancy indices is the need to define discrete functional units, or functional groups. The functional group approach in functional diversity has been criticized from a theoretical point of view by several authors. First of all, such classification tends to oversimplify functional differences between species as they consider a species totally redundant with the other species of its functional group and completely different from species of other groups (Rosenfeld, 2002). Another methodological issue lies in the subjective decisions such as the number of groups to consider and the classification of species into groups (Poos, Walker, & Jackson, 2009). Additionally, for the FredD index, for example, the classification of traits into effect and response represents another subjective step in the methodology. In the functional entities method from Mouillot *et al.* (2014), the transformation of continuous variable (predominant in plant ecology) into discrete categories is another subjective decision affecting the redundancy values. Those methodological considerations suggest that indices based on continuous metrics (Ur, TPDr, TPrr, etc.) are more comparable across studies, and should therefore be favoured.

One issue about linking functional redundancy with the community vulnerability to species loss can be shown in Fig. 2, focussing on community types A and C. In both cases, roughly half of the community is redundant, since no or little alteration of the community functional structure follows species loss. In type A, this is the case for the first half of species lost, and in type C it is for the last half of the species lost. Therefore, we already see that the uniqueness of the first species lost, and more generally the order in which species are lost, is a critical parameter of the community functional resistance to species loss. This explains why redundancy estimated as a static index (referring only to the initial organization of the community) might not be the best method to estimate communities’ vulnerability to species loss.

5. Conclusions and recommendations

This study contradicts the premise that functional redundancy indices should help predicting community resistance to species loss due to environmental change. On the contrary, when seeking information on the resistance of communities to species loss one can rather use classic indices such as species richness, FRic or FEve, or directly evaluate vulnerability with indices such as CV_{org} considered here. Species loss order seems to have an essential role in the vulnerability of communities to species loss. In the best case information about most probable species loss order is available as in Sasaki *et al.* (2014) and Carmona *et al.* (2017), otherwise repeated random species loss order can be use.

That redundancy indices developed so far might not be good predictors of community vulnerability to species loss could be explained by two main reasons. First, we saw that vulnerability was best predicted by a combination of high species richness with relatively low functional richness and high evenness, but the ideal redundancy index translating these characteristics into a measure is still missing and to be developed. Second, species loss is dynamic, and as shown in this study the order in which species disappear can have a strong influence on a community’s vulnerability. The reason why redundancy indices do not perform well as predictor of vulnerability might be that they only inform us relative to a static initial state of the community. This could also be a reason why dynamic vulnerability indices inform us better about the potential risk of species loss.

Functional redundancy indices could be theoretically relevant for other aspects of community stability, such as community resilience, with the hypothesis that more redundant communities have higher chances that the loss of one species can be replaced by a functionally similar one. However, redundancy indices that have trivial correlation with other indices (FredN, Ur and TPDr) will most likely not add any information to the classical community structural indices. On the other hand, FredD could potentially be useful in this sense, although it remains a complex index that requires several subjective steps for its calculation (number of functional groups, response/effect traits classification, etc.), and it has not proven to be efficient even in an a priori favourable scenario i.e. scenario 3. TPDrr would be the best recommendation as redundancy index as it is relatively independent from the classical community attributes and its calculation requires no other subjective step than the selection of functional traits. It presents the additional advantage of meaningful and comparable values i.e. the proportion of the community that could be removed without losing functional space.

In conclusion, our study supports the idea of Moriarty *et al.* (2018) in how crucial it is to evaluate ecological indices, i.e. the development and use of new indices should be tested for novelty and performance. Classical indices such as species richness, RaoQ, FEve and FRic are already good indicators of the community functional structure. For the evaluation of community vulnerability to species loss we recommend the use of vulnerability indices such as CV_{org} or comparable methods (Carmona *et al.*, 2017; Sasaki *et al.*, 2014) and for an independent and meaningful index of redundancy, we recommend the use of TPDrr.

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Supplementary material

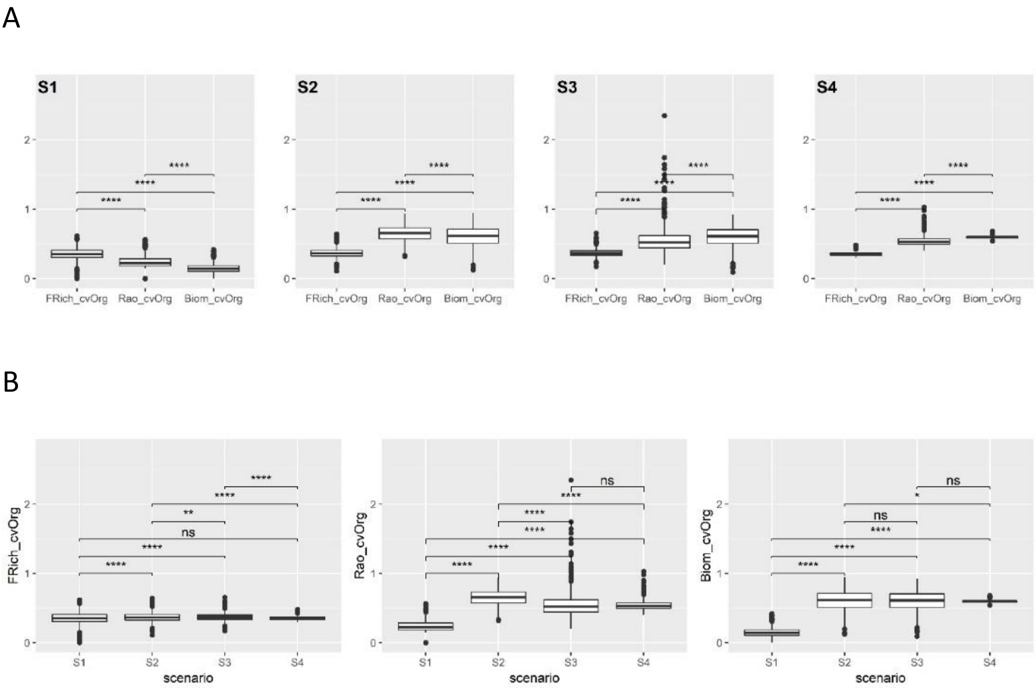


Figure S1: CV_{org} of different response variables within scenario (A) and across scenario (B). P-values significance levels from pairwise t test are represented above each pair of variables ("ns" for non-significant, "." for P <0.1, "*" for P <0.05, "**" for P <0.01, "***" for P <0.001, "****" for P <0.0001). S1 = Scenario 1 (abundance), S2 = Scenario 2 (uniqueness), S3 = Scenario 3 (environmental response), S4 = Scenario 4 (random), FRich = functional richness, Rao = functional divergence, Biom = Biomass.

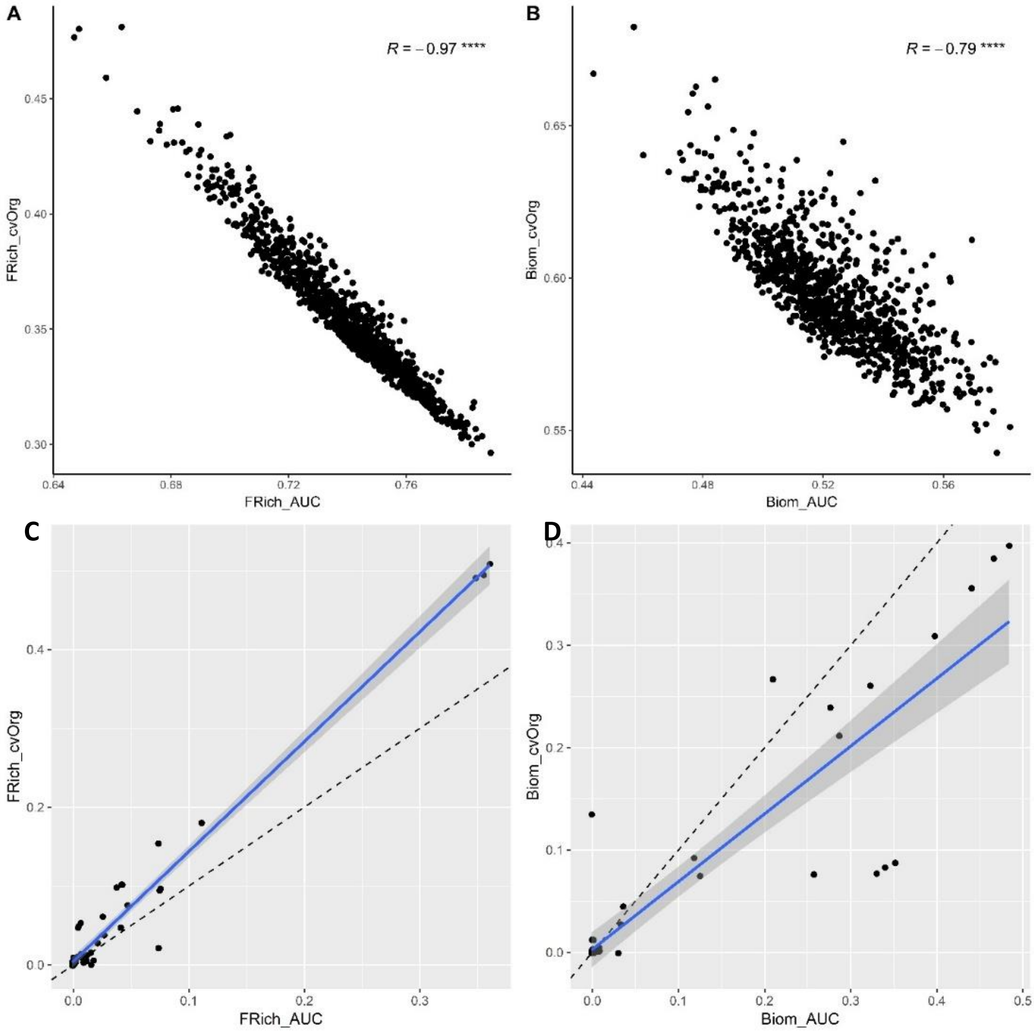


Figure S2: AUC (Area Under the Curve, or integral) versus CV_{org}. Vulnerability was estimated using FRich (A, C) and biomass (B, D) as response variable for the evaluation of the community resistance to species loss. Panels A and B shows correlation between vulnerabilities measures from scenario 4 (random species loss order) Pearson correlation coefficient and the significance of the correlation test are displayed on the top-right corner of the panels (“****” for $P < 0.0001$). Panels C and D presents the fit (R^2) of models using single predictors to explain vulnerability for each of the 4 scenarios. The dashed line represent the 1:1 diagonal. As the figure shows, for monotonic parameter, the AUC and CV_{org} approaches gives similar results.

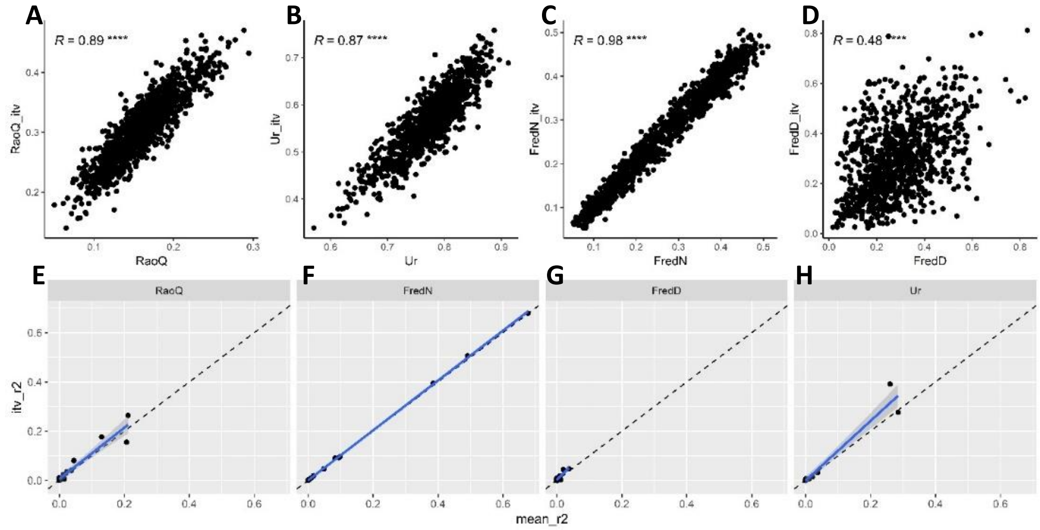


Figure S3: Mean trait values versus overlap method (i.e. accounting for intraspecific variability, itv). The four indices presented here are based on species pairwise distance matrices. The pairwise distances are calculated between the mean traits values of the species in the regular version of the indices and as 1-overlap (de Bello *et al.*, 2013) in the version of the indices accounting for itv. Panels A, B, C and D shows the correlations between indices of initial community for each index using or not the itv. Pearson correlation coefficient and the significance of the correlation test are displayed on the top-left corner of the panels ("****" for P <0.0001). Panels E, F, G and H presents the fit (R^2) of models using single predictors with or without itv to explain vulnerability for each of the 4 scenarios. The dashed line represent the 1:1 diagonal. As the figure shows, for the first three indices (RaoQ, Ur and FRedN), the correlations are strong between the version with and without itv of the indices.

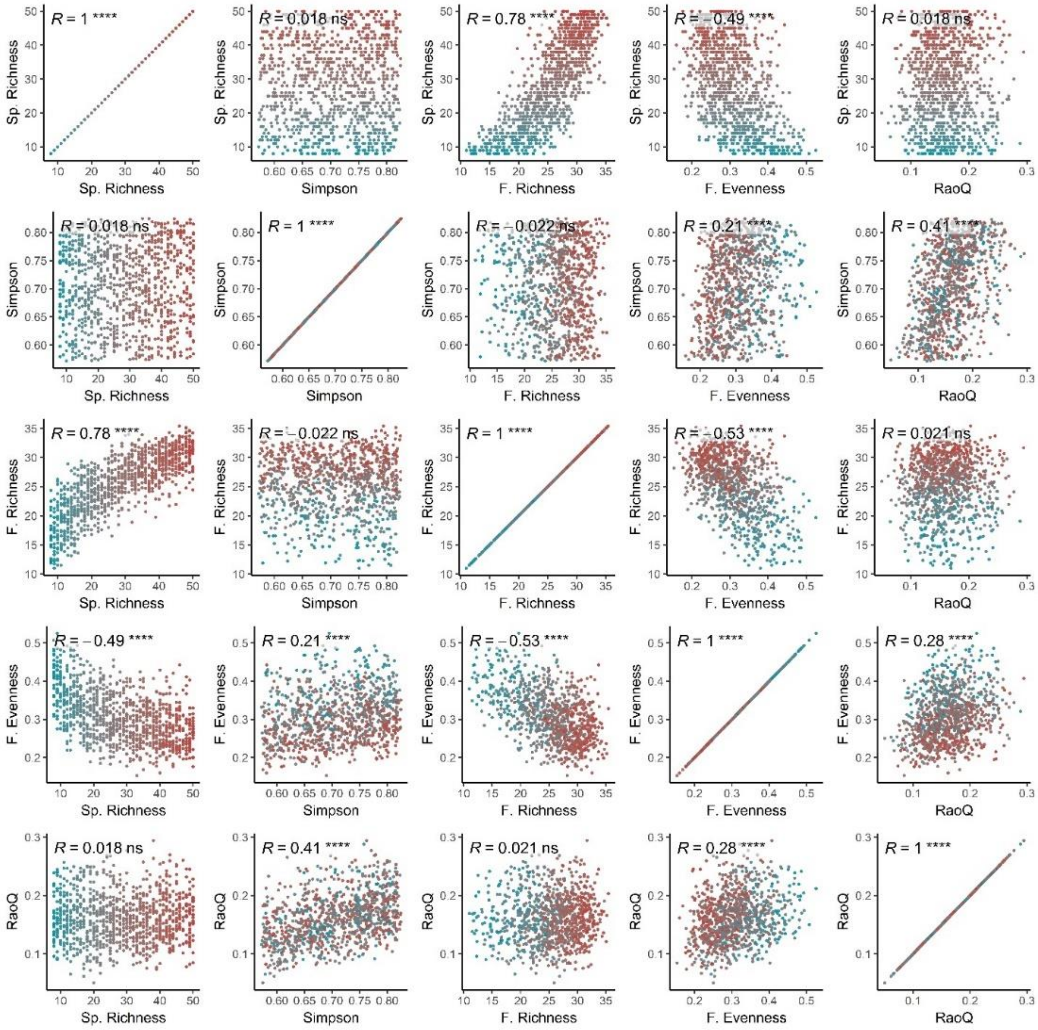
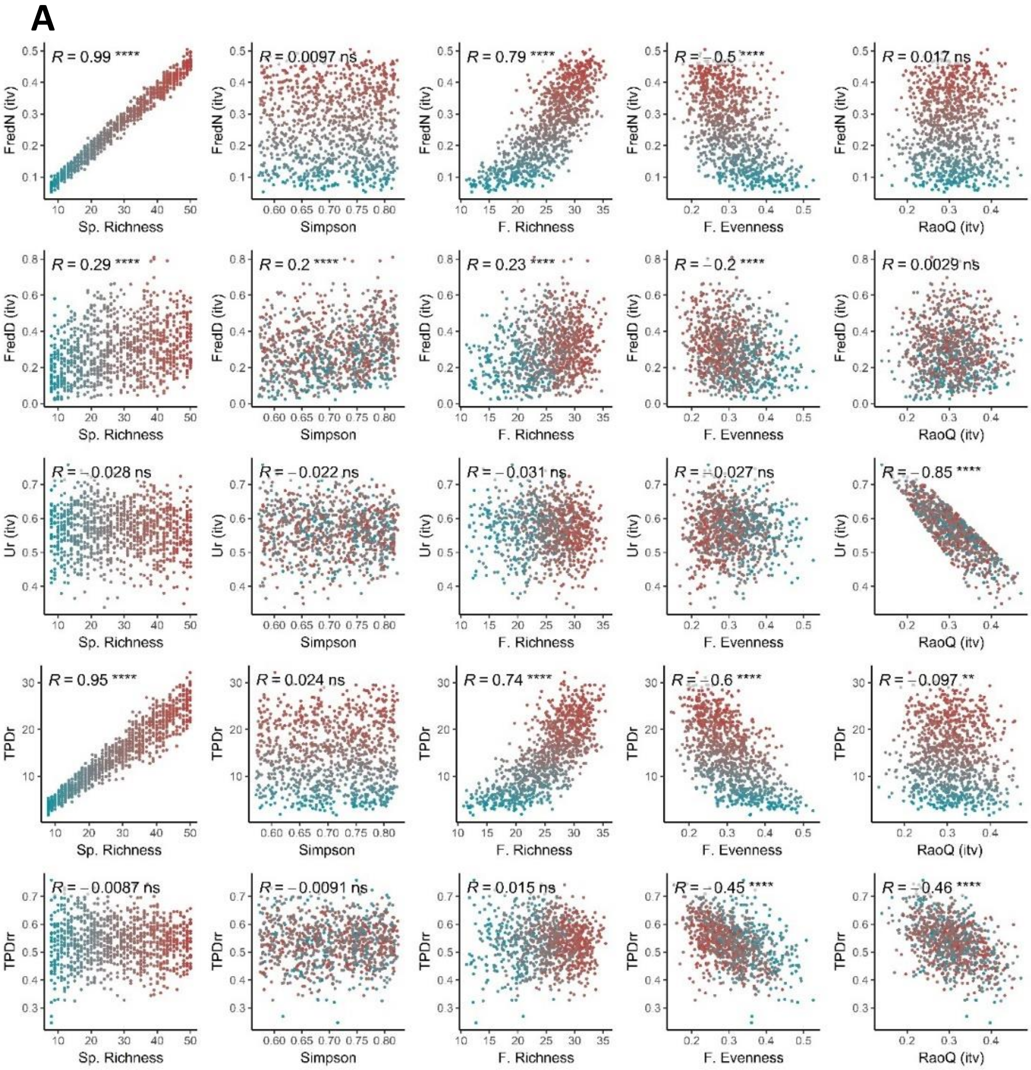


Figure S4: correlation between classical taxonomic and functional community structure indices.


A
R = 0.99 ****
R = 0.0097 ns
R = 0.79 ****
R = −0.5 ****
R = 0.017 ns
R = 0.29 ****
R = 0.2 ****
R = 0.23 ****
R = −0.2 ****
R = 0.0029 ns
R = −0.028 ns
R = −0.022 ns
R = −0.031 ns
R = −0.027 ns
R = −0.85 ****
R = 0.95 ****
R = 0.024 ns
R = 0.74 ****
R = −0.6 ****
R = −0.097 **
R = −0.0087 ns
R = −0.0091 ns
R = 0.015 ns
R = −0.45 ****
R = −0.46 ****
FredN (itv)
FredD (itv)
Ur (itv)
TPDr
TPDrr
Sp. Richness
Simpson
F. Richness
F. Evenness
RaoQ (itv)
10
20
30
40
50
0.60
0.65
0.70
0.75
0.80
15
25
35
0.2
0.3
0.4
0.5

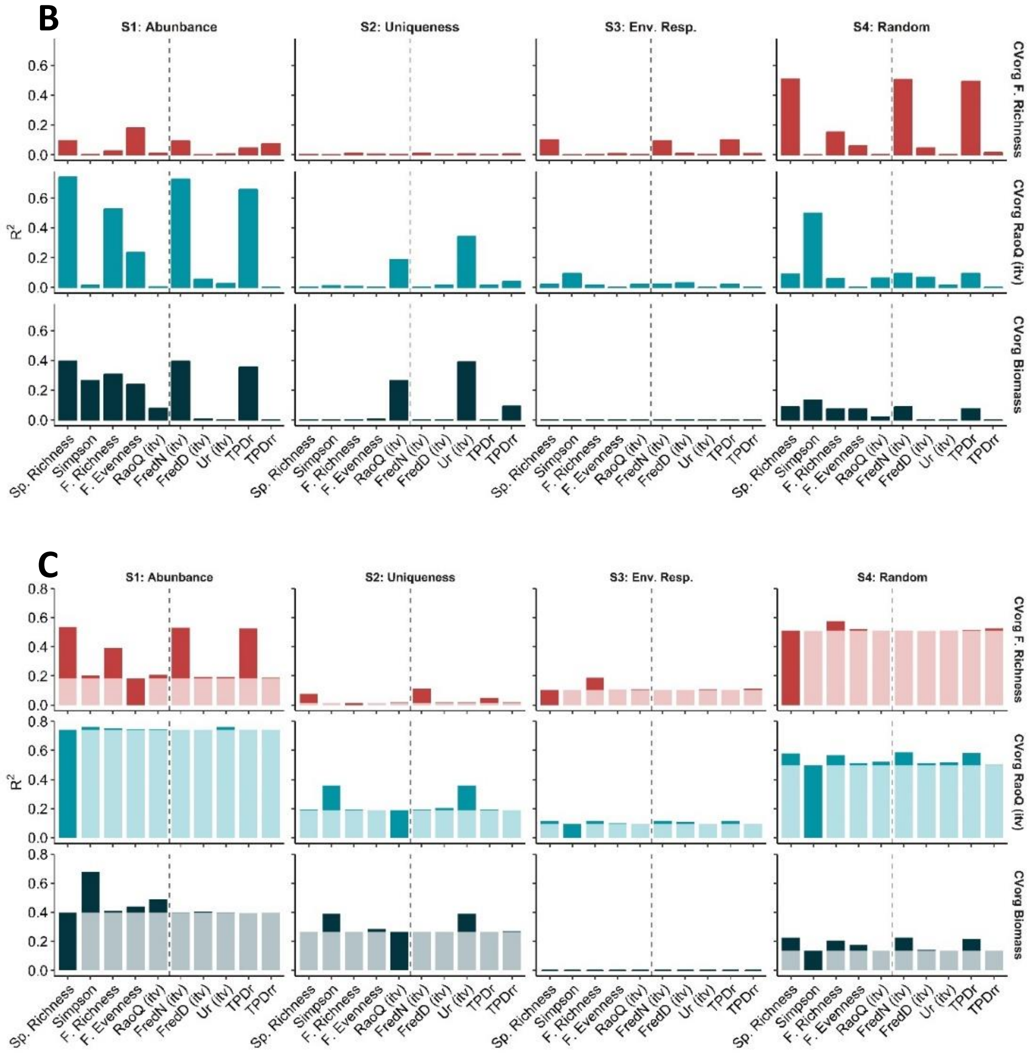


Figure S5: A reproduction of figures 3, 4 and 5 (panels A, B and C respectively) accounting for ITV (for indices RaoQ, FredN, FredD and Ur. TPD based indices including functional richness and evenness already account for ITV). Results are sensibly similar to those in the main text where RaoQ, FRedN, FRedD and Ur are calculated on mean traits values only.

General Discussion
& Perspectives

What have we learned?

In a context of increasing attention on the role of biodiversity in ecosystem functioning (Cernansky, 2017), this thesis shed some light on the effect of different facets of diversity, particularly at the community level, on various aspects of ecosystem functioning and stability. The thesis follows the development of biodiversity effects from community assembly to temporal stability trough the provision of plant and soil functions. Particularly, we explore the effect of different dimensions of community diversity and attempt to disentangle their independent effect on different aspect of ecosystem functioning, while specifically accounting for their covariations structure and their potential “redundancy”. Although increasing research has shown evidence for the effect of various dimensions of biodiversity (taxonomic, functional, phylogenetic; Le Bagousse-Pinguet *et al.*, 2019) on ecosystem functioning, it is not always clear whether those effect results from intrinsic effect or results from non-independence of particular diversity dimension with the “real” driver (Díaz *et al.*, 2013). Using various methodological approaches and different scales of study, this thesis presents empirical evidence that community diversity structure has an important and sometimes unexpected effect on ecosystem functioning.

This thesis is also a good example of the complementarity in the methodological tools available to better understand the role of biodiversity in ecosystem functioning: studying diversity effects requires a diversity of methods. Simulations offer a powerful instrument to evaluate the performance of the tools we design in our investigations and refine hypotheses (chapter IV). The experimental field approach provides an inimitable opportunity to balance the controlled experimental conditions with the realism of relatively natural conditions (chapters I and II). The extensive compilation of datasets offers a unique prospect on large trends governing our ecosystems on a global scale (chapter III), contributing to a more general understanding of patterns and processes. Evidently, any additional combination of dimension in space, time, ecological organisation level, controlled vs. natural conditions provides insight on the complex picture that represent our understanding of ecosystem functioning and the role of biodiversity in its dynamic.

First, using a field experiment specifically designed for disentangling functional and phylogenetic diversity, independently from species richness, we have shown the influence of community structure on community assembly (Chapter I). Most of the effect was driven by the functional component of sown community, while phylogenetic diversity brought only limited information, mainly as an interactive factor with functional diversity. This suggests that, when experimental communities are designed to avoid the inherent overlap between functional and phylogenetic diversity (Cadotte, Carboni, Si, & Tatsumi, 2019) and when trait information is not missing, then considering phylogenetic diversity can have relatively little additional power as predictor of ecosystem functioning. One interesting finding of our work is the, sometimes, *a priori* counterintuitive negative effect of functional diversity, specifically on community resistance to colonisation. This result supports earlier empirical findings from plant invasion studies (e.g. Loiola *et al.*, 2018) and makes sense if we consider that in certain conditions, functional diversity and redundancy are two sides of the same coin. In a non-uniformly distributed functional space with fixed species richness, lower diversity results in higher redundancy in the most densely populated part of the functional space, therefore limiting the opportunity for colonising species to successfully establish in the community.

Using the same experiment, we investigated several ecosystem functions involved in the plant-soil feedback system (Chapter II). Results show that plant functional structure parameters are good direct predictors of plant community ecosystem functions (biomass of sown community, community resistance to colonisation by weeds and community decomposability) and, again, better than phylogenetic differences between species. In a cascading effect, these plant ecosystem functions affect soil ecosystem properties. On the contrary, the direct effect of plant functional and phylogenetic structure on soil ecosystem properties are limited or null. Interestingly, and in accordance with findings from De Long *et al.* (2019) our results support also the importance of indirect effects of plant functional structure on the soil ecosystem functions mediated by i) the plant community EF (biomass production and decomposability) and ii) the modification of soil abiotic properties (pH, EC, GH). Novel methods, theoretical advances, and newly available data offer opportunities, but also pose challenges to the study of BEF. With increasing numbers of predictors and response variables, disentangling causal relationships from random patterns in covariation of factors requires careful design, analysis and interpretation.

Next, broadening our study scale in space and time (Chapter III) by compiling time series of permanent plot vegetation records from all around the world, we found that the temporal stability of communities is more dependent on the level of synchrony among species that compose the community, especially the level of synchrony among the most abundant species of the community, than on the species diversity. Our results show, across a wide diversity of ecosystems, the consistent importance of the interplay among species richness, synchrony and environmental parameters in the prediction of community stability. Similarly to previous findings (de Mazancourt *et al.*, 2013), low synchrony and high species richness defined the primary stabilizing pattern of communities. However, contrary to expectation, the stabilizing effects of species richness via synchrony were relatively weak. Yet, despite a prevalence of synchrony between species found in our communities, richness had a net positive association with stability, albeit weak, implying an existing effect of richness unrelated with synchrony. Environmental factors associated with different global change drivers also directly or indirectly affect stability and have the potential to reverse the effects of biodiversity and synchrony on stability, although biotic factors generally had a stronger effect. To consider these different drivers of stability in concert is critical for defining the potential of communities to remain stable in a global change context. Indeed, a perspective research following this baseline study, is applying the framework of different biodiversity components used in the previous chapters, to the stability of these communities.

Among the different components of biodiversity, temporal stability of a system is strongly determined by its resistance and resilience. Beyond synchrony and species diversity, functional redundancy has long been a strong candidate as driver of community stability through a positive effect on resistance and resilience to species loss via insurance mechanism (McCann, 2000). Our study (Chapter IV) shows that the quantification of this particular aspect of community functional structure and its relation to community resistance to species loss is not as straightforward as the wide collection of redundancy indices suggest. We found that the classic indices of community structure such as species richness, Functional richness and evenness were more performant in predicting community resistance than redundancy indices. We suggest that vulnerability indices (reciprocal of resistance), such as CV_{org} or other indices proposed by Sasaki *et al.* (2014) and Carmona *et al.* (2017), perform better because they account for the dynamic aspect of species loss, and not only the static initial state of the community like redundancy indices. This chapter suggest also that studies on community stability could focus on the integrity of the community functional structure.

Perspectives

This thesis opens new interesting perspectives for future research in the field of biodiversity effects on ecosystem functioning. These can be broadly grouped in two research lines, answering the following questions: i) What is the role of different functional structure components in temporal stability of species and communities? ii) Are changes in trade-offs of traits in plant communities associated with temporal consequences in other trophic levels and multiple ecosystem functions? Below we provide the baseline for future investigations on these ecological questions.

At the population level, theoretical assumptions (R. H. Macarthur & Wilson, 1967) as well as previous localized empirical evidence (Majeková *et al.*, 2014) on the interdependence between the general *conservative-acquisitive* trade-off, and species temporal stability are being generalised (Conti *et al*, unpublished) in an analysis that combines LOTVS (long term vegetation survey, Valencia *et al.* 2020) and TRY (plant trait database; https://www.try-db.org) database. We can expect that the drivers of species stability (e.g. LDMC) will scale up as driver of community stability (e.g. $\mathrm{CWM}_{\mathrm{LDMC}}$, Lepš, Osbornová-Kosinová, & Rejmánek, 1982). Other studies, however, have shown that greater diversity in trait values (e.g. higher diversity of LDMC, Pakeman, 2014) may promote community stability. Therefore, further studies focusing on trait diversity as well as on the synchrony of the species should be implemented in order to better understand the drivers of community stability.

As we saw in chapter II, the functional structure plays an important role in ecosystem functioning through direct and indirect effect. The maintenance of a stable functional structure trough time, potentially with changes in species richness and composition, could be a key parameter of the stability of ecosystem functions and services. With the simulation exercise in chapter IV, we improved our understanding of functional structure and its role in community resistance to species loss. The next step would be to use real communities, and test which dimensions of the functional structure are more or less stable. Identifying extreme climatic events through plant community time series records could be an opportunity to directly test the resistance and resilience of communities and their relation to functional redundancy and other metrics of functional and phylogenetic structure. The comparison of the temporal turnover (beta-diversity) in taxonomical and functional diversity could also be an interesting angle to study the insurance hypothesis. Indeed, identifying the characteristics of communities able to undergo taxonomical turnover without changes in functional structure could be a strong advance in the prediction of ecosystem vulnerability.

The integration of the trade-offs across trophic levels and ecosystem functions and their compartmentalisation (e.g. above vs. below ground) is a promising research topic. Continuing on the idea that temporal stability of ecosystem function and service is of prime interest not only in theoretical ecology but also for human societies, the direct repeated measurement of both community functional structure and ecosystem functions through time seems a key step in the validation of functional structure as driver of ecosystem functions. Unfortunately, these type of data are not yet available, or only measured on rather short periods of time (e.g. Sasaki, Lu, Hirota, & Bai, 2019).

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2011-2013: ***BSc Biology of Organisms, Populations and Ecosystem****. Paul Sabatier University (Toulouse, FR)*

2008-2010: ***Technical University Diploma (DUT) on Biology and Agronomy)****. Claude Bernard University (Lyon, FR)*

RESEARCHER EXPERIENCE & INTERNSHIPS

January-September 2020: International PhD stay. Miguel Verdú, Centro de Investigaciones sobre Desertificación CSIC-UV-GV (Valencia, Spain)

April-June 2019: International PhD stay. Miguel Verdú, Centro de Investigaciones sobre Desertificación CSIC-UV-GV (Valencia, Spain)

October-December 2018: International PhD stay. Eric Garnier, centre d'écologie fonctionnelle et évolutive, CNRS (Montpellier, France)

September 2018: Workshop "Linking functional traits to plant community stability" Institute for Integrative Systems Biology, Valencia (Spain)

January-August 2015: internship MSc Thesis, Aveliina Helm, University of Tartu (Estonia)

November 2010-May 2011: research & lab. assistant, Marina Von Keyserlingk, University of British Columbia (Vancouver, Canada)

PUBLICATIONS

Galland, T, Adeux, G, Dvořáková, H, E-Vojtkó, A., Orbán, I., Lussu, M., … & Götzenberger, L. (2019) Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology.* 107: 2090– 2104. https://doi.org/10.1111/1365-2745.13246

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Conti, L., Valencia, E., **Galland, T.**, Götzenberger, L., Lepš, J., E-Vojtkó, A., … & de Bello, F. Trade-offs among functional traits define plant population stability worldwide. *Ecology Letters*. (**Submitted**)

Conti L.; Malavasi M.; **Galland T.**; Komarek, J; Lagner O.; Carmona C.; de Bello F.; Rocchini D.; Šímová P. The relationship between species and spectral diversity in grassland communities is mediated by their vertical structure. *Applied Vegetation Science*. (**Submitted**)

Galland T., Valencia E., Carmona C.P., Goberna M., Götzenberger L., Lepš J., Verdú M. & de Bello F. Cascading effect from plant community functional structure to above and below ground ecosystem functions. (**In preparation**)

Medina N., de Bello F., Puy J., **Galland T**., Hájek T., Skuhrovec J., Dvořáková H., Cornelissen J. H., Latzel V. From memory to after-life: impacts of current and past environments on trait plasticity and decomposability of the clonal *Trifolium repens*. (**In preparation**)

Valencia E., de Bello F., Galland T., Götzenberger L., Lepš J., Durán J., Carmona C. P. Effects of functional and phylogenetic diversity on the temporal dynamic of N cycle. (**In preparation**)

CONFERENCE PRESENTATIONS

As first author:

October 2016: Community Ecology for the 21st Century: From Genes to Ecosystems. Evora (Portugal) Talk: “Selection and complementarity effect along functional and phylogenetic diversity gradient”

June 2017: IAVS annual Symposium. Palermo (Italy) Poster: “Are the redundancy indices redundant?”

October 2018: SFE conference Rennes (France) Talk : “ ‘Resistance is futile!’ - or is it? A study on natural colonisation resistance and colonisation success in experimental plant communities along functional and phylogenetic diversity gradients.”

As co-author (selection):

June 2017: IAVS annual Symposium. Palermo (Italy) Talk by Enrique Valencia: “Are compensatory dynamics a rare mechanism of temporal community stability? A plant global scale analysis of permanent plot data”

June 2017: IAVS annual Symposium. Palermo (Italy) Talk by Lars Götzenberger: “A test of synchrony indices for temporal community data”

July 2018: IAVS annual Symposium Bozeman (Montana, USA) Talk by Enrique Valencia: “A long-term vegetation sampling database and its possible application”

July 2019: IAVS annual Symposium. Bremen (Germany) Talk by Luisa Conti: “Linking spectral and functional diversity to predict ecosystem functions at community scale”

PROFESSIONAL ACTIVITIES

Reviewer in: *Journal of Vegetation Science* and *Functional Ecology*

Teaching: RStudio practical course 2019 (University of South Bohemia)

Field work: Sampling excursion in Ladakh (India) on a team from Institute of Botany of the Czech Academy of Sciences led by Jiri Dolezal.

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