

Abstract

1. Species-rich communities exhibit higher levels of ecosystem functioning compared to species-poor ones, and this positive relationship strengthens over time. One proposed explanation for this phenomenon is the reduction of niche overlap among plants or animals, which corresponds to increased complementarity and reduced competition.
2. In order to examine the potential of increased complementarity among plants or animals to strengthen the relationship between diversity and ecosystem functions, we integrated models of bio-energetic population dynamics and food-web assembly. Through the simulation of various scenarios of plant and animal complementarity change, we sought to elucidate the mechanisms underlying the observed increases in (1) primary productivity, (2) control of herbivores by predators, and (3) reduction of herbivore pressure on plants in species-rich communities.
3. Our findings reveal that increased niche complementarity of plants can steepen the diversity-function relationships if it does not increase their intraspecific competition, while increasing complementarity among animals during community assembly can also have a positive effect but with considerable variability.
4. The study highlights the importance of trait variation both among and within species, and the interplay between intra- and interspecific competition strength in shaping the functioning of ecosystems over time. These results offer insights into the mechanisms underpinning the diversity-functioning relationship, and have practical implications for ecosystem management and conservation efforts.

22

23 **Keywords:**

24 community assembly, competition, food-webs, herbivory, herbivory control, interspecific,
25 intraspecific, productivity, trophic niche

26

27 **Introduction**

28 An ecosystem's ability to function and thus provide services to humans depends on its
29 biodiversity (Hooper *et al.* 2005; Cardinale *et al.* 2012; Isbell *et al.* 2017). Positive effects of
30 biodiversity, have been reported for primary production (Cardinale *et al.* 2011), herbivory and
31 predation (Ebeling *et al.* 2014; Barnes *et al.* 2020), decomposition (Ebeling *et al.* 2014; Handa *et al.*
32 2014), as well as pollination (Gavini *et al.* 2021). Remarkably, these positive diversity-
33 ecosystem functioning relationships tend to establish during community assembly (Cardinale *et al.*
34 2007; Meyer *et al.* 2016; Eisenhauer *et al.* 2019). Therefore, they may be weak (Reich *et al.*
35 2012) or absent (Strecker *et al.* 2016) among communities in the first few years of their
36 establishment, becoming considerably more positive in later years (Reich *et al.* 2012; Huang *et al.*
37 2018; Wagg *et al.* 2022). Consequently, restored communities may require considerable time
38 for dynamic assembly processes to achieve a functioning level comparable to old natural
39 communities (Moreno-Mateos *et al.* 2020; Resch *et al.* 2021; Bannar-Martin *et al.* 2018;
40 Ladouceur *et al.* 2022). Understanding the mechanisms involved in establishing and steepening
41 the diversity-ecosystem functioning relationship is thus crucial for effective ecosystem
42 management, as they can tip the scales in conservation versus restoration decisions.

Competition for resources, such as light or nutrients, is instrumental in understanding the changes in plant community functioning over time (Reich *et al.* 2012). The strength of competition is often characterized by a gradient ranging from niche overlap (strong competition) to complementarity (weak competition or even facilitation) (Barry *et al.* 2019). Plant species grown in diverse plant communities (mixtures) become morphologically more dissimilar than the same species grown in monocultures (Zuppinge-Dingley *et al.* 2014; Roscher *et al.* 2015). This suggests that species respond to interspecific competition by shifting their niche to reduce overlap with other species, making them more complementary in their use of resources (Eisenhauer *et al.* 2019). However, intraspecific trait variability also allows individuals to escape competition from conspecifics (Jung *et al.* 2010). Avoiding interspecific competition by shifts along a finite niche axis to achieve species complementarity can come at the cost of increasing intraspecific competition. Consequently, plant productivity may decrease even when interspecific variability is high, if individuals of the same species become more clumped in the same area of niche space (Fig. 1a, clumped scenario). Therefore, we expect niche differentiation to have a net positive effect on productivity only if it reduces interspecific competition while maintaining a tolerable level of intraspecific competition (Roscher *et al.* 2015). This requires that species shift their location in niche space relative to each other while maintaining relatively high dispersion of niche positions among their individuals (Fig. 1a, spread-out scenario). Despite evidence that plant populations shift in their heritable traits over time (Zuppinge-Dingley *et al.* 2014) and thus change their niche spectrum, it is unclear how these changes affect the processes underlying the community's diversity-productivity relationship.

Moreover, plant diversity-productivity relationships may not only depend on plant-plant interactions, but also on multi-trophic interactions (Schneider *et al.* 2016; Seibold *et al.* 2018;

Wang & Brose 2018; Eisenhauer *et al.* 2019; Barnes *et al.* 2020; Albert *et al.* 2022). What becomes increasingly clear is the importance of expanding the focus of the field from primary productivity to functions performed by the consumer community (Poisot *et al.* 2013; Barnes *et al.* 2020; Maureaud *et al.* 2020) and the multitrophic control of plant diversity and productivity (Schneider *et al.* 2016; Wang & Brose 2018). This multi-trophic perspective is equally relevant in our effort to understand how community assembly across trophic levels can reshape this relationship over time (Duffy *et al.* 2007). Active dispersal enables consumers to colonize a location, provided they can find resources there (Gravel *et al.* 2011; Bauer *et al.* 2022), but after the early pioneer phase, the food-web they comprise will also be structured by competitive exclusion. Specifically, strong competitors can extirpate species that occupy a similar niche, while new species can succeed in invading the community only if they are sufficiently unique to avoid competition by existing species (Hui *et al.* 2021). In this sense, species' trophic links are a manifestation of their realized niche (Bolnick *et al.* 2011); species that share resources will experience high exploitative competition, while species that share consumers are subject to apparent competition (Holt 1977; Stouffer & Bascompte 2010; Holt & Bonsall 2017). The expected effect of time is, therefore, to restructure the animal community in a way that reduces the similarity of trophic interactions among species, thereby increasing trophic niche complementarity (Poisot *et al.* 2013; Bauer *et al.* 2022) (Fig. 1b, high-complementarity scenario), with potential cascading effects on the plant community. However, the impacts of such multi-trophic restructuring during community assembly processes on the strength of the relationship between plant diversity and primary productivity have remained largely unexplored. As these different competition mechanisms for plants and animals (Fig. 1a, b) are likely to act in concert, discerning their individual contribution to the observed patterns in plant diversity-

productivity relationships can be challenging. Therefore, in-silico biodiversity experiments allow us to investigate how the different niche shifts of animal and plant communities during assembly (illustrated in Fig. 1a, b) and their combinations modify the plant diversity-function relationship. Here, we investigated the potential for niche differentiation over time, in both plant and animal communities, to modify the relationship between plant diversity and three key ecosystem functions: primary productivity, herbivory pressure on plants, and herbivore control by predators. We hypothesized that steepening of the diversity-function relationship over time could result from (H1) plant species segregation on a niche axis (reducing interspecific competition) only with niche adaptation (similar levels of intraspecific competition), whereas (H2) niche concentration leading to clumped niches and higher intraspecific competition (Fig. 1a) should reduce ecosystem functioning. Additionally, we expected that (H3) increasing trophic complementarity of animals during assembly, which also decreases competition (Fig. 1b), should also steepen the biodiversity-functioning relationships.

Methods

Regional species pool

We generated a regional pool of 1000 species (250 each of plants, herbivores, omnivores, and predators). Species' body-masses (in grams), here defined as 10^x , where x was sampled from a uniform distribution in $[-9, 3]$. The links from plants to their consumers (herbivores and omnivores) were set according to a nested pattern. First, a 250x500 plant by plant-consumer matrix was generated. Then, every b_{ij} element of the matrix was given a value according to its position in the matrix:

$$b_{ij} = \left(\frac{i}{250}\right)^2 + \left(\frac{j}{500}\right)^2 \quad (1)$$

This function describes a paraboloid, giving the elements in the matrix' lower right corner higher values. If $b_{ij} \geq 1$, we set it equal to 1, and used b_{ij}^2 as a probability of a Bernoulli trial, replacing matrix elements with 0 or 1. The produced matrix was subsequently embedded in the square matrix that contained all the potential trophic interactions.

Predatory interactions were assumed to scale allometrically, adapted from Schneider *et al.* (2016): the feeding niche of each animal species was defined as the body-mass interval at which the Ricker function used in Schneider *et al.* (2016) returns values larger than a threshold θ :

$$M_{ij} = \begin{cases} 1, & \text{if } \left(\frac{m_j}{m_i R_{opt}} e^{1 - \frac{m_j}{m_i R_{opt}}}\right)^\gamma > \theta \\ 0, & \text{otherwise.} \end{cases} \quad (2)$$

Here m_j is the mass of the predator, m_i that of the prey, γ is the width of the Ricker function and R_{opt} is the optimal predator-prey mass ratio which we set to 3.98 (Brose *et al.* 2006). To produce a food-web for which allometry does not entirely determine consumption (i.e. non-interval food-web (Cattin *et al.* 2004)), the resulting interaction matrix was thinned by randomly removing 30% of produced interactions.

Establishment of local communities

Local communities of 2-16 plant species (2, 3, ..., 16) and 40 animal species (300 replicates for each plant diversity increment) were produced by randomly sampling the regional pool, while ensuring that all consumer species have at least one resource in the community (following Bauer *et al.* (2022)). For each community, we generated a plant competition matrix (representing resource competition), corresponding to a naive community (*sensu* Moorsel *et al.* (2018)) with

high niche overlap among species, i.e. the competition that each species experiences from all other species can be as high as the competition from conspecifics (Fig. 1a). The produced food-webs represent early pioneer communities without any shared time allowing for niche differentiation, where consumer occurrence is most contingent on the presence of their resources. Consequently, consumers have unrestricted trophic similarity and, therefore, limited complementarity.

Effect of history on plants

To simulate niche differentiation on plants, we directly manipulated the plant-plant interaction matrix (see *Community dynamics*, below). For each local community, we generated a competition matrix consistent with reduced niche overlap, but without niche spread-out, i.e interspecific competition is reduced but intraspecific competition increases, so the overall competition remains the same. We also generated a competition matrix consistent with reduced niche overlap combined with niche spread-out, such that species compete less with other species but without increased intraspecific competition; therefore the overall competition that a species experiences is reduced.

Effect of history on animals

The communities described above were then exposed to a simulation of turnover, based on a Metropolis-Hastings algorithm. The algorithm sequentially removed animal species from local communities with a probability depending on their linkage similarity to other local species (a proxy of niche overlap), replacing them with random species from the regional pool. If the average Jaccard similarity J' of this new community is larger than the Jaccard similarity J of the

community before replacement, then the swap becomes effective. Otherwise, the replacement could still be accepted with probability P :

$$P = e^{\left(\frac{J-J'}{J \cdot 0.01}\right)}. \quad (3)$$

This algorithm increases the probability of arriving at a community composition of reduced average similarity among local species (Bauer *et al.* 2022), representative of communities structured by history, where competitive exclusion is also at play.

The combination of two animal trophic complementarity scenarios (low, high, Fig. 1b) crossed with three plant niche complementarity scenarios (overlapping, clumped, spread-out, Fig. 1a) resulted in six versions of a focal community. Across 15 levels of plant richness (2-16 species) with 300 replicates for each community type, this produced 27,000 simulated food-webs.

Community dynamics

We simulated community dynamics with a bio-energetic model (Delmas *et al.* 2017; Gauzens & Berti 2022). Changes in plant biomass over time are described by

$$\frac{dB_i}{dt} = (r_i G_i - x_i) B_i - \sum_j x_j y_j B_j F_{ij}. \quad (4)$$

The first term in equation (4) describes biomass gains through growth: B_i is the biomass of species i , r_i is the mass-specific maximum growth rate, G_i is the net growth rate and x_i is the mass-specific metabolic rate, scaled to the growth rate r of the smallest basal species in the regional pool. The second term describes losses to consumption: B_j is the biomass of consumer j , y_j is the maximum feeding rate of j relative to its metabolic rate and F_{ij} is the per unit biomass feeding rate of species j on species i . The net growth rate of species i is defined as

$$G_i = 1 - \frac{s_i}{K_i/N}, \quad (5)$$

where K_i is the carrying capacity of species i , and N is the number of plant species in the corresponding community, ensuring that the total amount of available resources that plants implicitly compete for, does not change across the plant richness gradient. s_i depends on the inter- and intraspecific competition for resources a_{ij} :

$$s_i = \sum_j a_{ij} B_j, \quad (6)$$

The diagonal elements of matrix a correspond to intraspecific competition, while the off-diagonals to interspecific competition.

By manipulating the relative strengths of the a_{ij} elements, we implemented the different plant competition scenarios described above. While restricting row sums to 1, we set $\sum_j a_{ij} \leq a_{ii}$ for the overlap scenario, and $\sum_j a_{ij} \ll a_{ii}$ for the clumped scenario. Finally, combining the a_{ii} values of the former scenario with the a_{ij} values of the later scenario, we produced communities with an overall decrease of plant competition (spread-out scenario).

Changes in animal biomass over time are described by the equation

$$\frac{dB_i}{dt} = B_i(x_i y_i \sum_j F_{ji} e_j - x_i) - \sum_j x_j y_j B_j F_{ij}. \quad (7)$$

The first term in equation (7) describes biomass gains through consumption (after metabolic losses x_i), where B_i is the biomass of species i , F_{ji} is the per unit biomass feeding rate of species i on species j , and e_j is the assimilation efficiency of prey j . The second term describes losses to consumption as in eq. 4. The multi-prey (for k prey species) functional response F_{ij} of species j consuming i is described by the equation

$$F_{ij} = \frac{w_{ij}B_i^q}{B_0^q + c_jB_j + \sum_k w_{kj}B_k^q}, \quad (8)$$

where w_{ij} is j 's relative consumption rate when consuming i . q is the Hill exponent determining the shape of the functional response. B_0 is the half-saturation density, while c_j is the intraspecific interference factor.

We simulated community dynamics using the *ATNr* package (Gauzens & Berti 2022), and ran simulations for 40,000 time-steps.

Ecosystem functioning

To assess the effects of complementarity changes among animals and plants on ecosystem functioning, we examined primary productivity at the end of simulations. Herbivory pressure on plants was quantified as the total out-flux of energy from plants to their consumers, per unit of plant biomass. Finally, we quantified herbivore control by predators as the ratio of out-fluxes to in-fluxes of herbivores (after Barnes *et al.* 2020).

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Results

We initiated our model simulations with communities of 2-16 plant species and 40 animal species. The simulated communities reproduced the expected positive and saturating plant species richness-productivity relationship (Fig. 2a), and a positive relationship between plant species richness and standing plant biomass (Fig. S1).

We tested for effects of the two plant niche differentiation processes, concentration and adaptation (see Fig. 1a), on the plant diversity-productivity relationship. An increase in plant

212 complementarity through concentration (i.e. higher intraspecific competition) dampened the
213 diversity-productivity relationship (Fig. 2a, red versus yellow lines). The difference in
214 productivity in a focal community resulting from this complementarity change was, on average,
215 very limited for plant-poor communities (Fig. 2b), and unpredictable in terms of its sign. The
216 probability of being positive was almost as likely as being negative for communities with only
217 two plant species (Fig. 2b, red inlay plot). Communities with more plant species had more
218 pronounced negative differences in productivity (Fig. 2b) that were very consistent for plant-rich
219 communities. The probability of a positive difference was close to zero for eight species or more
220 (Fig. 2b, red inlay plot). Conversely, an increase of plant complementarity through adaptation
221 (i.e. lower interspecific competition with no change of intraspecific competition) produced a
222 pattern of a steeper diversity-productivity relationship (Fig. 2a, green versus yellow lines).
223 Consequently, differences in productivity in a focal community were more consistently positive
224 (Fig. 2b), and of higher magnitude for species-rich communities (Fig. 2b, green line and green
225 inlay plot). Together, these results demonstrate that plant diversity-productivity relationships
226 become shallower or steeper under the plant concentration or adaptation scenarios, respectively.

227 We also tested for effects of increasing complementarity in the trophic links of animal species
228 (i.e. trophic complementarity). An increase in trophic complementarity among animals also
229 contributed to the steepening of the diversity-productivity relationship on average, but this was
230 more pronounced in communities with high plant complementarity and low plant competition
231 (adaptation scenario, Fig. 2a, dashed versus solid green lines). There was considerable variation
232 in the difference in productivity in a focal community as a result of the transition from low to
233 high animal complementarity (Fig. 2c). For plant-poor communities, this difference was as likely
234 to be negative as positive, while among plant-rich communities with low plant competition, the

transition led to positive differences in productivity for 3 out of 4 communities (Fig. 2c, inlay plots). Our results show that the impact of increasing animal trophic complementarity on the plant diversity-productivity relationship depends on how plants increase their complementarity.

We next considered the effects of plant niche differentiation on the control of herbivores by predators. Control of herbivores had a hump-shaped relationship with plant richness, peaking between 4 and 8 plant species (Fig 3a). The difference in herbivore control by predators was generally positive when communities increased plant complementarity through niche adaptation (Fig. 3b, green line) and generally negative when they did so through concentration (Fig. 3b, red line). Differences in control due to adaptation were again more consistently positive (Fig. 3b, green inlay) and of higher magnitude for plant-rich communities.

The transition to higher trophic complementarity among animals had, on average, a positive effect on herbivore control (Fig. 3a, dashed vs solid lines and 3c). Again, there was considerable variation in the difference in control in a focal community as a result of this transition but for 3 out of 4 of plant-rich communities the difference was positive (Fig. 3c, inlays), regardless of the plant complementarity scenario that trophic complementarity was combined with.

We finally considered the effects of plant and animal complementarity changes on herbivory pressure. Like herbivore control, herbivory peaked in communities with ~4 plant species and declined with increasing plant richness (Fig 4a). The increase of plant complementarity through adaptation led to increased herbivory pressure (Fig. 4b, green line). This difference in herbivory pressure was consistently positive for plant species-rich communities (Fig. 4b green inlay). In contrast, increased plant complementarity through niche concentration had more variable effects on herbivory pressure. The average difference in herbivory pressure was negative for

communities with a low to medium number of plant species and was very close to zero for plant species-rich communities and communities with only two plant species (Fig. 4b, red line). Finally, the transition effect from low to high trophic complementarity among animals, while highly variable, was on average that of a reduction of herbivory pressure on plants. This average negative difference in pressure was more pronounced in communities of low to intermediate number of plant species (Fig. 4c) regardless of the plant complementarity scenario. Across the plant richness gradient, approximately 1 in 4 communities had a response against this general trend (Fig. 4c inlays).

Discussion

Simulating complex food-web dynamics, we found that shifts in plant resource niches to reduce interspecific competition only strengthen the diversity-functioning relationship if they do not come at the cost of increased intraspecific competition. The effects of increased complementarity among animals during community assembly are highly variable, yet positive on average. Together, these results indicate an interplay between plant niche shifts and animal community assembly in steepening biodiversity-functioning relationships over time.

Across experiments, it has been shown that biodiversity-functioning relationships steepen over time (Reich *et al.* 2012; Meyer *et al.* 2016; Huang *et al.* 2018; Wagg *et al.* 2022). Increases in plant niche complementarity have been suggested to explain this pattern (Zupping-Dingley *et al.* 2014; Eisenhauer *et al.* 2019). Our results demonstrate that temporal changes in biodiversity-functioning relationships largely depend on how increasing niche complementarity is achieved, due to implications for plant competition. If plants respond to interspecific competition by concentrating their niche (Fig. 1a, clumped scenario), thereby experiencing stronger intraspecific

competition, the diversity-function relationship is dampened. If plants can avoid interspecific competition by spreading out in niche-space (Fig. 1a, adaptation scenario), thereby maintaining low levels of intraspecific competition, the effect on the diversity-function relationship is generally positive and stronger with increasing plant richness. The importance of intraspecific trait variation for ecological processes has been repeatedly highlighted (Bolnick *et al.* 2011; Violle *et al.* 2012; Des Roches *et al.* 2018) with several studies examining its implications for leaf economics (Anderegg *et al.* 2018; Pichon *et al.* 2022), coexistence (Turnbull *et al.* 2013; Hart *et al.* 2016) and even niche differentiation (Roscher *et al.* 2015, 2018; Rodríguez-Alarcón *et al.* 2022). Our results support empirical evidence that the interplay between intra- and interspecific trait variation can be as important as species diversity for some ecosystem processes (Crutsinger *et al.* 2006; Des Roches *et al.* 2018). This underscores the need to examine shifts in the distribution of traits between and within species together (Roscher *et al.* 2015), when seeking explanations for the steepening of biodiversity-function relationships over time.

In complex food-webs, changes in plant diversity and productivity can cascade to higher trophic levels and feedback to plants by changes in herbivory (Barnes *et al.* 2020; Galiana *et al.* 2020). To address the importance of these cascading effects, we also studied how top-down herbivore control by predators and herbivory respond to changes in plant diversity and niche segregation. Along the plant diversity gradient, we found that control of herbivores by predators increased sharply from communities with two plant species to those with four to six plant species, before decreasing gradually. In consequence, herbivory strength followed similar trends along this gradient. Accordingly, a reduction of herbivore effects on plants in communities with higher plant diversity has been demonstrated experimentally (Barnes *et al.* 2020). These observed patterns in our model and prior empirical studies find an explanation in classic theory on biomass

pyramids along productivity gradients (Oksanen *et al.* 1981; Perkins *et al.* 2022). Increasing plant diversity increases plant biomass but also the biomass of higher trophic levels (Scherber *et al.* 2010). This increases herbivore biomass and thus herbivory at lower plant biomass levels (Oksanen *et al.* 1981). Further increases in herbivore and plant biomass generate higher predator biomass (Oksanen *et al.* 1981), leading to increasing dominance of higher trophic levels that control each other by intra-guild predation and dampen trophic cascades (Finke & Denno 2005; Schneider *et al.* 2012; Wang *et al.* 2019). The biomass distribution along the plant diversity gradient thus causes shifts in trophic cascades and energy fluxes to higher trophic levels (Barbier & Loreau 2018; Barnes *et al.* 2020; Galiana *et al.* 2020). This reduces fluxes among lower trophic levels, such as top-down pressure on herbivores and herbivory, with increasing plant diversity. Together, these findings explain the hump-shaped relationship between top-down pressure on herbivores as well as herbivory with plant diversity.

Despite increasing knowledge on how energy fluxes and trophic cascades vary with productivity, biomass distributions and plant diversity (Borer *et al.* 2005; Barnes *et al.* 2017; Barnes *et al.* 2020; Buzhdygan *et al.* 2020), the question of how dynamic plant niche differentiation modifies them remains unresolved. In our study, the effect of higher complementarity among plant species on herbivore control and herbivory pressure was also conditional on how this complementarity was achieved. Herbivory and predatory herbivore control increase under plant niche adaptation and decrease under concentration. Similar to the effects of plant diversity, these decreases are explained by changes in plant biomass production and the resulting biomass pyramids. Increases in plant productivity under adaptation yield higher fluxes to herbivores and higher trophic levels, whereas the decreased productivity due to strong intraspecific competition under concentration

324 causes decreased fluxes to higher trophic levels. Thus, our results link plant niche differentiation,
325 community biomass patterns, and energy fluxes in a general conceptual framework.

326 Our results confirm that higher complementarity among consumers, arising from ongoing
327 community assembly, leads to better herbivore control, on average. Additionally, if consumers in
328 a community become more complementary over time, herbivory pressure on plants is likely to be
329 reduced. Simultaneously, we demonstrate that the effects of increased complementarity among
330 consumers on ecosystem functioning can vary, so we should not necessarily expect higher
331 herbivore control or reduced herbivory pressure in communities with complementary consumers.
332 While this variability is partly a consequence of the random variability we imposed on food-web
333 parameters, it can also be explained by differences in consumer control via intra-guild predation
334 (Finke & Denno 2005; Wang *et al.* 2019). Therefore, our results suggest a complex interplay
335 between consumer complementarity and the network structures arising during community
336 assembly, generating feedbacks on the biodiversity-functioning relationships.

337 Seabloom *et al.* (2017) demonstrated that when plant communities are embedded in complex
338 food-webs, the effects of plant richness on productivity can be obscured, if biomass is used as a
339 proxy for productivity, due to the partial transformation of plant biomass to animal biomass. In
340 contrast, dynamic models allow us to consider plant productivity directly, while simultaneously
341 examining potential top-down effects of the animal community (Schneider *et al.* 2016). Our
342 results show that the magnitude of animal complementarity effects on plant productivity is
343 context dependent; it is stronger when both animals and plants have complementary niches as in
344 our spread-out scenario whereas it is less pronounced in the presence of high inter- or
345 intraspecific plant competition in the overlapping or clumped scenario, respectively. Similar to
346 the effects of animal complementarity on herbivory and top-down control of herbivores, the

effects on primary productivity were quite variable. As network properties that alter top-down control, such as intra-guild predation and modularity, vary with species richness (Riede *et al.* 2010), the resulting increased animal complementarity effects on plant diversity-productivity relationships may be idiosyncratic.

Our results augment the growing evidence that community assembly is important for ecosystem functioning (Bannar-Martin *et al.* 2018). We show that it can lead to shifts in animal species composition and plant niche distributions, resulting in a steepening of the biodiversity-functioning relationship. This illustrates a fundamental connection between ecosystem functioning and landscape processes that can accelerate or decelerate assembly. For instance, habitat fragmentation and anthropogenic disturbance together with species' dispersal capacities can impede the progress to mature, structured communities with high complementarity (Carrara *et al.* 2012; Arroyo-Rodríguez *et al.* 2013; Hirt *et al.* 2018). Indeed, consumers in disturbed habitats exhibit poor niche specialization (Korotkevich *et al.* 2018), suggesting that disturbance can have a regressive effect on assembly, preventing communities from increasing their ecosystem functioning. In this sense, our model informs our understanding of how such perturbations can impose costs by hindering assembly processes, which reduces ecosystem functionality beyond the direct effects of lower diversity.

As a simplifying assumption, we configured plant competition changes allowing plant niche adaptation to be unconstrained by the number of plant species. In reality, however, the capacity of species to avoid overlap within a finite niche space is constrained by niche space filling and thus by the number of coexisting species (Tilman 2004). Therefore, an increase in species richness will eventually lead to saturation of the niche space (Jousset *et al.* 2011; Eisenhauer *et al.* 2013). Regarding our approach, one could argue that shifting plant niches to avoid

interspecific competition could lead to a spread-out scenario under low plant diversity, whereas this is less likely at high plant diversity, where most of the niche space is occupied and the clumped or overlapping scenarios might be more realistic depending on the relative strength of intra- and interspecific competition. However, given our results, this would imply that primary productivity should increase especially when plant diversity is low with spread-out niches, resulting in a shallower relationship between diversity and productivity. As experimental results point in the opposite direction (Reich *et al.* 2012; Huang *et al.* 2018; Wagg *et al.* 2022), we conclude that the simplifying assumption of modeling niche shifts independently of species richness is unlikely to impact our conclusions.

We focused on complementarity-related processes driving the biodiversity-functioning relationship. Alternatively, selection effects may also become stronger over time to steepen the relationship. However, there is mounting evidence that complementarity, rather than selection, is driving the diversity-ecosystem functioning relationship (Loreau and Hector 2001; Cardinale *et al.* 2007; Reich *et al.* 2012; Huang *et al.* 2018; Wagg *et al.* 2022; but see Genung *et al.* 2020; Lisner *et al.* 2022). Accordingly, we focused on how complementarity among plants and animals can change the ecosystem functioning relationship. Although selection effects are implicit in our simulations because more productive species have higher survival rates, we refrained from including changes in selection effects over time without a clear hypothesis on their relation to assembly processes. However, if the assembly process correlates with global change factors such as nutrient addition, the overall niche space may become denser (Harpole & Tilman 2007), which could lead to stronger selection effects. Here, we provide a modeling framework that is flexible to include such changes in selection effects during community assembly, for example,

related to variations in intrinsic growth rates or asymmetric competition strengths of plants or maximum consumption rates of animals.

To achieve generality, we kept our model parameters at a generic level, while future studies could extend our approach to explore specific settings. For example, plant competition, which we modeled with a generic interaction strength matrix, could be replaced by explicitly modeling of differences in plant nutrient uptake, neighbor shading, and space use (Brose *et al.* 2008; Albert *et al.* 2022). Similarly, we modeled community assembly by sampling species from a pool without dispersal constraints. This could be replaced by linking dispersal capacity with species' traits and landscape characteristics (Hirt *et al.* 2018; Ryser *et al.* 2021). These examples illustrate how our modeling approach could integrate more explicit ecological processes to differentiate the reasons for the steepening of the diversity-function relationship over time, considering specific community and landscape types.

Conclusions

Our findings reveal that shifts in plant niches that reduce interspecific competition without increasing intraspecific competition provide a mechanism that strengthens the relationship between biodiversity and function. However, they also caution against any narrative that would suggest an uncomplicated relationship between niche complementarity and elevated ecosystem functioning. The restrictions imposed by intraspecific competition on complementarity's potential to act as a direct agent in the steepening of the relationship, highlight the need for empirical studies focusing on trait plasticity (Zuppinge-Dingley *et al.* 2014), explicit comparisons of inter- versus intraspecific trait variation (Roscher *et al.* 2015, 2018) and how their ratio changes over time. Such studies would help settle whether it is mainly niche adaptation or concentration occurring over time and therefore allow us to discern if

complementarity is directly responsible for increasing function, or whether any positive complementarity effect is instead mediated by its importance for species persistence.

Finally, we note that ecosystems that have reached a high level of functioning in the long process of their assembly history, are not easily replaceable. It is reasonable to expect that species turnover in multitrophic communities will increase complementarity over time, through a process of invasion, competitive exclusion and niche sorting. Despite evidence suggesting that plant communities can follow a predictable assembly (Petermann *et al.* 2010), the high unpredictability of multitrophic complementarity effects on different ecosystem functions shows that restoring an ecosystem after disturbance does not guarantee an assembly trajectory that will invariably lead to a functioning level necessary to provide desired ecosystem services (Arroyo-Rodríguez *et al.* 2017). Integration of ecosystem functioning into nature conservation concepts thus favors old-grown, mature communities over rewilding or reforestation strategies.

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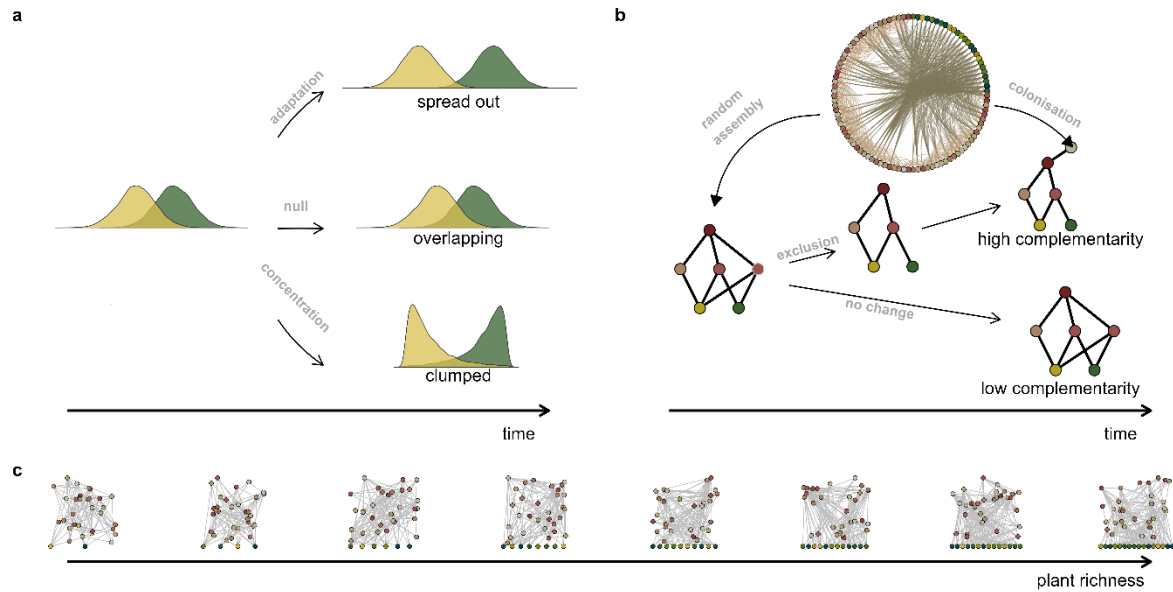


Figure 1. (a) Plant species in a community can reduce their niche overlap and therefore interspecific competition, either through niche concentration or adaptation. (b) In the early phase of community assembly, consumers may have high trophic similarity (low complementarity). A turnover process of competitive exclusion and colonisation of new species can reduce trophic similarity and therefore lead to high trophic complementarity. (c) These changes can take place in communities that contain a varying number of plant species.

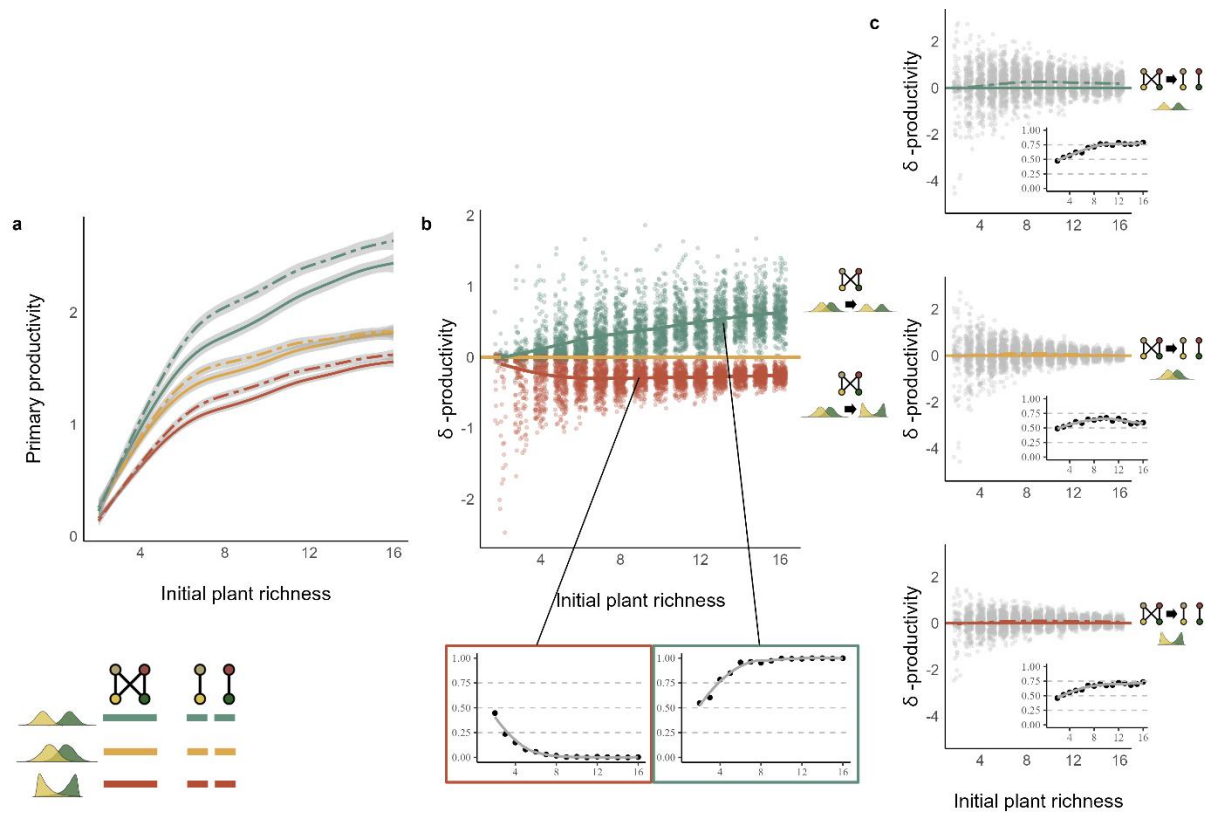


Figure 2. (a) The relationship between plant richness and primary productivity for communities with different combinations of plant and animal complementarity: communities with high niche overlap among plants (yellow lines), or reduced niche overlap either through niche concentration (red lines) or adaptation (green lines). Solid lines for communities with low animal complementarity and dashed lines for high animal complementarity. (b) The difference in primary productivity when plant complementarity increases through concentration (red points) or adaptation (green points). The red and green inset figures show the proportion of positive changes for each scenario. (c) The difference in primary productivity as communities transition from low to high animal complementarity. The colors correspond to the three different plant complementarity scenarios. Inset figures show the proportion of positive changes for each scenario.

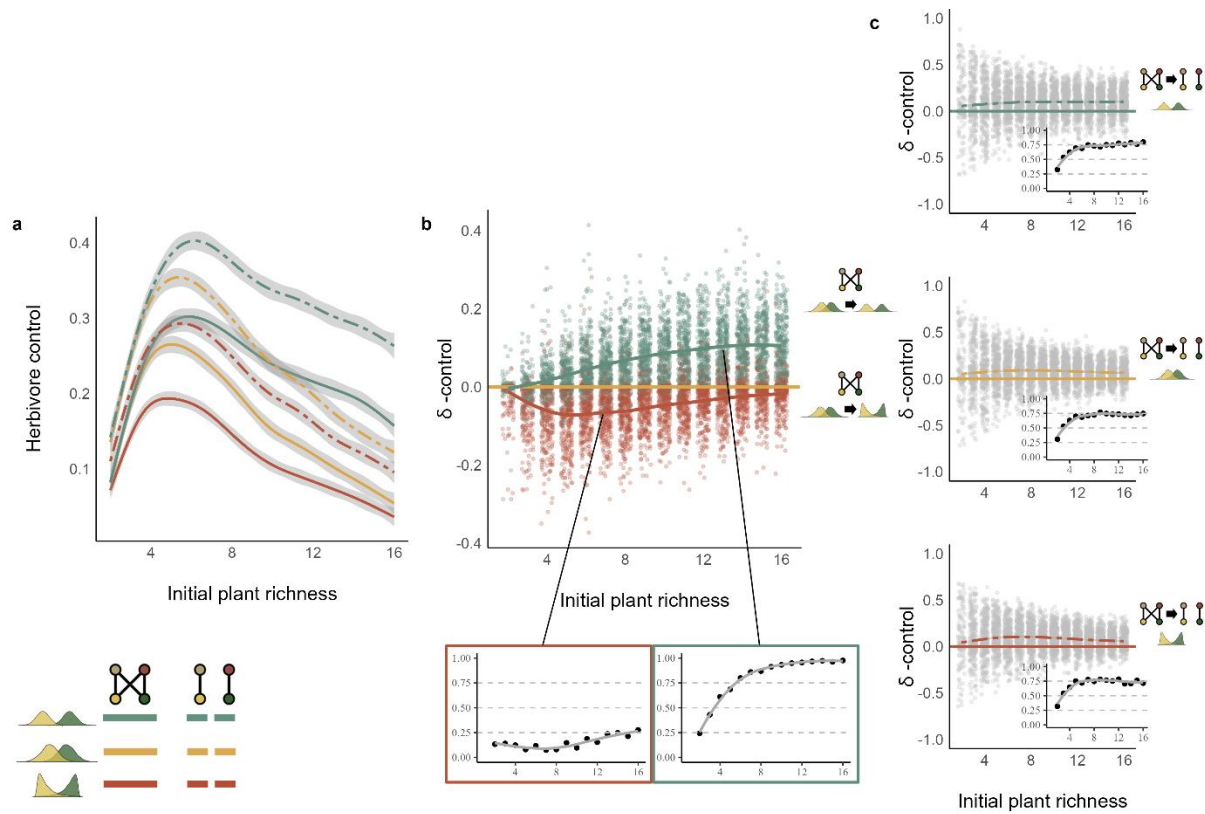


Figure 3. (a) The relationship between plant richness and herbivore control for communities with different combinations of plant and animal complementarity: communities with high niche overlap among plants (yellow lines), or reduced niche overlap either through niche concentration (red lines) or adaptation (green lines). Solid lines for communities with low animal complementarity and dashed lines for high animal complementarity. (b) The difference in herbivore control when plant complementarity increases through concentration (red points) or adaptation (green points). The red and green inset figures show the proportion of positive changes for each scenario. (c) The difference in herbivore control as communities transition from low to high animal complementarity. The colors correspond to the three different plant complementarity scenarios. Inset figures show the proportion of positive changes for each scenario.

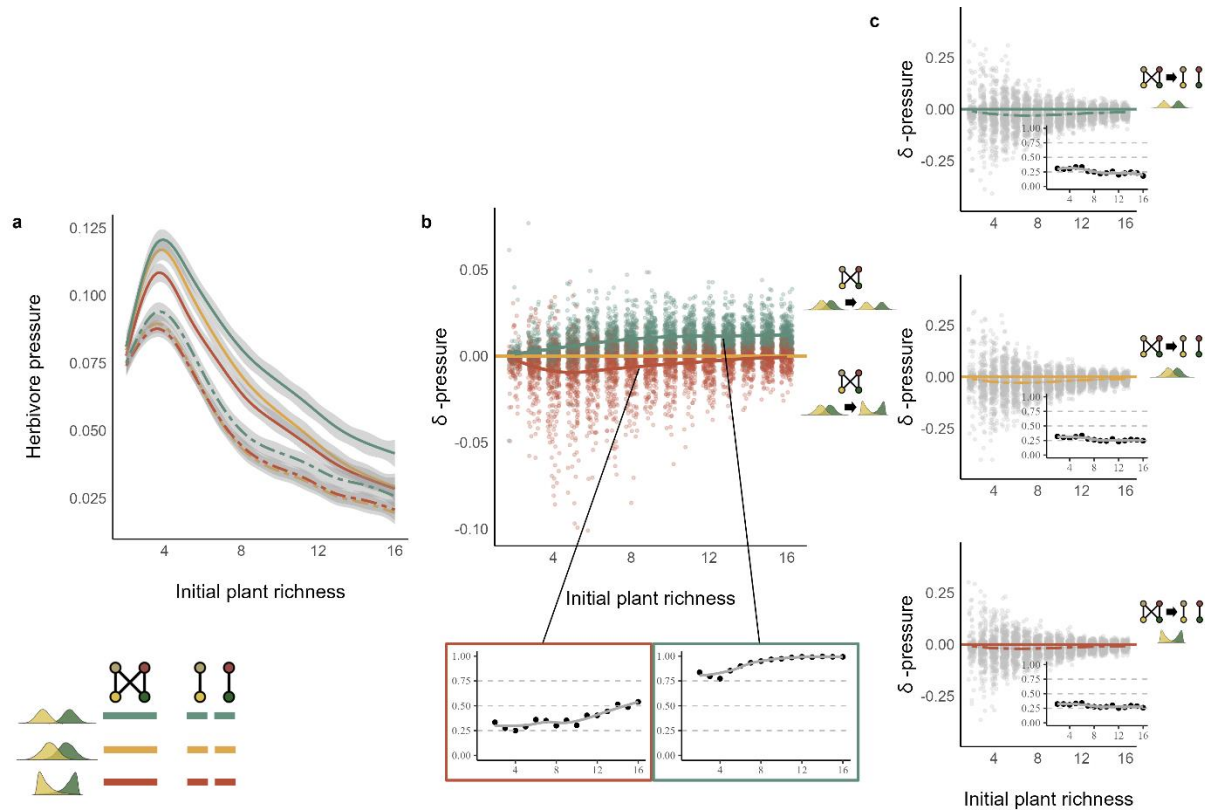


Figure 4. (a) The relationship between plant richness and herbivore pressure for communities with different combinations of plant and animal complementarity: communities with high niche overlap among plants (yellow lines), or reduced niche overlap either through niche concentration (red lines) or adaptation (green lines). Solid lines for communities with low animal complementarity and dashed lines for high animal complementarity. (b) The difference in herbivore pressure when plant complementarity increases through concentration (red points) or adaptation (green points). The red and green inset figures show the proportion of positive changes for each scenario. (c) The difference in herbivore pressure as communities transition from low to high animal complementarity. The colors correspond to the three different plant complementarity scenarios. Inset figures show the proportion of positive changes for each scenario.