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Carabid activity-density increases with forest vegetation diversity at different spatial scales

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Abstract. 1. More diverse forests are generally more resistant to insect herbivores. This might be due to positive effects of tree diversity on predation. Although the enemies hypothesis has received conflicting evidence in forest ecosystems.

2. Carabids were sampled by pitfall trapping in a tree diversity experiment, at the centre of plots ranging from one to five tree species mixtures. The composition and vertical structure of the vegetation was assessed at three scales, in the understorey, in the canopy of the experimental plots, and in the surrounding area of each plot.

3. None of the tested vegetation variables had an effect on the species richness of carabids. In contrast, the vegetation compositional diversity at the understorey, canopy and surrounding scales had additive and positive effects on the activity-density of the carabids.

4. Our findings indicate that more diverse forests can host a higher activity-density of predatory carabids, as a result of the combined effect of horizontal and vertical vegetation diversity, which might increase both habitat quality and the amount of feeding resources. This highlights the relevance of manipulative tree diversity experiments to identify the ecological filters shaping local carabid communities.

Key words. Biodiversity, carabids, *Carabus problematicus*, community ecology, *Harpalus rufipalpis*, mixed forests.

Introduction

Several reviews (Jactel & Brockerhoff, 2007; Castagneyrol *et al*., 2014; Jactel *et al*., 2017) have suggested that more diverse temperate forests would be more resistant to pest insect damage, supporting the *associational resistance* concept (Barbosa *et al*., 2009). Two main mechanisms have been proposed to account for reduced insect herbivory in mixed forests (Moreira *et al*., 2016). First, host trees may be less likely to be located and colonised by herbivores in mixed forests as a result of the presence of non-host trees, which would reduce the amount of resources to herbivores (i.e. resource concentration hypothesis, Root, 1973; Hamback & Englund, 2005; Underwood *et al*., 2014) and disrupt physical or chemical cues used to identify a suitable host; i.e. host apparency hypothesis (Jactel *et al*., 2011; Castagneyrol *et al*., 2013). Second, forests that are more diverse may host more abundant or more diverse natural enemies that would in turn be more effective at controlling insect herbivores through parasitism or predation, i.e. the *natural enemies* hypothesis (Root, 1973).

There are several theoretical arguments to support the enemies hypothesis. The community ecology theory predicts that multiple environmental filters shape local species communities. They include the biogeographical pools of species, dispersal abilities that limit habitat colonisation, abiotic factors of habitat quality, and ultimately biotic interactions (Hildrew & Giller, 1994; Stearns, 1994; Cardinale *et al*., 2011; 2018). The latter two filters can be modified by tree species mixing. Mixed species forests are known to provide more stable microclimatic conditions (Heilmann-Clausen *et al*., 2005; Melguizo-Ruiz *et al*., 2012), which might benefit to poikilothermic organisms like insect predators or parasitoids (Corcos *et al*. 2018). Species diverse forests are also generally more structurally complex, offering a larger array of nesting or overwintering resources to predators like birds and bats (Boyles, 2007; Charbonnier *et al*., 2016; Muiruri *et al*., 2016; Martins *et al*., 2017). In addition, species diversity effects can cascade across levels within the food webs

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(Fornoff *et al*., 2019), species rich plant communities offering larger food resources and thus host more diverse herbivore communities, which in turn may favour the establishment of more diverse predator assemblages (Scherber *et al*., 2010). Several studies have confirmed those correlations among species richness at both local (Castagneyrol & Jactel, 2012) and regional levels (Zhang *et al*., 2017).

Few observational studies have confirmed that associational resistance is mediated by better biological control. It was demonstrated for a birch defoliator (Riihimäki *et al*., 2005), a pine scale insect (Jactel *et al*., 2006), and aphids (Xoaquín *et al*., 2012) and suggested for the chestnut gall wasp (Guyot *et al*., 2016; Fernandez-Conradi *et al*., 2018). Experiments with dummy caterpillars have shown increased bird predation rates on trees surrounded by heterospecific neighbours (Muiruri *et al*., 2016). Although other studies using tree diversity experiments did not find a higher diversity of arthropod predators associated with more diverse forest plots, like spiders (Schuldt *et al*., 2011) and ants (Staab *et al*., 2014).

Similar questions arise for carabid beetles, a group that comprises both predatory and omnivorous species. Comparative studies of pure vs. mixed stands in managed forests (Walsh *et al*., 1993; Scheu *et al*., 2003; Oxbrough *et al*., 2012; Barsoum *et al*., 2014) and replicated in tree diversity experiments (Vehviläinen *et al*., 2008; Yeeles *et al*., 2017) consistently show no tree species richness (or mixture) effect on the abundance or diversity of carabids. To date such studies have not distinguished between carabid functional groups, making it difficult to precisely infer the response of carabid predators to tree diversity and their role in associational resistance in mixed species forests. Furthermore, prior studies did not take into account the effect of tree canopy diversity on understorey vegetation cover or diversity, which are known to shape ground beetle communities (Sitzia *et al*., 2015; Zou *et al*., 2015; Oxbrough *et al*., 2016). Finally, the surrounding area of sampled pure and mixed forest stands and their size were not controlled in observational studies. These two factors are known to influence the dispersal of carabids (Duflot *et al*., 2014) and might have obscured the effect of local tree diversity effect (Bommarco & Banks, 2003). For example, the carabid community of small forest plots might be more influenced by colonisation processes from neighbouring forest or grassland patches than by their own structure or composition (de la Pena *et al*., 2003; Decocq *et al*., 2016; Duflot *et al*., 2016). Small isolated forest patches are also known to have depleted assembly of carabids as compared to neighbouring large forest tracts (Lovei & Cartellieri, 2000).

Here, we used a systematic grid of pitfall traps in a manipulative experiment to test for the effect of vegetation diversity on carabid beetles while controlling spatial scale issues. For that, we considered three nested plant diversity scales: within plot understorey vegetation diversity (around pitfall traps), canopy tree diversity at the plot level, and tree cover diversity in the surrounding plots. We considered both the compositional and structural vegetation diversity using data on plant species abundance and size (height). In particular, we tested the hypothesis that the diversity of understorey vegetation, canopy trees and surrounding patches of experimental plots have additive effects on local species richness and activity-density of carabid beetles.

Materials and methods

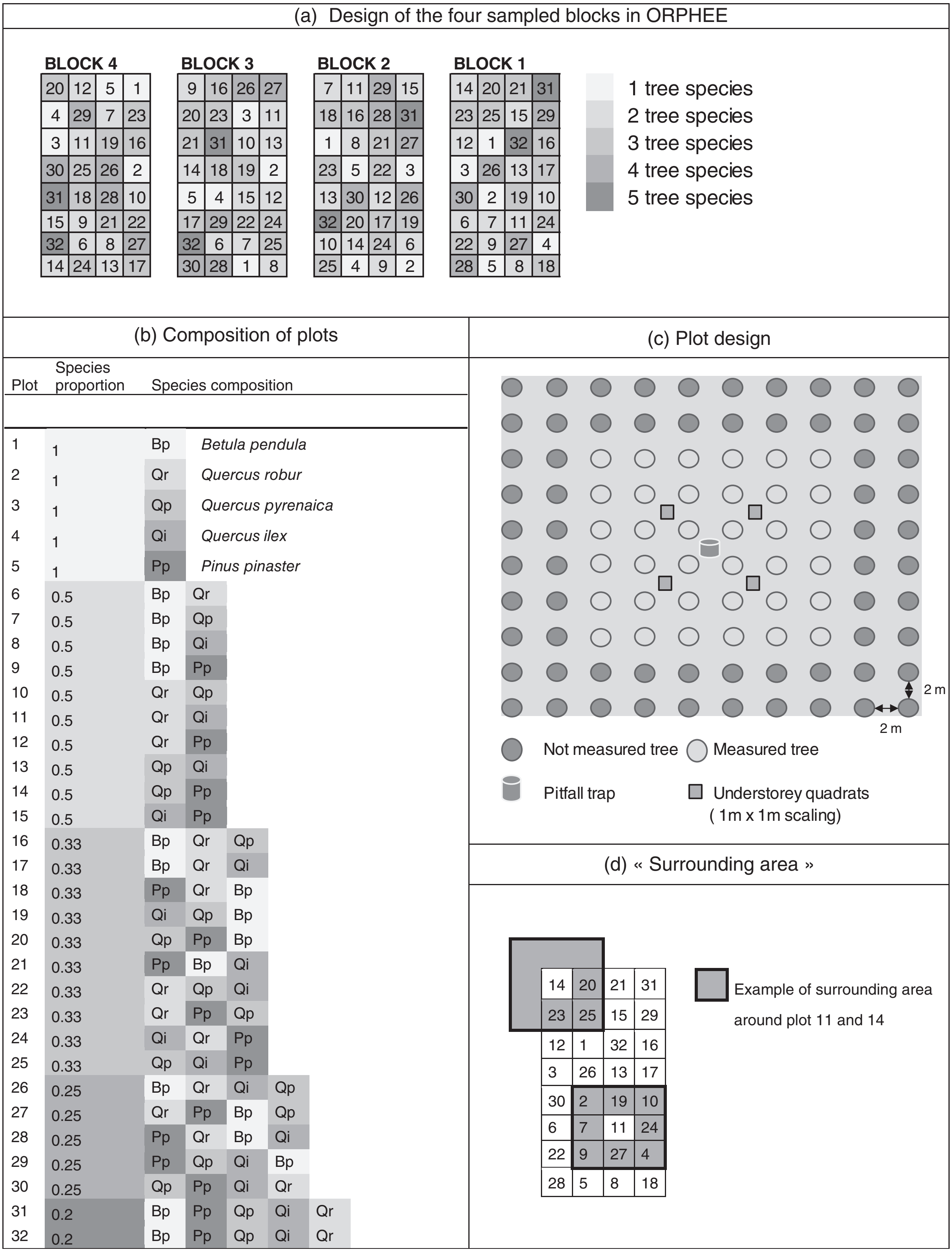
Study area

The study was conducted in the ORPHEE experiment, which belongs to the global TreeDivNet network (Paquette *et al*., 2018; Verheyen *et al.* 2016) The experimental plantation was established on a 12 ha clear-cut of maritime pine stands, on a sandy podzolic soil. It is located in southwestern France, 40 km south of Bordeaux, in a region characterised by a mild oceanic climate, with mean annual temperature of 12.5 °C and mean total precipitations of ca. 950 mm. The experimental site is in the heart of the Landes de Gascogne forest, the largest artificial forest in Europe, with about 1 million ha of pure maritime pine plantations. To establish the tree diversity experiment, in 2008, we planted 25 600 trees from five local, native species (European birch: *Betula pendula*, Roth; Pedunculate oak: *Quercus robur*, Linnaeus; Pyrenean oak: *Q. pyrenaica*, Willdenow; Holm oak: *Q. ilex*, Linnaeus; and Maritime pine: *Pinus pinaster*, Aiton). The experiment is composed of eight blocks, with 32 plots in every block corresponding to the 31 possible combinations of one to five species, with an additional replicate of the combination of the five species. Each plot contains 10 rows of 10 trees planted 2 m apart resulting in 100 trees per plot, with a plot area of 400 m^2. Tree species are planted according to a systematic alternate pattern, so that each tree of a given species is surrounded by at least one tree of all other tree species present in a given composition (see details in the study by Castagneyrol *et al*., 2013; Damien *et al*., 2016).

Carabid sampling

Carabid beetles were sampled with pitfall traps (Brown & Matthews, 2016; Engel *et al*., 2017), which were made of glass jars, 90 mm diameter, 100 mm high (445 ml volume) filled with ethylene glycol. One pitfall trap was placed at the very centre of all plots within four adjacent blocks (Fig. 1). This resulted in 32 traps per block (128 in total), which were thus established along a systematic grid of ca. 21.5 m × 21.5 m. Pitfall traps were used during the summer season, all installed the same day on the 4 June 2012 and emptied twice, all the same day (25 June and 17 July), hence 44 days of trapping. All pitfall traps were thus active for the same time period, i.e. performing the same sampling effort with no need for data rarefaction.

Captures from the two assessment periods were pooled for data analyses. Beetles were conserved in deep freezer prior identification. Insects were identified to the species level, using external morphological discriminating characters or genitalia and aedeagus examinations where required (Jeannel, 1955; Anichtchenko, 2013). Reference books were those for the French carabids fauna (Jeannel, 1941; 1942; Coulon *et al*. 2011a, 2011b; Maguère, 2016), and the European fauna (Trautner & Geigenmüller, 1987; Hurka, 1996). Carabid species were qualified as predator, phytophagous or omnivorous according to morphological characters of mouthparts, in particular mandibles and maxillae forms (Forsythe, 1982; Ribera *et al*., 2001).



(a) Design of the four sampled blocks in ORPHEE

BLOCK 4

20	12	5	1
4	29	7	23
3	11	19	16
30	25	26	2
31	18	28	10
15	9	21	22
32	6	8	27
14	24	13	17

BLOCK 3

9	16	26	27
20	23	3	11
21	31	10	13
14	18	19	2
5	4	15	12
17	29	22	24
32	6	7	25
30	28	1	8

BLOCK 2

7	11	29	15
18	16	28	31
1	8	21	27
23	5	22	3
13	30	12	26
32	20	17	19
10	14	24	6
25	4	9	2

BLOCK 1

14	20	21	31
23	25	15	29
12	1	32	16
3	26	13	17
30	2	19	10
6	7	11	24
22	9	27	4
28	5	8	18

(b) Composition of plots

Plot	Species proportion	Species composition				
1	1	Bp	*Betula pendula*			
2	1	Qr	*Quercus robur*			
3	1	Qp	*Quercus pyrenaica*			
4	1	Qi	*Quercus ilex*			
5	1	Pp	*Pinus pinaster*			
6	0.5	Bp	Qr			
7	0.5	Bp	Qp			
8	0.5	Bp	Qi			
9	0.5	Bp	Pp			
10	0.5	Qr	Qp			
11	0.5	Qr	Qi			
12	0.5	Qr	Pp			
13	0.5	Qp	Qi			
14	0.5	Qp	Pp			
15	0.5	Qi	Pp			
16	0.33	Bp	Qr	Qp		
17	0.33	Bp	Qr	Qi		
18	0.33	Pp	Qr	Bp		
19	0.33	Qi	Qp	Bp		
20	0.33	Qp	Pp	Bp		
21	0.33	Pp	Bp	Qi		
22	0.33	Qr	Qp	Qi		
23	0.33	Qr	Pp	Qp		
24	0.33	Qi	Qr	Pp		
25	0.33	Qp	Qi	Pp		
26	0.25	Bp	Qr	Qi	Qp	
27	0.25	Qr	Pp	Bp	Qp	
28	0.25	Pp	Qr	Bp	Qi	
29	0.25	Pp	Qp	Qi	Bp	
30	0.25	Qp	Pp	Qi	Qr	
31	0.2	Bp	Pp	Qp	Qi	Qr
32	0.2	Bp	Pp	Qp	Qi	Qr

(c) Plot design

(d) « Surrounding area »

14	20	21	31
23	25	15	29
12	1	32	16
3	26	13	17
30	2	19	10
6	7	11	24
22	9	27	4
28	5	8	18

Fig. 1. Design of the ORPHEE experiment. (a) The four blocks contain 32 randomly distributed plots. (b) Each plot contains one of the 31 possible combinations of 1, 2, 3, 4 or 5 tree species, except plots 31 and 32, which are the replicates of the five-species mixture. (c) All plots of the four blocks received a central pitfall trap and were assessed for vegetation diversity and structure. (d) The eight neighbouring plots of each sampled plots were used to define a *surrounding area*.

Vegetation diversity and structure variables

Understorey vegetation diversity and structure. Vascular plant surveys in the understorey layer of sampled plots were conducted in July 2012. In each plot, four quadrats of 1 × 1 m were established in the central area with the same, regular, position in each plot (Fig. 1). Abundance of each plant species was estimated in all quadrats using the Domin scale (MacLean *et al.*, 2015). A Shannon diversity index was calculated for each quadrat and then averaged at the plot level. Understorey vegetation height was measured at the four corners of each quadrat, yielding 4 × 4 = 16 height measurements per plot. They were used to calculate a mean and variance height value per plot.

Canopy tree diversity and structure of the plots. Canopy tree diversity was determined by the design of the experiment, as we had recorded <1% mortality in young trees since planting 4 years earlier. We thus simply calculated a Shannon tree diversity index per plot using the number of tree species planted (one to five) and the proportion of trees per species (e.g. 50% in a two-species mixture). The height of the 36 inner trees (six inner rows of six central trees), irrespective of the tree species, was measured in winter 2011–2012. It was used to calculate the mean and variance of tree height per plot.

Surrounding area diversity and structure. Each sampled plot was surrounded by eight neighbouring plots (Fig. 1), which were considered to form a *surrounding area* (Fig. 1d). In each surrounding area, we estimated a Shannon tree diversity index based on a tree species proportion calculated as the number of trees from a given species divided by 800 (8 plots of 100 trees). We used this theoretical maximum of trees in surrounding plots to take into account the fact that no trees were present in grassland edges (see example of surrounding area of plot 14 in Fig. 1d).

The mean height of trees in the eight neighbouring plots was used to calculate the mean and variance of tree height per surrounding area. The tree height was set to zero when the neighbouring edge was of grassland type.

Statistical analyses. Prior to inference modelling, we verified whether there was any spatial autocorrelation of carabid captures. Using longitude and latitude as geographical coordinates for each of the 128 pitfall traps (Fig. 1) and semivariogram graphs, we never detected any aggregation patterns, even at very low distances, on total or species-specific activity-density of carabids (Supporting Information Appendix S1).

For inference model construction, we used three types of variables describing vegetation composition (Shannon diversity) and structure (mean and variance of height) for three vegetation elements (understorey, canopy tree, and surrounding area). We also considered the mean cover of understorey vegetation. We did not test the effect of canopy tree cover as it was kept constant (100 trees/plot) by construction in the experiment. Explanatory variables are listed in Table 1.

We first built a complete, generalised linear mixed model (Bolker *et al.*, 2009) without interactions, with Block as random factor. We could introduce the nine variables in the complete model, as they were not strongly correlated with each other [variation inflation

Table 1. Vegetation elements, acronyms, explanatory variables, definitions, Mean, minima (Min.) and maxima (Max.) values across the 128 plots and VIF.

Explanatory compartments	Acronyms	Explanatory variables	Definition	Mean	Min	Max	VIF
Understorey plants	UND_DIV	Understorey diversity	Mean Shannon diversity ($\log_{10}$ base) of vascular plants in four quadrats per plot.	0.14	0.07	0.21	1.39
	UND_MH	Understorey mean height	Mean height of understorey vegetation averaged across 16 measure points (four per quadrat and four quadrats per plot) (in cm)	69.9	47.2	98.1	1.51
	UND_VH	Understorey height variance	Variance of understorey vegetation height across the 16 measure points (four per quadrat and four quadrats per plot) (in cm^2)	465.2	70.0	1203.3	1.64
Canopy trees	TREE_DIV	Tree diversity	Shannon diversity ($\log_{10}$ base) of trees per plot.	0.09	0.0	0.16	1.77
	TREE_MH	Tree height mean	Mean height of the 36 inner trees per plots (in cm).	196.8	55.5	426.1	1.69
	TREE_VH	Tree height variance	Height variance of the 36 inner trees per plots (in cm^2).	15814.3	620.8	35647.7	2.14
Surrounding area	SUR_DIV	Tree diversity in surrounding area	Shannon diversity ($\log_{10}$ base) of trees in the eight neighbouring plots	0.15	0.12	0.16	1.47
	SUR_MH	Mean tree height in surrounding area	Mean height of trees in the eight surrounding plots (in cm).	150.6	41.3	258.9	1.52
	SUR_VH	Variance of tree height in surrounding area	Variance of tree height in the eight surrounding plots (in cm^2).	11539.2	276.5	28916.9	1.15

factor (VIF)]. We applied a procedure of model selection based on AIC criteria corrected for small sample size (AICc). In the first step, we ranked the models according to the difference in AICc between a given model and the model with the lowest AICc (ΔAICc). ΔAICc revealed that no particular model was clearly better than the others. In the second step, a procedure of multimodel inference was thus applied on the set of best models, i.e. with a ΔAICc <2. Model averaging aimed at estimating parameters using all the models in the set. We chose the *full* average procedure to obtain unbiased values of parameters. The response variables were the species richness and total activity-density of carabids. Statistical analyses were performed using R software 3.3.2 (R Development Core Team, 2016) with the *MuMin* package for multi-model inference (Barton, 2018), and *vegan* package (Oksanen et al., 2018). We used the *HH* package to select variables with VIF value smaller than 10 (Dormann *et al.*, 2013). A Poisson distribution was used for the sampling distribution of count data (O'Hara & Kotze, 2010). For each final model, R^2 values were calculated based on the study by Nakagawa and Schielzeth (2013) to estimate the variance explained by fixed effects (marginal R^2, Rm^2) and by fixed and random effects (conditional R^2, Rc^2).

Results

Ground beetle community

A total of 26 carabid beetle species and 1258 individuals were caught in the experiment (Supporting Information Appendix S2). Twelve species and 829 individuals (66% of all carabids) were classified as predatory and 14 species and 429 individuals (34% of all carabids) as omnivorous. The species activity-density distribution was highly skewed, with two species *Carabus problematicus* (n = 768, 61% of all carabids) and *Harpalus rufipalpis* (n = 363, 29% of all carabids) representing 90% of total captures. *C. problematicus* represented 93% of all the predators and *H. rufipalpis* 85% of all the omnivores.

Effects of vegetation on carabid diversity and activity-density

We did not find any significant effect of any vegetation variables on carabid species richness (Supporting Information Appendix S3). We thus focused on activity-density data only.

Table 2. Summary of the best mixed-effect models testing the effects of understorey, canopy and surrounding area vegetation on all carabids activity-density (CAR_AD), *Carabus problematicus* activity-density (CARPRO) and *Harpalus rufipalpis* activity-density (HARRUF).

					Models comparison		
Response variables	Explanatory compartments	Explanatory variables	Parameter estimate (±SE)	z-value	R^2m (R^2c)	AICc	wi
CAR_AD (seven models)	Understorey plants	**UND_DIV**	**0.15** (0.03)	**4.411*** **	0.417 (0.484)	814.28	0.13
		UND_MH	**0.13** (0.03)	**3.863*** **	0.416 (0.476)	814.29	0.12
	Canopy trees	**TREE_DIV**	**0.13** (0.04)	**3.088** **	0.393 (0.466)	814.78	0.10
		TREE_MH	−0.03 (0.04)	0.686	0.402 (0.470)	814.88	0.09
		TREE_VH	0.05 (0.05)	0.984	0.403 (0.477)	815.17	0.08
	Surrounding area	**SUR_DIV**	**0.18** (0.04)	**4.909*** **	0.391 (0.455)	815.23	0.08
		SUR_MH	**−0.11** (0.04)	**3.044** **	0.396 (0.464)	816.26	0.05
		SUR_VH	0.03 (0.03)	0.788			
CARPRO (nine models)	Understorey plants	UND_DIV	0.08 (0.05)	1.419	0.324 (0.388)	769.47	0.08
		UND_MH	0.01 (0.03)	0.387	0.330 (0.399)	769.99	0.06
		UND_VH	−0.06 (0.06)	1.050	0.330 (0.385)	770.36	0.05
	Canopy trees	TREE_MH	0.00 (0.04)	0.190	0.336 (0.395)	770.89	0.04
		TREE_VH	**0.23** (0.04)	**5.740*** **	0.307 (0.381)	771.02	0.04
	Surrounding area	**SUR_DIV**	**0.16** (0.05)	**3.401*** **	0.326 (0.393)	771.09	0.04
		SUR_MH	**−0.14** (0.04)	**3.176** **	0.314 (0.394)	771.12	0.04
		SUR_VH	0.02 (0.04)	0.607	0.304 (0.351)	771.27	0.03
					0.311 (0.363)	771.42	0.03
HARRUF (four models)	Understorey plants	**UND_DIV**	**0.22** (0.07)	**3.023** **	0.431 (0.603)	543.44	0.22
		UND_MH	**0.31** (0.07)	**4.290*** **	0.427 (0.596)	544.14	0.15
		UND_VH	**0.16** (0.06)	**2.437** *	0.436 (0.603)	544.91	0.10
	Canopy trees	**TREE_DIV**	**0.20** (0.07)	**3.111** **	0.435 (0.608)	544.97	0.10
		TREE_MH	**−0.25** (0.08)	**3.302*** **			
		TREE_VH	−0.03 (0.07)	0.443			
	Surrounding area	**SUR_DIV**	**0.19** (0.07)	**2.824** **			
		SUR_MH	0.01 (0.03)	0.288			
		SUR_VH	−0.01 (0.03)	0.298			

AICc, AICc weight of models used in averaging (wi) and R^2m and R^2c between bracket. Only models with ΔAICc <2 are shown and were selected for averaging of model coefficient parameter estimates. We indicate in bold significant z-values and P (>|z|) values with following abbreviations to P(>|z|): *P < 0.05, **P < 0.01, and ***P < 0.001.

For total activity-density of carabids six models competed with the best model within 2 units of ΔAICc <2. They included all tested explanatory variables except the variance of understorey vegetation height (UND_VH), not selected by the model selection (Table 2). Their R^2 (m) was between 0.40 and 0.42 and R^2 (c) was between 0.46 and 0.49 (Table 2). Five explanatory variables had significant effects on carabid activity-density (Table 2), two at the understorey level (UND_DIV, UND_MH), one at the canopy tree level (TREE_DIV) and two at the surrounding area level (SUR_DIV and SUR_MH), thus including both compositional and structural variables of the three vegetation compartments.

Activity-density of all carabids significantly increased with the diversity of tree species per plot (Table 2 and Fig. 2b). The understorey plant diversity (i.e. UND_DIV Fig. 2a) and mean height (i.e. UND_MH Fig. 2d) had a significant positive effect on all carabids activity-density. The activity-density of all carabids significantly increased with the diversity of tree species in the surrounding area (SUR_DIV, Fig. 2c). Only the mean height of trees in the surrounding area (SUR_MH) had significant negative effect on carabid activity-density in the focal plot (Fig. 2f).

The activity-density of the two dominant carabid species (*C. problematicus* and *H. rufipalpis*) was influenced by the same combination of compositional and structural diversity factors, for the three vegetation compartments, as shown by the list of important variables retained in the best models (Table 2). Species-specific differences with the general response of carabids corresponded to the relative influence of the same set of explanatory variables. The activity-density of the dominant predatory carabid species (*C. problematicus*) was more affected by tree than by understorey variables (Table 2, Fig. 2). The activity-density of the omnivorous carabid (*H. rufipalpis*) decreased significantly with mean tree height at the plot level (Fig. 2e).

Discussion

The first important result of the study is that none of the tested explanatory variables could explain the species richness of carabid beetles. This could be due to the experimental constraints. The tree diversity experiment was young at the time of the survey (5 years) with a possible time lag in the colonisation process by the local fauna. On average, only 2.6 carabid species were caught per experimental plot and the species activity-density distribution was highly skewed, with two species dominating the overall trap catch. In addition, the plot size was quite small (20 × 20 m) compared to ground beetles' mobility, c.a. 100 m for *C. problematicus* (Dajoz 2002). Those characteristics probably made it difficult to distinguish more or less diverse species assemblages between plot compositions. More generally, congruence between plant and arthropods alpha diversities has been shown to be stronger for herbivores than for predators (Haddad *et al*., 2009; Scherber *et al*., 2010; Castagneyrol & Jactel, 2012; O'Brien *et al*., 2017). It is indeed likely that the effects of plant diversity on secondary consumers result from a cascading bottom-up effect of plant diversity on abundance and diversity of herbivores and detritivores acting as hosts and prey, with possible loose trophic links in the case of generalist predators, or antagonistic forces like intraguild predation. Most of the previous studies that compared carabid species richness in

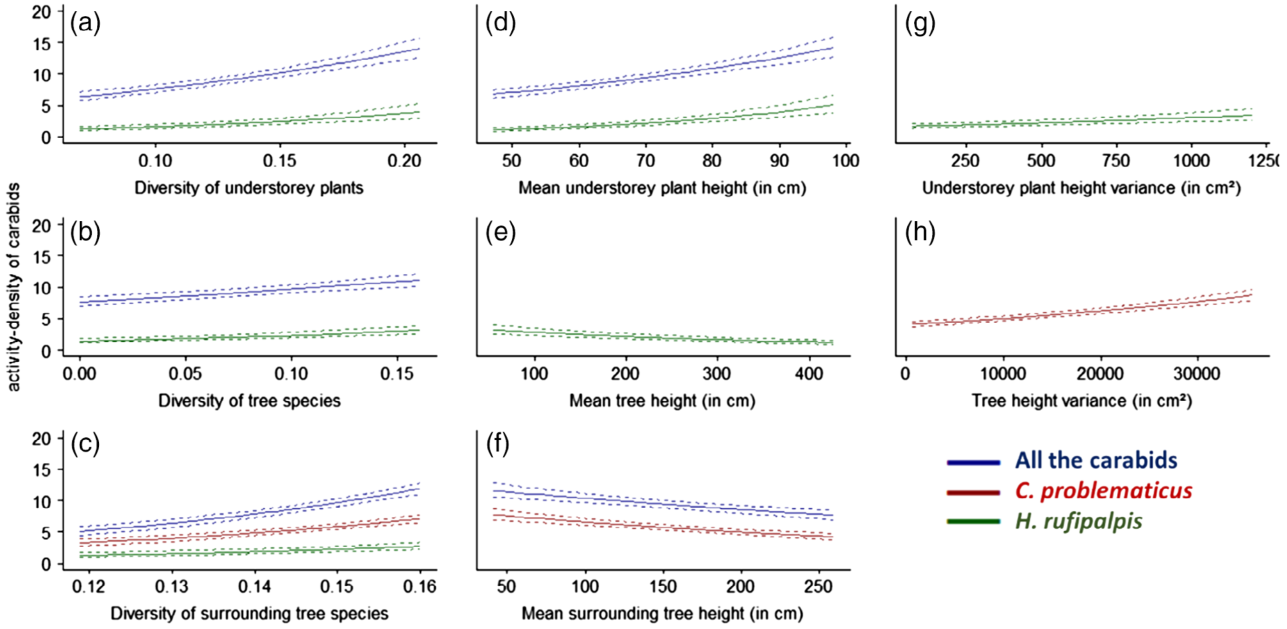


Fig. 2. Relationships between activity-density (number of individuals caught per pitfall trap over the entire trapping period, i.e. 44 days) of all carabids (blue lines), *Carabus problematicus* (red lines) and *Harpalus rufipalpis* (green lines) and a) diversity of the understorey plants (UND_DIV), (b) diversity of tree species (TREE_DIV), (c) diversity of surrounding tree species (SUR_DIV), (d) mean understorey plant height (UND_MH), (e), mean tree height (TREE_MH), (f) mean surrounding tree height (SUR-MH), (g) variance of understorey plant height (UND_VH), (h) variance of tree height (TREE-VH). Dashed lines around regression curve represent glmer prediction confidence intervals. [Color figure can be viewed at wileyonlinelibrary.com]

pure and mixed stands found no significant differences between forests of contrasting plant diversity (Walsh *et al.*, 1993; Work *et al.*, 2004; Oxbrough *et al.*, 2012; 2016; Barsoum *et al.*, 2014). This common pattern was explained by carabid beetles being generalist predators and mobile species. In comparison, ant species richness was shown to increase with tree species richness (Staab *et al.*, 2014; Yeeles *et al.*, 2017) which could be due to ant species being more sedentary as colonial insects, and more specialised on particular prey species like aphids.

The second, even more striking result of the experiment is that almost all explanatory variables related to compositional and structural diversity of the vegetation had significant and positive effects on carabids activity-density. The number of trapped beetles increased with the Shannon diversity of understorey vascular plants and tree species at both plot and surrounding scales. Results are less consistent when comparing activity-density of carabids in pure and mixed-species forests with either positive (Skłodowski *et al.*, 2018; Vehviläinen *et al.*, 2008) or neutral effects of higher tree species diversity (Vehviläinen *et al.*, 2008; Oxbrough *et al.*, 2012; 2016). To the best of our knowledge, our study is the first to test and demonstrate a positive response of carabid activity-density along a gradient of increasing tree and associated vegetation diversity.

Two main reasons might explain the increase in activity-density of carabid beetles in more diverse forests: (i) the improvement of habitat quality and (ii) the increase in abundance or diversity of food resources. Plant and tree diversity increase vegetation structural complexity, which can provide ground beetles with more shelters against adverse climate conditions or top predators (Brose, 2003) like birds. Intraguild predation is known to decrease with increasing vegetation complexity (Finke & Denno, 2002) as prey can hide from predation, thus resulting in higher abundance of predators. Carabids are sensitive to climatic conditions (Schuldt & Assmann, 2011; Viterbi *et al.*, 2013) the variation of which can be buffered in more diverse plant or tree communities, as shown by Lafage *et al.* (2014) and Ehbrecht *et al.* (2017) who found lower daily fluctuations of temperature and drought in forest stands with higher structural complexity. Further studies will be needed to verify such microclimatic variations between the small plots of our tree diversity experiment. Alternatively, the greater diversity of herbaceous and tree species usually increases the amount and diversity of food resources available to phytophagous and omnivorous species (Haddad *et al.*, 2009; Castagneyrol & Jactel, 2012; Ebeling *et al.*, 2014), which in turn represent a more abundant and diverse diet for predatory species (Scherber *et al.*, 2010; Hertzog *et al.*, 2016; Barbaro *et al.*, 2019). Density of carabids can increase with the number of prey items (Roubinet *et al.*, 2017) and a mix of prey species might benefit generalist predators through better nutrient balance and higher dilution of toxins (Evans *et al.*, 1999). The abundance and diversity of prey, particularly in the litter, will have to be better quantified along tree diversity gradients in the ORPHEE experiment.

We also found that carabid activity-density increased with the height of understory vegetation. Although we could not find in the literature any study dealing with the effects of understorey vegetation on carabids in mixed forests, grassland studies can provide relevant information. The results are actually inconsistent, with either positive (Lafage *et al.*, 2014), neutral (Wang *et al.*, 2018; Tsafack *et al.*, 2019) or negative effects (Liu *et al.*, 2016) of herbaceous plant height on activity-density of carabids. In the case of our experiment, we might hypothesise that higher understorey vegetation provided better shelter for carabids against adverse weather conditions or top predators such as birds.

One explanatory variables had a negative effect on general activity-density of carabids in the experiment, the mean height of trees in surrounding areas. This response pattern is consistent with the observation of Barbaro *et al.* (2005) who showed that the height of trees taken within a radius of 50 m around the pitfall trap had a negative effect on carabids abundance. Vele *et al.* (2011) also found that the abundance of carabids decreased in plots neighbouring older, and thus taller, trees. This might be due to a diversion of dispersing carabids towards forests with taller trees, either because they are easier to locate from distance, particular for flying macropterous carabid species, or because high forests are structurally more complex and provide better habitats or larger food resources. We are inclined to favour this second hypothesis because *H. rufipalpis*, a macropterous species was not negatively affected by surrounding plot heights whereas *C. problematicus*, an apterous species was. Conversely, the activity-density of the more specialised species (*C. problematicus*, an obligatory predator) was lower in plots surrounded by taller trees where they may have been attracted (positive effect of variance in tree height, TREE_VH, Table 2) while the more generalist species (*H. rufipalpis*, an omnivorous species) remained indifferent to surrounding plots structure.

The effect of the stratification of understorey vegetation (variance in plant height) had opposite effects on the two dominant carabid species, which can explain the lack of resulting effect on the total carabid density-activity. The influence of understorey height variance was negative for *C. problematicus* (although not significantly) and positive for *H. rufipalpis*. Here again the explanation might originate in the different feeding requirements of the species. The omnivorous (*H. rufipalpis*) might benefit from greater food diversity, including seeds from different plants of different heights, while the predator (*C. problematicus*) would have more difficulties to locate its prey items in a denser undergrowth. Further studies on the gut content of trapped carabids (Kamenova *et al.* 2018) in the tree diversity experiment will help disentangle those possible mechanisms of response.

Interestingly, our results confirm that the diversity of understorey vegetation, canopy trees and surrounding patches of experimental plots have complementary effects on local activity-density of carabid beetles. Many community ecology studies on drivers of carabid beetles' diversity and abundance have shown that species assemblages depend on both habitat and landscape attributes both in agricultural; e.g. (Liu *et al.*, 2015; Djoudi *et al.*, 2019) and forest ecosystems (Barbaro *et al.*, 2005; Pawson *et al.*, 2008). This confirms that ecological filters shaping carabid communities operate at different spatial scales, according to successive processes. Dispersal across landscapes mainly depends on configurational heterogeneity and habitat connectivity. Colonisation of habitat patches is driven by habitat quality and size, while survival results from biotic interactions, including finding suitable feeding resources and escaping predation. Another possible mechanism is that carabid species may benefit from habitat complementation or supplementation at larger spatial scale (Barbaro *et al.*, 2007), which would be particularly relevant to omnivorous species as observed with *H. rufipalpis* in our study.

Tree diversity experiments, with plots of different species compositions, and blocks with different patterns of plot heterogeneity, thus represent interesting miniature model ecosystems to test the influence of multiscale drivers on forest dwelling communities. A further step in the understanding of carabids' responses to both compositional and structural diversity of experimental forest plots will be to link them to relevant functional traits of carabid beetles, such as those related to dispersal and food requirements.

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Supporting information

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

Appendix S1. Supporting Information
Appendix S2. Supporting Information
Appendix S3. Supporting Information

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