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RESEARCH ARTICLE

Explaining variation in plant-herbivore associational effects in a tree biodiversity experiment

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Abstract

1. Within biodiversity-ecosystem function research, a major outstanding question is how herbivory, a critical ecosystem function at the base of the food web, changes along gradients of plant biodiversity.

2. Neighbourhood-level associational effects are hypothesised to be a strong driver of biodiversity-herbivory relationships, but we lack a successful framework that explains the wide variation observed in the sign and magnitude of plant-herbivore associational effects.

3. In this study, we combine measurements from a tree biodiversity field experiment with simulation to provide a framework for explaining variation in plant-herbivore associational effects, particularly when herbivores that feed on many different species (e.g. generalists) cause most damage. We show that monoculture herbivory levels of focal species and their neighbours predict the direction and strength of associational effects. We provide evidence that this may be due to a "spillover effect", in which some insect herbivores attracted to focal individuals ultimately end up feeding on neighbouring individuals.

4. With an empirically parameterised simulation, we explain how spatial organisation modifies biodiversity-ecosystem function relationships when associational effects operate. We suggest a set of experiments to test the generality of our conceptual framework, to elucidate the underlying mechanisms that produce the patterns we find, and to ultimately increase the predictability of plant-herbivore associational effects. We conclude by discussing how our results might inform pest management in diversified agroecosystems and reforestation sites.

5. *Synthesis*. Our results provide a potential framework for explaining why positive and negative plant-herbivore associational effects are often balanced in systems with primarily generalist herbivores and point to a path forward for predicting

when increased plant biodiversity will be associated with increased, decreased or unchanged levels of insect herbivory on individual plant species in such systems.

KEYWORDS

associational effects, biodiversity-ecosystem function, herbivory, MyDiv experiment, neighbourhood model, plant-herbivore interactions

1 | INTRODUCTION

Understanding the relationship between biodiversity and ecosystem functioning has been one of the major aims of ecological research over the past three decades (Cardinale et al., 2006; Eisenhauer et al., 2016; Loreau et al., 2001; Tilman et al., 2001, 2014). Biodiversity-ecosystem functioning (BEF) research has uncovered a critical role for species richness in promoting different ecosystem functions (Loreau et al., 2001; Scherber et al., 2010; Tilman et al., 2001). Early research on this topic focused on the effects of biodiversity on primary productivity, community stability and other functions within a single trophic level (Tilman et al., 2001). Following early BEF studies, interest soon broadened to "ecosystem multifunctionality" (Giling et al., 2019; Hector & Bagchi, 2007; Lefcheck et al., 2015; Manning et al., 2018) and a multitrophic perspective (Eisenhauer et al., 2019; Estes et al., 2011; Scherber et al., 2010). A current goal of BEF research is to become more realistic and useful in applied contexts (Jochum et al., 2020; Srivastava & Vellend, 2005). In addition to characterising how biodiversity affects a diverse range of ecosystem functions across multiple trophic levels, such realism also requires accounting for factors like the effects of spatial scale and organisation (Gonzalez et al., 2020; Srivastava & Vellend, 2005). In an era of widespread, accelerating global biodiversity loss (Ceballos et al., 2015; Dirzo et al., 2014), it is increasingly urgent to understand real-world, multi-trophic consequences.

As the main link between primary productivity and the rest of food webs, herbivory has cascading effects on many other ecosystem functions. Herbivory can influence plant population dynamics and community composition (Agrawal & Maron, 2022; Huntly, 1991; Verkaar, 2008), including playing an important role in the maintenance of genetic and species diversity (Gloss et al., 2013; Mortensen et al., 2018; Pacala & Crawley, 1992). In applied settings, including forestry and agriculture, increased plant biodiversity has long been thought to confer resistance to pests for individual species (Isbell et al., 2017; Jactel & Brockerhoff, 2007; Letourneau et al., 2011; Tahvanainen & Root, 1972). Negative effects of plant biodiversity on insect herbivory on individual species are most common, however, in systems with predominantly specialist herbivores, while plant biodiversity has, averaging across species in many different systems, a net-zero effect on herbivory by generalist insects (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel et al., 2021). This net-zero average masks the fact that biodiversity often has nonzero (positive or negative) effects on herbivory for individual species (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel

et al., 2021). Both the net-zero effect of biodiversity on herbivory as well as the variation of biodiversity effects across species have been found not just in meta-analyses (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel et al., 2021) but also in studies of many species within the same community (e.g. Cappelli et al., 2022). The emerging picture of the relationship between plant biodiversity and herbivory by generalist insects is not that biodiversity has no effect on herbivory, but rather that positive and negative effects are approximately equally common (Cappelli et al., 2022; Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel et al., 2021). The next step is to explain why positive and negative effects of plant biodiversity on generalist insect herbivory are equally common, and to understand under what circumstances to expect positive or negative effects. Like in many areas of BEF research, the effects of plant biodiversity on herbivory appear to exhibit strong context-dependency, and an important challenge is gaining a clearer understanding of the nature of this context-dependency (Barbosa et al., 2009; Jactel et al., 2021; Mutz et al., 2022).

Associational effects, in which the herbivory characteristics (e.g. magnitude of damage, patchiness) of a focal plant individual depend on neighbouring plant individuals, are a broad class of mechanisms that can give rise to biodiversity-herbivory relationships (Barbosa et al., 2009; Underwood et al., 2014). Neighbouring individuals can cause both decreases in herbivory of focal individuals (associational resistance; Andow, 1991; Castagneyrol et al., 2013; Field et al., 2020; Guyot et al., 2019; Hjältén et al., 1993; Jactel & Brockerhoff, 2007; Jactel et al., 2021; Orians & Björkman, 2009; Pfister & Hay, 1988; Zakir et al., 2013) as well as increases (associational susceptibility; Grossman et al., 2019; Loranger et al., 2014; Schuldt et al., 2010; White & Whitham, 2000). Associational effects may arise when neighbouring heterospecific plants lead to changes in plant traits of focal individuals, density and behaviour of herbivores and their natural enemies, or changes in environmental conditions (Kim, 2017). Under perhaps the simplest proposed mechanism for associational effects, the "spillover effect", herbivores are attracted to individual plants but feed on neighbouring individuals as well (Barbosa et al., 2009; Stiling et al., 2004; Wada et al., 2000; White & Whitham, 2000). For example, when grown near box elders, which are highly susceptible to fall cankerworms, cottonwood trees suffer increased damage due to spillover of cankerworms (White & Whitham, 2000).

Despite its simplicity, the spillover mechanism has received a relatively small amount of attention and has been used mostly to explain associational susceptibility in cases with 2–3 species (i.e.

herbivores attracted to one species spill over to one-to-two other species; Stiling et al., 2004; White & Whitham, 2000). Like many other hypothesised mechanisms for associational effects, scaling the spillover effect from individual species to community patterns remains a challenge. Associational resistance is among the many potential benefits of diversified agroecosystems (Isbell et al., 2017; Letourneau et al., 2011) and tree plantations (Verheyen et al., 2016), but given the variability of associational effects, increasing plant biodiversity cannot be expected to universally increase pest resistance. Understanding how species-specific associational effects scale up to produce community-level biodiversity-herbivory patterns will likely offer insight into both how to explain variation in biodiversity-herbivory patterns and how to leverage associational resistance in applied systems.

In this study, we used two similar tree biodiversity experiments to study the relationship between tree biodiversity and insect herbivory. We quantified leaf herbivory of 10 tree species across a diversity gradient of monocultures, two-species mixtures and four-species mixtures. We measured leaf traits (toughness, pubescence and palatability) and plant traits (apparency) related to susceptibility to insect herbivores. While Ferlian et al. (2021) examined broad controls on herbivory in one of these experiments and found an important role of leaf nutrients (carbon and nitrogen), we focus on finer-scale, species-specific biodiversity-herbivory relationships to explore associational effects. We address two main questions. (1) What is the relationship between tree biodiversity and both community-wide and species-specific herbivory? In particular, we investigated the prevalence of spillover effects by examining the relationship between species' levels of herbivory in monoculture and the species-specific effects of biodiversity on herbivory. Under ubiquitous spillover effects (i.e. occurring between all species), species with lower-than-average herbivory in monoculture would experience increased herbivory in higher diversity communities, as herbivores attracted to more attractive heterospecific neighbours would spill over to the less attractive focal species. Conversely, species with higher-than-average herbivory in monoculture would receive decreased herbivory in mixtures, as herbivores attracted to the more attractive focal species would ultimately end up feeding on less attractive neighbours. One manifestation of common spillover effects would thus be a negative correlation between species' levels of herbivory in monoculture and the effect of biodiversity on herbivory. Across the 10 species and three sampling periods in this study, we consistently found this negative correlation.

While spillover effects may produce this negative correlation between monoculture herbivory levels and biodiversity effects, other mechanisms may produce the same pattern. Alternative mechanisms that would produce such a pattern are less clear. If well-defended species are poor interspecific competitors, for example, they may be less able to devote resources to defences in mixtures, and thus show low herbivory in monoculture and higher herbivory in mixtures. Other species that engage in strong intraspecific competition might have weaker defences in monoculture but stronger defences

in mixture. Alternatively, well-defended trees that receive low herbivory in monoculture may compete and grow well in mixtures, thus becoming more apparent and receiving more herbivory in mixtures, while the converse might be true for less well-defended, poorer competitors. Therefore, we also ask: (2) Do leaf and plant traits mediate the effects of biodiversity on herbivory? Using measurements of a suite of traits related to herbivory to fit structural equation models (SEMs), we find that in most cases, direct effects of diversity far outweigh indirect effects, further evidence of spillover effects.

Finally, we used our measurements of field herbivory to construct and parameterise a mathematical model of neighbourhood-level associational effects, which we analysed through simulation. By generalising our model to incorporate variable spatial arrangements, we investigated a third question: (3) How might spatial organisation modify the biodiversity-herbivory relationship, as well other spatially structured BEF relationships, more broadly? Our simulation reproduced our empirical results and shows how intraspecific aggregation can weaken BEF relationships.

## 2 | MATERIALS AND METHODS

2.1 | Study site

Our empirical measurements took place within the MyDiv and mini-iMyDiv experiments at the Bad Lauchstädt Experimental Research Station of the Helmholtz Centre for Environmental Research-UFZ in Central Germany (Figure 1). The study site's climate is continental, with mean annual temperature of 8.8°C and mean annual precipitation of 484 mm (Ferlian et al., 2018). The site is located at an elevation of 115 m a.s.l., and the soil is a Haplic Chernozem (Altermann et al., 2005; Ferlian et al., 2018). Before the experiments began in 2015, the site had been a grassland for 2 years, prior to which it had been used for agriculture.

2.2 | Experimental design

We measured herbivory in two similar, co-occurring experiments: the MyDiv and miniMyDiv experiments. Both experiments were established in 2015. The MyDiv experiment includes a species pool of 10 tree species planted in 80 plots (Figure 1), with crossed treatments of tree species biodiversity and mycorrhizal type. The tree species biodiversity treatment includes monocultures (*n* = 20 plots), two-species mixtures (*n* = 30) and four-species mixtures (*n* = 30). Mycorrhizal treatments were equally balanced across biodiversity treatments and were not included in analyses.

The species pool includes deciduous angiosperms native to and common in Germany. Five species (*Acer pseudoplatanus*, *Aesculus hippocastanum*, *Fraxinus excelsior*, *Prunus avium* and *Sorbus aucuparia*) associate mainly with arbuscular mycorrhizal fungi, and five species (*Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Quercus petraea* and *Tilia platyphyllos*) associate mainly

FIGURE 1 The MyDiv experiment. (a) An overhead view of the MyDiv experiment, and (b) a representation of the spatial organisation of plots in the MyDiv and miniMyDiv experiments. Each colour represents a tree species, and each square represents an individual. The photograph in (a) was taken by T. Kattenborn.
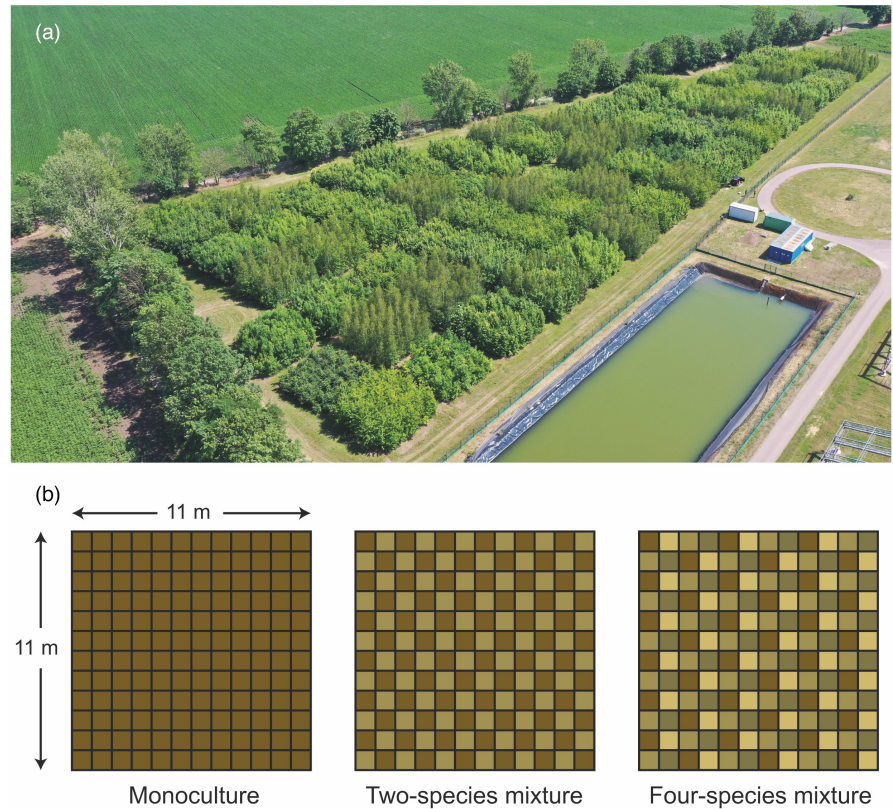
with endomycorrhizal fungi. The species represent a functionally and phylogenetically diverse selection of taxa (spread across 10 genera and six families). All tree individuals were planted in March 2015, at which time they were 2–3 years old. The insect herbivores that feed on the tree species in the experiment are likely to be predominantly generalists (Supporting Information, Figures S1 and S2; Rebollo Hernández, 2021).

The MyDiv experiment contains two equally sized blocks, with each block containing an equal number of each type of plot. Within each block, the spatial arrangement of plots was randomized. Each plot contains 144 trees arranged in a 12-by-12 grid of individuals, with individuals spaced 1 m apart (i.e. 11-by-11 m plots; Figure 1b). To avoid potential edge effects, we did not sample the two outermost trees in each row/column. Species are organised in a regular fashion, effectively maximising the number of heterospecific neighbours (Figure 1b). In two-species mixtures, an individual's four nearest neighbours are always heterospecific, and the four next-nearest neighbours are conspecific (Figure 1b). In four-species mixtures, all eight nearest and next-nearest neighbours are heterospecific (Figure 1b). While not all combinations of species are included in two- and four-species mixtures, combinations were chosen randomly, controlling for a balanced number of occurrences per species.

The miniMyDiv experiment used a similar design as MyDiv, was planted at the same time in the same location, and used the same species as the MyDiv experiment, but with trees spaced more closely together (15 cm apart), and in only monocultures ($n=20$) and two-species mixtures ($n=45$). The distance between plots was 1 m.

All possible two-species mixtures were included (but not replicated), resulting in 65 total plots.

2.3 | Field herbivory

Between the MyDiv and miniMyDiv experiments, we measured herbivory using multiple metrics across multiple years and seasons. In September 2016, in the miniMyDiv experiment, we measured the incidence of leaf herbivory due to any type of insect herbivore, using the following categories: leaf chewers (fully penetrating the leaf, including at the leaf margin), holefeeders (fully penetrating the leaf but not touching the margin), leaf miners (damaging the leaf tissue but not piercing the surface), gallers (creating swelling growths), leaf rollers (rolling and damaging the leaf surface) and skeletonizers (piercing only one side of the leaf surface). In May 25–29 and August 23–26, 2021, we measured incidence of leaf herbivory in the MyDiv experiment due to each of the above herbivore types. During the May sampling effort, we also measured the presence of sap-suckers (i.e. aphids), but these were uncommon (Figure S3) and omitted in the August 2021 sampling effort. To gain a more quantitative understanding of the variation in the magnitude of leaf herbivory, in the August 2021 sampling effort, we also measured a quantitative herbivory index, using six categories, as in Dirzo and Domínguez (1995): 1: 0% leaf area removed, 2: 1%–6%, 3: 6%–12%, 4: 12%–25%, 5: 25%–50%, 6: 50%–100%. Nearly all instances of herbivory were due to leaf chewers and holefeeders (Figure S3), making our herbivory index highly indicative of the total magnitude of

herbivory. The herbivory index categories are clustered more tightly at low herbivory levels to reflect the common occurrence (including in this study) of most leaves receiving a relatively small amount of herbivory.

During each sampling effort within the MyDiv experiment, within each plot, we chose three individuals from each species and three branches per individual, measuring herbivory on five haphazardly chosen, recently extended sun leaves per branch ($n = 15$ leaves per tree). Per species and sampling effort, we thus measured herbivory on 90 leaves per species in monoculture, 270 leaves in two-species plots and 540 leaves in four-species plots. Sampling was thus balanced across plots, but not across diversity levels. The unbalanced nature of this design takes into account the likely greater variation in herbivory within higher diversity plots due to the increasing variety of species mixtures present in plots with greater diversity. Additionally, unbalanced sampling across diversity levels poses no problem for the statistical methods described below. In total, we measured herbivory on 900 leaves per species per sampling effort ($N = 18,000$ leaves total across two sampling efforts) in the MyDiv experiment. Sampling in the miniMyDiv experiment followed the same protocols (described in Ferlian et al., 2021), but with two-to-four individuals (rather than strictly three) in each plot ($N = 3845$ leaves total). The number of individuals per plot sampled in miniMyDiv was inconsistent since individuals were young (approximately 4 years old) and not all individuals had enough biomass for sampling.

2.4 | Trait measurements

To test whether plant traits mediated effects of biodiversity on herbivory, we measured traits of individual leaves (across *Q. petraea*, *F. sylvatica*, *B. pendula* and *T. platyphyllos*) in the MyDiv experiment in late July and early August 2021, shortly before our final assessment of herbivory in the field. For leaf traits, we measured toughness using a leaf penetrometer, quantified pubescence by counting trichomes under a dissecting microscope, and estimated leaf palatability via controlled feeding trials with generalist *Spodoptera exigua* caterpillars.

We measured toughness on three leaves per tree and three trees per species per plot ($n = 180$ leaves per species), pubescence on one leaf per tree and three trees per species per plot ($n = 60$ leaves per species) and palatability on three leaves per tree and three trees per species per plot, but only in monocultures and four-species mixtures ($n = 126$ leaves per species) due to logistical constraints. For additional information on leaf trait measurements, see Appendix S3 in Supporting Information. We also measured tree height across all species. We included tree height as a metric of plant apparency. We constructed additional models with a metric of plant apparency from Castagneyrol et al. (2013) that takes into account the difference between focal plant height and the heights of the eight nearest neighbouring plants, weighted according to distance from the focal plant. However, raw plant height had greater explanatory power than the alternative metric (similar to Castagneyrol et al., 2013, in which plant height better predicted variation in herbivory due to leaf chewers), and our models thus used raw plant height.

2.5 | Statistical analysis

To quantify the effects of tree biodiversity on insect herbivory in the MyDiv and miniMyDiv experiments, we conducted two sets of empirical analyses. In the first analysis, we investigated both community-wide and species-specific effects of biodiversity on herbivory for all 10 species across all experiments, timepoints and sampling methods. In the second set of analyses, we incorporated leaf and plant traits measured in August 2021 to disentangle direct effects of tree biodiversity (e.g. spillover effects unmediated by traits) from indirect effects (i.e. effects mediated by traits).

2.5.1 | Experimental biodiversity-herbivory relationship

First, we investigated the effects of tree biodiversity on standing herbivory across all species in the two experiments. We sought to estimate monoculture herbivory levels and biodiversity effects in order to examine potential correlations between the two and to thus evaluate whether or not there was evidence of ubiquitous spillover effects occurring between species. To do so, we constructed four Bayesian generalised linear mixed models. In the first three models, we used incidence of leaf herbivory (due to any group of insect herbivores) in September 2016, May 2021 and August 2021, respectively, as the response variables. We modelled the incidence of leaf herbivory using a Bernoulli distribution, thereby modelling the probability of attack on a given leaf. In the fourth model, we used the quantitative herbivory index measured in August 2021 as the response variable. For this response variable, we conducted an ordered logistic regression. This type of regression effectively estimates the likelihood that the amount of herbivory on a leaf belongs to one of our herbivory categories (e.g. the likelihood that a leaf has 0% herbivory, the likelihood of 1%–6% herbivory, etc.). To summarise monoculture herbivory estimates from this model, we generated 90,000 predicted draws (conditioned on diversity being equal to one) per species, then used these draws to compute the mean herbivory index in monoculture for each species.

We modelled tree species biodiversity (1, 2 or 4 species) as a main effect and tree species identity as a random effect. Including species identity as a random effect allowed us to estimate both community-wide and species-specific effects of biodiversity on herbivory and to explicitly model the potential correlation between species-specific monoculture herbivory (i.e. model intercepts) and effects of biodiversity on herbivory (i.e. model slopes). For each model, we used weakly regularising priors. We ran 10,000 iterations across four chains, with the first 1000 iterations of each chain as warm-up to tune sampling. We checked for effective sampling of the posterior by inspecting trace plots, confirming that the

R-hat convergence diagnostics were less than 1.05, and verifying that effective sample sizes were at least 1000 (McElreath, 2018). To confirm that our model produced realistic predictions, we conducted posterior predictive checks, plotting model predictions against raw data. As a sensitivity analysis, we fit additional models in which intercepts could vary randomly across tree individuals. We fit all models in RStudio (using R 4.1.1) with the brms package, using the No U-Turn Sampler via Stan (Bürkner, 2017; Carpenter et al., 2017; Hoffman & Gelman, 2014; R Core Team, 2021; RStudio Team, 2020).

2.5.2 | Direct and indirect effects of biodiversity

To disentangle the direct effects of tree biodiversity from indirect effects, we constructed structural equation models. We first focused on species for which we had collected leaf trait data (*F. sylvatica*, *T. platyphyllos*, *Q. petraeus* and *B. pendula*). In addition to tree biodiversity, we included leaf and plant traits (toughness, pubescence, palatability and tree height) as covariates. Since traits were sampled in July and August 2021, we used herbivory measurements from August 2021 (from the MyDiv experiment) as the response variable. As trait and herbivory measurements were paired at the tree level, we used the proportion of herbivorized leaves per tree as the response variable. We used a beta distribution to model the response (Douma & Weedon, 2019). On some trees, we measured either no leaves or all leaves as being herbivorized. Since the standard beta distribution only accommodates proportions between 0 and 1 (but not 0 or 1), we applied a simple transformation to the data, described and discussed further in Supporting Information, Appendix S3 (and recommended by Douma & Weedon, 2019).

We constructed multiple sets of SEM's with varying levels of data. First, we constructed SEM's with all measured traits, but with data from only monocultures and four-species mixtures, as we only measured palatability in these plots. While these models allowed us to test whether biodiversity mediated through palatability strongly affected herbivory, they had decreased ability to accurately estimate other effects, including direct and indirect effects of biodiversity on herbivory. Therefore, we next constructed models that omitted palatability but included trait and herbivory data at all three diversity levels. Finally, as we collected leaf trait data for four species but plant height data for all 10 species, we constructed models for all species that tested whether plant height alone mediated biodiversity effects on herbivory. Unlike in many applications of SEM, in which the goal is to optimise the SEM, our goal of comparing direct and indirect effects required us to include paths independent of their statistical significance.

Across all SEM's, we averaged trait measurements for each tree individual and conducted analyses at the level of the tree individual. We used appropriate distributions (normal, log-normal, or hurdle log-normal) for response variables (besides proportion of herbivorized leaves, for which we used beta distributions, as described above). As for the model described in *Experimental*

biodiversity-herbivory relationship, we used the brms package to construct models, specifying weakly informative priors (Bürkner, 2017). For each response variable in our models, we computed Bayesian R^2. We calculated standardised path coefficients, multiplying each model slope by the ratio of the standard deviation in the predictor variable to the standard deviation in the response variable. To calculate indirect and total (direct + indirect) effects of diversity and to compute credible intervals with proper error propagation, we multiplied together posterior draws from sub-models. We graphically compared estimates of direct, indirect, and total effects of herbivory.

2.6 | Simulation

To better understand simple processes that may give rise to associational effects, we developed simulations for associational resistance and susceptibility due to spillover in multi-species neighbourhoods dominated by generalist herbivores. Our simulations assume that (1) species have different levels of average inherent attractiveness to herbivores, (2) species-specific inherent attractiveness follows a parameterisable distribution, (3) the degree to which herbivores feed on neighbours decays according to the distance from the focal individual, (4) herbivores attracted to focal individuals also feed on neighbouring individuals (i.e. high proportion of herbivory due to generalists) and (5) the overall level of herbivory in a mixture is equal to the summed attractiveness of all individuals. In communities in which plant species share similar defences (which may occur if phylogenetic distance between species is low or species have convergent defences), herbivores may not need to be broad generalists for (4) to hold.

Following from these assumptions, we implement simulations of a simple spillover process. In these simulations, we assume individuals are arranged on an evenly spaced lattice. Each individual has an innate attractiveness to herbivores, randomly drawn from a species-specific distribution. Following from the assumptions above, mean inherent attractiveness and mean average herbivory are equal in monocultures. Therefore, we used empirical means and variances for individual-level herbivory in monocultures to parametrise distributions for inherent attractiveness of simulated species. Specifically, we assigned each of our quantitative herbivory index measurements (from August 2021) to the midpoint of its corresponding range of percent leaf area removed. While this provides imperfect estimates of the true means and variances for species-specific percent leaf area removed, we believe this provides a sufficient approximation for the simulations of species-level variability in herbivory. We then computed means and variances of percent leaf area removed for each species. In the simulation, for each tree individual of species s, with mean μ_s and variance σ^2_s, we thus sample inherent attractiveness according to $X_{i,j}^{(s)} \sim \text{Lognormal}(\mu_s, \sigma^2_s)$, truncated so that values did not exceed 100 (which occurred less often than 1 in 100,000 samples).

In our simulations, spillover occurs between adjacent or diagonal neighbours (i.e. the nearest eight neighbours around a focal

individual), although in Appendix S1, we show results from simulations in which we included the 24 and 120 nearest neighbours. Spillover occurs as follows. A proportion p of the herbivores attracted to a focal individual actually end up feeding on that focal individual; $1-p$ of the herbivores thus do not contribute to herbivory on the focal individual. Similarly, a proportion of the herbivores attracted to each neighbour end up feeding on the focal individual. This proportion depends on p and is also a function of the distance from the neighbour. Total herbivory on each focal individual is thus the sum of its innate attractiveness plus spillover from neighbours minus spillover to neighbours.

We simulated sampling individual neighbourhoods from a very large community of individuals, rather than specifying the exact spatial organisation of an entire community. First, we simulated the regular arrangement of the MyDiv experiment, minimising intraspecific aggregation. For each species, we included 500 monoculture replicates, 504 two-species replicates and 504 four-species replicates, with the two-species and four-species replicates spread evenly across each combination of species. These sample sizes were relatively small to allow statistical analysis of simulated data described below, while still being large enough to accurately recover mean effect sizes. To quantify the importance of spatial arrangement, we simulated a scenario in which neighbours are sampled randomly from a uniform distribution (i.e. all 10 species have equal likelihoods of being a neighbour). We repeated this sampling process with $p=\{0.5, 0.8, 0.9\}$. Due to the relatively low levels of herbivory and spillover for most individuals, we never observed herbivory less than 0 or greater than 100. For additional mathematical formulation of the model, see Appendix S4 in the Supporting Information.

To understand the results of the simulations and to compare to our empirical results, for each combination of spatial arrangement and p ($N=6$ combinations), we repeated the statistical analysis described in *Experimental biodiversity-herbivory relationship*. We graphed the relationship between species-specific monoculture herbivory and biodiversity effects for each simulation. To be able to compare the simulations to our empirical data, we fit an additional empirical model, similar to those described in *Experimental biodiversity-herbivory relationship* but with the response transformed to percent leaf area removed. Though an imprecise model for correctly estimating quantities such as monoculture herbivory and biodiversity effects, we believe it is sufficient for comparison to simulation results. These comparisons are shown in the Supporting Information.

To some extent, a relationship between monoculture herbivory levels and biodiversity effects might be expected to emerge purely due to randomness. Even without species differences in innate attractiveness, species that, by chance, have lower or higher herbivory in monoculture would likely have closer to average herbivory in mixtures. Furthermore, since our empirical sampling included fewer samples in monocultures than mixtures, our monoculture herbivory estimates may have shown increased variance. Additionally, species with 0% or 100% herbivory in monoculture cannot decrease/increase in mixtures. To investigate the extent to which monoculture herbivory-biodiversity effect relationships can emerge from

randomness and limits to the scale of measurement, we simulated two null models. In the first, all individuals across all species and biodiversity levels received a random amount of herbivory, drawn from the empirical, community-wide distribution. In the second null model simulation, species received different levels of mean herbivory, but there was no spillover between individuals. In both simulations, we used sample sizes at each biodiversity level to match our empirical sampling.

3 | RESULTS

3.1 | Experimental biodiversity-herbivory relationship

Our general analysis of the biodiversity-herbivory relationship across all 10 species in the MyDiv and miniMyDiv experiments revealed a mix of positive and negative biodiversity effects, with a strong relationship between the level of herbivory in monocultures and the effect of biodiversity (Figure 2). These results were consistent through time, both within years (May and August 2021), and across years (in 2021 in the MyDiv experiment and in 2016 in the miniMyDiv experiment; Figure 2; Figure S4). The results were also consistent across herbivory measures (incidence and herbivory index; Figure 2; Figures S4 and S5). The net community-wide effect of biodiversity on herbivory across all species was statistically indistinguishable from zero in all models (Figure S5), but biodiversity effects were variable across species (Figure 2). The monoculture herbivory levels and biodiversity effects of individual species were somewhat consistent across years (Figure S6). Some species, however, (e.g. *S. aucuparia* and *A. hippocastanum*) showed seasonal and year-to-year swings in monoculture herbivory levels, with concordant swings in biodiversity effects (Figure S6). Across the full species pool and across all sampling efforts, we found a strong, consistent correlation between the level of herbivory in monocultures and the effect of biodiversity (Figure 2; Figure S4). Our sensitivity analysis with herbivory varying randomly across tree individuals showed the same patterns, with slightly shrunk estimates and marginally inflated variances (Figure S9).

3.2 | Direct and indirect effects of biodiversity

Structural equation modelling revealed that among species with non-zero biodiversity effects, direct effects of biodiversity on herbivory outweighed indirect effects (Figure 3; Figures S13–S18).

For the remaining species, there were no cases in which direct and indirect effects were strong but balanced (Figure 3). Among the four species for which we sampled leaf traits, biodiversity only had clear indirect effects on herbivory for *Q. petraea* and *F. sylvatica*. For both of these species, indirect effects were predominantly mediated through apparency (Figures S15 and S16). For this reason, and because leaf traits were only weakly related to herbivory, we show
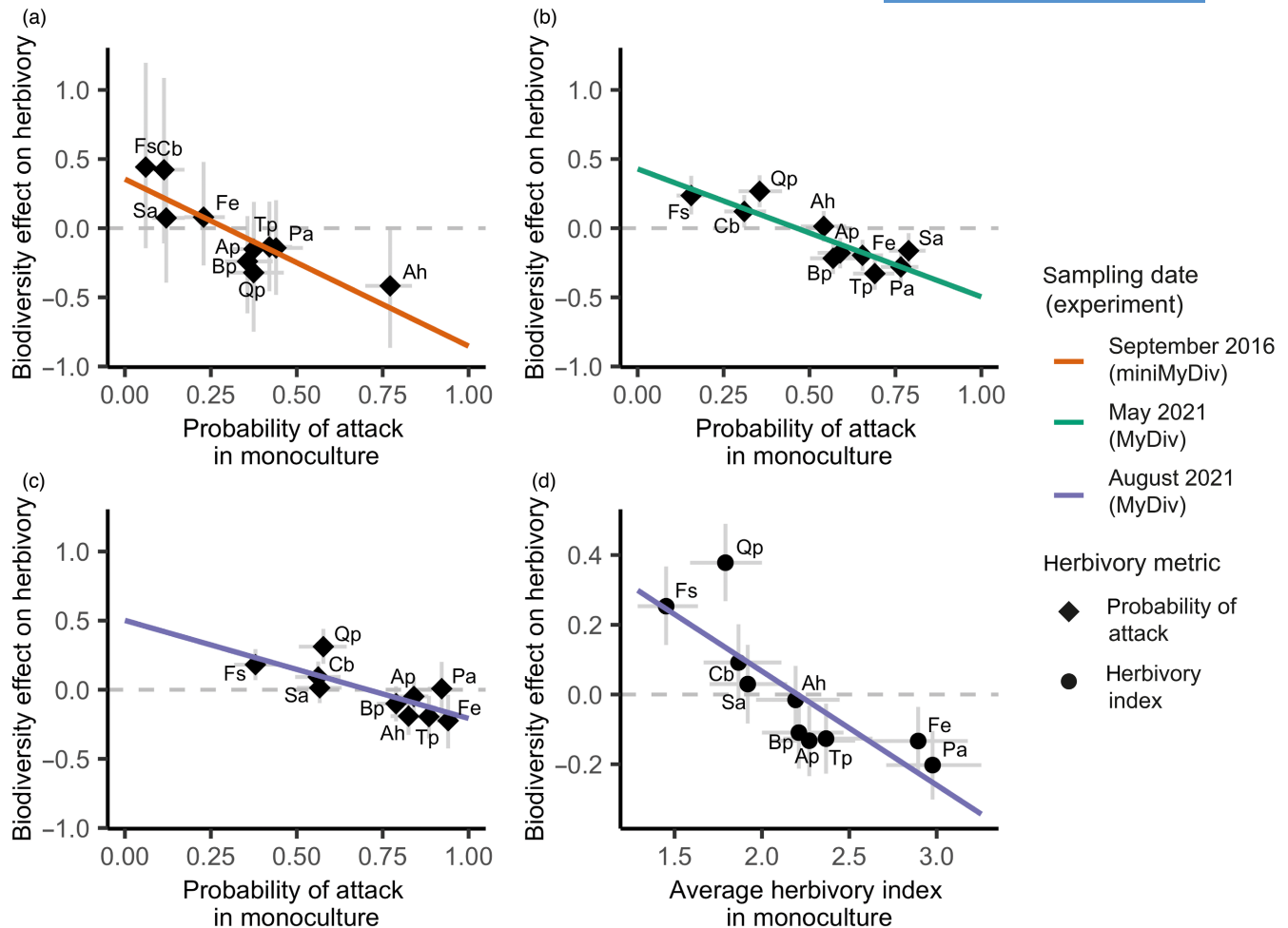
FIGURE 2 Negative correlation between monoculture herbivory and the effect of tree biodiversity. The panels (a–c) show the probability of a leaf being attacked in monoculture (species-specific random effect intercept) versus the effect of biodiversity on herbivory (species-specific random effect slope of biodiversity on herbivory) in September 2016, May 2021, and August 2021, respectively, as well as (d) our quantitative index of the amount of leaf area removed in monoculture versus the effect of biodiversity in August 2021. Each point represents a different tree species. The lines are best-fit lines to the model-derived points, provided to help see the negative correlations. Error bars represent 95% credible intervals for estimates. Labels correspond to the first letters of each species' genus and species name. See *Experimental design* for full species names.

and discuss in the main text, for all 10 species, the models in which apparency mediates biodiversity.

For five species with non-zero biodiversity effects, direct effects of biodiversity were 646.3× (*A. hippocastanum*), 10.5× (*B. pendula*), 2.9× (*F. excelsior*), 1.5× (*Q. petraea*) and 105.9× (*T. platyphyllos*) as strong as indirect effects. For the remaining species, *F. sylvatica*, the direct effect of biodiversity on herbivory was 0.9× as strong as the indirect effect. Among the six species with clear biodiversity effects, biodiversity had non-zero indirect effects for three species (*F. excelsior*, *F. sylvatica* and *Q. petraea*). Across all three species, tree height had a negative effect on herbivory (Figures S17 and S18). For *F. sylvatica* and *Q. petraea*, biodiversity had a negative effect on tree height, while the opposite was true for *F. excelsior* (Figures S17 and S18). Though traits explained little intraspecific variation in herbivory, some traits appeared to be related to interspecific variation in herbivory. Taller species and those with less tough, more palatable leaves experienced higher levels of herbivory (Figure S10).

3.3 | Simulation

Our simulation replicated the negative empirical relationship between monoculture herbivory and the effect of biodiversity on herbivory, with a mix of positive, negative and neutral biodiversity effects (Figure 4). Increasing *p*, the proportion of food that herbivores obtain from the intended host tree, decreased the magnitude of the negative relationship between biodiversity and herbivory: nonzero biodiversity effects decreased in magnitude as *p* increased (Figure 4). The strength of the simulated monoculture herbivory-biodiversity effect relationship was most similar to the empirical relationship when *p*=0.5, that is when herbivores only obtained half of their food from intended host trees (Figure S19). At equivalent levels of *p*, biodiversity effects were weaker in the uniform random design than in the regular design (Figure 4). At *p*=0.5, effects of biodiversity on herbivory for simulated species with monoculture herbivory levels similar to *F. sylvatica*, *Q. petraea* and *P. avium* were 12.9%, 19.3% and 20.7% greater, respectively,
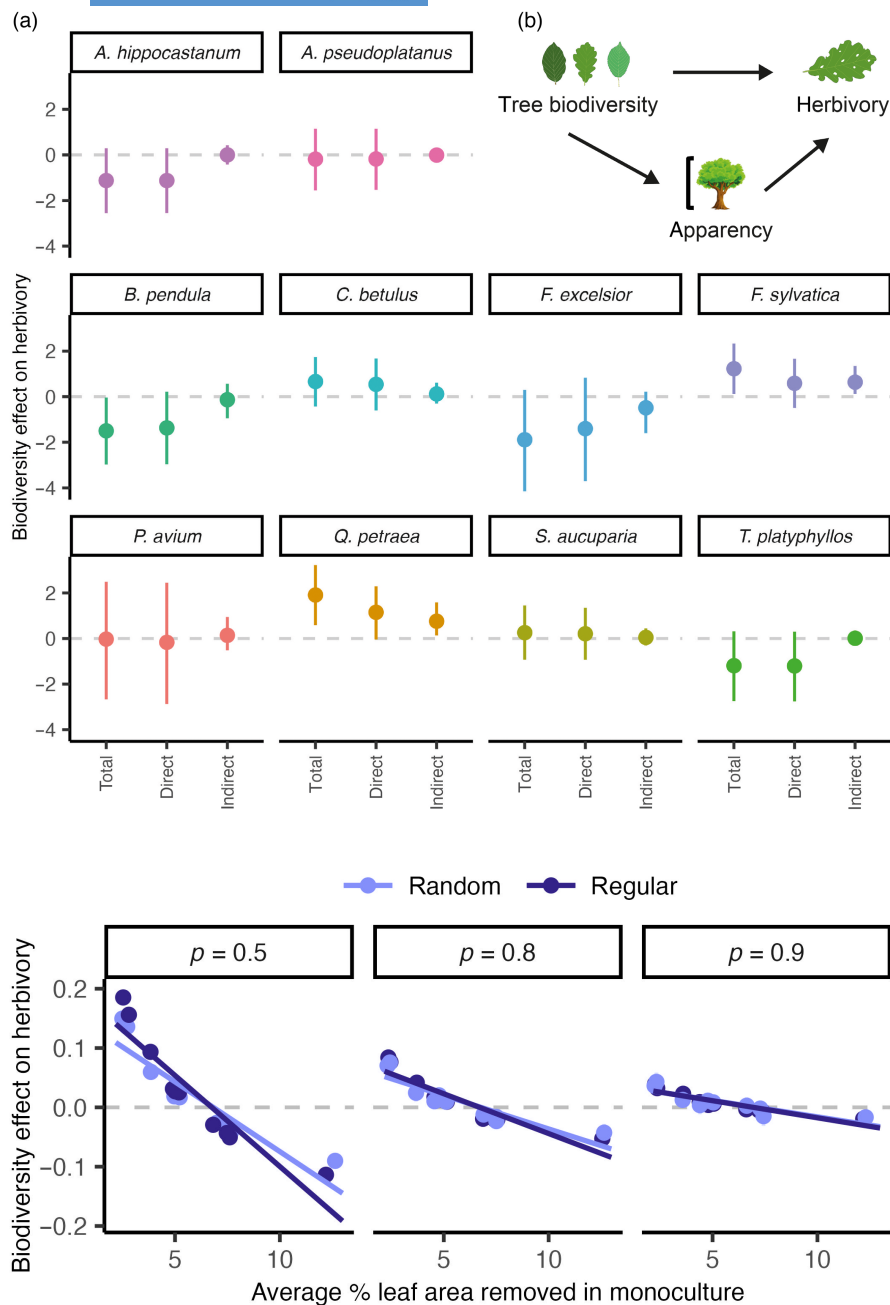
FIGURE 3 Direct effects of biodiversity outweigh indirect effects. (a) The structure of our SEM model, applied to all 10 species, testing whether apparency (quantified as tree height) mediated effects of tree biodiversity on herbivory. (b) Estimates of the direct, indirect and total effects of biodiversity on herbivory (specifically, proportion of herbivorized leaves per tree in August 2021), as derived from structural equation models with the format shown in (a). Error bars represent 95% credible intervals for effect sizes.
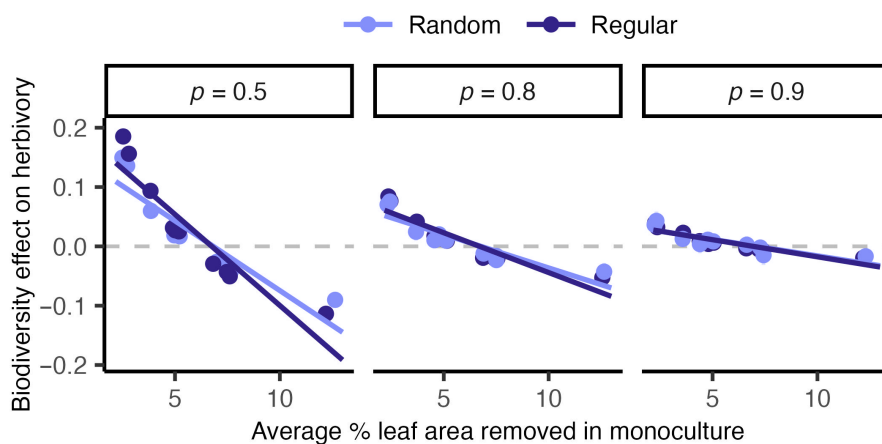
FIGURE 4 The strength of associational effects and spatial organisation modify the biodiversity-herbivory relationship. This figure shows the output of simulations of associational effects across various levels of p, the proportion of herbivore food intake ultimately derived from intended host trees. In each facet, we show the results using a regular spatial organisation (as in MyDiv) in addition to a uniform random organisation, in which all species are equally likely to be neighbours.

in the regular arrangement than in the random arrangement (Figure 4). This effect of spatial organisation was weaker, though still present, in simulations with larger neighbourhood sizes (Figure S19), since in a regular design, intraspecific disaggregation is most pronounced in the immediate neighbourhood of focal individuals (Figure 1). The results from our null models showed that stochasticity and unbalanced sampling across diversity levels are highly unlikely to have given rise to our empirical results (Figure S20).

4 | DISCUSSION

Using a combination of empirical observations from a tree biodiversity experiment and empirically motivated simulations, we found

strong evidence for spillover associational effects driving species-specific and community-wide relationships between tree biodiversity and insect herbivory. We offer four main lines of evidence for the prevalence of spillover associational effects. First, and most importantly, we found a strong negative relationship between the level of herbivory a species experienced in monoculture and the effect of tree biodiversity on herbivory for that species. Consistent with spillover associational effects, species with lower than/equal to/higher than average herbivory in monoculture experienced increased/unchanged/decreased herbivory in mixtures, respectively. This effect was consistent across years (2016 and 2021), seasons (May and August 2021) and the metric used to quantify herbivory (probability of attack and herbivory index). Second, we found that across all species pooled together, biodiversity had no overall effect

on herbivory. A net-zero effect of biodiversity is consistent with an ultimately neutral process by which spillover associational effects drive even mixing between levels of herbivory among species. Third, SEMs revealed that the plant traits we measured did not strongly mediate biodiversity effects, evidence against alternative hypotheses that might rely on biodiversity effects due to changes in plant traits driven by mixing with heterospecifics. Finally, with a simulation of neighbourhood-level spillover associational effects, we reproduced the relationship between monoculture herbivory and the effect of biodiversity, verifying that ubiquitous spillover associational effects could give rise to our empirical results. We extended our simulation to show how spatial organisation can modify biodiversity-herbivory relationships. Our results provide a potential framework for eventually predicting the direction and strength of associational effects, particularly in systems where herbivores that feed on many species (e.g. generalists) inflict most damage, with implications for other biodiversity experiments, future research and applied purposes (see below).

4.1 | Connections to past studies and other systems

Studies in a variety of systems have found strong variation in the magnitude and direction of associational effects (Andow, 1991; Barbosa et al., 2009) and plant biodiversity-herbivory relationships (Jactel & Brockerhoff, 2007; Jactel et al., 2021) and we both find and explain similar variation. A meta-analysis of associational effects on plant damage by Barbosa et al. (2009) found a nearly even split between associational resistance ($n=25$ effect sizes) and associational susceptibility ($n=24$). More recent, larger-scale meta-analyses have found the level of herbivore host specialisation to be an important variable moderating the relationship between diversity and herbivory: associational resistance is predominant with monophagous and oligophagous herbivores (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel et al., 2021). With polyphagous herbivores, however, a zero net-effect of biodiversity on herbivory masks substantial variation: associational resistance and susceptibility are equally common and often strong (Castagneyrol et al., 2014; Jactel et al., 2021). This variation implies a need to move beyond trying to determine whether associational resistance or susceptibility is the rule, instead aiming to predict when and how strongly each will occur.

Our results suggest that in systems dominated by polyphagous herbivores, the spillover mechanism may be responsible for producing variation in associational effects. According to many previously hypothesized mechanisms of associational effects on herbivory (e.g. altered availability of soil nutrients due to neighbouring plants; plant–plant communication, such as through volatile organic compounds; plant–plant competition altering plant resource allocation), biodiversity affects herbivory indirectly, via plant traits (Barbosa et al., 2009). Biodiversity, however, can also influence plants without modifying plant traits, especially through mechanisms in

which neighbourhood composition influences characteristics (e.g. behaviour or density) of herbivores, rather than changing characteristics of plants (Barbosa et al., 2009; Stiling et al., 2004; Wada et al., 2000; White & Whitham, 2000). Our results point to the importance of direct effects of biodiversity on herbivory via spillover, in which herbivores are attracted to some species more than others, but feed on neighbouring individuals as well.

More specifically, we suggest that ubiquitous spillover, in which herbivores are constantly spilling over between all species, may occur in systems dominated by generalist insects. As we show, ubiquitous spillover can produce both the neutral community-wide effect of biodiversity on herbivory as well as the broad species-specific variation in associational effects commonly observed in the literature (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Jactel et al., 2021). Intriguingly, Cappelli et al. (2022) found a similar pattern across 18 species in a biodiversity experiment in a Swiss perennial grassland. Performing a similar analysis to ours, Cappelli et al. (2022) found that species with monoculture herbivory lower than their neighbours had increasing herbivory in mixtures, species with monoculture herbivory higher than their neighbours had decreasing herbivory in mixtures, and that biodiversity had a neutral community-wide effect on herbivory (see fig. 5 in Cappelli et al., 2022). The similarity of results between our species and theirs, despite their focus on herbaceous plants in a different system, suggests the potential generality of our results and framework. Many factors that have been hypothesised to control the magnitude and direction of associational effects broadly, including herbivore taxonomic group (e.g. mammal vs. insect), herbivore diet breadth (specialist vs. generalist), and phylogenetic relationships between neighbouring plants, may drive variation in the magnitude of spillover (Barbosa et al., 2009; Jactel et al., 2021; Mutz et al., 2022). For the framework of spillover effects to become a truly predictive framework, identifying which underlying mechanisms explain the prevalence and strength of spillover effects will be critical.

4.2 | The importance of spatial organisation

While the importance of neighbourhood effects has a strong theoretical and empirical basis (Bergelson, 1990; Pacala, 1986; Pacala & Deutschman, 1995; Stoll & Prati, 2001), our results suggest the need for an increased focus on the influence of neighbourhood-scale spatial organisation in biodiversity-ecosystem function research and beyond. Neighbourhood models have been successful, for example, in predicting multi-species plant population dynamics in annual plants (Pacala, 1986; Silander & Pacala, 1985). The potential importance of local spatial organisation in BEF experiments has been acknowledged (Scherer-Lorenzen et al., 2005; Underwood et al., 2014) but actual tree biodiversity experiments most often use regular arrangements (Bruelheide et al., 2014) and almost never include explicit spatial organisation treatments (Forest & Nature Lab, n.d.). Our empirically parameterised simulation shows that when spillover associational effects determine

biodiversity-herbivory relationships, the strongest biodiversity effects occur in regular designs. These results can be straightforwardly extended to any BEF relationship driven by neighbourhood-level associational effects: whenever close proximity to heterospecific individuals creates a BEF relationship, the relationship will be stronger when individuals tend to be surrounded by heterospecific rather than conspecific individuals. Since some level of intraspecific aggregation seems to be the rule in natural ecosystems (Hubbell, 1979), future BEF experiments explicitly manipulating intraspecific aggregation can offer valuable insight into real-world BEF relationships in addition to informing agricultural and reforestation planting schemes.

The potential importance of spatial organisation for the biodiversity-herbivory relationship, as documented here, also suggests an explicit relationship between BEF patterns and mechanisms of coexistence in forest ecosystems. The Janzen-Connell hypothesis explains how specialised natural enemies can create regular spatial patterns of individuals of different species and maintain high biodiversity in species-rich tropical forest ecosystems (Connell, 1971; Janzen, 1970). The results of our simulation show that under regular patterning, the monoculture herbivory-biodiversity effect relationship will be maximised. The spillover effects we investigate, however, likely depend on generalist herbivores inflicting the majority of damage. In cases where most herbivory is due to generalists, but specialist pathogens or seed predators maintain tree diversity, regular patterning due to Janzen-Connell effects may still exist in systems where generalist herbivores are responsible for most herbivory. Yet, if specialist herbivores are responsible for maintaining tree diversity, spillover effects may be weak. In this case, niche differences, which are necessary for other types of BEF relationships (Eisenhauer et al., 2019; Turnbull et al., 2013, 2016), may ultimately weaken biodiversity-herbivory relationships.

4.3 | Applications

Due to its value for pest resistance, ecologists and agriculturalists have been interested in associational resistance since before the modern field of BEF research existed (Aiyer, 1949; Altieri et al., 1984; Smith & McSorley, 2000; Uvah & Coaker, 1984). A great deal of evidence for associational resistance comes from agricultural studies (Andow, 1991; Barbosa et al., 2009; Underwood et al., 2014). In crop-trapping, a centuries-old technique, attractive species planted nearby and/or prior to focal species are used as a sink for pests (Altieri et al., 1984; Holden et al., 2012). Alternatively, when unpalatable plants are planted near focal species, they may create associational refuges by repelling herbivores from the local neighbourhood (Erfanian et al., 2021; Pfister & Hay, 1988). Although we do not incorporate them explicitly, such associational refuges emerge organically in our simulation. Our simulation rests on a process by which herbivores attracted to focal individuals ultimately feed partially on neighbours. This includes the possibility that herbivores find focal

individuals and explicitly spill over to neighbours as well as the possibility that herbivores simply fail to properly locate focal individuals. Indeed, in some of the earliest research on associational resistance, Tahvanainen and Root (1972) found that in an agricultural system, when a host plant of an agricultural pest was interspersed with heterospecific neighbours, these neighbours interfered with the host-finding ability of an agricultural pest, resulting in associational resistance. While our results support this strategy of planting unpalatable/non-host heterospecific individuals near target crops, we do not dispute the long-standing benefits of crop-trapping, which could be compatible with a more biologically detailed extension of our model. Our findings can also be applied in the context of tree plantations and reforestation sites, which typically use regular designs (Scherer-Lorenzen et al., 2005). In these contexts, if focal tree species are highly palatable, our results suggest that mixtures with unpalatable species in a regular design minimises herbivory to the focal species. Alternatively, if focal species are unpalatable, an aggregated arrangement in mixtures would minimise herbivore damage to the focal species.

For our framework to become predictive and more useful in applied settings, understanding what causes variation in monoculture herbivory is an important next step. We provide evidence that toughness, palatability and apparency are somewhat predictive of interspecific variation in monoculture herbivory, but our data also show pronounced variation in herbivory between seasons and years. Ontogenetic variation in plant defences (Boege & Marquis, 2005) may contribute to some of this between-year variation, and its effects on variation in spillover should be studied further.

4.4 | Future experiments

In addition to experiments directly manipulating spatial organisation, our results suggest other measurements and experiments to more strongly test our hypothesis of ubiquitous spillover associational effects. First, we suggest investigating the relationship between monoculture herbivory and biodiversity effects in other BEF experiments like MyDiv (as in Cappelli et al., 2022), including in systems with specialists and different types of trees, such as evergreen species, where results will likely differ (Grossman et al., 2018; Paquette et al., 2018; Verheyen et al., 2016). Collecting the multi-species data necessary for such an analysis is straightforward and can generally be done in a short amount of time (e.g. 3–4 days per sampling effort in this study). Second, within experiments like MyDiv, measurements of focal individuals and all surrounding individuals within a chosen neighbourhood would enable stronger, more detailed tests of our hypothesis regarding associational effects. Such measurements would also allow specification of how associational effects decay with distance. Third, coupling neighbourhood-specific herbivory measurements with taxon identification of herbivores feeding on host and focal trees would provide a test of the degree to which herbivores are attracted to focal trees and feed partially on neighbours. Coupling

neighbourhood-specific herbivory measurements with herbivore identification would enable more careful parametrisation of p, the parameter that controls the degree to which herbivores attracted to focal trees also feed on neighbours. Future studies might also include species-specific p parameters, or even pairwise p parameters between each pair of species, which would model herbivore specialisation (as in Hambäck et al., 2014). In our simulations, we found that a high value of spillover ($p \approx 0.5$) was needed to reproduce empirical results. While our SEM's show that incorporating some level of indirect effects would lower this value, potential explanations for such strong spillover effects are weak herbivore preferences or very low host-finding ability. Measurements that parametrise p, as well as experiments that explicitly link herbivore behaviour to individual-level plant herbivory, would enable clearer estimation of the strength of spillover and the mechanisms driving it.

Expanding beyond this study, herbivory is a multi-scale process (Hambäck et al., 2014; Jactel et al., 2021), and we only considered the neighbourhood scale. In addition to how herbivores choose individuals within neighbourhoods, how herbivores locate and choose neighbourhoods is important, too. Explicit quantification of this multi-scale process—modelled in Hambäck et al. (2014)—would provide a more mechanistic understanding of associational effects. Our theoretical framework can be straightforwardly extended to accommodate additional relevant details, such as density-dependent herbivory, but experimental manipulations will be necessary for quantifying the influence of such details (Hambäck et al., 2014; Kim & Underwood, 2015; Merwin et al., 2017).

Similarly to Mutz et al. (2022), we found that leaf traits commonly thought to be important for defence (toughness, pubescence, and lab-quantified palatability) were relatively poor predictors of intraspecific variation in herbivory. Following standard practice, we measured physical defence traits and field herbivory on separate leaves, specifically choosing undamaged leaves for trait measurements but not for herbivory assessments. If physical defence traits vary greatly within trees, however, or if undamaged leaves used for trait measurement differ from (potentially) damaged leaves used to assess herbivory, predicting standing herbivory using measurements of nearby leaves on the same tree will be difficult. We also found, surprisingly, that within species in which biodiversity had indirect effects on herbivory via apparency, more apparent (i.e. taller) trees experienced less herbivory. While taller trees may be more apparent to herbivores, if better competitors grow faster and have better defences, perhaps due in part to their superior growth, more apparent trees might have less herbivory. In the future, more rigorous quantitative analysis of how trait-mediated biodiversity effects on herbivory vary between species (e.g. through a multigroup SEM) would provide further insight into why and how associational effects vary between species. Regarding palatability, we measured palatability using *Spodoptera* caterpillars, which are not the most important herbivores in our study site. If more locally relevant herbivores have different preferences than *Spodoptera*,

palatability might still explain some intraspecific variation in herbivory. A previous study with a similar design found a relationship between nutrient status (carbon and nitrogen) and herbivory (Ferlian et al., 2021) across species. Individual-level measurements of nutrient status and additional plant traits relevant to herbivory (e.g. emissions of volatile organic compounds, though Ferlian et al., 2021 found that VOC's did not predict variation in herbivory) and investigation of potential biodiversity effects on top-down regulation of herbivory (Barnes et al., 2020) would enable a more rigorous comparison between direct and indirect effects of biodiversity.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14212.

DATA AVAILABILITY STATEMENT

Data is stored in the Dryad Digital Repository: https://datadryad.org/stash/dataset/doi:10.5061/dryad.9kd51c5pv (Leonard et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Figure S1. Biomass of insect herbivore families in the MyDiv experiment.

Figure S2. Biomass of herbivores in MyDiv on different tree species.

Figure S3. Herbivory due to different herbivore feeding modes.

Figure S4. Negative correlation between monoculture herbivory and the effect of biodiversity is consistent through time and across herbivory metrics.

Figure S5. Net-zero total effects of biodiversity on herbivory through time and across metrics.

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