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Cappelli, Seraina Lisa

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ARTICLE

Partitioning the effects of plant diversity on ecosystem functions at different trophic levels

Seraina L. Cappelli^{1,2}  | Noémie A. Pichon^{1,3}  | Tosca Mannall¹  | Eric Allan¹ 

¹Institute of Plant Sciences, University of Bern, Bern, Switzerland

²Research Centre for Ecological Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

³Department of Ecology and Genetics, University of Oulu, Oulu, Finland

Correspondence

Seraina L. Cappelli

Email: seraina.cappelli@helsinki.fi

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Abstract

Biodiversity effects on ecosystem functioning can be partitioned into complementarity effects, driven by many species, and selection effects, driven by few. Selection effects occur through interspecific abundance shifts (dominance) and intraspecific shifts in functioning. Complementarity and selection effects are often calculated for biomass, but very rarely for secondary productivity, that is, energy transfer to higher trophic levels. We calculated diversity effects for three functions: aboveground biomass, insect herbivory and pathogen infection, the latter two as proxies for energy transfer to higher trophic levels, in a grassland experiment (PaNDiv) manipulating species richness, functional composition, nitrogen enrichment, and fungicide treatment. Complementarity effects were, on average, positive and selection effects negative for biomass production and pathogen infection and multiple species contributed to diversity effects in mixtures. Diversity effects were, on average, less pronounced for herbivory. Diversity effects for the three functions were not correlated, because different species drove the different effects. Benefits (and costs) from growing in diverse communities, be it reduced herbivore or pathogen damage or increased productivity either due to abundance increases or increased productivity per area were distributed across different plant species, leading to highly variable contributions of single species to effects of diversity on different functions. These results show that different underlying ecological mechanisms can result in similar overall diversity effects across functions.

KEYWORDS

additive partitioning, biodiversity experiment, complementarity effect, ecosystem functioning, grassland, insect herbivory, pathogen infection, selection effect, tripartite partitioning

INTRODUCTION

Biodiversity affects ecosystem functions, such as biomass production or energy transfer to higher trophic levels, through different underlying mechanisms (Cardinale et al., 2006, 2012). A mechanistic

understanding of biodiversity–functioning relationships is of fundamental interest and is important to predict and manage the consequences of biodiversity declines. An approach to understanding the underlying mechanisms is to determine whether biodiversity effects occur due to simultaneous changes in multiple species

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(complementarity effects) or because single species drive the functioning of diverse plant communities (selection effects, Loreau & Hector, 2001). Single species with particular characteristics can drive polyculture functioning by outcompeting other species, in this case the selection effect is driven by interspecific changes and species with high monoculture functioning drive polyculture functioning by dominating mixtures. However, it is possible for single species to drive polyculture functioning without impacting others, that is, through intraspecific changes, for example by growing taller or more densely

(Fox, 2005). It is likely that the importance of these different effects varies between functions and also depends on environmental conditions, that is, the effects are context dependent (Figure 1a). For example, complementarity in nutrient use strategies is more likely to drive productivity of diverse communities in nutrient poor environments than when nutrients are not limiting (Tilman, 1985). Partitioning diversity effects into complementarity and selection effects in different ecological contexts can therefore provide important insights into the role of diversity in driving functioning and might

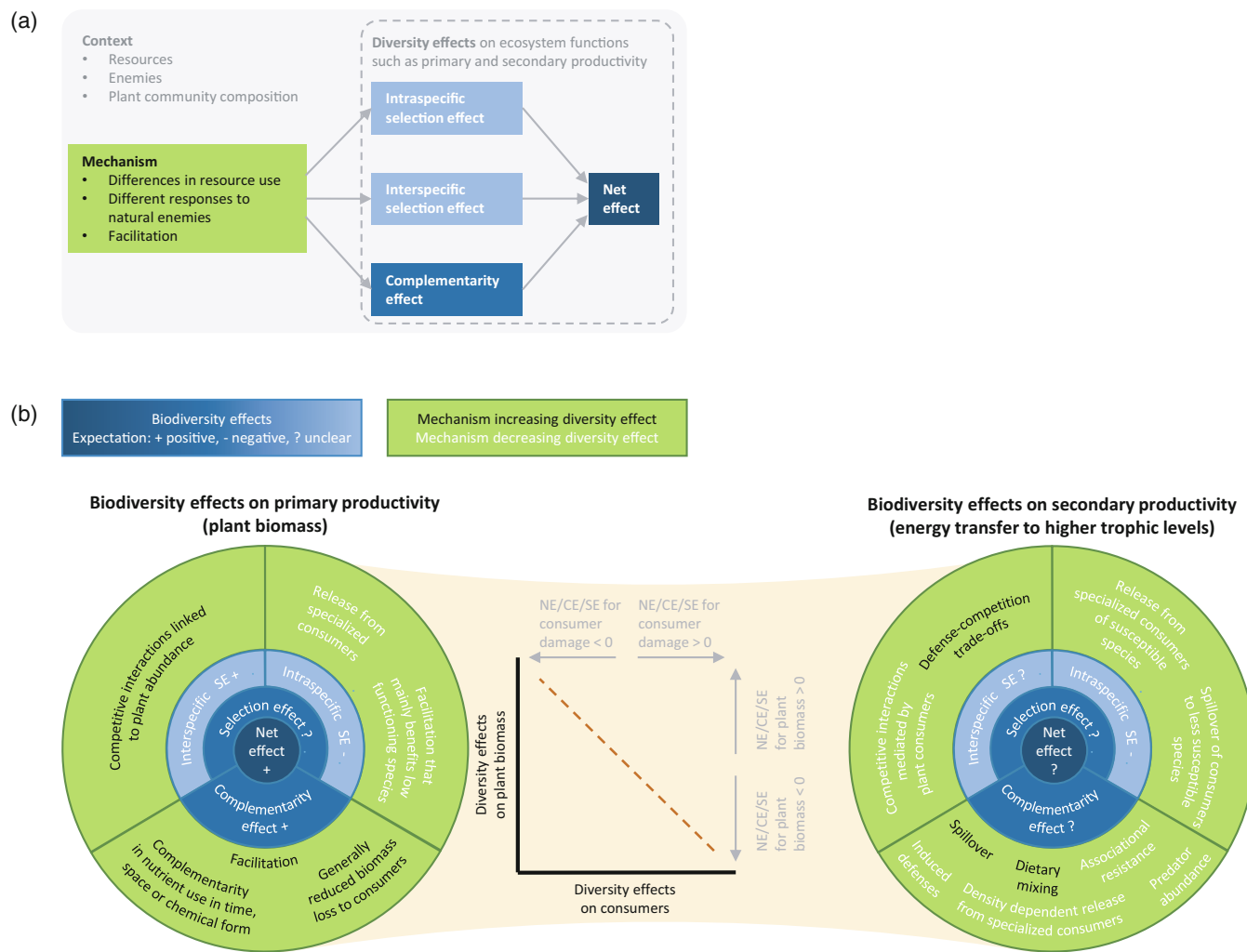


FIGURE 1 (a) With increasing plant diversity, ecosystem functioning often increases, too (net effect, NE). This can be because many species contribute to increased functioning (complementarity effects, CE) or few species drive polyculture functioning (selection effects, SE). Various underlying ecological mechanisms can lead to complementarity and selection effects and the mechanisms driving complementarity and selection effects may depend on the environmental context. (b) Diversity effects (inner circle, blue) can be caused by various underlying mechanisms (outer circle, green), as has been reviewed in detail by Barry et al. (2019) for biomass production. Here we do not list all possible mechanisms but highlight some of the most commonly discussed ones. The mechanisms can increase (written in black) or decrease (written in white) diversity effects. Whether the diversity effects for the different functions are expected to be positive or negative or unclear, is indicated with +, -, and ? respectively. If diversity changes energy transfer to higher trophic levels, by affecting herbivory and pathogen infection, this might also affect biomass production. If so, diversity effects for herbivory and infection should be negatively correlated with diversity effects for biomass. Because diversity likely affects pathogen infection and herbivory in similar ways, diversity effects for infection and herbivory are likely positively correlated with each other

help to identify which underlying mechanisms are responsible for the overall diversity effects overall (Figure 1b).

Biodiversity effects on primary productivity (plant biomass)

Plant biomass production, the most commonly studied ecosystem function, is usually increased by diversity through positive complementarity and selection effects in terrestrial ecosystems (Cardinale et al., 2011). There is evidence that processes like differentiation in nutrient use in time (Kahmen et al., 2006), space (Mamolos et al., 1995), or chemical form (Ashton et al., 2010), the action of specialist herbivores and pathogens (Eisenhauer, 2012) and facilitative interactions between species all contribute to positive complementarity effects (Wright et al., 2017). It is likely that several such mechanisms operate simultaneously and we therefore expect to observe positive complementarity effects for biomass production (Hypothesis [H1]; Table 1 and Figure 1b). Selection effects are partly driven by competitive interactions: a species can dominate polyculture biomass by increasing in abundance at the cost of other species in the community (interspecific shifts). The species that are able to dominate in mixtures are likely to be those that have high competitive ability under the prevailing environmental conditions (Laliberté et al., 2012). And these species would also be expected to grow well in monocultures. We would therefore expect to see a positive correlation between abundance in monoculture and dominance of mixtures, which would result in positive interspecific selection effects (H2; Table 1 and Figure 1b). However, overall selection effects also depend on whether species with low or high monoculture biomass benefit from complementary interactions, for example, through the release from their specialist pathogens in mixture. It is likely that species that do not grow well in monoculture would benefit particularly from such interactions, even if they remain at relatively low abundance in mixtures. Such increases in biomass could occur without affecting other species and would then contribute to negative intraspecific selection effects (H3; Table 1 and Figure 1b). We therefore expect opposing inter and intraspecific selection effects, leading to no clear prediction for the overall selection effect.

Biodiversity effects on secondary productivity (energy transfer to higher trophic levels)

Energy transfer to higher trophic levels is a key aspect of ecosystem functioning and is often strongly affected by plant diversity (e.g., Ebeling et al., 2018; Knops et al., 1999;

Liu et al., 2016; Mitchell et al., 2002; Rottstock et al., 2014). Although the overall effect of plant diversity on a range of different ecosystem functions has been widely studied, we know much less about the importance of complementarity and selection effects for ecosystem functions other than biomass (but see Grossiord et al. [2013] for water use efficiency and Pires et al. [2018] for decomposition). The damage caused by natural enemies such as fungal pathogens or insect herbivores is frequently used as a proxy of the energy transferred from plants to consumers and there is a range of different processes that can mediate effects of plant diversity on damage. It is generally assumed that diversity reduces the abundance of, and damage caused by, (specialized) natural enemies through dilution effects (Keesing et al., 2006). Such dilution effects should lead to negative complementarity by causing a general reduction in enemy damage across plants in the community. For example, a reduction in damage on a particular plant species, and thus reduced energy transfer to higher trophic levels can occur due to density dependence in enemy attack (resource concentration effect, e.g., Rottstock et al., 2014), associational resistance and induced defense by neighboring plants (e.g., Morrell & Kessler, 2017), or an increase in predators at high diversity (e.g., Haddad et al., 2009; Sanders et al., 2008). If dilution effects are important mechanisms, we would expect to see negative complementarity effects of plant diversity on energy transfer to higher trophic levels (H4a; Table 1 and Figure 1b). However, there is also evidence that some species suffer from spillover of generalist enemies in diverse communities, especially in the presence of species that tolerate a particular natural enemy and support a high abundance of it (Halliday et al., 2017; Power & Mitchell, 2004). Further, the dietary mixture hypothesis suggests that generalist herbivores benefit from feeding on a variety of different plant species, due enhanced nutrient balance or dilution of harmful plant secondary compounds (Bernays et al., 1994), which could lead to an increase in herbivory with increasing plant diversity. Both spillover and diet mixing would thus lead to positive complementarity effects, which can be interpreted as a contribution of most plant species to energy transfer to higher trophic levels in diverse communities (H4b; Table 1 and Figure 1b). Plant fungal pathogens and insect herbivores are two very diverse and heterogeneous groups and whether dilution or spillover is more prevalent is probably dependent on the specific composition of the natural enemy community. It is thus difficult to predict the direction of the complementarity effect for natural enemy damage and thus energy transfer to higher trophic levels (H4a vs. H4b).

Plant diversity might also increase or decrease energy transfer to higher trophic levels through selection effects. It is likely that species with high monoculture damage

TABLE 1 Overview over all tested hypotheses and which ecosystem function (biomass production or energy transfer to higher trophic levels) it is about

Hypothesis no.	Hypothesis description	Function
H1	There should be positive complementarity effects for biomass production, due to complementary resource use, reductions in natural enemies, or facilitation in diverse communities.	Biomass
H2	There should be positive interspecific selection effects for biomass production, because species that grow well alone are likely to be good competitors in mixtures.	Biomass
H3	Negative intraspecific selection effects for biomass are likely, if species that do not grow well in monoculture disproportionately benefit from complementary interactions between species in mixtures.	Biomass
H4	If dilution effects decrease enemy damage in mixtures, we expect positive complementarity effects for energy transfer to higher trophic levels (a), but if processes increasing enemy damage such as spillover or dietary mixture prevail, we expect negative complementarity effects for energy transfer to higher trophic levels (b).	Energy transfer
H5	There should be negative intraspecific selection effects for energy transfer to higher trophic levels, because species with high enemy damage in monoculture likely benefit from dilution and/or species with low enemy damage in monoculture likely suffer from processes promoting enemy damage.	Energy transfer
H6	If species with high natural enemy pressure benefit from enemy release in diverse communities and increase in abundance at the cost of species with lower enemy pressure, we expect negative interspecific selection effects for energy transfer to higher trophic levels (a) but if they are tolerant to enemies and at the same time more competitive, we expect positive interspecific selection effects for energy transfer to higher trophic levels (b).	Energy transfer
H7	We expect negative correlations between diversity effects for biomass and diversity effects for energy transfer to higher trophic levels if reduced pressure by natural enemies in diverse communities increases biomass production.	Biomass, energy transfer
H8	We expect positive correlations between diversity effects for herbivory and infection, because the same processes should drive diversity effects for both proxies of energy transfer to higher trophic levels.	Energy transfer
H9	We expect diversity effects to become stronger with increasing diversity (negative diversity effects becoming more negative and positive diversity effects becoming more positive).	Biomass, energy transfer
H10	With increasing functional diversity, complementarity effects, in particular, should become stronger.	Biomass, energy transfer
H11	Selection effects are better predicted by species mean traits than by functional diversity.	Biomass, energy transfer
H12	Plant communities consisting of slow-growing species are expected to have higher positive complementarity effects for biomass production, than plant communities consisting of fast-growing species, due to stronger differentiation in resource use strategies in slow-growing species.	Biomass
H13	Plant communities consisting of fast-growing species should have more positive interspecific selection effects for biomass than communities of slow-growing species, due to stronger competitive interactions.	Biomass
H14	We expect complementarity and intraspecific selection effects for energy transfer to higher trophic levels to be more pronounced in communities of fast- than of slow-growing species, since well defended slow-growing species are likely less affected by changes in enemy abundance in their surroundings.	Energy transfer
H15	When well-defended slow-growing species are attacked nonetheless, their competitive ability is likely diminished more than the competitive ability of tolerant, fast-growing species, which should result in lower interspecific selection effects in communities of slow-growing species.	Energy transfer

(Continues)

TABLE 1 (Continued)

Hypothesis no.	Hypothesis description	Function
H16	We expect nitrogen enrichment to reduce complementarity effects if resource partitioning is a driver of positive complementarity effects.	Biomass
H17	We expect nitrogen enrichment to increase selection effects for biomass if resource partitioning is a driver of positive complementarity effects.	Biomass
H18	We expect fungicide treatment to reduce complementarity effects for biomass if fungal pathogen dilution is a driver of positive complementarity effects.	Biomass
H19	We expect fungicide treatment to increase selection effects if fungal pathogens mainly suppress dominant plant species.	Biomass

would benefit from growing in mixtures and would have reduced enemy pressure (see also H4a), while species with low monoculture damage would suffer from spillover (see also H4b). Such shifts in enemy damage would reduce total selection effects and would lead to negative intraspecific selection effects, if they are not correlated with shifts in the abundance of the plant species (H5; Table 1 and Figure 1b). However, if plants with high monoculture damage are also top-down controlled by their enemies, they may be outcompeted by more resistant species in mixtures, which would lead to negative interspecific selection effects (H6a, Table 1 and Figure 1b). Alternatively, fast-growing plants may be the ones that suffer most from natural enemies (Cappelli et al., 2020; Heckman et al., 2019) and they may be able to tolerate herbivory (Coley et al., 1985). Fast growth is also linked to a high competitive ability for light (Diaz et al., 2016; Wright et al., 2004), which leads to a competitive advantage in nutrient rich habitats (Hautier et al., 2009). Thus, fast-growing, heavily infected species may tolerate attack and still be able to outcompete slower-growing neighbors with lower enemy damage. This process would be especially pronounced if the species with high enemy damage additionally benefit from dilution effects, and would lead to positive interspecific selection effects for energy transfer to higher trophic levels (H6b, Table 1, Figure 1b). Whether diversification leads to negative (H6a) or positive (H6b) interspecific selection effects for energy transfer to higher trophic levels, depends on how strongly enemy release and spillover affect the competitive ability of the different plant species.

Links between the mechanisms underlying diversity effects on different ecosystem functions

Biodiversity drives many ecosystem functions (Cardinale et al., 2006, 2012). If the same species are responsible for

driving multiple functions (Sullivan et al., 2007), then complementarity and selection effects of different functions are also likely to be correlated, but this has not been tested. Negative correlations between selection and complementarity effects for energy transfer to higher trophic levels and for plant biomass could arise if positive diversity–productivity relationships are driven by the suppression of specialist herbivores and pathogens through dilution effects (Barry et al., 2019; Eisenhauer, 2012; Keesing et al., 2006; H7, Table 1 and Figure 1b). Further, pathogenic fungi and herbivorous insects are both primary consumers of plants and many theories about the drivers of infection and herbivory are identical for both (Raffa et al., 2019). For example, if a growth–defense trade-off prevails for both herbivore and pathogen defense, then plant traits, such as specific leaf area (SLA), should be linked to both high infection and high herbivory (e.g., Blumenthal, 2006; Heckman et al., 2016). If energy transfer to fungal pathogens and insect herbivores is driven by the same mechanisms and species, then selection and complementarity effects for infection and herbivory, the two proxies for energy transfer to higher trophic levels, should be positively correlated (H8, Table 1).

Context dependency of biodiversity effects

The strength and nature of diversity effects are likely to depend on characteristics of the plant community and the biotic and abiotic environment. Understanding such context dependence is critical to predict when diversity is an important driver of functioning and it might also help to understand the mechanisms driving diversity effects. Complementarity effects are frequently stronger in more diverse communities (e.g., Spehn et al., 2005, van Ruijven & Berendse, 2003, but see Mahaut et al., 2019), suggesting that underlying mechanisms such as resource partitioning or enemy dilution operate more efficiently at high diversity. We thus expect stronger positive complementarity effects for biomass and energy transfer (see

also H1), and/or stronger negative intraspecific selection effects for energy transfer (see also H5) at high plant diversity (H9; Table 1). An increase in functional diversity should strengthen diversity effects, especially complementarity. This might be even more pronounced than with richness, because some species are likely to be functionally redundant so that differences in functional traits might better capture the complementary interactions that lead to enhanced functioning in diverse communities (Cadotte, 2017; Marquard et al., 2009; Roscher et al., 2012, H10, Table 1). Selection effects are driven by single species and their characteristics, which makes it likely that they are predicted by community means of key traits (Cadotte, 2017; Roscher et al., 2012, but see Mahaut et al., 2019, H11; Table 1).

Several key functional traits relate to the leaf economics spectrum, which categorizes plants based on their growth strategy. Slow-growing plants, with traits adapted to nutrient-poor environments, such as low SLA and high leaf dry matter content are at one end of the spectrum and fast-growing plants, with traits adapted to resource rich environments such as high SLA or high nitrogen content are at the other end (Diaz et al., 2016; Wright et al., 2004). In unproductive environments, species are expected to be strong competitors for nutrients, and given trade-offs in competitive abilities for different nutrients, they are expected to differ in their resource use (Tilman, 1985). It is therefore likely that plant communities composed of slow-growing plants have higher complementarity effects for biomass (H12; Table 1) than plant communities with fast growing species, which might be more characterized by higher interspecific selection effects for biomass (H13; Table 1). The growth strategy of plants also links to their defense against natural enemies, and therefore to the extent of energy transfer to higher trophic levels. Slow-growing plant species are often better defended against natural enemies (like insect herbivores and fungal pathogens) (Blumenthal et al., 2009; Cappelli et al., 2020; Coley et al., 1985), however fast species may be more tolerant, as they can easily replace tissue that was damaged or eaten (Gianoli & Salgado-Luarte, 2017). Well defended plants may be less affected by dilution or spillovers in diverse communities, which would mean that communities containing fast-growing species will have stronger complementarity and intraspecific selection effects on energy transfer to higher trophic levels, while diversity will have few effects on energy transfer in communities containing slow-growing species (H14; Table 1). However, if slow-growing species are attacked by natural enemies despite their high defense, they are likely to suffer more, leading to dominance of diverse slow-growing communities by those species with the lowest attack in monoculture (i.e., negative interspecific selection effects; H15, Table 1).

It is often suggested that resource partitioning is a driver of positive complementarity effects (e.g., Kahmen et al., 2006; Mamolos et al., 1995). Nitrogen, for example, occurs in different chemical forms and if species specialize on different forms, they can collectively access a larger pool of nitrogen and produce more biomass than they could in monoculture. For example, legumes increase complementarity effects for biomass, because their symbiotic rhizobacteria help to fix atmospheric nitrogen, which is otherwise inaccessible to plants (e.g., Marquard et al., 2009). Adding nitrogen to an ecosystem, through aerial deposition or in the form of fertilizer (Battye et al., 2017), would remove the benefits of resource partitioning and should thus reduce complementarity effects for biomass, as has been observed for nutrients in general (Craven et al., 2016) and nitrogen specifically (Roscher et al., 2016, Yin et al., 2018, but see Wacker et al., 2009). Further, high nutrient levels often favor a few species that are well adapted to productive environments, which would be reflected in increased inter- and potentially also intraspecific selection effects for biomass, which has also been previously observed for nutrient addition in general (Siebenkaes et al., 2016) and nitrogen specifically (Roscher et al., 2016, but see Yin et al., 2018). We thus hypothesize that nitrogen enrichment reduces complementarity effects (H16; Table 1) and increases selection effects (H17; Table 1) for biomass production. Further, nitrogen enrichment can accelerate energy transfer to higher trophic levels, by providing higher quality resources for plant consuming organisms (Altieri & Nicholls, 2003; Mitchell et al., 2003). Yet, whether this varies with plant diversity is not known and making predictions about how nitrogen enrichment may alter diversity effects on energy transfer to higher trophic levels is difficult. The outcome depends on many different factors, such as how much the natural enemies benefit from nitrogen enrichment, the degree to which different plant species can compensate for tissue lost to natural enemies or the efficiency of dilution effects under altered nutrient availability.

Similarly, if release from natural enemies in diverse communities is a driver of positive complementarity effects for biomass (see also H7), then removing natural enemies for example by spraying pesticides, would reduce complementarity effects for biomass (H18, Table 1). Also, if natural enemies mainly affect dominant plant species (e.g., Mitchell et al., 2002; Root, 1973; Rottstock et al., 2014), removing them will likely increase interspecific selection effects for biomass (H19; Table 1). Again, it is difficult to predict if and how pesticides would affect diversity effects for energy transfer to higher trophic levels. Overall, pesticides should reduce the damage caused by pests (e.g., Cappelli et al., 2020), but the consequences for complementarity and selection effects remain largely unstudied.

This study analyses data from an experiment manipulating plant species richness, plant functional composition (gradient in community mean SLA), nitrogen addition, and foliar fungal pathogen exclusion. We calculate biodiversity effects across these three functions related to primary productivity and energy transfer to higher trophic levels (aboveground plant biomass, insect herbivory, and pathogen infection). Through manipulation of nitrogen enrichment, pathogen abundance and community functional composition and diversity (based on mean and variance in SLA) along a species richness gradient we can test for context dependency in diversity effects on primary productivity and energy transfer to higher trophic levels. We tested the 19 hypotheses outlined in Table 1.

METHODS

Study site

The study was conducted in the PaNDiv experiment, established on an extensively managed grassland in the Swiss lowlands in autumn 2015 (47°03' N, 7°46' E, 564 m above sea level, mean annual temperature and precipitation of 9.2°C and 1051 mm/year, respectively, MeteoSchweiz, 2019). The experiment consists of 336 4-m² plots differing in plant species richness (1, 4, 8, 20 species), functional composition and functional diversity (a gradient of sown SLA was created by grouping species into fast- [high SLA] and slow- [low SLA] growing species and creating plots with only fast, only slow, or a mix of growth strategies), nitrogen enrichment (in the form of urea; 0, 100 kg ha⁻¹ year⁻¹) and foliar fungicide treatment (Score Profi by Syngenta Agro AG, 24.8% difenoconazole and Ortiva by Syngenta Agro GmbH, 22.8% azoxystrobin). Ten slow-growing and 10 fast-growing common perennial grassland species were used to create the plant communities (Appendix S1: Table S1, Figure S1). Species combinations were randomly selected from the respective species pool (i.e., fast, slow, or all) and the experiment contained 84 unique species compositions (Appendix S1: Table S2). Polycultures contained both grasses and non-leguminous forbs. The plots were arranged in four blocks and all species compositions (richness × functional composition and diversity) occurred once per block. Each composition received the four combinations of fungicide × nitrogen treatments, while the particular treatment that a given composition received was randomly allocated to each block. The plots were separated by 1-m grass paths. To maintain species compositions, the experiment was weeded three times per year. The whole experiment was

mown twice a year, which reflects typical extensive grassland management in this area.

Sown SLA (functional composition) and diversity in SLA (functional diversity) of a plant community was calculated based on SLA measurements in the control (without fungicide or nitrogen treatment) monocultures in three subsequent years (2016, 2017, and 2018). Each time, SLA was measured on five healthy and mature leaves following the protocol of Garnier et al. (2001) and averaged. The average SLA per species across the years was used to characterize the species and the average SLA of all species in a plot was used as the sown SLA and thus the (initial) growth strategy of the communities (further details on the experiment design in Pichon et al., 2020). We therefore used the functional categories (fast, slow) in the design, to ensure that functional composition was crossed with species richness, but we used the continuous measure mean SLA in the analysis to account for the fact that SLA varies within the slow and fast groups.

Ecosystem function measurements

We measured three functions related to primary productivity and energy transfer to primary consumers: plant aboveground biomass, aboveground insect herbivory (herbivory thereafter), and foliar fungal pathogen infection (infection thereafter).

We visually estimated the percent cover of all sown (target) plant species, bare ground, and weeds, in all plots. The sum of cover values per plot could exceed 100%, due to the layered vegetation structure. Cover was estimated twice a year between 2016 and 2018, once at the beginning of June and once at the beginning of August. In 2016, we only used the August data, once the field was fully established. This resulted in total of five “sampling periods” distributed over 3 years. Target species cover values were transformed to relative abundances (calculated relative to total target cover, i.e., without the weeds or bare ground). Over these 3 years, we measured biomass, infection, and herbivory during different sampling periods.

Shortly after the abundance measurements, we cut biomass in two 50 × 20 cm areas per plot (total of five sampling periods). The samples were dried at 60°C for at least 24 h, before weighing and we used the mean biomass of the two measurements. The abundance data were used to calculate the biomass produced by each species. We multiplied the proportional abundances of each plant species by the total plot biomass to obtain biomass values per species. In order to check that these estimates of species-specific biomass were accurate, we also sorted the biomass from 84 plots (two samples per plot) in June

2017 and from 216 plots (one sample per plot) in August 2017. The estimated biomass values per species were very close to the sorted biomass values in June, overall $R^2 = 0.87$ for untransformed and 0.67 for log-transformed values (Appendix S1: Figure S2). The correlation was less strong in August ($R^2 = 0.4$ for untransformed and 0.59 log-transformed values) presumably because we sorted only one out of two samples, leading to less accurate estimates of species abundances due to spatial variation. The strong correlation between predicted and observed species biomass means we are confident that our approach is suitable for estimating species biomasses.

We estimated infection on 10 plants in the central 1 m^2 of the plots in 2016, 2017, and 2018 in September when infection intensity is highest (Rottstock et al., 2014). In 2018, we also estimated infection in June (four sampling periods). Infection was measured as the proportion of individuals with signs of infection. We used incidence-based infection measures instead of severity-based measures, as we pooled different pathogen types. This way, easily visible pathogens like powdery mildews are not overestimated in comparison to pathogens that have a larger proportion of mycelium within leaves and are only partly visible, for example rusts. However, plant communities with high disease incidence did also generally have high disease severity (Appendix S1: Figure S3). If the central 1 m^2 did not contain enough individuals, we scored additional plants from the rest of the plot and if less than 10 individuals could be found in the whole plot, the proportion was calculated based on all individuals found in the plot. Herbivory was assessed at the end of May and August 2018 (two sampling periods). Five individuals of each target species were haphazardly selected from the central square meter of each plot, where five leaves per individual were assessed for damage. Leaves were selected from the middle tier of each individual, excluding juvenile and senescing leaves. Damage was assessed as presence or absence of each damage type per leaf (chewing, sucking, leaf mining, or rasping (Loranger et al., 2014)). From these we calculated the mean (across damage type) proportion of damaged leaves.

Additive partitioning

We calculated net, selection, and complementarity effects using the additive partitioning framework of Loreau and Hector (2001) for biomass and the adjusted framework of Grossiord et al. (2013) for fungal infection and insect herbivory. As the different functions were measured in different units, we scaled all functions between 0 and 1, per sampling period, before calculating additive partitioning.

The net effect of diversity (NE) is the difference between the observed functioning of a polyculture and its expected functioning assuming all species are at equal abundances and have the same functioning as they do in monocultures (illustrated with arrow a in Figure 2). In our case, we always compared to monocultures from the corresponding nitrogen and fungicide treatment, at the same time point. NE is the sum of complementarity (CE) and selection effect (SE):

$$NE = CE + SE = N \times \overline{\Delta RF} \times \overline{M} + N \times \text{cov}(\Delta RF; M) \quad (1)$$

where N is the number of species in the polyculture, M_i is the functioning of species i in monoculture, and ΔRF_i is the difference between the relative observed functioning of species i in polyculture ($RF_{\text{observed},i}$) and the relative expected functioning of species i in polyculture ($RF_{\text{expected},i}$). Positive (negative) complementarity effects occur when, on average, species increase (decrease) their relative functioning in polyculture compared to their monocultures. Usually, complementarity effects are driven by, and interpreted as, shifts in functioning across most of the species although it is mathematically possible that species with disproportionately large shifts drive complementarity effects. When species with above average monoculture functioning drive the functioning of mixtures (either through dominance or through further increases in functioning), this is reflected in positive selection effects. If species with below average monoculture functioning drive polyculture functioning (either through dominance or through disproportional increase in functioning) this is reflected in negative selection effects.

ΔRF_i is calculated as

$$\Delta RF_i = RF_{\text{observed},i} - RF_{\text{expected},i} = \frac{F_{\text{observed},i}}{F_{\text{expected},i}} - \frac{1}{N} \quad (2)$$

where $RF_{\text{observed},i}$ is the ratio between the observed functioning of species i in polyculture ($F_{\text{observed},i}$) and the expected functioning of species i in polyculture ($F_{\text{expected},i}$). $RF_{\text{observed},i}$ equals the sown abundance of species i , which is $1/N$ when species are equally abundant. Note that for biomass, the actually observed biomass of a species in a polyculture is used as $F_{\text{observed},i}$. For herbivory and pathogen infection, the observed functioning per species is obtained by weighing the observed function per species with the relative abundance of species i in polyculture (a_i). The reason for this is that for the functions other than biomass, the observed functioning per species does not have to be correlated with its abundance, while for biomass production,

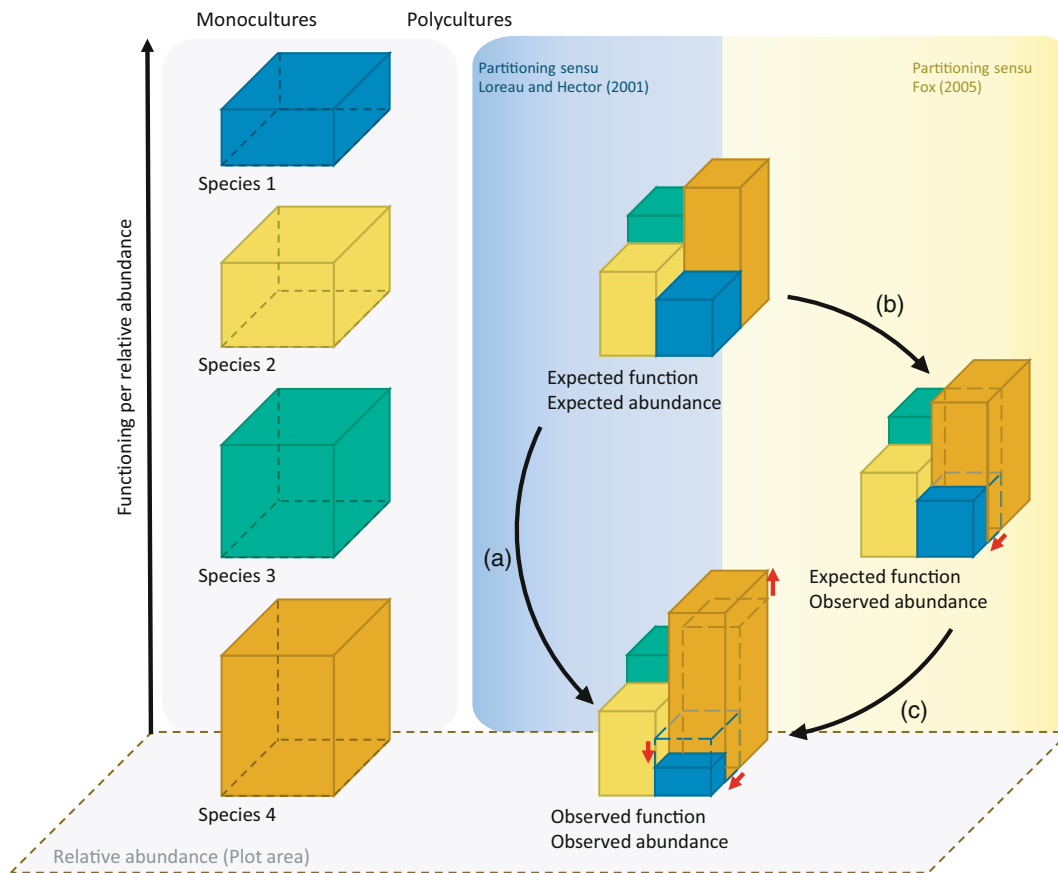


FIGURE 2 Graphical illustration of the additive partitioning frameworks sensu Loreau and Hector (2001) and Fox (2005). The differently colored cubes illustrate single species. The ground area of the cubes represents the species relative abundance, the height of the cubes represents the function provided by the species per relative abundance (or area covered), which makes the volume of a cube the contribution of the given species to the polyculture function. Due to equal sown abundances, we expect the relative abundance of each species to equal $1/N$. Based on the monocultures we expect the species to have a certain value of the function per relative abundance/area (expected polyculture). In reality, species in polycultures deviate from these expectations and might show higher (Species 4) or lower (Species 1) relative abundances (a) than expected and higher (Species 4) or lower (Species 1) than expected functioning (observed polyculture). (Total) net, complementarity, and selection effect sensu Loreau and Hector (2001) are calculated by comparing functioning of the expected community with the functioning of the observed community (a). For the tripartite partitioning sensu Fox (2005), the contribution of inter- (b) and intraspecific (c) shifts to total selection effects are further partitioned by comparing the functioning of both the expected and the observed polyculture with the functioning of an “intermediate” polyculture. For this “intermediate” polyculture, only interspecific abundance shifts are considered (Species 4 expands in relative abundance at the cost of Species 1). Note that interspecific abundance shifts (b) are a zero-sum game. Because of this, the complementarity effect between the expected and the “intermediate” polyculture (b) is always zero. The complementarity effect between the “intermediate” and the observed polyculture (c) equals the total complementarity effect between the expected and the observed polyculture (a)

abundance and contribution to function are the same (see also Grossiord et al., 2013).

In order to assess how much changes in species abundances (interspecific shifts) and changes in species functioning per unit ground area (intraspecific shifts) contributed to selection effects, we further partitioned the selection effects of all functions using the tripartite partitioning of Fox (2005). The contribution of interspecific shifts to the selection effect (SE_{inter} , equivalent to Fox’s “dominance effect”) is calculated as

$$SE_{inter} = N \times cov(\Delta RF_{inter,i}; M) \quad (3)$$

where $\Delta RF_{inter,i}$ is the difference between the expected functioning of species i in the polyculture, based on its observed abundance and monoculture functioning, and its expected functioning, based on its sown abundance and monoculture functioning. Simplified, this is the difference between the observed and the expected relative abundance of species i in polyculture (see arrow b in Figure 2)

$$\Delta RF_{\text{inter},i} = a_i - \frac{1}{N}. \quad (4)$$

The expected relative abundance equals $1/N$ as all species were sown at equal abundances. The contribution of intraspecific shifts to the selection effect (SE_{intra} , equivalent to Fox's "trait-dependent selection effect") are calculated as

$$SE_{\text{intra}} = N \times \text{cov}(\Delta RF_{\text{intra},i}; M) \quad (5)$$

Where $\Delta RF_{\text{intra},i}$ is the relative difference between observed functioning in polyculture and expected functioning based on the monoculture values and the observed abundances, thus

$$\Delta RF_{\text{intra},i} = \frac{F_{\text{observed},i}}{F_{\text{expected},i}} - a_i \quad (6)$$

(see arrow c in Figure 2). SE_{inter} and SE_{intra} together sum up to the total selection effect.

$$SE = SE_{\text{inter}} + SE_{\text{intra}}. \quad (7)$$

More details on the calculations are provided in Appendix S1: Table S3. In order to clarify the link between the total selection effect and the contribution of inter- and intraspecific shifts to the total selection effect, we do not use the terminology of Fox (2005), who calls SE_{inter} "dominance effect," SE_{intra} "trait dependent complementarity effect." and CE "trait independent complementarity effect."

We excluded *Heracleum sphondylium* L. and *Antirrhiscus sylvestris* (L.) Hoffm. from all calculations because of their poor establishment (details in Appendix S1: Section S1, Figure S4). Further, when a species was missing from a plot, we could not measure consumer damage. The missing values were replaced with the monoculture values of the same species in the same treatment, which leads to conservative estimates of selection and complementarity effects. When monoculture values were missing (2 out of 400 samples), we modeled them based on the other monoculture values, including species identity, sampling period, and fungicide and nitrogen treatment as explanatory variables. Zero monoculture values were possible for herbivory and fungal infection and these cause infinitely big complementarity and selection effects. To avoid this, zero values were set to half of the observed minimum function (11 out of total 320 monoculture measurements for infection and 2 out of total 160 monoculture measurements for herbivory).

A caveat of the additive partitioning approach is the importance of the monoculture values, as they are

included in all measures of net, complementarity and selection effects. Ideally, we would replicate all the monocultures with the different treatments, which would provide more precise estimates and reduce the impact of random variation. However, due to the high number of species and treatment combinations (80), we could not replicate the monoculture \times treatment combinations. The detailed analyses of the treatment effects might be less robust than overall effects because they are based on a single monoculture measurement. However, we measured all functions at least two times, which does not provide replication but does reduce the influence of extreme measurements.

Analysis

We first analyzed the net, complementarity, selection, and intra- and interspecific selection effects for each function, including all measures over time. All effects on biomass, infection, and herbivory were log-transformed, keeping the original sign, to achieve a normal distribution. We constructed linear mixed effects models (*lme4* package, Bates et al., 2015) including all the treatment variables (nitrogen, fungicide, sown SLA, sown mean pairwise distance in SLA, and plant richness) as fixed effects. We excluded interactions between the treatments, even though our experimental design would allow us to test the full five-way interaction, to reduce the number of terms tested, as we were fitting many different models. We included random intercepts for block, plot, species composition and sampling period in all models. We also tested if including slopes of fungicide and nitrogen against sampling period and random intercepts for the interactions between sampling period and plant composition improved model fit (assessed with likelihood ratio tests). Using these mixed effect models, we first calculated the values for each biodiversity effect by fitting intercept only models, using the chosen random structure per effect, to determine how complementarity and selection effects varied between functions (H1–H6). We then tested for context dependency in complementarity and intra- and interspecific selection effects by examining the fixed effects (H9–H19). Fixed effect structures were simplified by progressively excluding nonsignificant effects, using likelihood-ratio tests (Zuur, 2009). In addition we visually checked that there was no temporal autocorrelation in the residuals of the models for biomass and infection (as they were measured over multiple sampling periods) using the *ACF_gam* function of the R package *itsadug* (van Rij et al., 2015; Appendix S1: Figures S5 and S6).

To better visualize the overall intra- and interspecific selection effects and single-species contributions to them, we calculated relationships between the mean

monoculture function per species, across treatments and sampling periods (scaled relative to the mean of all monocultures), and the mean change in function between monocultures and polycultures. We did this for both interspecific and intraspecific effects.

To check whether complementarity effects are driven by multiple species rather than a few species with disproportionately large differences between mono- and polyculture functioning, we plotted complementarity effects against the proportion of species with positive ΔRF_i (Appendix S1: Figure S7).

We also looked at how diversity effects correlated across functions (H7–H8). We calculated the mean net, complementarity, intraspecific selection, and interspecific selection effects per function, across all sampling periods (with the untransformed values), because we did not measure all functions in all sampling periods. We then calculated Pearson correlation between mean values. All calculations and analyses were done in R (R Core Team, 2020).

RESULTS

Intercepts and species contributions

To test average effect sizes per diversity effect and function (H1–H6), we fitted intercept only models. The net

effect of diversity was negative for herbivory, positive for biomass, and not significantly different from zero for infection, meaning that polycultures yielded more biomass and had lower herbivory than expected (Figure 3). Complementarity effects were positive or neutral for all functions. Positive complementarity for biomass and infection means that, on average, species produced higher than expected biomass and had higher than expected infection in polycultures (Figure 3).

For biomass, 12 out of 18 species contributed to the positive complementarity effect, for infection nine species and for herbivory seven (Figure 4). There were six species, all of them forbs, that increased complementarity effects for all functions: *Achillea millefolium*, *Centaurea jacea*, *Salvia pratense*, *Crepis biennis*, *Plantago media*, and *Prunella grandiflora*. With the exception of *P. grandiflora* and *P. media*, all of these species had positive interspecific shifts, which indicates they had higher than expected abundances in mixtures. *P. grandiflora* had lower than expected abundance, but higher than expected biomass, infection, and herbivory (per area), which led to an overall higher than expected contribution to functioning (Figure 4). Five species, all of them grasses, reduced complementarity effects for all functions: *Helictotrichon pubescens*, *Holcus lanatus*, *Antioxanthum odoratum*, *Bromus erectus*, and *Dactylis glomerata*. They all had negative interspecific shifts

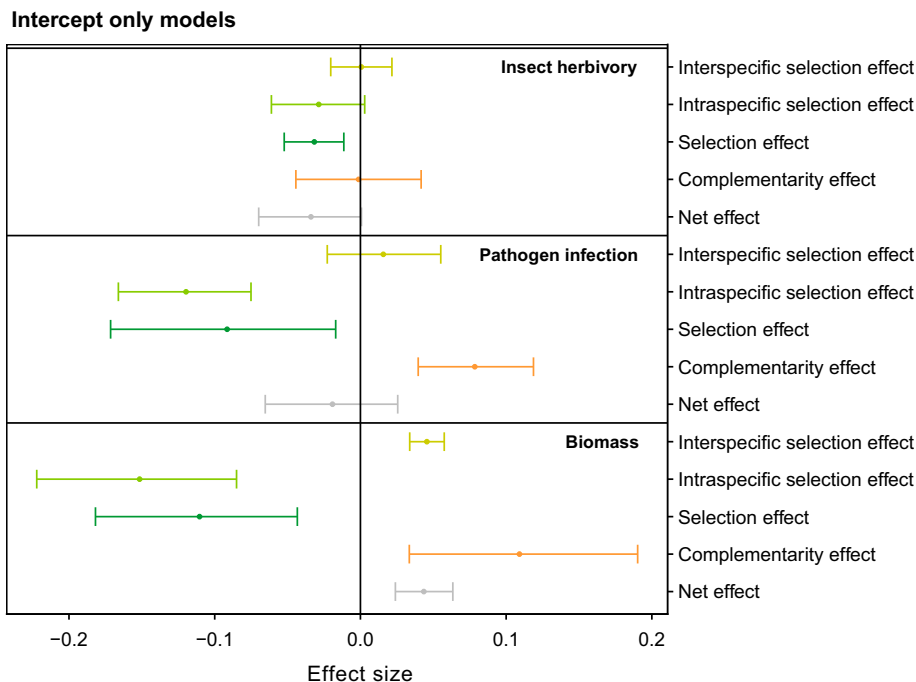


FIGURE 3 Intercept only models of all additive partitioning measures for all the functions. The data for the herbivory, pathogen, and biomass models were log-transformed for the analysis. The estimates and the upper and lower boundaries of the confidence intervals were back-transformed to show values on the original standardized scale, which is why the CI bars are asymmetric. Details about how different species contribute to the inter- and intraspecific selection effects of the different functions can be found in Figures 4 and 5

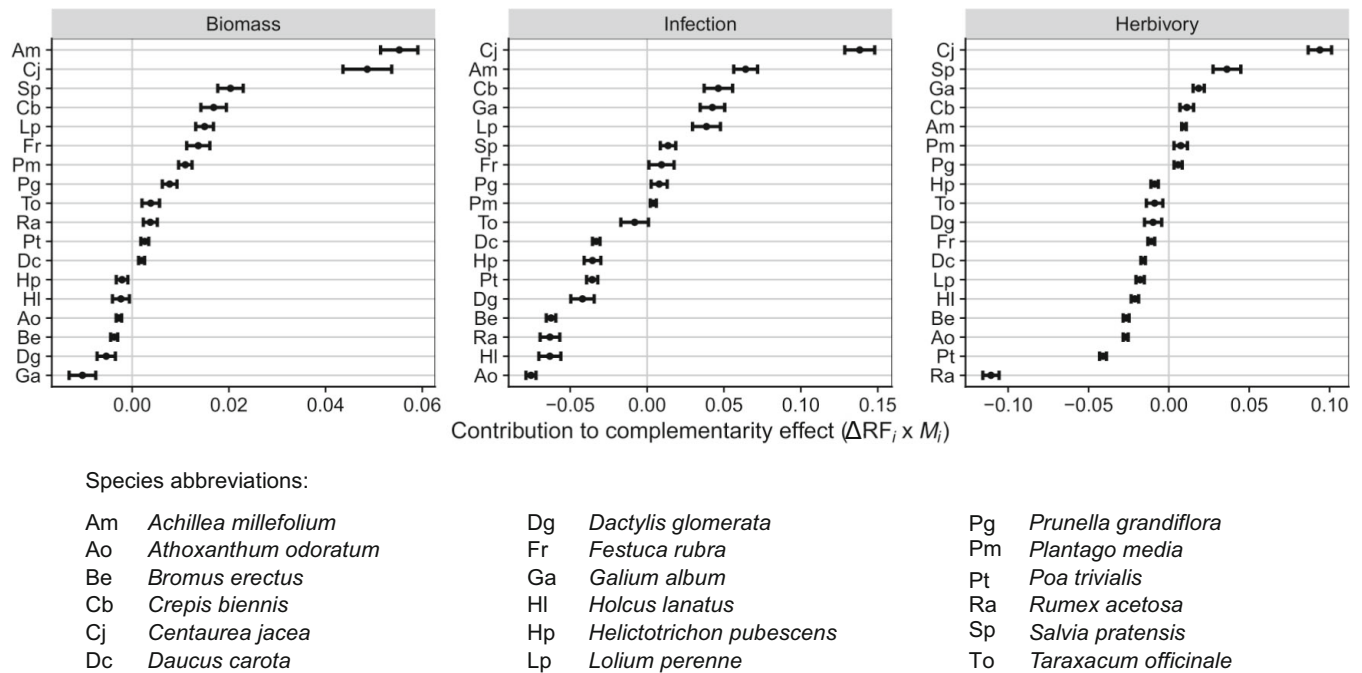


FIGURE 4 Average contributions of each species to complementarity effects for biomass, infection, and herbivory, calculated by multiplying the monoculture functioning of the species (M_i) with its delta relative functioning (RF_i) in polyculture

(lower than expected abundances), and even when they increased functioning per area in mixture (positive intraspecific shifts), this was not enough to compensate for the interspecific shifts (Figure 4). Four species increased complementarity effects for biomass but reduced complementarity effects for infection and herbivory: *Taraxacum officinale*, *Daucus carota*, *Poa trivialis*, and *Rumex acetosa* (Figure 4). Except for *T. officinale*, they all had lower than expected abundances in mixtures (negative interspecific shifts, Figure 6). For biomass, increases in productivity (positive intraspecific shifts, Figure 5) compensated for the reduced abundances and led to overall positive contributions to the complementarity effect. For infection and herbivory, intraspecific shifts in these species were weak overall and often negative (Figure 5). Thus, intraspecific shifts were not big enough to compensate for negative interspecific shifts or even further reduced the species contribution to the complementarity effect for infection and herbivory. *Galium album*, *Lolium perenne*, and *Festuca rubra* had mixed contributions (Figure 4). In general, complementarity effects were most positive when a majority of the species in the polyculture had higher than expected relative functioning and most negative when a majority of the species had lower than expected relative functioning. However, for infection positive complementarity effects were sometimes driven by a minority of species with large increases in infection (Appendix S1: Figure S7).

Selection effects were negative across all functions (Figure 3), meaning that species with low monoculture function contributed more to polyculture functioning than expected. We decomposed the selection effect into contributions of inter- and intraspecific shifts. Negative intraspecific shifts outweighed neutral or positive interspecific shifts and led to negative total selection effects for all functions (Figure 3). For biomass, negative intraspecific selection effects were driven by disproportionate increases in biomass for species with low monoculture biomass, like *Daucus carota* and *Poa trivialis*, and by lower (or no) increases in species with high monoculture biomass like *Achillea millefolium*, *Centaurea jacea*, or *Galium album* (Figure 5). For infection, negative intraspecific shifts were primarily driven by disproportionate increases in infection for species with low monoculture infection, especially *Festuca rubra*, *Plantago media*, and *Salvia pratensis* (Figure 5). Negative intraspecific shifts for herbivory were driven by increases in herbivory for species with low monoculture herbivory (*Achillea millefolium* and *Galium album*) as well as decreases in herbivory for species with high monoculture herbivory (*Salvia pratensis* and *Centaurea jacea*; Figure 5). There were positive interspecific selection effects on biomass (Figure 3) as the species dominating the polycultures were those with high monoculture biomass (especially *Centaurea jacea* and *Achillea millefolium*) and species with low monoculture biomass such as *Daucus carota* and *Anthoxanthum odoratum* were excluded (Figure 6).

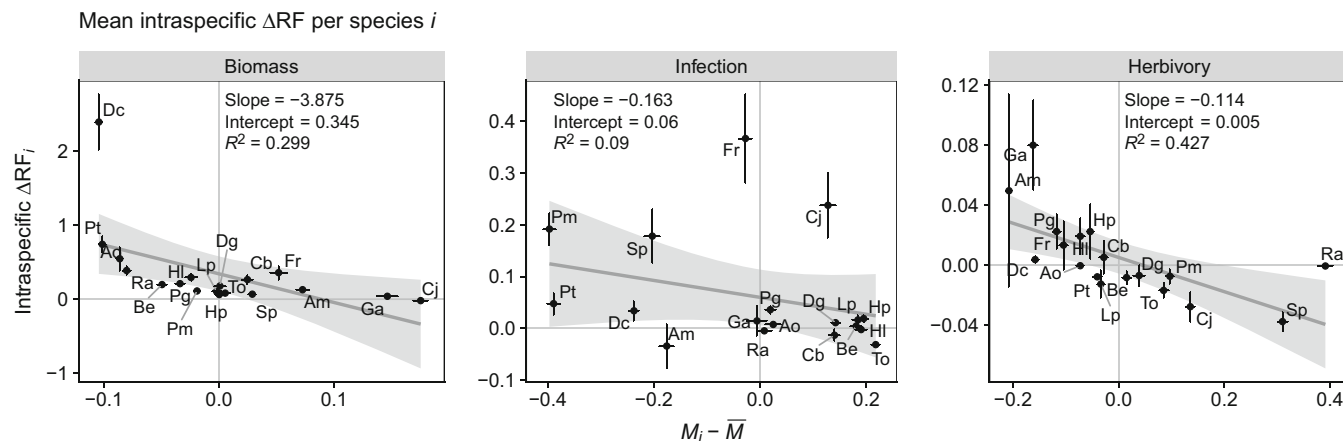


FIGURE 5 Overall intraspecific effects per function. The relationship between monoclature function per species relative to the mean of its neighbors in the polycultures across the sampling periods and treatments ($M_i - \bar{M}$) and intraspecific shift in polyculture (mean intraspecific ΔRF_i). Slopes, intercepts, and R^2 for the relationship across all species are given in the plots. For species abbreviations, see legend in Figure 4

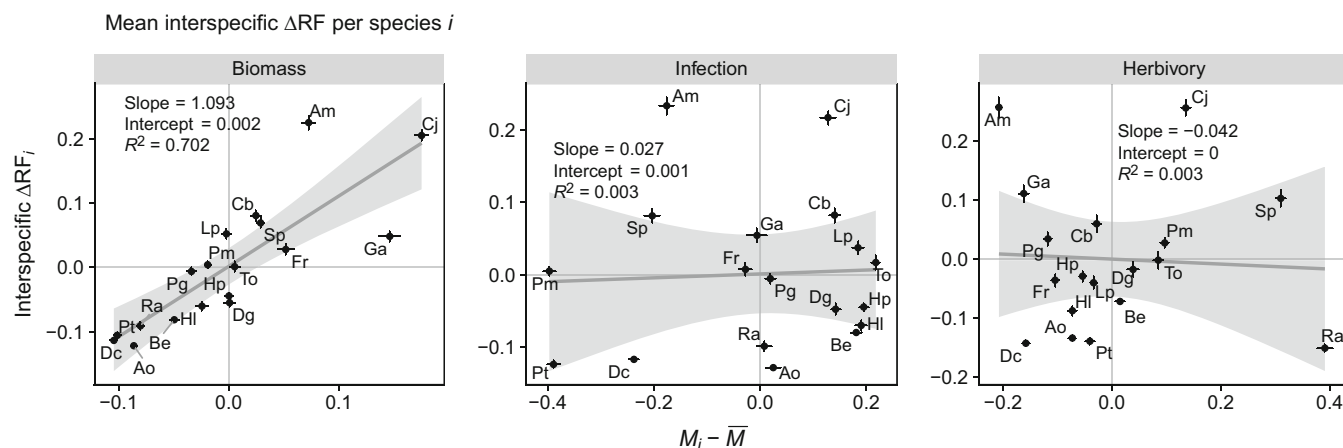


FIGURE 6 Overall interspecific effects per species function. The relationship between monoclature function per species relative to the mean of its neighbors in the polycultures across the sampling periods and treatments ($M_i - \bar{M}$) and abundance shift in polyculture (mean interspecific ΔRF_i). Species with high monoclature biomass dominated the polycultures. Monoclature pathogen infection and herbivory did not greatly impact abundance. Slopes, intercepts, and R^2 for the relationship across all species are given in the plots. For species abbreviations see legend in Figure 4

Monoclature infection or herbivory did not predict dominance in polycultures, leading to neutral interspecific selection effects (Figure 6).

Correlations

To better understand simultaneous changes in biodiversity effects (H7–H8), we calculated correlations between all effects, within and across functions. Within functions, all complementarity and selection effects were highly significantly negatively correlated (blue squares in Figure 7a,d,f), mainly due to a strong trade-off between

complementarity and intraspecific selection effects. This negative correlation occurred because species with low biomass, infection, and herbivory in monoclature substantially increased their per-area functioning in mixtures.

Complementarity and intraspecific selection effects for biomass and infection were slightly positively correlated (Figure 7b). In other words, species with low monoclature infection and biomass increased their infection and biomass per unit area in mixtures. Net effects and interspecific selection effects for biomass were positively correlated with the corresponding effects for herbivory (Figure 7c), due to dominance of species with both high

	Biomass				Pathogens					Herbivores					
Biomass	(a) Expected				(b) Expected					(c) Expected					
	NE	0.40 ***	-0.22 ***	0.28 ***	-0.25 ***	0.04	0.09	-0.08	-0.03	-0.08	0.23 ***	0.07	0.08	0.24 ***	-0.07
		CE	-0.98 ***	0.18 **	-0.98 ***	0.01	0.16 **	-0.16 *	-0.06	-0.16 **	0.12 *	0.01	0.07	0.17 **	-0.03
			SE	-0.14 *	0.99 ***	0.00	-0.15 *	0.15 *	0.06	0.16 *	-0.08	0.01	-0.06	-0.13 *	0.02
				SE intra	-0.24 ***	0.05	0.06	-0.05	-0.02	-0.05	0.09	-0.07	0.12 *	0.11 *	0.07
					SE inter	-0.01	-0.16 *	0.16 *	0.06	0.16 *	-0.09	0.01	-0.07	-0.14 *	0.01
Pathogens	(d) Expected				(e) Expected										
	NE	0.20 **	0.13 *	0.62 ***	-0.06	0.06	0.07	-0.02	0.02	-0.04					
		CE	-0.95 ***	-0.34 ***	-0.97 ***	0.17 **	0.02	0.08	0.22 ***	-0.05					
			SE	0.54 ***	0.96 ***	-0.15 *	0.00	-0.09	-0.21 ***	0.03					
				SE intra	0.30 ***	0.02	0.05	-0.03	-0.04	-0.02					
				SE inter	-0.18 **	-0.02	-0.09	-0.23 ***	0.04						
Herbivores	(f) Expected														
	NE	0.13 *	0.48 ***	0.84 ***	0.02										
		CE	-0.80 ***	-0.14 *	-0.93 ***										
			SE	0.63 ***	0.83 ***										
				SE intra	0.10										
				SE inter											

	Significant correlation as expected
	Insignificant correlation as expected
	Significant correlation other than expected
	Insignificant correlation other than expected
	Correlation between CE and SE
	Correlation between CE and intra- and interspecific SE
	Correlation between intraspecific SE and

FIGURE 7 Correlations between all measures of net effect (NE), complementarity effect (CE), and total, intra-, and interspecific selection effect (SE) of biomass, pathogen infection, and herbivory damage. More details can be found in Appendix S1: Figure S10. The expectations are described in Appendix S1: Table S4

monoculture herbivory and high monoculture biomass in mixtures. Complementarity and selection effects for infection and herbivory were not significantly correlated (Figure 7e).

Context dependency

To explore potential underlying mechanisms of diversity effects we analyzed context dependency in the diversity effects on biomass and enemy damage (H9–H19). Diversity effects for biomass were stronger with higher species richness (H9). Positive complementarity effects became more positive, and negative intraspecific selection effects became more negative, in species rich communities, while interspecific selection effects were not affected (Figure 8; Appendix S1: Figure S8c): Therefore the more

diverse a community became the more species increased their productivity on average and the more species with low monoculture biomass increased their per area biomass production. Species with high monoculture biomass had higher than expected abundance in polycultures, but this was constant across different species richness levels. In contrast, diversity effects for herbivory and infection did not change with species richness.

The functional composition (H11–H15) of the plant community (sown SLA) had the biggest impact on diversity effects on infection (Figure 8; Appendix S1: Figure S8d). The net effect was negative in slow-growing communities but increased to slightly positive in fast-growing communities, which means that diverse slow-growing communities had lower, and fast-growing communities higher, infection than expected. Increases in the net effect were driven by increases in intra- and

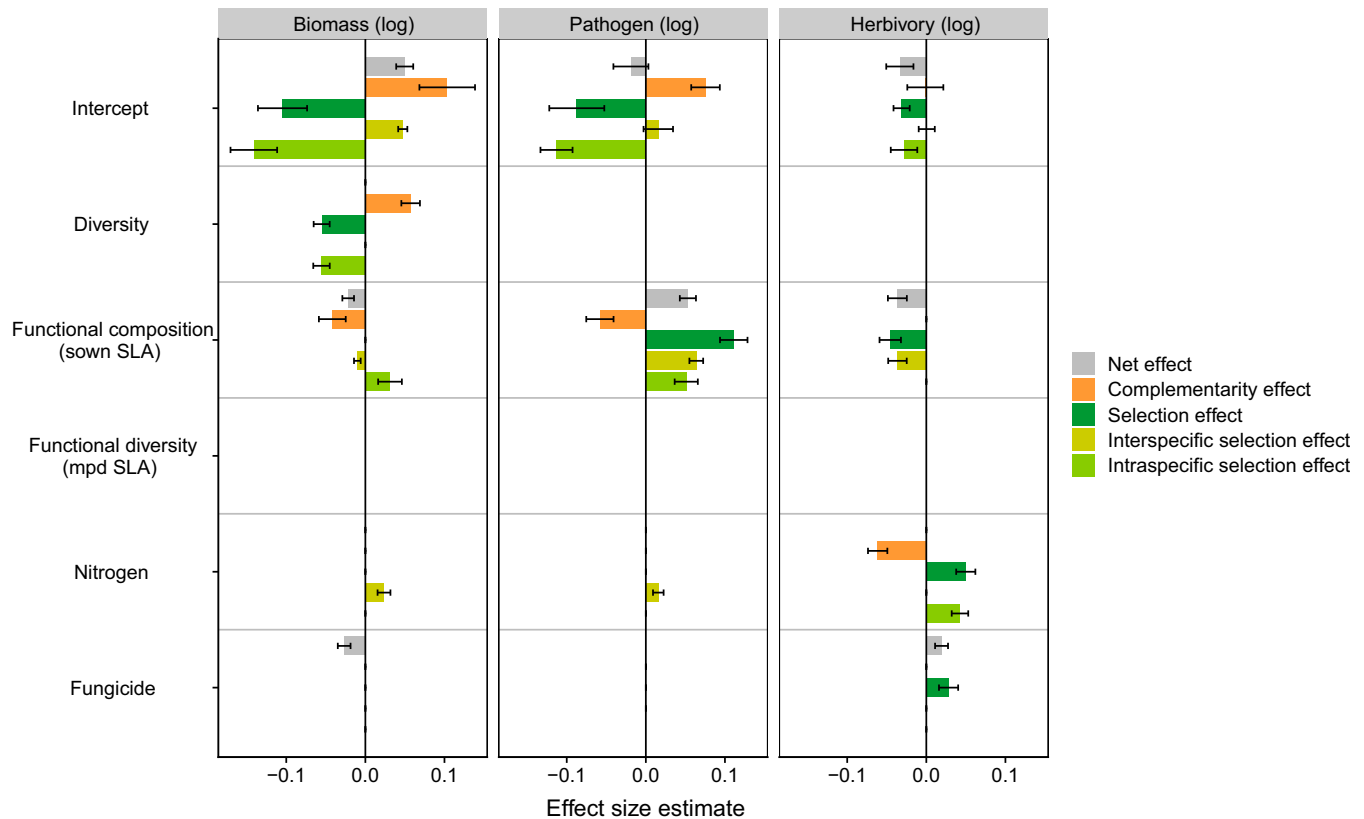


FIGURE 8 Effect sizes (and SE) of the linear mixed effects models for net effect (gray), complementarity effect (orange), selection effect (dark green), intraspecific selection effect (yellow-green), and *i* (light green) of all functions: biomass, pathogens and herbivory. All explanatory variables were standardized and centered, which means that the displayed effect sizes reflect the effect size of variable(s) of interest at the mean of all other variables. Selected plots of model predictions can be found in Appendix S1: Figure S8 and the detailed model results can be found in Appendix S1: Tables S5–S7

interspecific selection effects (Figure 8): in slow-growing communities, species with low monoculture infection increased in abundance (negative interspecific selection effect), while fast-growing communities were dominated by species with high monoculture infection. However, the complementarity effects followed the opposite pattern: on average, plants had higher infection than expected (positive complementarity effect), particularly in slow-growing communities. The lower complementarity effects in fast-growing communities arose because many fast-growing species had very high monoculture infection (close to 100%) and cannot increase their infection further in polycultures.

The growth strategy of the plants also determined the effect of diversity on herbivory. The net effect on herbivory shifted from zero in slow-growing, to negative in fast-growing communities, which was driven by the interspecific selection effect (Figure 8, Appendix S1: Figure S8d). In other words, in fast-growing communities, species with low monoculture herbivory increased in abundance at the cost of species with high monoculture herbivory, leading to overall lower than expected herbivory in

fast-growing communities. The net effect of diversity on biomass was slightly lower in fast-growing than in slow-growing communities (Figure 8), due to complementarity effects, and partly to inter- and intraspecific selection effects (Figure 8), indicating that many species with low monoculture biomass benefitted from growing in polycultures and produced more biomass mainly in slow-growing communities. Despite these large effects of average growth strategy, functional diversity (differences in SLA, H10) never altered diversity effects.

Nitrogen enrichment (H16–H17) increased the interspecific selection effect for biomass and infection (Figure 8, Appendix S1: Figure S8a). Nitrogen enrichment therefore favored plant species with high monoculture biomass and infection and allowed them to increase in abundance at the cost of species with lower monoculture biomass and infection. However, nitrogen enrichment did not alter the net effect. Weak changes in complementarity and intraspecific selection effects may have balanced changes in the interspecific selection effect. Nitrogen enrichment further decreased positive complementarity and increased negative intraspecific

selection effects for herbivory (Figure 8). Thus, under nitrogen poor conditions, many species with low monoculture herbivory suffer from increased herbivory in polycultures, while under nitrogen enrichment mostly species with high monoculture herbivory benefit from reduced herbivory in polycultures.

Fungicide (H18–H19) decreased the positive net effect for biomass and removed the negative net effect of herbivory (Figure 8; Appendix S1: Figure S8b). These changes could not be attributed to complementarity or selection effects, probably because they were too weak. Fungicide did not change net, complementarity or selection effects of infection (Figure 8).

DISCUSSION

We always observed neutral or positive complementarity (supporting H1 and H4b) and negative selection effects for all functions, which shows that diversity has broadly similar effects on primary and secondary productivity (energy transfer from plants to higher trophic levels) (Figure 3). However, contrary to our expectations (H7 and H8) the lack of strong correlations between most diversity effects (Figure 7), and the fact that different species drove the diversity effects for different functions (Figures 4 and 5), suggest diverse underlying mechanisms. This idea is further supported by the different effects of the context drivers on the various diversity effects. Differences in the balance of effects also led to different net effects of diversity: as in many studies, we found positive net effects for biomass largely due to positive complementarity (e.g., Mahaut et al., 2019; Spehn et al., 2005; van Ruijven & Berendse, 2003; Yin et al., 2018). We also found negative effects of diversity on herbivory, in line with the idea that diverse communities are better protected against herbivores (Barnes et al., 2020), which implies reduced energy transfer to higher trophic levels and reduced secondary productivity in diverse plant communities. However, we found that this was driven by only a few plant species: those with highest herbivory in monoculture had reduced herbivory in mixture, but species on average did not differ in herbivory between monocultures and mixtures (negative intraspecific selection and neutral complementarity). Plant diversity did not seem to protect as well against pathogens because of counteracting effects: negative selection and positive complementarity. Expanding our analysis of diversity effects beyond plant biomass, therefore shows some consistent patterns: generally negative selection effects due to intraspecific shifts (supporting H3 and H5) and positive or neutral complementarity (supporting H1 and H4b). However, there was variation

in overall effects and large variation in the effects of different context drivers on the different diversity effects.

Interspecific selection effects: Species that are productive in monoculture dominate mixtures

Interspecific selection effects varied between functions (Figure 3). This variation arises because the species that increased in abundance in polycultures varied in their contributions to different functions. The shifts in abundances were most strongly related to monoculture biomass: species with high (monoculture) biomass increased in abundance at the cost of species with low biomass (Figure 6), as expected (H2). Monoculture infection and herbivory were generally not related to abundance shifts (Figure 6), which is in contrast to our expectations (H6a and H6b), but this varied depending on the experimental treatment (see below *Variable context dependencies*). Contrary to our expectations (H7), the interspecific selection effects of herbivory and biomass were positively correlated, indicating that at least some of the species that increased in abundance had both high monoculture biomass and high monoculture herbivory and thus increased both primary and secondary productivity. This might indicate that the most competitive species have a tolerance strategy and can produce high biomass despite losses to herbivores (Gianoli & Salgado-Luarte, 2017). The variation in interspecific selection effects between functions indicates that the dominant plant species in polycultures did not supply all functions at a high level.

Negative intraspecific selection effects

In contrast to the inconsistent interspecific selection effects, the intraspecific selection effect was on average negative (significant for biomass and infection, nonsignificant for herbivory (Figure 5), mostly because species with low monoculture functioning increased their functioning in mixtures. This result is consistent with our expectations (H3 and H5) and findings of other studies, showing that negative intraspecific selection effects are common (plant traits: Roscher et al., 2018, decomposition: Pires et al., 2018, biomass: e.g., Liu et al., 2018; Wagg et al., 2017, but see Pontes et al., 2012). Negative density dependence, caused by strong intraspecific competition or specialist enemies (de Kroon et al., 2012), or even facilitation of low functioning species (Soliveres et al., 2015), could have resulted in increased biomass for low yielding species in polyculture. For secondary productivity (herbivory and infection), negative intraspecific

selection effects were mostly caused by species with high consumer damage in monoculture benefiting from host dilution (e.g., Keesing et al., 2006; Mitchell et al., 2002, H5). For herbivory, species with low monoculture consumer damage also suffered from spillover (Power & Mitchell, 2004; H5). Thus, plant species varied in how they contributed to energy transfer to higher trophic levels in diverse communities: the species that contributed a lot in monoculture contributed less in mixtures, and species that contributed little to energy transfer to higher trophic levels in monocultures contributed more in mixtures. Intra- and interspecific selection effects varied greatly for all functions and even had opposite signs in the case of biomass because the species that were productive in monoculture and that dominated the mixtures did not increase biomass per area, whereas the least productive species did. This indicates that low biomass production in monoculture is mostly driven by low density. The contrasting selection effects further highlight the importance of partitioning total selection effects (see also Fox, 2005).

Complementarity effects: Multiple, but different species drive different functions

We found mostly positive complementarity effects (positive for biomass and infection, neutral for herbivory; Figure 2), as predicted by H1 and H4b (but not H4a). Multiple species increased their functioning in polycultures (Figure 5) and contributed more to polyculture functioning than expected (Figure 4), and the functioning of mixed plant communities was typically driven by several species (Appendix S1: Figure S7). However, complementarity effects were sometimes driven by a few species with extraordinarily large increases in functioning (especially for infection; Appendix S1: Figure S7, see also Mahaut et al., 2019), highlighting the importance of examining individual species contributions to function, especially when they vary dramatically (Roscher et al., 2007). Several species either increased or decreased complementarity effects for all functions. The species that increased complementarity across functions were generally those that increased their abundance in mixtures (mostly slow-growing herbs, such as *Achillea millefolium*) and those that reduced complementarity for all functions (all grasses) were those that decreased in mixtures. This shows that changes in abundance contribute strongly to complementarity effects on both primary and secondary productivity. However, even if species consistently increased or decreased complementarity, they generally varied substantially in the magnitude of their contribution to complementarity effects for the different

functions, because their intraspecific shifts varied. Changes in functioning per area were therefore important in causing species to have different contributions to complementarity effects for different functions. Some of the species that increased complementarity across functions were slow growing (low SLA) plants. For biomass, this is predicted by H12. However, it might seem surprising that slow-growing (low SLA) species would increase infection and herbivory and thus energy transfer to higher trophic levels in polyculture as slow growth is usually linked to high defense against natural enemies (Blumenthal et al., 2009; Coley et al., 1985; Liu et al., 2017). Most of these species do have low pathogen infection in monoculture, however, it seems they suffer from pathogen spillovers when growing next to poorly defended plants with higher pathogen loads (Halliday et al., 2017; Power & Mitchell, 2004), resulting in increased pathogen infection per area in mixture, as predicted by H5. This indicates associational susceptibility, and a reduction in the effectiveness of anti-pathogen defenses for plants growing with infected neighbors as underlying mechanisms shaping diversity effects on energy transfer to fungal pathogens. For herbivory, certain species (especially *Galium album* and *Achillea millefolium*) suffered more damage in mixtures but others suffered less per area (mostly *Centaurea jacea* and *Salvia pratensis*, although they increased complementarity for herbivory overall because of their large increase in abundance). This suggests a mix of associational susceptibility and resistance against herbivores in diverse communities and/or a shift from specialist to generalist herbivores with increasing diversity, and possibly varying impact of specialists and generalists on different plant species as reasons that herbivory shows varying responses to diversity between plant species. Such opposing mechanisms led to overall neutral complementarity effects for energy transfer to insect herbivores. Certain species (e.g., *L. perenne* and *F. rubra*) also suffered from associational susceptibility to pathogens but resistance against herbivores in diverse communities and several plant species also increased complementarity for primary productivity but reduced it for secondary productivity: for example *T. officinale* (a fast-growing herb) increased biomass per area and had reduced infection and herbivory and may have benefitted from dilution effects in mixture. Taken together, these results indicate that changes in diversity are likely to have complex effects on the response of different species to changes in natural enemy groups and ultimately on energy transfer to higher trophic levels.

Given that species varied substantially in their contribution to complementarity effects for biomass, infection and herbivory it is not surprising that the complementarity effects did not correlate strongly with each other (Figure 7f), and therefore that our initial hypothesis was not supported (H7, H8). Further, the one weak positive

correlation that occurred, between complementarity effects for biomass and infection, was unexpected based on H7, as it means that when diversity led to more infection, it also led to more biomass. This means that decreased enemy pressure with increasing diversity is an unlikely mechanism driving positive complementarity effects for biomass, and that at least certain plant species are good at promoting both primary productivity and energy transfer to fungal pathogens.

Interestingly, complementarity effects were neutral for herbivory but positive for infection (Figure 3; supporting H4b, but not H4a) and did not correlate with each other (Figure 7e), even though herbivores and fungal pathogens are both primary consumers and might be expected to respond similarly to plant richness (e.g., Blumenthal, 2006; Heckman et al., 2016; H8). Stronger complementarity for infection than herbivory might indicate a greater shift in the composition of the pathogen community with plant diversity or a greater importance of spillovers because pathogens are less mobile than herbivores and more likely to spread only between neighboring hosts (Raffa et al., 2019). This result indicates that energy transfer to insect herbivores occurs largely independently of energy transfer to fungal pathogens. It is therefore likely that different types of complementary interactions between species are important for different functions. Overall, the lack of strong correlations and the different sets of species contributing to complementarity effects highlight the high importance of species richness for maintaining multiple ecosystem functions simultaneously (Hector & Bagchi, 2007; Isbell et al., 2011).

Variable context dependencies

We found strong, but variable, context dependency in the diversity effects for different functions (Figure 8; Appendix S1: Figure S8). The diversity effects for infection responded strongly to community functional composition, while diversity effects for herbivory were mainly altered by nitrogen, and diversity effects for biomass mainly changed with further increases in plant diversity. Different environmental contexts are therefore likely to alter the effects of diversity on different functions in various ways and it will be important to better understand the underlying mechanisms driving the diversity effects on different functions in order to predict how they will change with alterations in the abiotic and biotic environment.

Diversity effects (complementarity and intraspecific selection effects) only strengthened with increasing plant species richness for biomass (Figure 8; Appendix S1: Figure S8c, only diversity effects for biomass support H9).

Increasing positive complementarity and decreasing negative selection effects with increasing species richness are often found for biomass, showing that underlying mechanisms, such as enhanced nutrient use efficiency or reduced consumer attack, are more effective at higher species richness (Craven et al., 2016). For the other functions, this was not the case. Diversity effects on plant enemies are often related to the abundance of host plants (Keesing et al., 2006) and the biggest decline in host abundance occurred between one and four species (Appendix S1: Figure S9). This likely explains why diversity effects for herbivory and infection did not change when plant species richness increased from four to 20 species. Increasing species richness to a high level, will therefore not further change energy transfer to higher trophic levels. Comparable results have been found for different functional traits (Roscher et al., 2018) and water use efficiency (Grossiord et al., 2013). Thus, diversity effects on several functions saturate at low species richness, probably especially when they occur due to density-dependent mechanisms. However, underlying mechanisms promoting biomass complementarity operate more effectively at higher species richness.

Community functional composition altered the strength of diversity effects for several functions (Figure 8; Appendix S1: Figure S8d), in contrast to our expectations (H11) it did not predominantly change selection effects. Diversity effects on herbivory were enhanced in fast-growing communities (partly confirming H14, but not H15), while diversity effects on biomass and infection were maximal in slow-growing communities (confirming H12 and H15, but not H13 and H14). For biomass production stronger complementarity in slow-growing communities might reflect more strongly differentiated resource competition among species from low-resource environments, allowing more opportunities for coexistence between them (Tilman, 1982). For infection, stronger complementarity among slow species probably arises because fast-growing species always had high infection regardless of the community context (Cappelli et al., 2020), while slow species suffered spillovers when growing in diverse communities. Spillover of pathogens to less infected plants therefore seems to be an important mechanism driving increased energy transfer to higher trophic levels in diverse, but slow-growing communities. The interspecific selection effect was also affected by functional composition and changed in opposing directions for infection and herbivory. Species with low infection and high herbivory increased in abundance in slow-growing communities, while species with high infection and low herbivory increased in fast-growing communities. This could mean that fast-growing plants are susceptible to herbivores but tolerant of infection,

while slow-growing plants are less competitive in the presence of pathogens but tolerant of herbivory. This would suggest that different trade-offs between defense, growth, and tolerance exist for herbivores and pathogens, and that growth-defense trade-offs might be more complex than previously described (Lind et al., 2013). Wagg et al. (2017) found that functional diversity, like species richness, should enhance diversity effects, which we cannot confirm here (see also H10). Community functional composition has rarely been considered as a modifier of diversity-functioning relationships, but our results suggest that it alters diversity effects for several functions.

Resource levels and fungal pathogen abundance altered diversity effects for some functions (Figure 8; Appendix S1: Figure S8a,b). Nitrogen enrichment increased the interspecific selection effect for biomass and infection, showing that productive species with high infection benefit from nitrogen enrichment, as expected based on H17 (Heckman et al., 2016; Liu et al., 2017; Pontes et al., 2012; Siebenkaes et al., 2016). Both effects are, at least partially, driven by the same species, as the intraspecific selection effects of biomass and infection were correlated. The fact that nitrogen enrichment allowed species with high infection to increase in abundance at the cost of less infected species, could mean that nutrient enrichment can compensate for negative impacts of fungal infection on the competitive ability of highly infected species and thus promote energy transfer to higher trophic levels by favoring plant species that contribute a lot to this energy transfer. This is in accordance with other studies showing that nitrogen enrichment causes dominance of species susceptible to pathogens (Blumenthal et al., 2009; Heckman et al., 2019; Liu et al., 2017). Nitrogen enrichment also altered diversity effects for herbivory: complementarity decreased from positive to negative with nitrogen and intraspecific selection became less negative. It is possible that nitrogen enrichment enabled species to outgrow their herbivores, diluting herbivory damage. However, in contrast to our expectations (H16) nitrogen enrichment did not reduce complementarity effects for biomass.

Fungicide had relatively small effects but changed effects of diversity on biomass and herbivory. Reducing fungal pathogen abundance weakened the positive net effect of diversity on biomass, which might suggest that fungal pathogens play some role in driving positive effects of diversity on biomass as expected by H18 (but not H19). Together with the positive correlation between the complementarity effects for biomass and infection and potential bottom-up effects of biomass on infection, this indicates complex feedback loops between the biomass and fungal pathogens, which we cannot resolve here. A reduction in pathogens also

reduced the extent to which diversity protected against herbivory.

CONCLUSION

Negative selection effects and positive complementarity effects were the rule and led to weak net effects. However, the lack of strong correlations between diversity effects on different functions and the fact that different species drove these diversity effects suggest that changes in enemy pressure are an unlikely reason for increased productivity in diverse plant communities. It has recently been shown that, for biomass production, diversity effects link to coexistence processes, so that the most stably coexisting communities produced most biomass (Godoy et al., 2020). This link was not apparent for other functions, agreeing with the idea that different underlying mechanisms operate for different functions. This highlights the importance of high biodiversity for the provision of multiple functions. Further research needs to look in detail into the processes underlying diversity effects to mechanistically understand the consequences of global diversity loss.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Seraina L. Cappelli, Noémie A. Pichon, and Eric Allan designed and set up the PaNDiv experiment. Noémie A. Pichon, Tosca Mannall, and Seraina L. Cappelli collected the data. Seraina L. Cappelli analyzed the data and wrote the manuscript with substantial input from Eric Allan, Noémie A. Pichon, and Tosca Mannall.

DATA AVAILABILITY STATEMENT

Data (Cappelli et al., 2022) are available in the Dryad digital repository at <https://doi.org/10.5061/dryad.zs7h44jbp>.

ORCID

Seraina L. Cappelli  <https://orcid.org/0000-0002-8141-404X>

Noémie A. Pichon  <https://orcid.org/0000-0003-2972-1912>

Tosca Mannall  <https://orcid.org/0000-0003-0802-3971>

Eric Allan  <https://orcid.org/0000-0001-9641-9436>

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