

Woody plant richness does not influence invertebrate community reassembly trajectories in a tree diversity experiment

PETER YEELES,^{1,5} LORI LACH,^{2,3} RICHARD J. HOBBS,² MARY VAN WEES,¹ AND RAPHAEL K. DIDHAM^{1,4}

¹*School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009 Australia*

²*School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009 Australia*

³*Centre for Tropical Environmental and Sustainability Science, James Cook University, Cairns, Queensland 4870 Australia*

⁴*Centre for Environment and Life Sciences, CSIRO Land & Water, Underwood Avenue, Floreat, Western Australia 6014 Australia*

Abstract. Understanding the relationship between plant diversity and diversity at higher trophic levels is important from both conservation and restoration perspectives. Although there is strong evidence for bottom-up maintenance of biodiversity, this is based largely on studies of simplified grassland systems. Recently, studies in the TreeDivNet global network of tree diversity experiments have begun to test whether these findings are generalizable to more complex ecosystems, such as woodlands. We monitored invertebrate community reassembly over 5 yr of experimental woodland restoration at the TreeDivNet Ridgefield site in southwest Australia, testing the effects of woody plant species richness and herb-layer manipulation on invertebrate community structure and ant species composition. From 2010 to 2014, we sampled ground-dwelling invertebrates using pitfall traps in herbicide vs. no-herbicide subplots nested within each of 10 woody plant treatments varying in richness from zero (bare controls) to eight species, which produced a total of 211,235 invertebrates, including 98,979 ants belonging to 74 species. In mixed model analyses, the presence of woody plants was an important driver of faunal community reassembly (relative to bare control plots), but faunal responses to woody plant treatment combinations were idiosyncratic and unrelated to woody plant richness across treatments. We also found that a herbicide-induced reduction in herbaceous plant cover and richness had a positive effect on ant richness and caused more rapid convergence of invertebrate community composition toward the composition of a woodland reference site. These findings show that woody plant richness did not have direct positive effects on the diversity and community reassembly trajectories of higher trophic levels in our woodland system. From a management perspective, this suggests that even low-diversity restoration or carbon sequestration plantings can potentially lead to faunal reassembly outcomes that are comparable to more complex re-planting designs.

Key words: ants; biodiversity; bottom-up diversity; community reassembly; faunal restoration; Formicidae; succession.

INTRODUCTION

Global biodiversity loss has led to an upsurge in research linking biological diversity and ecosystem functioning (BEF). The dependence of functional outcomes, such as ecosystem productivity and stability, on biodiversity is now well demonstrated across a range of systems (Hooper et al. 2005, Naeem et al. 2012). In light of this knowledge, it is vital that we understand the processes that promote and maintain biological diversity, to allow us to better develop practices to conserve and restore stable, functioning ecosystems (Cardinale et al. 2012).

The importance of bottom-up processes in the maintenance of terrestrial biodiversity (i.e., those effects that cascade from lower to higher trophic levels) has been widely demonstrated (Knops et al. 1999, Haddad et al. 2009), but with a strong bias toward studies in northern hemisphere grasslands (Symstad et al. 2000, Haddad

et al. 2001, Ebeling et al. 2014). These studies have largely concentrated on the effects of herbaceous plant taxonomic richness (Ebeling et al. 2014), functional diversity (Haddad et al. 2001), and phylogenetic diversity (Dinnage et al. 2012) on arthropod diversity. Other studies have built on these findings to include the responses of higher trophic level consumers to grassland plant diversity (Siemann et al. 1998, Haddad et al. 2009) and potential cascading effects across species interaction networks (Scherber et al. 2010). Typically, these have exhibited similar, but weaker relationships than observed for primary producer diversity. However, a key limitation in interpreting these findings is that there has been comparatively little research investigating whether the conclusions from experimental grassland systems hold true for forest and woodland systems as well, which is especially relevant given the magnitude of global forest loss (Crowther et al. 2015).

The few studies that have been conducted in woodland systems have tended to find a relatively weak positive correlation between plant and consumer diversity (Sobek et al. 2009a, Scherber et al. 2014). Broadly, then, this

Manuscript received 20 June 2016; revised 21 October 2016; accepted 7 November 2016. Corresponding Editor: Nathan J. Sanders.

⁵E-mail: peter.yeeles@grs.uwa.edu.au

might suggest that similar mechanisms operate in both grassland and woodland systems, with an increase in such factors as resource niche dimensions and structural heterogeneity leading to a bottom-up increase in herbivore diversity (Hutchinson 1959). For instance, in European forests Sobek et al. (2009b) found that temporal patterns of resource availability were broader in more diverse, heterogeneous assemblages, leading to a higher diversity of true bugs. Moreover, there is potential for cascading bottom-up effects of woody plant diversity on the diversity of higher-level consumers, such as predatory ants (Staab et al. 2014), in at least some systems.

However, it can be difficult to disentangle the drivers of faunal responses in studies that focus on correlative spatial gradients in diversity across natural systems (Sobek et al. 2009a, Gunawardene et al. 2012, Staab et al. 2014). For example, Scherber et al. (2014) found that Diptera responded to tree cover, not tree richness, across a tree diversity gradient in Germany, noting that the observational nature of their study meant it was difficult to infer causality between multiple drivers. It is likely that this problem will be even more challenging to overcome when studying bottom-up diversity effects in woodlands, compared to purely herbaceous systems, because woody species typically make up a relatively small proportion of total plant diversity in forests (Gilliam 2007), yet dominate forest biomass and vegetation structure, and indirectly influence understory vegetation where the majority of plant diversity occurs (at least in temperate regions; Ampoorter et al. 2015). For instance, woody overstory species can facilitate increases in understory plant diversity through altered microclimate and soil temperature, while at the same time competing for light, nutrients, and water availability (Messier et al. 1998). This means that woody species diversity is likely to have both direct effects on the diversity of higher trophic levels (Sobek et al. 2009a), as well as indirect effects mediated by their influences on the herb layer (Scherber et al. 2014).

To address the inherent limitations on teasing out plant richness effects from correlative data, a network of tree diversity experiments, TreeDivNet, has been established to directly manipulate woody species richness under controlled conditions (Verheyen et al. 2016). With the maturation of woody species across this network of experiments, results of research testing whether higher plant diversity begets higher consumer diversity are emerging (e.g., Staab et al. 2015). Some of these studies have focused on the diversity responses of primary consumers (e.g., Haase et al. 2015), and there is significant scope for testing cascading bottom-up influences on the diversity and composition of higher-level consumers. For instance, recent findings from the BEF-China experiment suggest that bottom-up diversity effects operate across multiple trophic levels (Staab et al. 2015). Surprisingly, though, the tendency in these studies is to take a snap-shot of spatial variation in woody plant diversity effects at one point in time, even though there is a large potential for effects to vary temporally with stage of growth and community assembly.

Here, we utilize a tree diversity experiment in southwest Australia to test if the presence, diversity, and composition of woody species have bottom-up effects on the diversity of higher trophic level consumers in woodland systems, whether in the presence or absence of an experimentally manipulated weedy herbaceous layer. For the first time, we also test temporal variation in these effects over five years of invertebrate colonization and community succession (i.e., reassembly “trajectories” of invertebrate communities as they become progressively more similar to the communities typical of a nearby reference woodland site) at the Ridgefield TreeDivNet experiment (Perring et al. 2012). We address three questions that are fundamental to an improved understanding of bottom-up drivers of biodiversity in woodland and forest ecosystems: (1) Does increasing woody plant diversity have a cascading bottom-up effect on the composition and diversity of higher-level consumers? (2) Does removal of a complex herbaceous understory have negative effects on the diversity and composition of higher-level consumers? (3) Does increasing woody plant diversity positively influence invertebrate community reassembly trajectories?

METHODS

Experimental design

This study was conducted at the Ridgefield woody plant diversity experiment (Perring et al. 2012), which was established to investigate the relative contributions of woody plant species and functional richness to the restoration of multiple ecosystem services. The experiment was set up on the University of Western Australia’s Future Farm, approximately 130 km southeast of Perth (elevation 350 m). The site is located on the western margins of the Western Australian wheat belt, a 150,000-km² region of agricultural land that has experienced over 93% land clearing since the settlement of Western Australia. The site has a Mediterranean-type climate, with a mean annual rainfall of 445 mm that falls primarily in winter, a mean summer daily maximum temperature of 31.8°C, and a mean winter daily minimum temperature of 5.9°C (Perring et al. 2012).

The experimental design at Ridgefield consists of nine woody species treatments and one unplanted control treatment, with each treatment replicated 10 times, blocked by soil characteristics and site aspect, for a total of 100 plots of 21 × 23 m (for this study, we used only the plots established on previously grazed land, not the previously cropped plots; see Perring et al. 2012). Eight woody species were planted: two eucalypt trees (York gum, *Eucalyptus loxophleba* ssp. *loxophleba*, and brown mallet, *Eucalyptus astringens*), two myrtaceous shrubs (*Callistemon phoeniceus* and *Calothamnus quadrifidus*), two proteaceous shrubs (*Hakea lissocarpha* and *Banksia sessilis*), and two fabaceous shrubs (*Acacia microbotrya* and *Acacia acuminata*). These were planted into the

following treatments: (1) York gum only, (2) eucalypt trees, (3) eucalypt trees plus myrtaceous shrubs, (4) eucalypt trees plus proteaceous shrubs, (5) eucalypt trees plus fabaceous shrubs, (6) eucalypt trees plus myrtaceous and proteaceous shrubs, (7) eucalypt trees plus myrtaceous and fabaceous shrubs, (8) eucalypt trees plus proteaceous and fabaceous shrubs, (9) all species, and (10) unplanted control. The site was plowed to a depth of 30 cm and pre-treated with a site-wide herbicide application in 2010. A total of 110 seedlings were planted in each of 90 woody plant treatment plots in August 2010, with the distribution of tree species detailed in Perring et al. (2012) and the 10 bare control plots remaining unplanted. For further details regarding the experimental design and overarching goals of the Ridgefield woody plant diversity experiment, see Perring et al. (2012).

Sub-plot level treatments

A two factor split-plot treatment combination of herbicide application and nitrogen addition was also included in plot quarters. Herbicide application at the sub plot level allowed us to measure the influence of woody species without potential mediating effects of a herbaceous understory. Glyphosate herbicide was applied on average twice per year to herbicide-treated quarters, with additional spot spraying of herbaceous plants (predominantly nonnative weed species) as required (Perring et al. 2012). Herbicide treatment greatly reduced both understory cover ($80.5\% \pm 21.1\%$ in control vs. $9.7\% \pm 13.2\%$ in treatment) and species richness (10.8 ± 2.9 in control vs. 3.9 ± 3.4 in treatment). The subplot level nitrogen addition treatment used ammonium nitrate at an application rate of $10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, a potential threshold at which various ecosystem functions might be affected (e.g., primary productivity; Bobbink et al. 2010).

Woodland reference site

We sampled invertebrate communities in a remnant she-oak (*Casuarina* sp.)/eucalypt woodland as a reference site to compare against the reassembly trajectories of invertebrate communities in the treatment plots. We selected the woodland site that was the closest likely source of dispersing invertebrates, including ant propagules, located approximately 100 m up-slope from the eastern side of the tree diversity plots. Our qualitative initial surveys suggested it was representative of the vegetation and condition of remnant woodlands in the region. Woody species composition did somewhat differ from the experimental plots, with a higher proportion of *Acacia* sp. and a lower proportion of eucalypts. We make no inference or assumption about whether this reference site represents the final “end-point” of succession for invertebrate communities in the experimental plots, but we use it as the best available proxy for local woodland conditions. Five equivalent-sized plot areas ($21 \times 23 \text{ m}$)

were randomly located in the woodland, with sampling points at the center of each plot quarter.

Invertebrate sampling

Invertebrate sampling was conducted using pitfall traps set in late spring (November) each year between 2010 and 2014. A 10 cm length of 67 mm internal diameter PVC pipe was dug into place between two York gum trees in the center of each plot quarter, in October 2010. The use of a sleeve for pitfall trap placement ensured the consistent location of the trap, and minimized any “digging-in” effect during each sampling period. Pitfall traps consisted of a plastic cup of 69 mm diameter and 62 mm depth. Empty pitfall cups with lids were set flush to ground level with minimal soil disturbance. After seven days, lids were removed and the cups filled with 50 mL of a pre-mixed 50:50 solution of filtered water and propylene glycol. A drop of unscented detergent was added to each 5-L container of the premixed solution to reduce surface tension. The traps were collected after a further seven days, and the samples were washed through a $125\text{-}\mu\text{m}$ sieve before being stored in 70% ethanol at 4°C .

All samples were sorted to invertebrate class, order, and a nominal “higher taxa” level. We utilized the same higher taxon approach as Didham et al. (2009). This approach allows for further division of order-level taxa by developmental stage, sub-order, and family, providing higher resolution with minimal requirements for specific taxonomic expertise during sorting. We did not count or analyze data for Acari or Collembola due to their extremely high abundances (often exceeding 20000 individuals per trap in 2010 and 2011). We elected to use ants (Hymenoptera: Formicidae) at a finer taxonomic resolution as their high local diversity and relatively stable spatial dynamics (being colonial animals) makes them ideally suited to studying patterns of biodiversity at relatively small spatial scales (Agosti et al. 2000). A specialist taxonomist confirmed ant species identifications and morphospecies delimitation, and a voucher collection has been lodged at the Western Australian Museum.

Statistical analysis

We pooled data from the nitrogen addition and nitrogen control subplots after preliminary analyses (likelihood ratio tests on a series of generalized linear mixed models for ant abundance and richness; Appendix S1: Table S1) showed that the nitrogen treatment did not improve model fit. In order to maintain equivalent sample sizes for sub-plot-level comparisons with the woodland reference site, the four traps from each woodland remnant plot were also randomly pooled into two groups of two traps. This pooling resulted in a five-year total of 50 samples from the woodland reference site (two samples per plot, with five plots per year over 5 yr), and an expected 1,000 samples from the tree diversity plots (two samples per plot, 10 plots per block, 10 blocks over 5 yr).

However, 64 samples were discarded from 2014 because of the potential influence of an ant colony exclusion experiment conducted at three locations within the plot network. To avoid these manipulations compromising our data set, we established a 40-m radius “zone of influence” around each manipulated colony based on observed foraging distances of the manipulated species. All traps within this distance were excluded from the data set for the final sampling year, resulting in 136 pitfall samples in 2014, rather than a full 200.

Response variables.—We compared reassembly trajectories of higher taxa by calculating changes in community similarity to the reference woodland through time, using the Morisita-Horn index on square-root-transformed abundance data (after excluding ants). The Morisita-Horn index has a lower weighting for rare species, which makes it ideal for investigating dissimilarity in the more dominant, and potentially functionally important, members of a community (Magurran and McGill 2011). We then visualized the trajectory of change in community similarity to the reference woodland site using non-metric multidimensional scaling (NMDS) calculated with 999 random starts, in the R package *vegan* (Oksanen et al. 2016).

For ants, we calculated measures of richness, abundance, and evenness across treatments, and used the Sorensen index (presence/absence) as a measure of community similarity to the reference woodland. Presence/absence is often preferred over abundance for ant communities sampled with pitfall traps as abundances can be spuriously inflated if a trap is located near an ant colony. Dissimilarity (presence/absence) among samples was then visualized using NMDS, using the same method described above for the higher taxa ordination. Ant species evenness was calculated by decomposing Hulbert’s Probability of Interspecific Encounter (PIE) into its evenness component, via conversion to effective number of species (ENS) (Jost 2006), prior to dividing by ant species richness. ENS represents the number of equally abundant species that would be required to attain the same PIE value as was achieved for each community (Chase and Knight 2013), and by dividing this value by richness we isolate the evenness-only component of diversity. To further investigate variation in responses across functionally different components of the ant communities, we used a trait-based approach to establish trait functional groupings of species based on nine traits related to environmental use and resource acquisition strategies (as described in Appendix S2).

Model fitting.—We tested the effects of time since planting, woody species treatment, and herbicide application on five response variables (the similarity of higher taxon composition to the reference woodland, ant species richness, ant abundance, ant evenness, and ant community similarity to the reference woodland) using separate generalized linear mixed models (GLMMs) in the *lme4*

package (Bates et al. 2015) in R version 3.2.0 (R Development Core Team 2015). In addition to the treatment predictors, we used an additional covariate for treatment divergence in all models. We required the treatment divergence covariate because not all woody plants survived throughout the experiment, and woody plant death was uneven across plots, which may have influenced microclimate, resource distribution, and invertebrate responses. The number of individual tree deaths of each species was recorded for each plot (in each year), and this was converted to a community-wide measure of compositional divergence from the original woody plant treatment composition using a Bray-Curtis measure of dissimilarity. In the ant species richness model, we used a covariate of ant abundance to account for any changes in richness that could be attributed to changes in sample abundance. Random intercepts were included for block and for plot nested within block to account for non-independence within the experimental design. A random slope for year was used to account for longitudinal repeated measures within plots.

Models were fitted using a Poisson error distribution for ant richness and abundance, while Gaussian errors were used to model all other responses. Where a continuous response variable was bounded by zero and one (i.e., for community similarity and evenness responses) a logit transformation was used to meet model assumptions (Warton and Hui 2011). Continuous predictor variables were centered and scaled by two standard deviations to ensure unbiased comparison of model predictors measured on different unit scales (Gelman 2008). We inspected Gaussian model residuals for violations of normality and homoscedasticity, and Poisson model residuals for over-dispersion. Where required, we addressed over-dispersion of residuals using an observation level random effect (Harrison 2014). Data inspection revealed that responses were not necessarily linear through time, so we tested all models for non-linearity using likelihood ratio tests between models with and without a second-order polynomial term for year. Model simplification of global models was carried out using Akaike’s information criterion (AIC) to compare models with all possible subsets of fixed predictors. The model with the smallest number of parameters within 2.0 Δ AIC of the top model was selected as the best model (Arnold 2010). We assessed raw responses and model residuals for spatial autocorrelation using Moran’s *I*, calculated with the *ncf* package in R (Appendix S3: Fig. S1). Final estimates of model fit were calculated as marginal R^2_{glmm} (for fixed effects only) and conditional R^2_{glmm} (for fixed plus random effects) using the approach of Nakagawa and Schielzeth (2013).

RESULTS

Over the five years of the study, 211,235 invertebrates were captured (excluding Acari and Collembola), with 206,669 individuals from the 936 samples taken in the experimental plots and 4,566 from the 50 samples in the woodland remnant. The most abundant taxa were

Formicidae (47%), followed by Diptera adults (13%), Araneae (8%), Coleoptera adults (7%), and Thysanoptera (7%). A total of 98,979 ants were captured in experimental plots and 1,492 in the woodland remnant (99,671 in total). Overall, 60 ant species were detected in experimental plots, with 31 of these species plus a further 14 unique species found in woodland reference plots, giving a total of 74 species across all samples (see Appendix S4 for species accumulation curves of the tree diversity plots and woodland reference site, and Appendix S5: Tables S1 and S2, for details of species captured).

Higher taxa responses

Community composition of the 35 higher taxa changed substantially through time (Fig. 1a), and temporal

trajectories were not consistent across all treatments (Table 1, Fig. 2). Instead, there were strong interaction effects between year and woody species treatment, and between year and herbicide treatment (Table 1). Compositional reassembly trajectories were clearly not linear through time, with best-fit models having strong polynomial trends (Fig. 2). Compositional similarity of herbicide plots converged rapidly on woodland reference plots, whereas the no-herbicide controls initially started on a similar trajectory but increasingly diverged in composition in later years (Fig. 1a). This manifested as strong effect sizes for the positive interactions between both year and herbicide (0.29 ± 0.04 [mean \pm SE]), and year squared and herbicide (0.36 ± 0.11), with the strength of the non-linear relationship being moderated by woody species treatment (Table 1, Fig. 2).

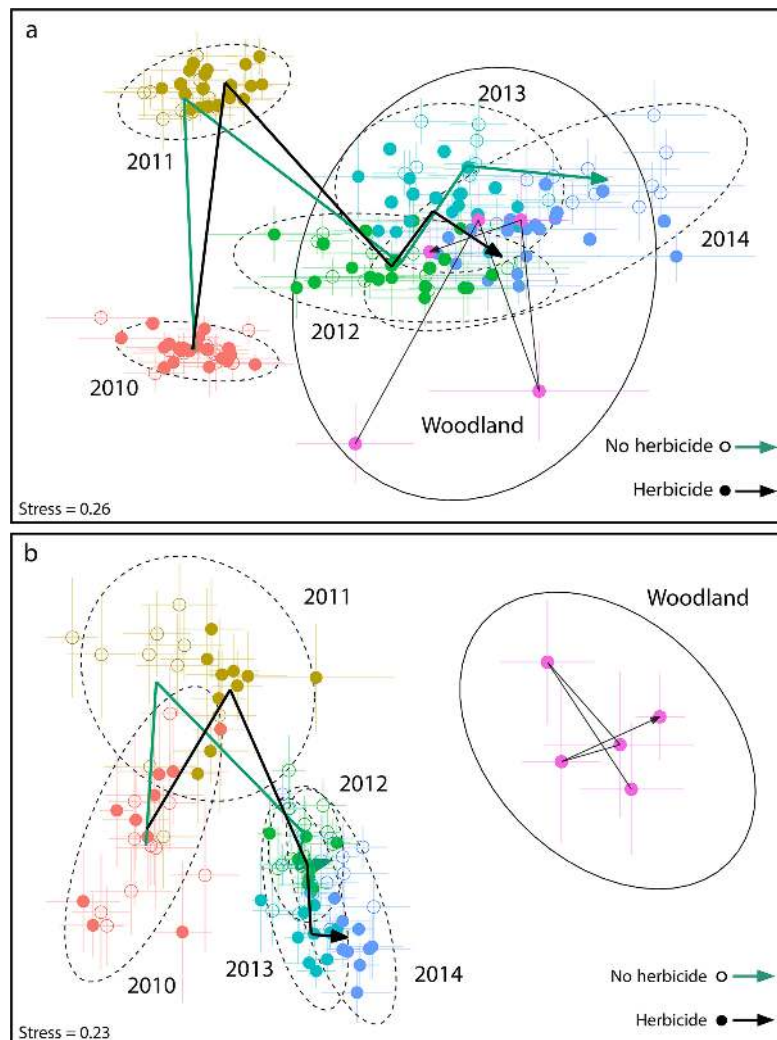


FIG. 1. Nonmetric multidimensional scaling of (a) invertebrate higher taxa and (b) ant species communities by year and herbicide treatment. Dashed ellipses show each annual sampling in the restoration plots, with points representing the mean of 10 replicate community samples from each woody plant treatment. The solid line ellipse shows the woodland reference site, with pooled samples for each year. Arrows illustrate temporal trajectories. Error bars show standard error of the mean. Ellipses show 95% CI. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1. Parameter estimates (*b*) from generalized linear mixed models (GLMMs) fitting responses of higher taxa and ant community similarity to woodland, as well as ant species richness, abundance, and evenness against our experimental variables.

	Higher taxa community similarity to woodland	Ant community similarity to woodland	Ant species richness	Ant abundance	Ant species evenness
Fixed treatment effects					
Intercept	-0.01 (0.06)	0.28 (0.003)	1.83 (0.04)	3.63 (0.11)	0.01 (0.06)
Year (linear component)	-0.01 (0.37)	0.07 (0.005)	0.57 (0.03)	1.29 (0.10)	-0.74 (0.06)
Year ² (quadratic component)	-0.46 (0.19)				
Herbicide	0.13 (0.04)	-0.01 (0.007)	0.09 (0.02)	0.25 (0.05)	-0.03 (0.05)
Trees (1 Euc species)	0.32 (0.08)		0.15 (0.05)	0.34 (0.12)	
Trees (2 Euc species)	0.35 (0.08)		0.19 (0.05)	0.47 (0.12)	
Trees (+ Myrt shrubs)	0.32 (0.08)		0.19 (0.03)	0.29 (0.12)	
Trees (+ Prot shrubs)	0.39 (0.08)		0.13 (0.06)	0.23 (0.13)	
Trees (+ Fab shrubs)	0.35 (0.08)		0.22 (0.05)	0.35 (0.12)	
Trees (+ Fab + Prot shrubs)	0.18 (0.08)		0.21 (0.06)	0.34 (0.12)	
Trees (+ Fab + Myrt shrubs)	0.41 (0.08)		0.19 (0.05)	0.29 (0.12)	
Trees (+ Myrt + Prot shrubs)	0.24 (0.08)		0.21 (0.06)	0.44 (0.12)	
Trees (+ shrubs (all spp.))	0.30 (0.08)		0.14 (0.06)	0.45 (0.12)	
Year × Herbicide	0.29 (0.04)	-0.03 (0.007)		0.47 (0.10)	
Year ² × Herbicide	0.36 (0.11)				
Year ² × Trees (1 Euc species)	-0.73 (0.27)				
Year ² × Trees (2 Euc species)	-0.92 (0.27)				
Year ² × Trees (+ Myrt shrubs)	-0.54 (0.27)				
Year ² × Trees (+ Prot shrubs)	-0.57 (0.27)				
Year ² × Trees (+ Fab shrubs)	-0.77 (0.28)				
Year ² × Trees (+ Fab + Prot shrubs)	-0.35 (0.28)				
Year ² × Trees (+ Fab + Myrt shrubs)	-1.22 (0.28)				
Year ² × Trees (+ Myrt + Prot shrubs)	-0.14 (0.27)				
Year ² × Trees (+ shrubs (all spp.))	-0.62 (0.27)				
Covariate, treatment divergence			-0.09 (0.03)	-0.15 (0.08)	
Covariate, ant abundance			0.21 (0.02)		
Null model (intercept only)	0.43 (0.03)	-1.03 (0.02)	2.05 (0.02)	4.07 (0.06)	0.01 (0.05)
PCV from null (random intercept, block)	6.3%	8.7%	93.3%	-24.5%	-21.0%
PCV from null (random intercept, plot/block)	12.9%	3.8%	99.9%	>-100.0%	-6.2%
PCV from null (random slope, year)	88.6%	98.9%	100.0%	88.0%	82.3%
$R^2_{\text{GLMM}(M)}$	28.9%	20.0%	46.7%	42.5%	16.1%
$R^2_{\text{GLMM}(C)}$	38.7%	22.3%	46.7%	51.4%	25.6%
Null model, AIC	1,211.3	-2,458.0	4,549.0	10,158.2	2,390.5
Final model, AIC	968.7	-2,595.0	4,188.8	9,968.7	2,309.4

Notes: The intercept (*b*) is the non-herbicide quarter of woody control treatment at mean centered position of the year effect. Parameter estimates with 95% confidence intervals that do not overlap zero are in boldface type. Values are means with SE in brackets. See Nakagawa and Schielzeth (2013) for details on PCV. SE, standard error; PCV, proportion change in variance; AIC, Akaike information criterion. Woody treatments are described in *Methods: Experimental design*.

Ant species richness, abundance and evenness responses

The best fit models (Appendix S6) for ant species richness ($R^2_{\text{GLMM}(M)} = 46.7$, $R^2_{\text{GLMM}(C)} = 46.7$) and ant abundance ($R^2_{\text{GLMM}(M)} = 42.5$, $R^2_{\text{GLMM}(C)} = 51.4$) included woody species treatment and indicated a positive effect of trees compared to unplanted controls (Table 1, Fig. 3). However, responses to treatments were highly variable and there was no identifiable tree treatment differentiation in relation to tree species richness driving these effects. The smallest effect size was seen in the trees + proteaceous shrub treatment for both ant richness (0.13 ± 0.06) and ant abundance (0.23 ± 0.13),

while the largest effect was in trees + fabaceous shrubs for ant richness (0.22 ± 0.05) and eucalypt-only trees for ant abundance (0.47 ± 0.12). The woody species treatment parameter was dropped from the final model when testing its effects on ant community evenness.

The herbicide treatment parameter was retained in all final models, and had a strong positive effect on ant abundance (0.25 ± 0.05) and, to a lesser extent, on ant species richness (0.09 ± 0.02), but no detectable effect on ant species evenness (-0.03 ± 0.05). As in higher taxa models, herbicide treatment effects on ant abundance were temporally inconsistent, instead showing a significant time × herbicide interaction (0.47 ± 0.10), with the

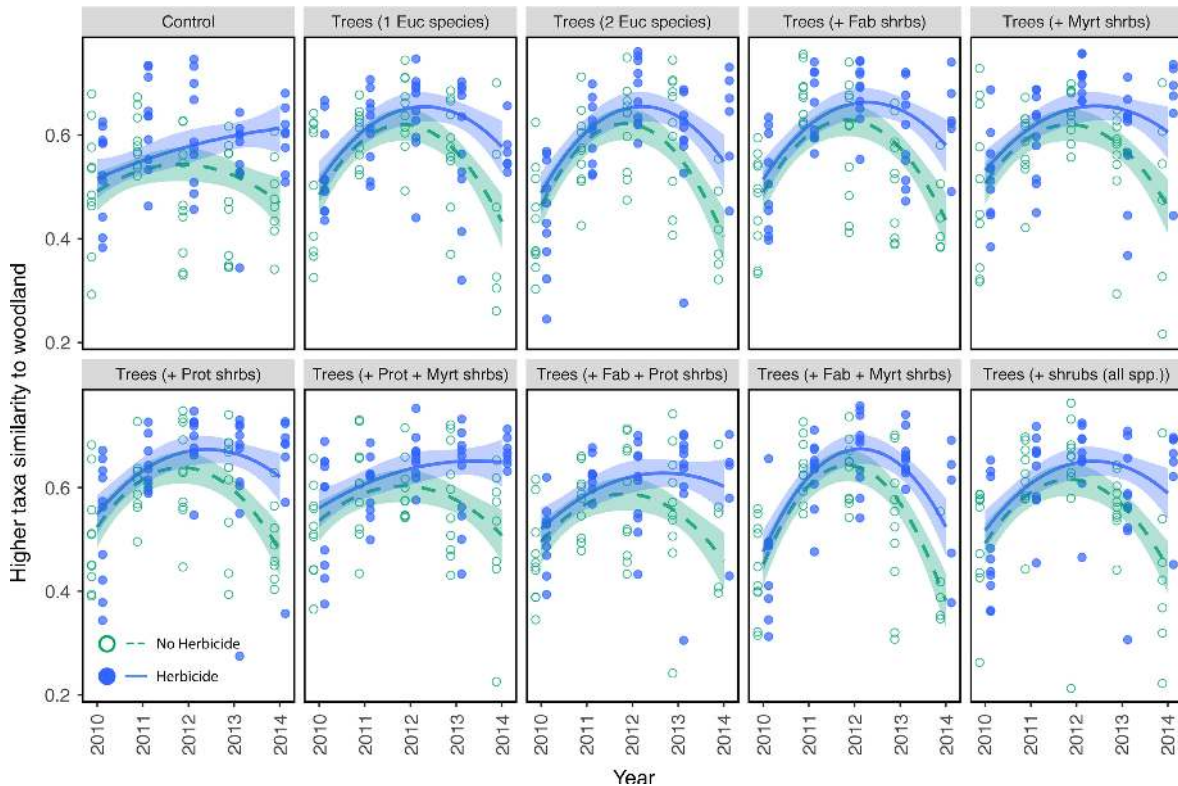


FIG. 2. Invertebrate higher taxa compositional similarity (Morisita-Horn index) to the pooled woodland reference community by woody species treatment over time in herbicide treated and no-herbicide control quarters. Shaded regions show 95% CI. See Table 1 for full results. Woody treatments are described in *Methods: Experimental design*. [Color figure can be viewed at wileyonlinelibrary.com]

herbicide effect increasing in later years of the study. We confirmed this temporal effect was not a spurious artefact of differences in herbicide effectiveness through time, by comparing the absolute difference in ant captures between herbicide and no-herbicide subplots against the absolute difference in percent herbaceous cover in the same subplots, across all years (Appendix S7). Temporal differences in the magnitude of the herbicide effect on ant abundance were unrelated to differences in the magnitude of the herbicide effect on absolute plant cover (Appendix S7; Fig. S1).

Time since planting had a strong positive effect on ant richness (0.57 ± 0.03) and abundance (1.29 ± 0.10), but a negative effect on ant species evenness (-0.74 ± 0.06). Over the five years of the study, average (model-predicted) values for ant species richness increased from 4.9 ± 0.23 to 11.3 ± 0.48 per sample for no-herbicide control, and from 5.4 ± 0.25 to 12.4 ± 0.53 for herbicide-treated quarters. Ant abundance showed a similar pattern, with abundance increasing from 22.0 ± 3.0 to 146.4 ± 19.7 ants per sample in no-herbicide control quarters, and 20.5 ± 2.8 to 274.0 ± 36.9 in herbicide-treated quarters. These increases occurred with a corresponding decrease in ant species evenness over the five years, indicating increasing disparity in levels of dominance and rarity across the communities.

Ant community compositional responses

Variation in ant community composition was best modeled by time since planting, herbicide treatment, and their two-way interaction ($R^2_{\text{GLMM}(m)} = 20.0$, $R^2_{\text{GLMM}(c)} = 22.3$). Time since planting had a small positive effect on ant community similarity to the reference woodland (0.07 ± 0.01) that was partly moderated by a weak negative interaction with herbicide application (-0.03 ± 0.01) (Fig. 1b). Interestingly, the direction of the time by herbicide interaction effect on community similarity was reversed compared to the response of ant abundance to herbicide treatment, resulting in the herbicide treated quarters being on a shallower reassembly trajectory than that seen in the no-herbicide control quarters (Fig. 3).

Differing trajectories of functional groups

Five functional groups, based on variation in traits related to differential habitat use and resource acquisition strategies (Appendix S2; Fig. S1), showed strong temporal shifts in relative abundances through time (Appendix S2; Fig. S2). The principal shift was from a dominance of functional group 5 (*Pheidole* species) in early years, to a dominance of functional group 3

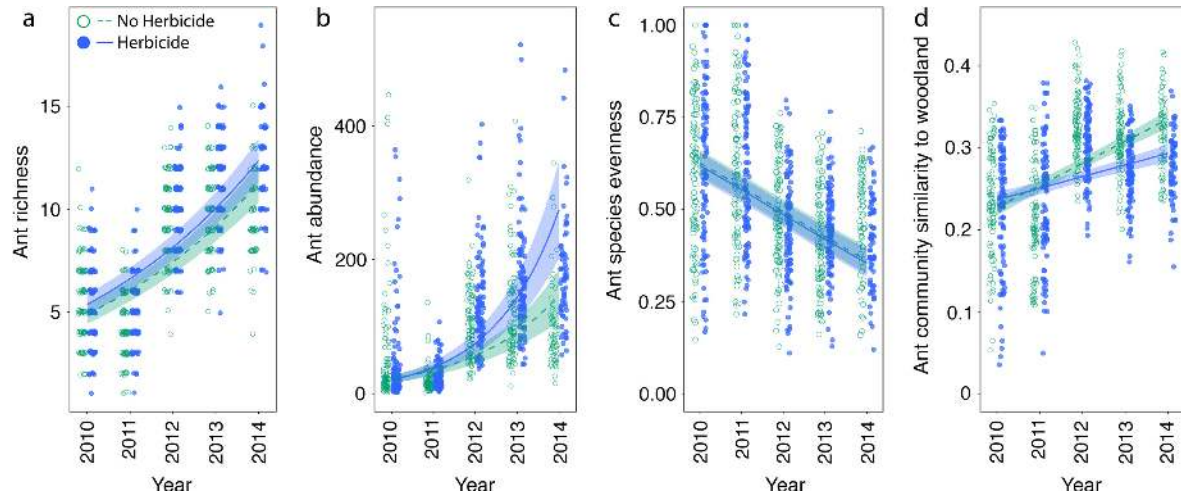


FIG. 3. Predicted values from the *Eucalyptus*-only woody species treatment, generated using the best-fit mixed models (from Appendix S6: Table S1) for (a) ant species richness, (b) ant abundance, (c) ant species evenness and, (d) ant community similarity to woodland, over time, in herbicide-treated and no-herbicide control quarters. Shaded areas represent 95% CI. [Color figure can be viewed at wileyonlinelibrary.com]

(*Iridomyrmex* species) in later years. Captures of functional group 2 (*Melophorus* and *Camponotus* species), and 4 (small generalist species; *Monomorium* spp., *Doleromyrma* sp., and *Tapinoma* spp.), remained relatively stable throughout the experiment.

DISCUSSION

One of the central pillars of the conservation and restoration ethos is that “diversity begets diversity,” such that the maintenance or restoration of diverse plant assemblages will accrue collateral benefits in the assembly of diverse faunal communities (e.g., Palmer et al. 1997). Here, we present findings of one of the first studies utilizing a woody species biodiversity experiment to investigate bottom-up diversity effects across higher-level consumers (see also Staab et al. 2015, 2016). In this system, we found a clear, strong effect of the presence of woody plants on various measures of invertebrate diversity, but no evidence of a bottom-up diversity effect. Moreover, herbicide application to experimentally reduce understory weed cover and richness had strong positive effects on the rate at which ant and invertebrate species composition became more similar to the woodland reference site, a result that is counter to what might be expected in the context of bottom-up diversity drivers. Taken together, these results suggest a lack of bottom-up diversity effects in our system, which has implications spanning both basic and applied ecology.

Woody plant presence promotes invertebrate diversity

We found that the presence of woody plants, irrespective of their species identity, diversity or composition, had a strong positive effect on invertebrate communities. Over five years, the establishment of woody plants in the

experimental plots led to the reassembly of invertebrate communities of (generally) increasing similarity to our woodland reference site. The trajectory of reassembly was more rapid for invertebrate higher taxa than for ant species assemblages, potentially due to the coarser level of resolution of the higher taxon data and limited ability to discriminate species turnover within such broad groupings. Although our study did not aim to establish the mechanism(s) behind the woody species effect on invertebrate community change, it is likely to occur through increases in resource and habitat niche dimensionality (Hutchinson 1959), and increasing ecosystem productivity leading to “more individuals” (Srivastava and Lawton 1998). Woody species add both vertical and horizontal structure on different scales to herbaceous species, produce slow decomposing litter, and increase shading (Messier et al. 1998). Through these and other processes, woody species can alter the abiotic conditions of their immediate surroundings, changing understory light availability, altering soil temperatures, and capturing litter moisture. Our findings were consistent with studies investigating the ecological value of woody species presence, such as those that promote the conservation benefits of planting monocultures of plantation timber (e.g., Brockerhoff et al. 2008). Timber plantations have been shown to support increased diversity of higher-level consumers when compared to the surrounding agricultural matrix (Cunningham et al. 2005), but typically with a distinct species composition (and often with lower abundances) relative to that of remnant vegetation in the region (Irwin et al. 2014). We identified a pattern of increasing higher taxa similarity to the woodland between 2010 and 2012, which subsequently decreased in later years as the invertebrate community appeared to diverge on a differing successional trajectory. Potentially such a pattern could indicate that the woodland was the source

of early colonizers of the experiment, but as the trees in the experimental plots matured, differences in floral composition between the experimental site and the reference woodland became larger, and successful later colonists may have arrived from other source localities.

Woody plant diversity does not influence invertebrate diversity

Bottom-up diversity effects driven by woody species appeared to have little role in shaping the diversity and composition of invertebrate communities during the early stages of habitat restoration. Differences in diversity and compositional responses detected among woody species treatments were idiosyncratic, showing no consistent evidence of tree species-identity, composition, or diversity effects. While we found some consistencies in the magnitude of effects for particular tree treatments (e.g., trees + fabaceous shrubs), we found no evidence of a true bottom-up diversity effect where increased woody species diversity drives ant diversity. Importantly, this lack of effect was evident over the full 5 yr of this experiment, with no evidence for any interaction between diversity treatment and time since planting. This is perhaps surprising, given the strong observational and experimental evidence for grassland diversity effects on invertebrates and the fact that forest plant diversity has been found to be a good predictor of invertebrate community diversity and functional performance, at least in some studies (Riihimäki et al. 2005, Basset et al. 2012, Haase et al. 2015). However, the majority of the apparent tree diversity effects in previous studies has been based on correlational evidence across natural gradients among sites or habitat types, and the causal drivers of these relationships have not been identified. For example, when assessing ant diversity across a tree diversity gradient in China, Staab et al. (2014) found that higher tree diversity increased the richness of ants at higher trophic levels. However, both tree and ant diversity could have been driven by underlying extrinsic drivers and they may not, in fact, be causally linked. Furthermore, several studies (Sobek et al. 2009c, Scherber et al. 2014) have noted that correlations between tree diversity and faunal diversity across systems are often taxon specific, potentially due to the complex nature of the indirect links through which woody species influence diversity at higher trophic levels. Just as in the earlier grassland diversity literature, the key need is for careful experimental manipulation to control for potential confounding effects of extrinsic drivers so that we can discriminate the true causal link between tree diversity and faunal diversity. Recently, a study at the BEF-China experiment found that multiple facets of woody species diversity can influence the stability and diversity of species interactions across several trophic levels (Staab et al. 2015). However, in our system, where we have also undertaken a controlled comparison, there appears to be no clear effect of tree diversity or composition on ant diversity over the early stages of experimental woodland restoration.

An obvious limitation of testing faunal responses to tree diversity manipulation is the greater dispersal range of many generalist species at consumer trophic levels. We countered this as much as possible by focusing primarily on social taxa, with relatively fixed colony locations. However, we acknowledge that a weakness of all tree diversity experiments conducted so far is that plot sizes are small relative to the dispersal distances of most key target taxa. Another caveat is that the relatively young age of current tree diversity experiments may reduce our ability to detect the effects we hypothesized, as bottom-up diversity effects are likely to be slower to manifest in tree-dominated rather than grassland-dominated systems (Leuschner et al. 2009). Revisiting these questions after longer periods of time, using our experimental site and others like it, will be needed to further corroborate the lack of relationship that we found. As the trees mature, the invertebrate communities might also vertically stratify to some degree, meaning that future studies should also account for variation in communities between the ground stratum and the canopy (Floren et al. 2014). In such structurally diverse forests, it would also be more important to use a broader range of sampling methods that target different suites of taxa with different life history strategies, as there can be limitations in focusing solely on the surface-active epigeic fauna, as is the case with pitfall trapping.

Removal of weedy understory leads to biodiversity gains

Interestingly, the use of herbicide application to experimentally reduce understory plant cover and richness had positive effects on ant species richness and abundance, as well as positive effects on rates of community reassembly of invertebrate “higher taxa” composition towards the reference woodland. This is contrary to expectations from bottom-up diversity effects, and we propose two potential explanations for these findings. First, in the context of old-field succession (in which the tree diversity experiment was established), one of the most important factors for faunal recolonization might be the degree to which biotic and abiotic conditions within treatment plots match conditions typical of remnant vegetation in the region. In undisturbed woodlands in southwest Australia, the understory generally has a very open structure and there is rarely any substantial ground cover present, except for short intervals after winter rains. Dense herbaceous understories only occur at woodland remnant edges that are heavily invaded by nonnative plants from adjacent agricultural land subject to high fertilizer addition (Hobbs and Huenneke 2002). In our study, the herbicide treated plot quarters appeared (qualitatively) to more closely match the structure and abiotic understory conditions of local remnant vegetation, potentially providing more natural conditions for ground-dwelling woodland invertebrates.

Secondly, differences in invertebrate capture rates between herbicide and no-herbicide treatments might result from sampling bias in invertebrate trappability in

bare vs. vegetated substrates (Melbourne 1999). Although it is never fully possible to overcome trapping artefacts when using activity-based trapping methods, this is unlikely to explain our conclusions because the magnitude of herbicide treatment effect was unrelated to the magnitude of structural differences in vegetation that likely influenced trappability. Therefore, models of ant abundance in which the herbicide treatment effect increased through time cannot be explained by varying trappability of ants as a function of herbaceous vegetation cover.

Implications for conservation and restoration practices

Understanding the temporal patterns, magnitude and mechanisms of bottom-up diversity effects in woodland systems is important for both conservation and restoration. All too commonly, ecological restoration has been carried out with the assumption that successful plant community reassembly toward an idealized historic state will also result in faunal community reassembly (Majer 2009). Unfortunately, this so-called “field of dreams hypothesis” (Palmer et al. 1997) has received limited empirical support, with community reassembly frequently occurring on alternative trajectories that do not converge toward the desired reference state, even after long periods of time (e.g., Majer et al. 2013). Determining the underlying causes of this lack of convergence has been hampered by the lack of experimental manipulations of potential drivers of bottom-up diversity effects on higher-level consumers. Studies examining bottom-up effects across gradients of woody species diversity have usually used space-for-time substitution along habitat restoration or forestry plantation chronosequences. For example, Barton et al. (2013) studied arthropod assemblages in monoculture and mixed species plantings of between 6 and 20 yr old, finding that increased tree diversity in mixed plantings did not increase the diversity of sampled arthropods. In fact, diversity of consumer trophic levels followed a “more individuals” pattern, with greater herbivore abundances in *Eucalyptus* monocultures driving higher diversity of secondary consumers. Similarly, in our study, there was no effect of woody species diversity on ground-dwelling invertebrate communities, over and above the tree monoculture effect, suggesting that the most important factor (at least in early succession) is the structural element to woody plant cover, rather than tree richness, composition, or identity. It is important to note, though, that there is observational evidence from long-term restoration chronosequences suggesting that differences between monospecific vs. diverse tree plantings might increase over longer time intervals (Cunningham et al. 2005, Grimbacher et al. 2007). Balancing short- and long-term faunal restoration goals with financial and logistic constraints will be important when selecting woody species for revegetating degraded land. Interestingly, our experimental findings also show that some potential problems encountered in monoculture plantings in natural systems, such as high

understorey weed invasion rates, can be mitigated to rapidly and effectively enhance faunal reassembly trajectories. By combining monoculture planting of a rapidly growing native tree with understorey management of non-native weeds we were able to push recolonizing invertebrate communities onto reassembly trajectories that, in early succession at least, more rapidly converged with communities found in local remnant vegetation, producing a simple and effective win-win for both carbon sequestration and biodiversity conservation.

ACKNOWLEDGMENTS

We acknowledge funding from the Australian Research Council, via Discovery grant DP130102203 awarded to Richard Hobbs. We thank Mike Craig, Helen White, and an anonymous reviewer for comments on earlier versions of this manuscript, and Brian Heterick for confirming ant identifications. We also thank those who planted and maintained the Ridgefield Tree Diversity experiment, in particular Rebecca Campbell, Kris Hulvey, Tim Morald, Michael Perring, and Rachel Standish, and many volunteers who assisted with pitfall trapping over the years, including Russell Dinnage, Laura Fagan, Camilla Gallagher, Bridget Johnson, Fransina Latumahina, Mark Murphy, Rachel Standish, Helen White, Thomas Windsor, and Wayne Zilko.

LITERATURE CITED

- Agosti, D., J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. 2000. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, D.C., USA.
- Ampoorter, E., L. Baeten, M. Vanhellefont, H. Bruelheide, M. Scherer-Lorenzen, A. Baasch, A. Erfmeier, M. Hock, and K. Verheyen. 2015. Disentangling tree species identity and richness effects on the herb layer: first results from a German tree diversity experiment. *Journal of Vegetation Science* 26: 742–755.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike’s information criterion. *Journal of Wildlife Management* 74:1175–1178.
- Barton, P. S., M. J. Colloff, K. R. Pullen, and S. A. Cunningham. 2013. Arthropod assemblages in a focal tree species (*Eucalyptus microcarpa*) depends on the species mix in restoration plantings. *Biodiversity and Conservation* 22:2091–2110.
- Basset, Y., et al. 2012. Arthropod diversity in a tropical forest. *Science* 338:1481–1484.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bobbink, R., et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20:30–59.
- Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008. Plantation forests and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation* 17:925–951.
- Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 489:59–67.
- Chase, J. M., and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: Why standardised sampling is not enough. *Ecology Letters* 16:17–26.
- Crowther, T. W., et al. 2015. Mapping tree density at a global scale. *Nature* 525:201–205.
- Cunningham, S. A., R. B. Floyd, and T. Weir. 2005. Do *Eucalyptus* plantations host an insect community similar

- to remnant Eucalyptus forest? *Austral Ecology* 30: 103–117.
- Didham, R. K., G. M. Barker, J. A. Costall, L. H. Denmead, C. G. Floyd, and C. H. Watts. 2009. The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. *New Zealand Journal of Zoology* 36:135–163.
- Dinnage, R., M. W. Cadotte, N. M. Haddad, G. M. Crutsinger, and D. Tilman. 2012. Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecology Letters* 15: 1308–1317.
- Ebeling, A., S. T. Meyer, M. Abbas, N. Eisenhauer, H. Hillebrand, M. Lange, C. Scherber, A. Vogel, A. Weigelt, and W. W. Weisser. 2014. Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. *PLoS ONE* 9:e106529.
- Floren, A., W. Wetzel, and M. Staab. 2014. The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. *Myrmecological News* 19:65–74.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27:2865–2873.
- Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845–858.
- Grimbacher, P. S., C. P. Catterall, J. Kanowski, and H. C. Proctor. 2007. Responses of ground-active beetle assemblages to different styles of reforestation on cleared rainforest land. *Biodiversity and Conservation* 16:2167–2184.
- Gunawardene, N., J. D. Majer, and J. Edirisinghe. 2012. Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. *Myrmecological News* 17:81–90.
- Haase, J., B. Castagneyrol, J. H. C. Cornelissen, J. Ghazoul, J. Kattge, J. Koricheva, M. Scherer-Lorenzen, S. Morath, and H. Jactel. 2015. Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos* 124:1674–1685.
- Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158:17–35.
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029–1039.
- Harrison, X. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616.
- Hobbs, R. J., and L. F. Huenneke. 2002. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324–337.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hutchinson, G. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145–159.
- Irwin, S., et al. 2014. The value of plantation forests for plant, invertebrate and bird diversity and the potential for cross-taxon surrogacy. *Biodiversity and Conservation* 23:697–714.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Knops, J. M., et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286–293.
- Leuschner, C., H. F. Jungkunst, and S. Fleck. 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. *Basic and Applied Ecology* 10:1–9.
- Magurran, A. E., and B. J. McGill, editors. 2011. *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford, UK.
- Majer, J. D. 2009. Animals in the restoration process—progressing the trends. *Restoration Ecology* 17:315–319.
- Majer, J. D., B. Heterick, T. Gohr, E. Hughes, L. Mounsher, and A. Grigg. 2013. Is thirty-seven years sufficient for full return of the ant biota following restoration? *Ecological Processes* 2:1–12.
- Melbourne, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Australian Journal of Ecology* 24:228–239.
- Messier, C., S. Parent, and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9:511–520.
- Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The functions of biological diversity in an age of extinction. *Science* 336: 1401–1406.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Oksanen, J., et al. 2016. *vegan: Community Ecology Package*. R package version 2.3-5. <https://CRAN.R-project.org/package=vegan>
- Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291–300.
- Perring, M. P., R. J. Standish, K. B. Hulvey, L. Lach, T. K. Morald, R. Parsons, R. K. Didham, and R. J. Hobbs. 2012. The Ridgefield Multiple Ecosystem Services Experiment: Can restoration of former agricultural land achieve multiple outcomes? *Agriculture, Ecosystems and Environment* 163:14–27.
- R Development Core Team. 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Riihimäki, J., P. Kaitaniemi, J. Koricheva, and H. Vehviläinen. 2005. Testing the enemies hypothesis in forest stands: The important role of tree species composition. *Oecologia* 142: 90–97.
- Scherber, C., et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553–556.
- Scherber, C., E. A. Vockenhuber, A. Stark, H. Meyer, and T. Tscharntke. 2014. Effects of tree and herb biodiversity on Diptera, a hyperdiverse insect order. *Oecologia* 174: 1387–1400.
- Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* 152:738–750.
- Sobek, S., M. M. Goßner, C. Scherber, I. Steffan-Dewenter, and T. Tscharntke. 2009a. Tree diversity drives abundance and spatiotemporal β -diversity of true bugs (Heteroptera). *Ecological Entomology* 34:772–782.
- Sobek, S., C. Scherber, I. Steffan-Dewenter, and T. Tscharntke. 2009b. Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia* 160:279–288.
- Sobek, S., T. Tscharntke, C. Scherber, S. Schiele, and I. Steffan-Dewenter. 2009c. Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecology and Management* 258:609–615.
- Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory

- using tree-hole communities. *American Naturalist* 152: 510–529.
- Staab, M., A. Schuldt, T. Assmann, and A.-M. Klein. 2014. Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. *Ecological Entomology* 39:637–647.
- Staab, M., N. Blüthgen, and A.-M. Klein. 2015. Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. *Oikos* 124:827–834.
- Staab, M., H. Bruelheide, W. Durka, S. Michalski, O. Purschke, C. Zhu, and A.-M. Klein. 2016. Tree phylogenetic diversity promotes host – parasitoid interactions. *Proceedings of the Royal Society B* 283:20160275.
- Symstad, A. J., E. Siemann, and J. Haarstad. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. *Oikos* 89:243–253.
- Verheyen, K., et al. 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* 45:29–41.
- Warton, D., and F. K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:276–281.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1662/supinfo>