

Biodiversity and Temporal Stability of Naturally Assembled Ecosystems Across Spatial Scales in a Changing World

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9.1. Introduction

Both theory and experiments have demonstrated the positive effect of biodiversity on the temporal stability of aggregated ecosystem properties (Chapters 7 and 8). Hereafter, by temporal stability, we mean the temporal invariability of ecosystem properties (e.g. primary productivity) measured as the inverse of the coefficient of variation. While biodiversity experiments have established the causal effects of biodiversity on functional stability, the transferability of these results to the management of real-world ecosystems has been questioned for several reasons (Wardle 2016).

First, most experiments simulate a random loss of diversity from a local species pool and minimize variability in abiotic conditions. However, in natural ecosystems, species loss is not random but the result of multiple factors such as nutrient availability, climatic conditions, and land use (Selmants *et al.* 2012). For example, nutrient

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enrichment usually leads to the dominance of a few fast-growing or taller species that exclude slow-growing or smaller species due to increased competition for light (Hautier *et al.* 2009). As a result, in natural systems, dominant and rare species have an unequal probability of being lost, with rare species being more at risk (Gaston 2008). Additionally, biodiversity is likely not the only driver of ecosystem function responses and abiotic conditions could outweigh biodiversity effects (Diaz *et al.* 2007).

Second, most experiments prevent immigration by continuously removing non-target species. This limits the role played by species dispersal and species sorting in maintaining both biodiversity and ecosystem functioning across temporal and spatial scales (Leibold *et al.* 2017). For example, dispersal helps species with different environmental optima to effectively track spatial changes in local environmental conditions, promoting species persistence and increasing ecosystem functioning (Loreau *et al.* 2003).

Third, experimental studies have primarily focused on plant responses at relatively small spatial scales (i.e. within plots with a median size of 3 m²) (Cardinale *et al.* 2012). This hinders our ability to predict the extent to which biodiversity will maintain ecosystem services at broader spatial scales most relevant for policy, nature management, and biodiversity conservation (Isbell *et al.* 2017). Understanding whether biodiversity safeguards ecosystem functioning against environmental fluctuations in natural ecosystems at larger spatial scales has thus become a major challenge of modern ecology (Isbell *et al.* 2017; Gonzalez *et al.* 2020). This is of particular importance given rapid biodiversity changes at multiple spatial scales due to anthropogenic activities, including habitat loss and fragmentation, climate change, pollution, overexploitation, and species introductions (Chase *et al.* 2019; McGill *et al.* 2015).

Although earlier examples exist (Dodd *et al.* 1994; McNaughton 1978), a new generation of research quantifying biodiversity–stability relationships in natural and semi-natural ecosystems has emerged. These studies can be classified into two types. First, there are observational studies linking natural gradients of biodiversity with the temporal stability of ecosystem functioning (Path 1 of Figure 9.1). Second, there are global change experiments assessing how environmental drivers influence temporal stability directly (Path 3 of Figure 9.1) or indirectly by jointly changing biodiversity and stability (Paths 2 and 3 of Figure 9.1) or by changing the biodiversity–stability relationship (Path 4 of Figure 9.1).

Since biodiversity and ecosystem functioning are shaped by environmental drivers and global change factors, the link between biodiversity and stability in these studies is correlational and inference relies upon statistical control of covariates (Duffy *et al.* 2017). However, confident inference of causal links is limited due to the high probability of missing important variables that can confound the

relationship between them (Ferraro *et al.* 2019). Despite this limitation, studies of natural ecosystems are a crucial step towards transferring knowledge from controlled experiments with high internal validity (confidence in the result) to natural settings with high external validity (generality of the result).

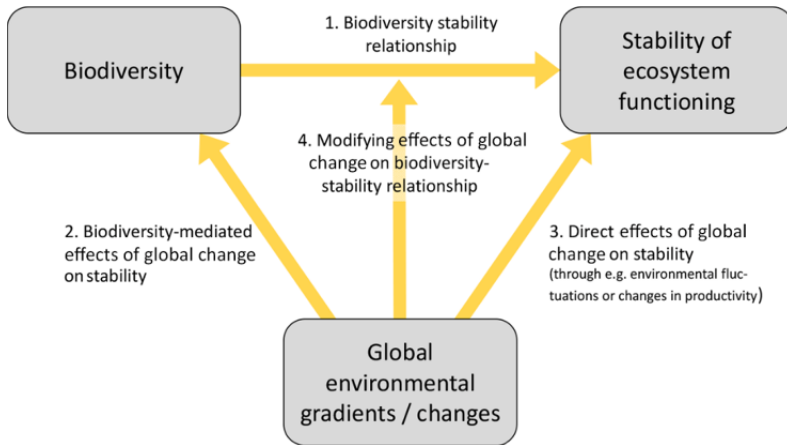


Figure 9.1. Conceptual framework illustrating how global change drivers (e.g. fertilization, increased livestock densities, and climate change) can affect biodiversity, stability, and their relationships

Concurrently to the emergence of these empirical studies in natural ecosystems, new theoretical developments have contributed to clarifying the mechanisms by which biodiversity can stabilize functioning at different spatial scales (Chapters 4 and 7). Local species diversity (α -diversity) can provide *local insurance* effects to enhance community stability (α -stability) because different species with different functional traits exhibit asynchronous temporal responses to their shared local environment (species asynchrony) (Figure 9.2). Similarly, variation in species composition among local communities (β -diversity) can provide *spatial insurance* effects to enhance stability at the larger spatial scale (γ -stability) because communities with different species compositions exhibit asynchronous responses to a spatially correlated environment (spatial asynchrony) (Figure 9.2). Hence, global change drivers that reduce biodiversity in local communities or homogenize community composition across space should reduce the local or spatial insurance effects of alpha or beta diversity respectively (Path 2 of Figure 9.1). Additionally, global change drivers may alter the stabilizing effects of biodiversity, leading to a decoupling of biodiversity and stability in systems highly altered by global change drivers (Path 4 of Figure 9.1) (Hautier *et al.* 2020; Hautier *et al.* 2014).

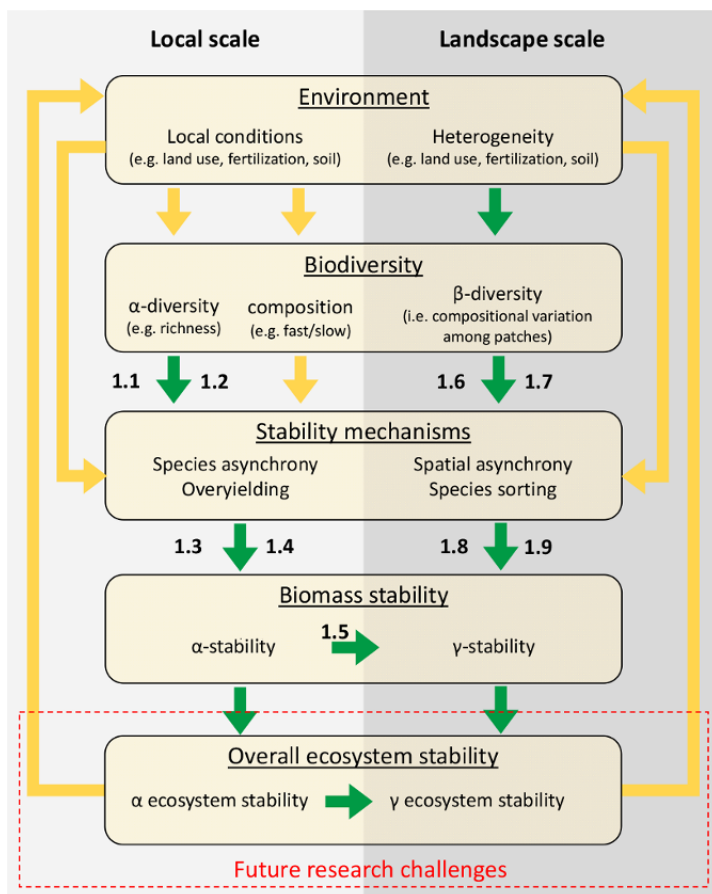


Figure 9.2. Mechanisms by which environmental conditions (including global change drivers) influence biodiversity, and by which biodiversity influences stability in biomass production, at both local and landscape scales. Eventually, “overall ecosystem stability”, that is, the stability of multiple ecosystem functions (not exclusively biomass production), may be influenced by biodiversity, which is generally an avenue for future research. Paths depict hypothesized, causal relationships and are green when expected to be positive and yellow when expected to be context dependent. Numbered paths depict relationships that receive special attention in this review. Path 1.1: effect of α -diversity on species asynchrony. Path 1.2: effect of α -diversity on overyielding. Path 1.3: effect of species asynchrony on α -stability. Path 1.4: effect of overyielding on species asynchrony. Path 1.5: effect of α -stability on γ -stability. Path 1.6: effect of β -diversity on spatial asynchrony. Path 1.7: effect of β -diversity on species sorting. Path 1.8: effect of spatial asynchrony on γ -stability. Path 1.9: effect of species sorting on γ -stability. For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip

Here, we first review the literature and assess the balance of evidence regarding the direction of biodiversity–stability relationships and underlying mechanisms in (semi-)naturally assembled communities at the local and larger spatial scales. Studies include both observational studies linking natural gradients of biodiversity with the temporal stability of ecosystem functioning as well as global change experiments assessing how environmental drivers influence temporal stability, either by jointly changing biodiversity (thus altering biodiversity–stability relationships *across* gradients created by the global change driver), or by changing the biodiversity–stability relationship *within* global change contexts. Next, we discuss the contributions of dominant and rare species to functional stability. Finally, we identify knowledge gaps and opportunities for future research.

9.2. Biodiversity–stability relationships along natural gradients

We found 39 publications assessing biodiversity–stability relationships along natural gradients (see the online supplementary material¹). Most were carried out in North America, Europe, and Asia (Figure 9.3a), especially in drylands, temperate grasslands, and temperate forests (Figure 9.3b). Some other ecosystem types, such as tropical rainforests and the open ocean, have not been studied at all, despite their widespread global distribution. Furthermore, most studies focused on relationships between plant diversity and the stability of primary production, rather than on higher trophic levels (Figure 9.3c).

Across the 39 publications, 63 biodiversity–stability relationships were tested. The majority (44 out of 63) showed positive relationships between α -diversity and α -stability along natural gradients (Figure 9.4) (e.g. Blüthgen *et al.* 2016). Negative relationships were found in some contexts in two papers only (Polley *et al.* 2007; Jourdan *et al.* 2020). Thus, along natural gradients, more biodiverse communities are generally more stable, and this pattern applies to plants, as well as to higher trophic levels such as birds and bats (Blüthgen *et al.* 2016), fishes (Franssen *et al.* 2011), and invertebrates (Blüthgen *et al.* 2016).

In line with theory (Chapter 7), higher α -diversity was associated with a higher species asynchrony in 21 out of 28 studies (e.g. Gilbert *et al.* 2020), and higher species asynchrony was associated with higher stability in 32 out of 33 studies (e.g. Zhang *et al.* 2018). Various mechanisms can cause asynchrony in the fluctuations of co-occurring species, including stochasticity, species interactions and responses to environmental fluctuations (Chapter 7). Fluctuations in precipitation and temperature throughout years may play a key role in driving relationships between α -diversity

1 Available at: ww.iste.co.uk/loreau/biodiversity.zip.

and species asynchrony, so that asynchronous responses of plants to weather conditions may promote stability in more diverse communities (Gilbert *et al.* 2020). In contrast, Lamy *et al.* (2019) suggested that resource competition, rather than responses to environmental fluctuations, was most important in driving a relationship between α -diversity and α -stability. However, with so few studies assessing which mechanism is most important, this remains an unresolved issue.

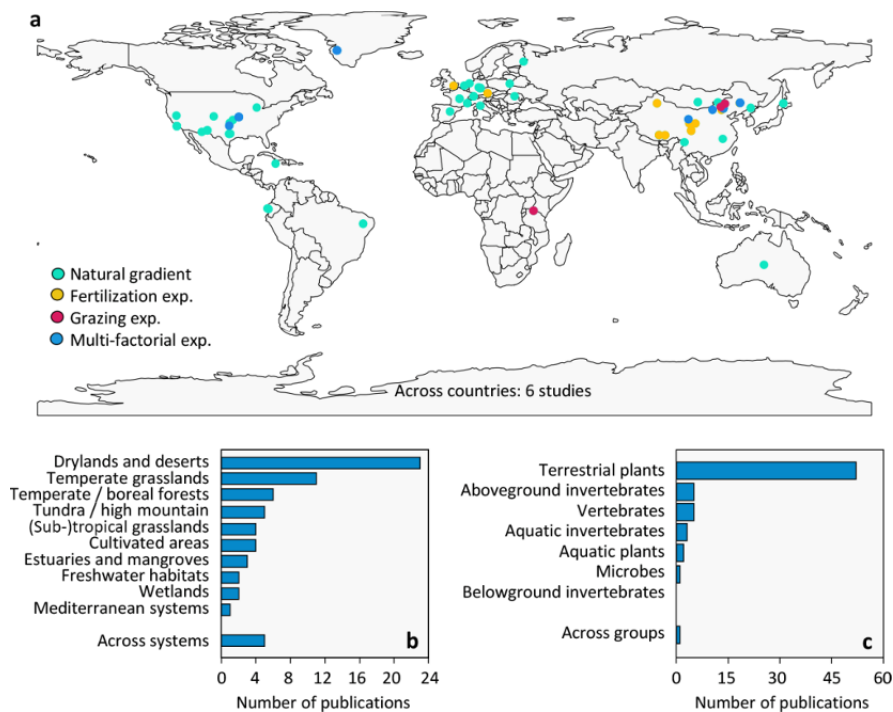


Figure 9.3. Overview of studies assessing relationships between biodiversity and stability, along natural gradients or in global change experiments. A) Map with locations of studies. Colors indicate whether the study was along a gradient or based on a fertilization experiment, grazing experiment, or a multi-factorial global change experiment. B) Main ecosystem types in which studies were carried out. C) Taxonomic groups for which biodiversity was studied. For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip

Theory suggests that biodiversity may also promote biomass stability through overyielding, that is, higher biomass in mixtures than expected based on

monocultures (Chapter 7). While many studies along natural gradients found that diverse communities produce on average more biomass than species-poor communities (e.g. Zhang *et al.* 2018, Chapter 6), evidence that overyielding promotes stability was rather mixed (Figure 9.4), with some studies finding positive relationships (e.g. Dolezal *et al.* 2020), but many others finding neutral relationships (e.g. Gilbert *et al.* 2020). Our results indicate that at the local scale, species asynchrony, rather than overyielding, plays the most important role in underlying positive biodiversity–stability relationships.













Response	Driver	Path	N	Results
Spec. asynchrony	α -diversity	1.1	28	
Overyielding	α -diversity	1.2	17	
α -stability	Spec. asynchrony	1.3	33	
α -stability	overyielding	1.4	8	
α -stability	α -diversity	1.1–1.4	63	
γ -stability	α -stability	1.5	5	
γ -stability	α -diversity	1.1–1.5	3	
Spat. asynchrony	β -diversity	1.6	8	
Species sorting	β -diversity	1.7	0	
γ -stability	Spat. asynchrony	1.8	5	
γ -stability	Species sorting	1.9	0	
γ -stability	β -diversity	1.6–1.9	2	

Figure 9.4. Balance of evidence regarding the different mechanisms by which biodiversity may affect biomass stability. Response: the variable whose response to the driver is assessed. Path: the corresponding path of the assessed relationship in Figure 9.2. N: the number of studies that assessed the relationship. The bars indicate the proportion of positive (green), neutral (yellow), and negative (red) relationships reported in studies, while the arrows indicate whether relationships are, across studies, generally positive (green, up) or unresolved (white, horizontal). For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip

Larger scale γ -stability can simply arise from α -stability (and hence α -diversity) or from processes taking place at larger spatial scales, such as species sorting and spatial insurance effects (Chapter 7). Few studies (e.g. Hautier *et al.* 2020; Wilcox *et al.* 2017) have investigated how α -stability relates to γ -stability, but their outcomes are consistent and show that γ -stability generally increases with α -stability (Figure 9.4). Thus, local scale mechanisms, such as local insurance effects, driving positive

biodiversity–stability relationships can propagate to larger spatial scales. Only two studies (Zhang *et al.* 2019; Hautier *et al.* 2020) assessed the overall relationship between β -diversity and γ -stability, which was found to be positive (Figure 9.4). This indicates that larger scale processes may also contribute to positive relationships between biodiversity and stability.

Some studies tested the idea that spatial asynchrony can drive relationships between β -diversity and γ -stability. Although studies are only starting to emerge, most show that β -diversity is positively related to spatial asynchrony (e.g. Hautier *et al.* 2020; Wilcox *et al.* 2017) (Figure 9.4) and thereby to γ -stability (e.g. Catano *et al.* 2020; Hautier *et al.* 2020).

Positive relationships between β -diversity and γ -stability may also occur through species sorting, that is, where patches with different abiotic conditions are occupied by different species, so that each species is present in the environment where it grows best (Loreau *et al.* 2003). However, the importance of this biomass-enhancing mechanism in driving relationships between β -diversity and γ -stability has not been directly assessed along natural gradients (Figure 9.4). That said, there is indirect evidence that this mechanism may be important, as different species maximize biomass production in different environments (Isbell *et al.* 2011) and because β -diversity can be positively related to biomass production (Grman *et al.* 2018). Thus, it is possible that β -diversity can promote γ -stability through species sorting processes, although this merits further study.

9.3. Global change drivers and biodiversity–stability relationships

We found 27 studies experimentally assessing how single (e.g. McNaughton 1985) or multiple (e.g. Ma *et al.* 2017) global change drivers influence relationships between biodiversity and stability (see the online supplementary material). Effects of fertilization were most often assessed (19 studies), while effects of grazing (7 studies), warming (6 studies), and changes in precipitation (4 studies) or other global change drivers (e.g. fire, increased CO₂, tilling and mowing, in single studies only) were less frequently assessed (Figures 9.3 and 9.5). Many of the studies assessed the joint effects of the given global change driver on biodiversity and stability directly (Paths 2 and 3 in Figure 9.1), while modifying effects on biodiversity–stability relationships (Path 4 in Figure 9.1) were less frequently assessed. Almost all studies focused on plant diversity and its relationship to the stability of primary production, except for Wagg *et al.* (2018), who studied how microbial diversity related to their biomass stability in experimentally disturbed soils.









Response	Driver	Path	N	Results
Biodiversity and stability	Fertilization	2+3	19	
Biodiv–stability relationship	Fertilization	4	2	
Biodiversity and stability	Grazing	2+3	7	
Biodiv–stability relationship	Grazing	4	2	
Biodiversity and stability	Warming	2+3	6	
Biodiv–stability relationship	Warming	4	1	
Biodiversity and stability	Drought	2+3	5	
Biodiv–stability relationship	Drought	4	1	

Figure 9.5. Balance of evidence regarding how global change drivers affect biodiversity, biomass stability, and their relationship, either through joint responses of biodiversity and biomass stability or through direct effects on their relationship. Response: the variable whose response to the driver is assessed. Path: the corresponding path of the assessed relationship in Figure 9.1. N: the number of studies that assessed the relationship. For the response “biodiversity and stability”, the bars indicate the proportion of cases where the variables responded qualitatively in the same direction (either both positive or both negative; Figure 9.6a–c) to the global change driver (green), in opposite directions (biodiversity positive and stability negative, or vice versa; red; Figure 6d–f), or whether responses were unrelated, because at least one of the variables did not respond significantly to the global change driver (Figure 9.6g–i). The bars on lines assessing the “biodiversity–stability relationship” as the response indicate whether this relationship was strengthened (more positive or less negative; green), not affected, or weakened (less positive or more negative; red) by the global change driver. The arrows indicate whether relationships were, across studies, generally positive (green, up), negative (red, down), or unresolved (white, horizontal). For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip

Most studies showed that biodiversity and stability respond similarly to fertilization (Figure 9.5, Hautier *et al.* 2015), which is in line with existing meta-analyses (Midolo *et al.* 2019; Avolio *et al.* 2020). The joint negative responses suggest that along gradients in fertilization, biodiversity and stability should be positively related to each other (right panels in Figure 9.6), as found in most studies (e.g. Zhang *et al.* 2017). However, studies assessing the impact of fertilization on the relationship between biodiversity and stability found weaker relationships under fertilized compared to unfertilized conditions (e.g. Hautier *et al.* 2020), as conceptually illustrated in Figure 9.6c.

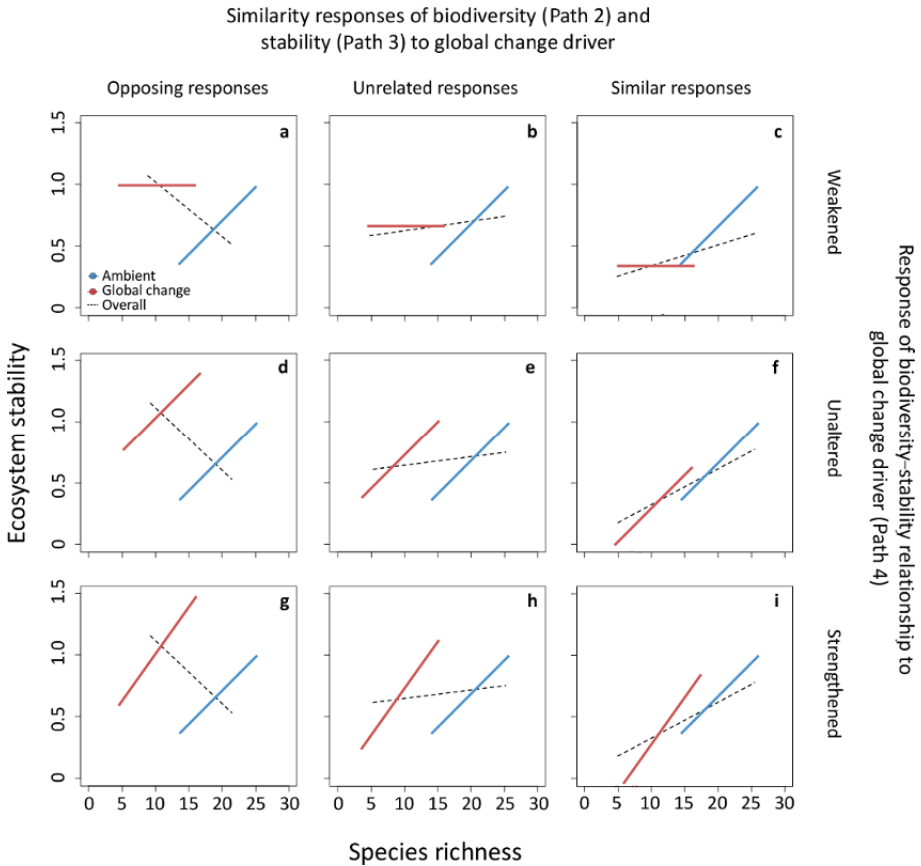


Figure 9.6. Possible scenarios of how biodiversity, stability, and relationships between them respond to global change drivers. *a, b, c*: scenarios where the relationship between biodiversity and stability is weakened by the global change driver (compare the blue and red relationships). *d, e, f*: scenarios where the relationship between biodiversity and stability is unaltered by the global change driver. *g, h, i*: scenarios where the relationship between biodiversity and stability is strengthened by the global change driver. *a, d, g*: biodiversity and stability have opposing responses (positive and negative, respectively) to the global change driver, causing a negative overall relationship (dashed black line) between them. *b, e, h*: biodiversity and stability have unrelated responses (neutral and negative, respectively) to the global change driver, thereby having a limited effect on the overall relationship between them. *c, f, i*: biodiversity and stability have similar responses (both negative, respectively) to the global change driver, strengthening the overall relationship between them. For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip

Seven studies on biodiversity–stability relationships assessed the effects of grazing on biodiversity and stability. Three studies reported that biodiversity and stability responded similarly to grazing, although one of these showed joint positive responses (Post 2013), while the others showed joint negative responses (Qin *et al.* 2019; Liang *et al.* 2020) (right panels in Figure 9.6). Four other studies showed qualitatively unrelated responses of biodiversity and stability (e.g. Hautier *et al.* 2015; Xu *et al.* 2020). Thus, while gradients in grazing intensity can cause positive relationships between biodiversity and stability, in some cases they do not. Only two studies investigated whether grazing altered the strength of the relationship between biodiversity and stability. One found a strengthening effect (Post 2013), while the other found a neutral effect (McNaughton 1985). Thus, it is too early to draw conclusions concerning an overall grazing effect on the strength of biodiversity–stability relationships.

Six studies on biodiversity–stability relationships reported on the effects of experimental warming. While one study found joint negative effects of warming on biodiversity and stability (Ma *et al.* 2017), other studies showed unrelated responses (e.g. Yang *et al.* 2020). Only one study (Post 2013) investigated the effect of warming on the strength of the biodiversity–stability relationship, and it found a neutral response (Figure 9.5). This suggests that biodiversity should be equally strongly related to stability in future, warmer climates as in present-day conditions.

Studies on the joint effects of drought on biodiversity and stability are still relatively rare. Two studies showed joint negative responses (Muraina *et al.* 2020) and three other studies showed unrelated responses (e.g. Hautier *et al.* 2015). Only one study assessed the impact of drought on the strength of the biodiversity–stability relationship, and it found no significant response (Muraina *et al.* 2021). Thus, more studies are needed to draw general conclusions on how climate change may alter the relationship between biodiversity and stability.

In summary, global changes can alter biodiversity and stability in many ways. Fertilization usually decreases both plant diversity and stability, leading to positive biodiversity–stability relationships. At the same time, relationships between biodiversity and stability are weakened in fertilized areas (Figure 9.6c). Other global change drivers, such as grazing management, global warming, and precipitation, can strengthen or weaken relationships between biodiversity and stability, although it is still too early to say which scenario is most common. However, our findings suggest that in many scenarios of global change, relationships between biodiversity and stability may weaken. The predominantly positive relationships along natural gradients we observed when reviewing the literature contrast somewhat with the less frequent positive relationships found in other meta-analyses (e.g. Valencia *et al.*

2020), which lumped studies along natural gradients with global change experiments. Possibly, the inclusion of various global change contexts may have weakened the strength of relationships between biodiversity and stability. On the other hand, truly “natural” gradients are extremely rare, and almost all observational studies include sites that vary at least to some extent regarding global change drivers such as land use. Thus, more studies on how global change drivers affect biodiversity, stability, and the relationships between them, are urgently needed.

9.4. Contribution of dominant and rare species to stability

High dominance in natural ecosystems can lead to a stronger contribution of the dominant species to the stability of aggregate properties relative to rare species (Grime 1998), thereby diminishing the role of biodiversity per se (Loreau and de Mazancourt 2013). This would lead to a positive selection effect when the dominant species have lower variance than expected (compared to monocultures or to ambient conditions) and a negative selection effect when the dominant species have higher variance than expected.

Supporting this idea, many real-world studies have shown that the temporal stability of the dominant species disproportionately contributes to the temporal stability of community productivity (e.g. Xu *et al.* 2015). As predicted by theory (Haegeman *et al.* 2016), most of these studies found a positive selection effect where dominant species were more stable than expected. Another way dominance could disproportionately contribute to stability and override diversity effects is through higher species asynchrony; that is, when species asynchrony is higher in communities with low evenness that are dominated by a few species compared with communities with high evenness. This could be the case when species-rich communities contain many species with similar ecological attributes that respond similarly to environmental fluctuations, as found in some studies (Song *et al.* 2020; Valencia *et al.* 2020).

Accordingly, most of the studies discussed above found a stronger contribution of dominant species stability or dominant species asynchrony to α -stability compared to species richness, and a high frequency of neutral or negative biodiversity–stability relationships (Valencia *et al.* 2020). These results contrast with theoretical predictions (de Mazancourt *et al.* 2013), as well as with results from along natural gradients of biodiversity (Figure 9.4) (Houlahan *et al.* 2018; Hautier *et al.* 2020), and from synthetic ecosystems (Cardinale *et al.* 2012), which all show a strong association between biodiversity and temporal stability. This discrepancy can be explained by two reasons.

First, neutral or negative richness–stability relationships found in real-world ecosystems are almost exclusively based on single site studies in which biodiversity and stability respond to global change treatments (but see Polley *et al.* 2007; Jourdan *et al.* 2020). However, the simultaneous effect of global change drivers on both biodiversity and functioning is likely to confound the relationship between biodiversity and functional stability (Huston 1997). For example, a simultaneous increase or decrease in both diversity and stability in response to global changes would lead to a positive diversity–stability relationship (Figure 9.6c,f,i; e.g. Tilman 1996; Ma *et al.* 2020). In contrast, a simultaneous decrease (increase) in diversity and increase (decrease) in stability would lead to a negative diversity–stability relationship (Figure 9.6a,d,g; e.g. Polley *et al.* 2007; Yu *et al.* 2020). Additionally, global changes that simultaneously increase or decrease stability (diversity) but have no effect on diversity (stability; as often happens: see Figure 9.5) would lead to a neutral or very weak diversity–stability relationship (Figure 9.6 b,e,h; e.g. Yang *et al.* 2017).

Second, in synthetic experiments, communities are usually initiated with even relative-abundance distribution and the random loss of species gives equal probability to rare and abundant species of being lost. While patterns of dominance can quickly develop (Hector *et al.* 2010), ecosystem responses in experiments may, at least in the short-term, largely be influenced by an initially very even abundance distribution and depend on the identity of the species being added or excluded from the community (Huston 1997). However, the only experiment, to our knowledge, that manipulated species diversity together with species abundance found no evidence that stabilizing effects of diversity are influenced by abundance distribution (Isbell *et al.* 2009). This could be because experimentally imposed differences in evenness quickly dissipated. Additionally, the range of the diversity gradient may be relatively small in observational studies, and particularly in global change experiments, as compared to that of synthetic experiments (Hautier *et al.* 2015). This may limit diversity effects when dominant species effects are strong.

In addition to the strong contribution of dominant species, there is growing evidence that rare species may significantly and disproportionately contribute to ecosystem functioning (Dee *et al.* 2019) and functional stability (Xiong *et al.* 2020). New theoretical advances have clarified the role of species abundances in shaping the diversity–stability relationships in response to perturbations (Chapter 7). In particular, perturbations that predominantly affect the many rare, highly unstable species lead to a negative diversity–stability relationship. In contrast, perturbations that predominantly affect the dominant, stable species lead to a positive diversity–stability relationship.

Finally, the type of perturbation that dominates depends on the spatial scale considered and thus may determine the diversity–stability relationships at multiple spatial scales (Arnoldi *et al.* 2019). For example, at the small spatial scale, communities are expected to be driven by demographic stochasticity and thus to depend more on the gains and losses of species compared to environmental perturbations. This suggests a stronger role of the rare species at small spatial scales. In contrast, at larger spatial scales, the role of environmental perturbations is expected to become more important compared to demographic stochasticity and dominant species could play a stronger role.

9.5. Future directions

While it is clear that the diversity of various taxonomic groups is related to stability in natural settings, various questions remain. Some of the questions we addressed here remain partly unresolved: for example, to what extent and how biodiversity at larger spatial scales contributes to stability, and to what extent global change drivers alter biodiversity–stability relationships. Biodiversity loss occurs at multiple spatial scales and many communities are homogenizing in their composition (β -diversity loss) (McGill *et al.* 2015). An emerging insight is that these larger scale biodiversity losses also hamper stability, but whether the consequences are less, equally, or more detrimental than local biodiversity loss is unresolved. Furthermore, it is likely that several global change drivers will become more important in the future. For example, continued and increasing global warming is almost inevitable in the coming decades, but to what extent this will strengthen or weaken links between biodiversity and stability is unknown. Thus, increased efforts into the effects of climate change on biodiversity–stability relationships are much needed.

Furthermore, existing biodiversity–stability studies are highly biased towards terrestrial, temperate systems and towards primary producers (Figure 9.3). However, in various understudied ecosystems, stability is also of great importance. For example, the oceans provide a great source of food for humans in the form of fish and seafood. While it is known that a high fish marine diversity is generally associated with high fish biomass (e.g. Lefcheck *et al.* 2019), to what extent this biomass is also more stable over time is unknown. Similarly, tropical forests harbor the most aboveground carbon of all terrestrial systems (Crowther *et al.* 2019). However, relationships between tree diversity and aboveground carbon sequestration are generally weaker in tropical forests than in temperate forests (van der Plas 2019). Whether this is also the case for stability in carbon sequestration is unknown. Thus, we urgently need to investigate the role of

biodiversity for stability among higher trophic levels and in both marine and tropical systems.

Future studies could also focus more on how organisms' traits drive relationships between biodiversity and stability. Under optimal conditions (e.g. resource rich environments), primary production is often maximized by plant species that have "fast" traits that maximize photosynthetic rates, such as high specific leaf area (e.g. Grigulis *et al.* 2013). On the other hand, in stressful situations, more conservative traits enable a species to conserve resources and maintain moderate growth (Ruiz-Benito *et al.* 2014). Therefore, it has been proposed, and shown in experiments, that plant communities containing both "slow" and "fast" species are most stable in their biomass production when environmental conditions change over time (Craven *et al.* 2018). Similarly, across drylands, natural gradients in functional diversity are a stronger predictor of stability than species richness per se (Garcia-Palacios *et al.* 2018). It is likely that, for higher trophic levels also, a high functional diversity in traits related to the "speed of life" (i.e. traits related to growth rates) may be crucial for biodiversity–stability relationships.

Another question still hardly addressed is to what extent biodiversity regulates the stability of ecosystem functions other than biomass production. While primary productivity is only one property of ecosystems, ecosystems consist of multiple organisms across multiple trophic levels, which are intricately related to each other. Therefore, a high primary productivity may have propagating effects on higher trophic levels by also promoting their biomass stocks and process rates (e.g. Barnes *et al.* 2018) and may thereby also affect ecosystem functions, such as pollination or soil carbon storage, and their stability. On the other hand, levels of different ecosystem functions can also trade off (Lavorel and Grigulis 2012). The main questions include how 1) biodiversity regulates the stability of other ecosystem functions and 2) whether biodiversity can promote "multifunctional stability", that is, the stability of multiple ecosystem functions simultaneously (Figure 9.2). Orford *et al.* (2016) found that a high pollinator diversity is associated with a higher temporal stability in flower visitation and hence likely with a higher stability in pollination services. Similarly, Wagg *et al.* (2021) found that microbial diversity is positively related to the stability of multiple functions, including plant biomass production, litter decomposition, and carbon assimilation. On the other hand, Sasaki *et al.* (2019) show that plant diversity had an overall negative effect on multifunctional stability. So, while in theory one would expect biodiversity to promote "multifunctional stability", the few studies so far (mostly performed in experimental settings) offer rather mixed evidence. Hence, one of the main open questions is whether, along natural gradients, positive or negative relationships between biodiversity and multifunctional stability are most common.

A key challenge is also to apply our current understanding of biodiversity–stability relationships for the stabilization of ecosystem services that we depend on. One promising study in this direction showed that countries with a higher diversity of crop species also had a higher temporal stability of agricultural production (Renard and Tilman 2019). Famines are typically caused by years in which local agricultural production is lower than in normal years, rather than by overall low productivity across years. Thus, to avoid famines it is important that food production is stable, and the study by Renard and Tilman (2019) suggests that diversifying cropping systems at national levels is a promising way to do so.

In summary, in line with theory and experimental findings, the biodiversity of multiple trophic levels is typically associated with a high stability in biomass production. While these relationships have only been explored for a subset of ecosystem types and organisms, patterns to date are generally consistent, and indicate that the conservation and restoration of biodiversity in natural systems has several benefits for the stability of biomass production. It is possible that this is also true for other types of ecosystem functions, such as soil carbon storage, pollination services, and nutrient cycling. Knowledge on biodiversity and stability in natural systems is starting to have applied benefits for the design of natural and semi-natural systems, and these benefits may become greater with an increased understanding yielded by future studies.

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