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Restoring tree species mixtures mitigates the adverse effects of pine monoculture and drought on forest carabids

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Abstract

1. Habitat degradation and climate change are main drivers of insect species loss worldwide, raising concern about natural forest replacement by tree monocultures in a context of more frequent disturbances like drought. Carabid beetles are emblematic species in ecology because they are often used as indicators of biodiversity and they have important functional roles, particularly predation.
2. We used a tree diversity experiment with half of the plots irrigated and the other half under summer water stress to test the combined effects of tree species mixing and drought on carabid species and functional diversity.
3. We observed a qualitative effect of drought on carabid communities, with species turnover mainly due to predator species loss in the drier (non-irrigated) plots.
4. We also found that species richness and activity density were lowest in pure pine plots and highest in mixture of pine and birch at low tree density. The likely underlying mechanism is the better provision of food and shelter resources in mixed forests.
5. The association of pine with birch species could compensate for the loss of carabid beetles observed between pine monocultures benefiting from the water regime of the last century and those subject to current droughts. This suggests that diversifying plantation forests is a promising way to increase their resilience to the adverse effects of climate change.

KEYWORDS

biodiversity, functional diversity, ground beetles, mixed forests, ORPHEE, plantations

INTRODUCTION

Alarming news are piling up about the loss of global biodiversity (Dirzo et al., 2014), as highlighted by converging reports from IUCN, WWF and IPBES (IPBES, 2019; IUCN, 2020; Living Planet Report, 2020). In particular, a series of recent studies have drawn attention to the decline of insects worldwide (Córdoba-Aguilar &

Roitberg, 2021; Didham et al., 2020; Jactel et al., 2020; Wagner et al., 2021). Among the best-studied insects, carabids show the same signs of severe decline, with losses around 30%–50% in Europe during the last 30–50 years (Brooks, Bater, et al., 2012; Brooks, Storkey, et al., 2012; Hallmann et al., 2020; Homburg et al., 2019; Kotze & O'Hara, 2003). Apart from their gleaming beauty and high relevance as bio-indicators, carabids play a key role in many ecosystem

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functions such as pest regulation (Alalouni et al., 2013) nutrient cycling and improvement of soil structure (Loreau, 1987). They are also frequently used as indicators of the effect of natural or anthropogenic disturbances on forest biodiversity (Kotze et al., 2011; López-Bedoya et al., 2021; Rainio & Niemelä, 2003).

Habitat loss and degradation are the main causes with climate change of biodiversity loss in different ecosystems, including forests (IPBES, 2019). As a striking example of habitat degradation, deforestation (De Castro Solar et al., 2016) or conversion of natural forests into plantations, mostly tree monocultures (Holloway et al., 1992; Lucey & Hill, 2012) have caused dramatic reduction of insect abundance and diversity (Cardoso et al., 2020; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020).

As poikilothermic organisms, many insects can benefit from rise in temperature to increase their number of generations or extend their geographical range (Jactel et al., 2019). However, they are also sensitive to thermal shocks and heat waves, especially when temperatures exceed lethal thresholds (Soroye et al., 2020; Wang et al., 2020). Intensified droughts may be also harmful to insects because they are organisms with a low weight-to-surface area ratio, making them particularly sensitive to desiccation (Wagner, 2020). Homburg et al. (2014) found a steeper decline in the abundance of carabid species overwintering as imagos, which may be explained by the activity of their larvae in summer, when they are possibly exposed to severe drought or high temperatures. Both Sustek et al. (2017) and Šiška et al. (2020) found a negative effect of drought on the abundance and diversity of ground beetles with a lag effect of 1–2 years. This has been interpreted as an effect of drought on reduced activity and increased mortality of snails, slugs, earthworms, and other soil organisms that represent the primary food sources for carabid beetles while being highly dependent on soil moisture. In addition, higher moisture conditions are known to select for larger and primarily predatory species of carabid beetles (Kansman et al., 2021; Schirmel et al., 2015; Tsafack et al., 2019), possibly due to an increase in hibernation sites needed by larger species and a more abundant and diverse prey source. More disturbed environments, including those exposed to drought events, would therefore favour small, mobile and omnivorous carabid species (Magura et al., 2002).

Tree canopies are known to buffer forest floor temperatures against extreme heat, hence desiccation (De Frenne et al., 2019). This effect of canopy cover on the abiotic conditions of the understorey is known to favour forest-dwelling carabid beetles, while it disadvantages open-habitats species that prefer drier conditions (Ings & Hartley, 1999; Negro et al., 2014). This generally results in an overall decrease in species richness and functional diversity of carabid beetles as tree density or canopy closure increases (Lange et al., 2014; Niemelä et al., 1996) due to the loss of these open-habitat species (Spake et al., 2016; Wang et al., 2021). However, daily temperature and amplitudes of vapour pressure deficit also decrease with increasing stand structural complexity (Ehbrecht et al., 2017), which has been shown to be greater in mixed species forests. Similarly, the density and diversity of understorey vegetation decrease with increasing canopy cover, but more in pure forest stands than in mixed species

forests (Ampoorter et al., 2020; Corcket et al., 2020), providing less shelters for carabids to hide from drought or fewer seeds for herbivorous carabids species. In addition, soil fauna generally increases with tree diversity (Ampoorter et al., 2020; Korboulewsky et al., 2016) while most endogeic or epigeic organisms need soil humidity to move and survive, suggesting that the amount of prey for predatory carabids would be reduced in less diverse and drier forest stands. Mixed forests could therefore provide refuge for carabid beetles with different habitat and diet preferences, even under high canopy cover. Recently, we have shown that carabid diversity and abundance both increase with increasing tree species diversity in young forest plantations, an effect we hypothesised to be related to improved biotic and abiotic conditions (Jouveau et al., 2020).

While conversion of natural forests into tree monocultures is detrimental to biodiversity conservation in general (Brockerhoff et al., 2008) and particularly in the context of climate change (Pawson et al., 2013), the opposite trajectory of diversifying plantation forests could help restore forest biodiversity (Messier et al., 2022). For example, it has been shown that enriching pine monocultures with broad-leaved tree species has increased carabid beetle diversity (Sklodowski et al., 2018).

To address these questions, we studied carabid abundance and diversity in a manipulative experiment that controlled both tree species diversity and drought via irrigation. More particularly, we used pitfall traps in irrigated or non-irrigated (dry) forest plots in pure and mixed pine plantations to investigate the numerical and functional response of carabid communities to drought reduction and forest diversification. With regard to carabid abundance, we first hypothesised that both reduced forest diversity (e.g. tree monocultures) and drier soil conditions (no irrigation) would reduce the availability of microhabitats and of food resources for ground beetles. Functionally, our second hypothesis was that because individual carabid species should respond to biotic and abiotic conditions according to their life traits and more particularly their body mass, diet and habitat, the ground beetle species assemblages would differ with drought conditions and tree species composition. By testing these hypotheses, we aimed at building toward a more comprehensive understanding of the interactive effects of habitat degradation (here reduced tree diversity) and climate change (here increasing drought) on forest insect decline and conversely to propose ways to restore insect biodiversity through plantation forest diversification.

MATERIALS AND METHODS

Experimental site

The study was conducted in the manipulative tree diversity experiment of ORPHEE, which belongs to the global TreeDivNet network (Paquette et al., 2018; Verheyen et al., 2016). It is located in South-west of France (44°44'24.9"N; 00°47'48.1"W) and consists of a 25,600 trees plantation covering 12 ha. It was planted in 2008 on a sandy soil. The local climate is temperate, with mean annual

temperature of 13.6 °C and mean annual cumulated rainfall of 893 mm, with chronic summer droughts. The experiment involves five tree species: maritime pine (*Pinus pinaster*), silver birch (*Betula pendula*), pedunculate oak (*Quercus robur*), Pyrenean oak (*Quercus pyrenaica*) and green oak (*Quercus ilex*). Each block of the experiment consists of 32 randomly distributed plots corresponding to all the possible combinations of one to five tree species: each species monoculture and each two- to five-species mixture, the five-species mixture being duplicated. Each plot is 20 m × 20 m and contains 100 trees planted in 10 rows of 10 trees spaced 2 m apart. Plots are 3 m apart from each other and separated by a regularly mowed grass strip. Mixed plots were planted following a substitutive design with a regular alternate pattern (Damien et al., 2016).

Four out of eight blocks are irrigated since 2015 while the other four blocks receive only natural rainfall. All plots of irrigated blocks are sprinkled at night with 1.2 m³ of water per plot (i.e. 3 mm precipitation, plot area 400 m²), every night from May to October. This volume was calculated on the basis of regional climatic data (evapotranspiration) and is assumed to avoid soil water deficit in the irrigated plots during the whole growing season. And we were indeed able to confirm that the water deficit was eliminated in the irrigated blocks in 2015–2017 (see Maxwell et al., 2020; Figure S1).

Plot selection

Previous studies at the same experimental site have shown that pines and birches are much taller than oaks because the latter have a lower growth rate (Damien et al. 2016; Toïgo et al., 2022). While maritime pines were on average 7.80 m tall in 2016 and birches 6.48 m, oaks were only 1.38 m (Pyrenean oak), 1.42 m (pedunculate oak) and 1.77 m (green oak), that is, similar average height as the understory vegetation 1.03 m (Figure S2). We therefore considered oak trees to be an integral part of this understory vegetation at the time of our study.

The silver birch (*B. pendula*) is a pioneer species with a very large distribution in Eurasia and growing naturally in the Southwest of France. Like the maritime pine (*P. pinaster*), it is a pioneer species that needs light and shows a rapid growth during its juvenile phase (Dubois et al., 2020). The two species therefore often co-occur in the process of natural forest regeneration in our study area. In addition, birch appears to create favourable conditions for the establishment of other tree species through the process of facilitation (Dubois et al., 2020). Birch resists moderate drought by reducing its transpiration through yellowing or leaf fall (Dubois et al., 2020).

In this study, with a view to testing an approach to converting pure maritime pine plantation forests into mixed plantations, we worked on maritime pine and silver birch mixtures. We focused on a subset of five tree composition treatments replicated in six blocks (three irrigated and three non-irrigated; 30 plots in total). For a given sampled block, the plot selection comprised:

- the monoculture of *P. pinaster* (*Pp*) at the density of 100 trees per plot (hereafter *Pp100*), and the mixture planted with maritime pine

and pedunculate oak (*Pp + Qr*), considered here as a maritime pine monoculture, since the oaks were in fact integrated into the understory, at a density of 50 trees per plot (hereafter *Pp50*)

- the two-species mixtures of pine and birch (*Pp + Bp*) at the density of 100 trees per plot according to the substitutive design of ORPHEE, hereafter (*Pp50.Bp50*), the composition (*Bp + Qr + Pp*) corresponding to the mixture of pine and birch with 33 trees of both species (*Pp33.Bp33*) and the composition (*Bp + Qr + Pp + Qi + Qp*), corresponding to the mixture of pine and birch with 20 trees of both species (*Pp20.Bp20*). It should be noted here that because planting pattern on ORPHEE followed a systematic substitutive design, the pines and birches were always evenly distributed in the plots and not aggregated in these mixtures.

By doing this selection of tree species compositions, we could compare pure and mixed plots of maritime pine according to a substitutive approach (*Pp100* vs. *Pp50.Bp50*) or an additive approach (*Pp50* vs. *Pp50.Bp50*). We could also investigate the effect of tree density in mixed plots at equal proportion of each species (*Pp50.Bp50* vs. *Pp33.Bp33* vs. *Pp20.Bp20*).

Vegetation diversity assessment

We assessed understory vegetation in irrigated and non-irrigated plots in 2016. In the central area of each sampled plot, we established four quadrats of 1 × 1 m where the abundance of each vascular and fern species was estimated using the Domin scale (see Corcket et al., 2020 for details). A Shannon diversity index of understory plants (*SDI_UNDER*) was calculated for each quadrat and then averaged at the plot level.

Carabid sampling

Carabid beetles were sampled using pitfall traps (Brown & Matthews, 2016; Hohbein & Conway, 2018), consisting of 90-mm-diameter, 100-mm-high glass jars (445-ml volume) filled with mono-propylene glycol and covered with a 3-mm-thick, 200-mm-square clear plastic roof located 50 mm above the trap to protect it from rain.

Four pitfall traps were placed at each corner of an 8 m × 8 m subplot in the centre of the sampled plots to avoid edge effects. A total of 144 traps were used in the study (4 traps × plots × 6 blocks).

Pitfall traps were activated 2 weeks per month for 6 months between April and September 2017 (traps were plugged during the 2 weeks of inactivation). Catches from all six-assessment periods were pooled for data analyses. Trapped carabid beetles were identified to species level, using morphological examinations and reference works for the French carabid fauna (Coulon et al., 2011a, 2011b; Jeannel, 1941, 1942; Maguère, 2016), and the European fauna (Hurka, 1996). We used these data to estimate the activity density, species richness and Shannon diversity index of carabids.

Life history traits of carabids species and functional diversity

We focused on one quantitative and four qualitative life history traits that could be assessed for all carabid species captured (Table S1) and that we considered relevant to explain the response of carabid beetles to forest habitat quality via the quantity of available resources and microclimate. *Body length* was the quantitative trait and defined as the average of body lengths (in mm) found in the literature for a given species. *Wing morphology* was coded as brachypterous or macropterous. *Habitat type* was coded as open habitat specialisation, forest habitat specialisation, and generalist habitat carabids. *Diet* was coded as phytophagous, predatory or omnivorous. *Overwintering stage* was coded as larva, imago, or both. Trait values of each species were extracted from the published literature (Table S2). Life traits associated with the local species *Pterostichus gallega* were documented using information from the closest congeneric species present in the rest of France, *Pterostichus madidus*. The life traits missing in the literature were completed by a specialist (F. Soldati, personal communication).

We used the trait values of captured species to calculate indices of functional richness, functional evenness, functional divergence and functional dispersion for each plot. These functional indexes were calculated with the package FD in R, using the function dbFD (Villéger et al., 2008) for the carabid assemblage of each sampled plot. Functional richness (FRic) estimates the dispersion of species in the trait space and does not account for species abundance. Functional evenness (FEve) measures both the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species. Functional divergence (FDiv) represents how the abundance spreads along a functional trait axis, within the range occupied by the community. Functional dispersion (FDIs) is the weighted mean distance in multi-dimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species (Laliberté & Legendre, 2010). For the traits with continuous value (body size), the calculation of functional richness was based on the average of the differences between the maximum and minimum trait values for each species in the community. For categorical traits, functional richness was calculated in the same way except that each trait factor value was transcribed into a binary trait (0 and 1) depending on whether the species has it or not. In addition, for these categorical traits, we calculated community weighted mean (CWM) values as the proportion of individuals per species in each class (Lavorel et al., 2008).

Statistical analysis

All statistical analyses were carried out using R software 4.1.2 (R Development Core Team, 2021). We applied non-metric multidimensional scaling (NMDS) to characterise differences in carabid species assemblages between plots of different composition and drought

levels. We used the function metaMDS in the package vegan (Oksanen et al., 2018). We applied these analyses to the dataset with and without the species represented by singletons and as the results were the same we decided to keep the latter. Significant environmental variables were fitted to the ordination using the function envfit with 1000 permutations. We carried out a multivariate analysis of variance, using the adonis2 function of the vegan package (Oksanen et al., 2018) with 1000 permutations, with the Bray Curtis dissimilarity index and a marginal test, to test the effect of environmental variables on species assemblages. We tested the effects of interactions between irrigation and vegetation on the composition of carabid communities using the adonis2 function (with 1000 permutations, the Bray Curtis dissimilarity index and a marginal test). Because we did not detect any significant interactions, we decided not to retain them in the study.

We used linear mixed models to test the effects of tree species composition (*TREE_COMP*) and drought (*irrigation*) on the carabid community numerical and functional characteristics, that is, species richness, activity-density, Shannon diversity index, functional richness, functional evenness, functional divergence, functional dispersion and CWM of body length, wing morphology, habitat specialisation, diet and overwintering stage (Table 1).

We analysed the data with generalised linear mixed effect models (GLMMs) with Poisson and Gaussian error distribution for species richness and activity-density of carabid beetles, respectively. Before model analyses, all continuous explanatory variables (predictors) were centred and reduced to obtain model coefficients that were comparable within and between models (Schielzeth, 2010). Because the ORPHEE experiment is a split-plot experiment (all plot compositions in each block and irrigation applied at the block level), we had to adapt the calculation of degrees of freedom and mean sum of squares of residuals. We used *Block* and *Irrigation* in interaction (*Block* × *Irrigation*) as random factors to account for this nesting between *Block* and *Irrigation* in the linear mixed effect models (Castagneyrol et al., 2017; Schielzeth & Nakagawa, 2013).

In R language, the general model equation for the full model was the following:

$$Y \sim (TREE_COMP + SDI_UNDER)^* Irrigation + (1|BLOCK : Irrigation),$$

with irrigation as categorical variables (irrigated vs. non-irrigated).

We proceeded to model selection using a procedure based on AIC criteria corrected for small sample size AICc (Burnham et al., 2011) to identify the best, most parsimonious model for each response variable. First, we ran every model nested within the full model, calculated model AICc and ranked them according to the difference in AICc between a given model and the model with the lowest AICc ($\Delta AICc$). Second, Model averaging was used to estimate parameters using the set of best models, that is, with a $\Delta AICc < 2$. For each final model, R^2 values were calculated to estimate the variance explained by fixed effects (marginal R^2 , R^2_m) and by both fixed and random effects (conditional R^2 , R^2_c) (Nakagawa & Schielzeth, 2013).

TABLE 1 Response variables, definitions, minima (Min) maxima (Max) and median values across the plots

Carabid response variables	Definitions	Min	Max	Median
Species Richness	Number of carabid species trapped per plot	2	10	6
Activity-Density	Number of carabid individuals trapped per plot	7	40	17
Shannon Diversity	Shannon diversity of carabids species trapped per plot	0.06	0.20	0.13
Functional Richness	Amount of niche space occupied by the species within a community	0.00	1.04	0.44
Functional Evenness	Evenness of abundance distribution in a functional trait space	0.39	0.90	0.71
Functional Divergence	Abundance distribution within the volume of functional trait space occupied by species	0.64	0.98	0.90
Functional Dispersion	Weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species	0.02	0.39	0.27
CWM of Body Length	Average of carabids body length in mm per species per plot	9.83	26.87	20.40
CWM of Brachypterous		0.17	1.00	0.71
CWM of Macropterous		0	0.83	0.29
CWM of Forest habitat specialisation		0.13	1	0.65
CWM of Generalists habitat carabids	Mean proportion of individuals of all species having this life trait value (0 or 1 for each species) out of the total number of trapped individuals	0	0.70	0.14
CWM of Open habitat specialisation		0	0.56	0.16
CWM of Omnivores		0	0.10	0
CWM of Phytophagous		0	0.31	0.07
CWM of Predators		0.69	1	0.92
CWM of Overwintering at all stage		0.10	1	0.80
CWM of Overwintering at Imago stage		0	0.73	0.16
CWM of Overwintering at Larval stage		0	0.39	0

RESULTS: EFFECTS OF VEGETATION DIVERSITY AND IRRIGATION ON CARABID DIVERSITY

Numerical responses of carabid species communities

We captured and identified 559 individuals of 24 carabid beetle species from 14 genera (see Table S1). This represents the same number of species compared to the same site studied for carabid biodiversity 5 years earlier (Jouveau et al., 2020) and two thirds of the regional pool of 36 species associated with maritime pine forest (Barbaro et al., 2006).

We found that the best-explaining, most parsimonious model of carabid activity-density included the tree species composition of sampled plots as only significant predictor (Figure 1, Table S3), explaining 31% of the variability in carabid species activity density. The density of carabid species was the lowest in the pure maritime pine plots (Pp100 and Pp50) and significantly higher in mixed plots of pine and birch (Pp50.Bp50, Pp33.Bp33, Pp20.Bp20), irrespective of irrigation (Figure 2a).

The response of carabid species richness to tree species composition followed exactly the same pattern, although the effect was not statistically significant (Figure 2b).

Functional response of the carabid community

For each of the model sets testing the effect of irrigation, tree species composition and understory vegetation on the functional diversity

(functional richness, dispersion, divergence and evenness) of carabid beetles, the null model was retained in the set of models within 2 units of Δ AIC to the best model (Table S4). This indicates that there was no statistically clear relationship between potential predictors and these components of the carabid beetle community.

When traits were analysed separately, irrigation was the only predictor that had a significant effect on their CWM. In particular, carabid beetles consisted of larger species (Figure 3a), with greater specialisation towards forest habitats in non-irrigated plots (Figure 3b). For all other CWM traits (Figure 1), the null model was competing with other models with Δ AIC < 2.

Composition of carabid communities

The three most abundant species represented 68% of the total specimens (*Carabus violaceus* 35%, *Carabus problematicus* 20%, *Carabus nemoralis* 13%). Six species were represented by a single individual (i.e. singletons, 1% of the total).

Carabid beetle assemblages significantly differed between irrigation treatments (Table 2, Figures 1 and 4). Three species were present only in non-irrigated plots: *Amara communis* and *Harpalus affinis* are macropterous, prefer open habitats and are phytophagous whereas *Philorhizus melanocephalus* is macropterous, prefers forest habitats and is predator. All these species were captured as singletons. Six species were present only in irrigated plots, which were mainly macropterous, open habitat-specialists and exclusively predatory species:

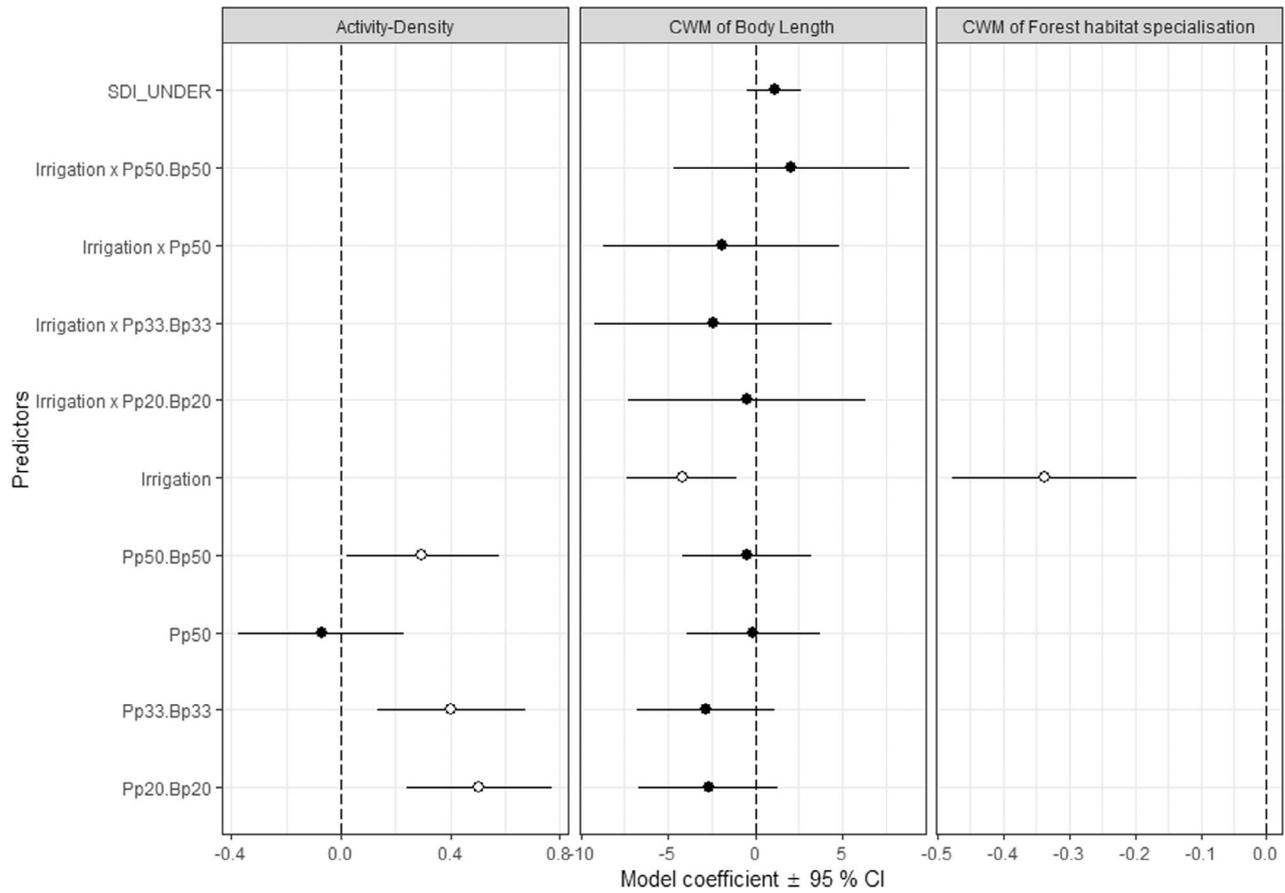


FIGURE 1 Model coefficient parameter estimates from the linear mixed models testing the effect of Irrigation, understorey diversity (SDI_UNDER), tree species composition (TREE_COMP), and their two-ways interactions on carabid species activity-density and the community weighted means (CWM) of body length and forest habitat specialisation. Parameters estimates correspond to averaged parameter estimates across models within a Δ AICc < 2 of the best models (i.e. the model with the lowest AICc). White and black dots are significant and non-significant predictors respectively, as determined by 95% CI.

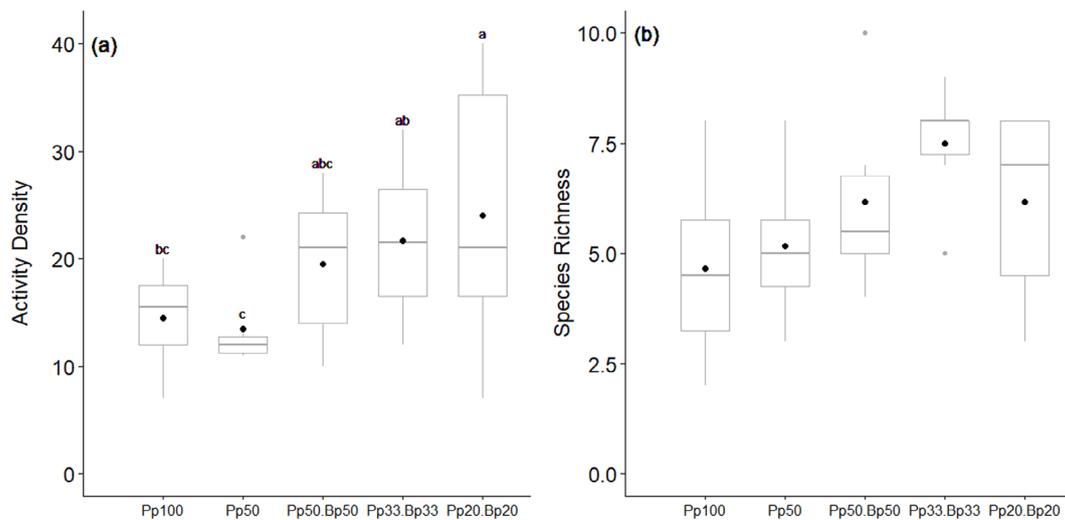


FIGURE 2 Numerical responses of carabid communities to tree species composition: (a) activity-density, (b) species richness. Box plots represent mean (black dots), median, 25% and 75% percentiles. Means not sharing the same letters are significantly different (LSD post hoc test).

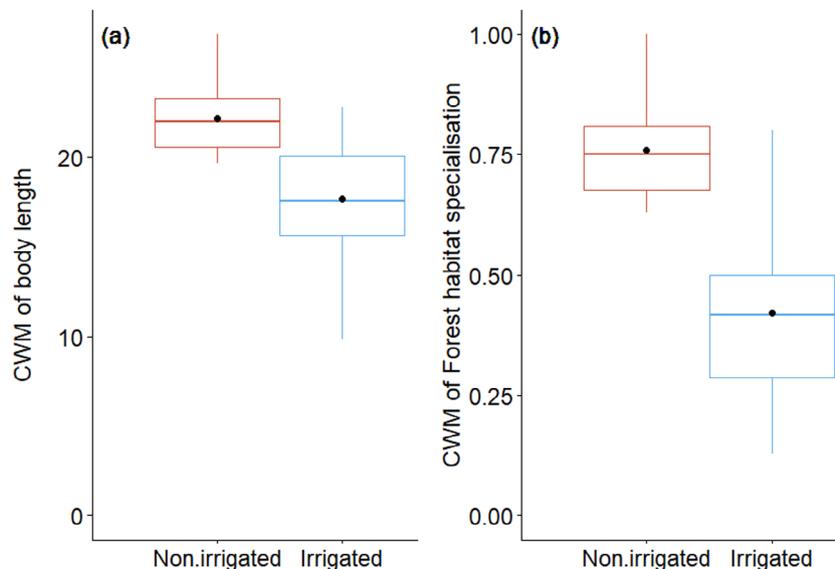


FIGURE 3 Functional responses of carabid communities to irrigation: (a) community weighted means of carabid body length, (b) community weighted means of species with forest habitat specialisation. Blue boxes and lines represent Irrigated plots. Red boxes and lines represent non-irrigated plots. Box plots represent mean (black dots), median, 25% and 75% percentiles.

TABLE 2 Results of permutational multivariate analyses of variance of the effects of environmental variables on the composition of carabid beetles' communities

Environmental variable	Df	Sum of squares	R ² m	F value
Irrigation	1	1.34	0.23	8.54***
TREE_COMP (Trees composition per plot)	4	0.48	0.080	0.77
SDI_UNDER (Shannon diversity index of understorey plants)	1	0.34	0.056	2.14*

Note: Significant F values are bold with the following abbreviations: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Leistus ferrugineus, *Leistus fulvibarbis*, *Bembidion (Nepha) callosum*, *Platynus livens*, *Pterostichus (Steropus) maddidus* and *Stomis pumicatus*. Three of these species were captured as singletons (*L. ferrugineus*, *P. livens* and *S. pumicatus*). The other 15 species were present in both irrigated and non-irrigated environments (Figure 4). Irrigation treatment thus seems to have mainly separated species according to their diet (predators vs. herbivores).

Carabid species assemblages were also significantly but marginally ($R^2m = 0.06$) influenced by the diversity of understorey plants (SDI_UNDER, Table 2, Figure 4). On the diversity-rich side of the understorey gradient were positioned *Amara communis*, *Badister bullatus*, *Harpalus rufipalpis*, *Harpalus latus*, and *Calathus (Neocalathus) erratus*, which shared common functional traits: they are 9–10 mm long, macropterous, specialised in open habitats, phytophagous or omnivorous diets (only *B. bullatus* and *C. erratus* are predators). On the low-diversity side of the gradient were positioned *Notiophilus biguttatus*, *Notiophilus quadripunctatus*, *Nebria salina*, *Notiophilus substriatus* and *Leistus spp.*, which are predatory, macropterous, ubiquitous or from open habitats, and smaller in size (5–8 mm long). This environmental gradient therefore seems to differentiate carabid species based on their size and main diet (predators vs. herbivores or omnivores).

DISCUSSION

Using a dedicated experimental set-up, with an irrigation system, our study revealed a significant effect of reduced water availability on the composition of carabid communities, with a species turnover between irrigated and non-irrigated plots. We also found that carabid activity-density, and in a lower extent species richness, was mainly driven by tree species composition, being lowest in pure pine forests and highest in mixed pine and birch forests, irrespective of water availability. Our results suggest that converting pine monocultures to mixed-species plantations by introducing broadleaved species would increase the diversity and abundance of carabids.

Effects of tree species mixing on the carabid community

Our study showed a positive effect of mixing pine with birch trees on numeric (activity-density) and marginally on taxonomic (species richness) characteristics of the carabid community. The effect of mixing conifers and broadleaves on the abundance and diversity of carabid beetles is a matter of debate in the literature. Magura et al. (2000)

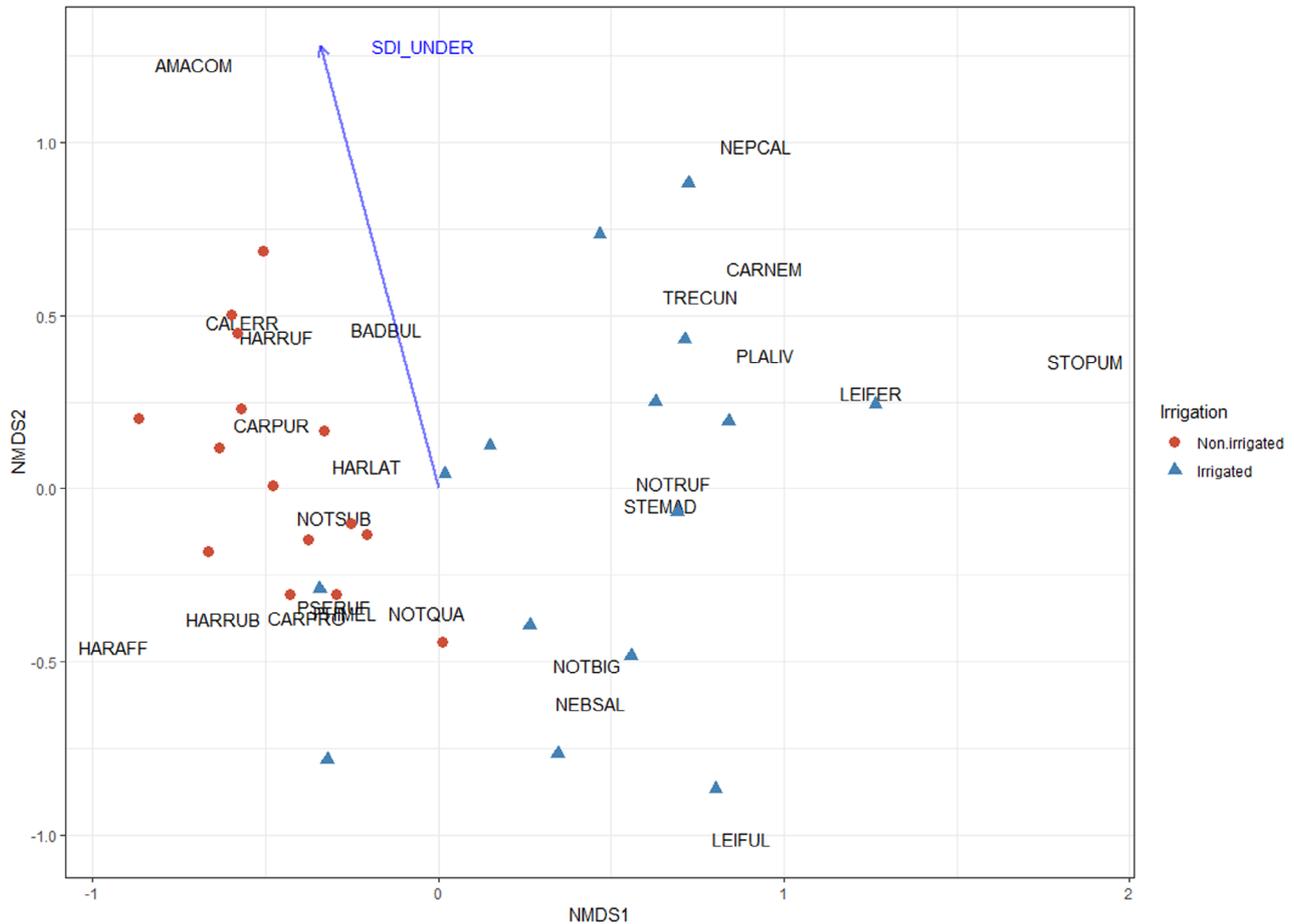


FIGURE 4 Non-metric multidimensional scaling (NMDS) of ground beetle assemblages: Distribution of species according to the irrigation treatment (ellipses show standard deviation of plot type scores) and the significant effect of understorey vegetation diversity (SDI_UND, blue arrow). The three overlapping species labels are *Carabus problematicus* (CARPRO), *Harpalus (Pseudoophonus) rufipes* (PSEUF) and *Philorhizus melanocephalus* (PHIMEL).

found that *Picea abies* plantations re-invaded by native broadleaved species (oak and hornbeam) contained greater abundance and diversity of carabid beetles than pure spruce plantations. Sklodowski et al. (2018) showed that complementing pine stands with broadleaved species as second story or understorey species results in more abundant and more species rich communities of carabids, and so did Jouveau et al. (2020). Zou et al. (2019) found a positive correlation between tree species richness and carabids species richness in mature temperate forests. Wehnert et al. (2021) found more carabid species in mixed pine-oak forests than in pure Scots pine stands. In contrast, several articles reported no difference in carabid species richness between pure and mixed forests (Barsoum et al., 2014; Oxbrough et al., 2016; Vehviläinen et al., 2008; Zou et al., 2019). However, they all concerned young forests that had perhaps not yet had time to be recolonised by the local fauna, all the more impoverished because the surrounding landscape was itself degraded by intensive management.

The positive effect of tree diversity on carabid abundance (activity-density) and diversity could be explained by two non-exclusive mechanisms. The first is that the diversity of tree species results in a greater complexity of vegetation structure, offering more resting,

breeding or hiding sites and thus reducing the risks of mortality for ground dwelling organisms (Brose, 2003; Niemelä et al., 1996). In our experimental site, we showed an increase in abundance and diversity of carabid beetles as the structure of the pine plots became more complex due to the introduction of birch, a species characterised by a less dense crown. These positive changes appear to have been further exacerbated by decreasing tree density, as carabid abundance increased in these mixed forests when the total number of trees per plot was reduced from 100 to 66 and 40. This positive effect of reduced forest density on carabid abundance is consistent with previous studies (Ings & Hartley, 1999; Lange et al., 2014; Wang et al., 2021; Yi & Moldenke, 2005), showing that that greater canopy openness could promote more abundant or diverse understorey vegetation, providing more hunting and foraging niches and protection from predators and desiccation. This would also explain why the reduction in tree density had no effect in pure stands of maritime pine (Pp100 vs. Pp50), which shaded the understorey vegetation even at the reduced density.

The second mechanism is an indirect effect of tree diversity on carabids through an increase in food resource abundance or diversity

for carabids (Schuldt et al., 2019). Komonen et al. (2015) found higher abundance and diversity of carabids in birch forests than in pine forests, which was attributed to a more abundant leaf litter, with higher pH, in the birch stands. Thicker litter has often been shown to increase carabid diversity by providing more favourable microsites for carabids (Loreau, 1987; Magura et al., 2000, 2003; Niemelä et al., 1996). In addition, less acidic litter appears to allow for better survival of carabid eggs and larvae (Lövei & Sunderland, 1996), while being more favourable to most carabid prey species (Koivula et al., 1999; Magura et al., 2003).

Effects of drought on the carabid community

We detected no numerical response of the carabid community to irrigation, suggesting that summer drought had no significant effect on carabid abundance or species richness in the plots surveyed. These results are not consistent with recent studies addressing the effect of drought on carabids, which showed reduced abundance and diversity of ground beetles in drier forests (Skłodowski et al., 2018; Sustek et al., 2017). Two hypotheses are commonly proposed to explain these patterns of response to drought. First, drought could indirectly affect the carabid community through negative effects on plant growth (Kansman et al., 2021). Well-watered forests have denser and more complex vegetation structure hence providing more refuges for carabid beetles, limiting intra- or inter-guild predation (Finke & Denno, 2006) or adverse effects of the microclimate (Langellotto & Denno, 2004). A second explanation is that drought had a negative effect on carabid food resources since many soil organisms, such as slugs, snails, earthworms, arthropods, are hygrophilous and cannot survive in soils that are too dry (Šiška et al., 2020). A first explanation for the discrepancies with our results may be that the amount of water applied and the duration of irrigation (for 3 years) were not sufficient to drastically modify the structure of the vegetation and the quantity of microhabitats favourable to carabid beetles. In a study dedicated to this question, we found no effect of irrigation in our experimental site on the composition or diversity of the understory (Corcket et al., 2020). This could be partly due to the buffering effect of the forest cover on the microclimate and in particular the higher relative humidity in the forest understory (Davis et al., 2019). It has also been found that leaf litter in forest can buffer evaporation, providing more stable humidity for ground beetles (Koivula et al., 1999). A second explanation could be that the local carabid fauna is well adapted to the climatic conditions of the region, with recurrent summer droughts and therefore not very sensitive to the variations experienced during the sampling year.

Nevertheless, we observed that reducing forest exposure to summer drought through irrigation qualitatively altered the carabid community associated with pine forests, as a result of species turnover. More precisely, the community of carabids found in dryer (non-irrigated) forest plots was characterised by larger species. This contradicts recent studies showing that environments most exposed to drought events were characterised by smaller carabid beetles (Kansman

et al., 2021; Schirmel et al., 2015; Tsafack et al., 2019) mainly as a result of food shortage. However, it should be noted that these studies have all been conducted in open habitats (grasslands or croplands) while ours concerns the forest environment, where the microclimate is characterised by higher and more stable humidity. This could also explain why the relative proportion of forest-dwelling species was also higher in the non-irrigated plots, as carabid species of open environments may be less drought tolerant.

The species only present in the irrigated plots in our experiment were all predatory, suggesting the importance of soil moisture in providing prey for carnivorous carabids (Šiška et al., 2020). This highlights the fact that the greatest risk posed by an increase in drought would be the loss of carabid predator species, and with it a decrease in the trophic regulation service they provide. However, this consequence needs to be confirmed by further research as half of the species only found in irrigated plots were caught as singletons and we did not find a significant effect of irrigation on CWM of predators.

Tree species enrichment helps restore carabid diversity

Simplification of forest composition to maximise productivity, such as the eradication of hardwoods in coniferous forests in Europe, has led to an impoverishment of insect biodiversity (Siitonen & Martikainen, 1994). Here, we have shown that the reverse path, consisting of reintroducing a deciduous species, birch, in maritime pine plantations, allows restoring a part of the carabid biodiversity. Comparing pure pine plots between irrigated and non-irrigated blocks provides a way to trace the trajectory of carabid biodiversity loss caused by increased drought in maritime pine plantations (Pp plots, bottom part of Figure 5). It corresponds to an average loss of 1.5 species in the densest pine plot with 100 trees and an even greater loss of ca. 2.5 species in less dense pine plot of 50 trees. It should be noted that mixed pine and birch forests would have experienced the same type of reduction in carabid richness under drought conditions (blue vs. red Pp.Bp plots). We can then assess how increasing tree diversity would have prevented for the losses due to increasing drought in pure pine plantations by observing biodiversity change in plots mixing maritime pine with birch in the non-irrigated blocks (Pp.Bp plots, red dots, upper part of Figure 5). All tested non-irrigated mixed plots with pine and birch exhibited greater abundance and richness of carabids than non-irrigated pure pine plots. The best combination was the mix of 33 pine and 33 birch (1650 t/ha), which resulted in a gain in richness of one to two species and a doubling of carabid abundance compared to the initial reference of pure pine plots without drought. This suggests that diversification and reduction of tree density are two complementary avenues for promoting carabid biodiversity in pine plantations, likely through their combined effect on stand complexity and litter quality. It should also be noted that diversification approaches by substitution (Pp100 vs. Pp50 Bp50) or addition (Pp50 vs. Pp50 Bp50) appear to confer the same benefit.

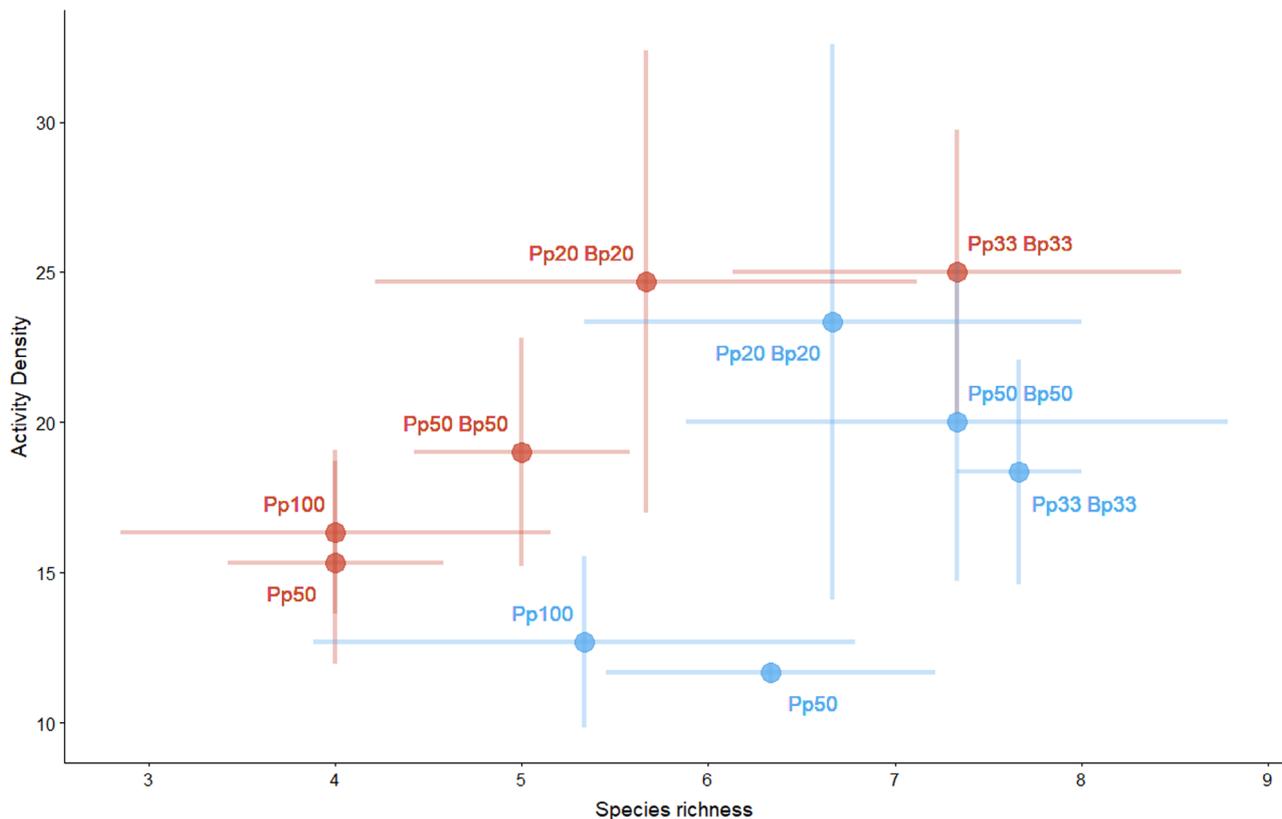


FIGURE 5 Diagram showing changes in carabid species richness and activity-density (proxy of abundance) (mean and standard error) in pine forests along a trajectory tracing the effect of increasing drought in pure forests (blue dot to brown dot) and then the effect of forest diversification based on the addition or substitution with birch. Pp: *Pinus pinaster*. Bp: *Betula pendula*. The numbers indicate the number of trees per species and per plot of 400 m². Blue dot: irrigated forest plot. Brown dots: non-irrigated plots

In terms of community composition, the path from pure maritime pine forests (Pp100 and Pp50) well-watered to the corresponding pure pine forests under drought conditions was characterised by the loss of six carabid species, *B. callosum*, *C. nemoralis*, *H. rubripes*, *L. fulvibarbis*, *N. rufipes*, and *S. pumicatus*, all but one (*H. rubripes*) being predators. The transition from pure pine forests under drought conditions to mixed pine-birch forests with 33 trees of each per plot (Pp33. Bp33) under the same drought conditions resulted in a recruitment of four predator species, *B. bullatus*, *C. erratus*, *H. rufipes*, *N. substriatus*, the recruitment of three phytophagous species *A. communis*, *H. affinis*, *H. rubripes* that compensated for the loss of *N. salina*.

CONCLUSIONS

Our study shows, for the first time experimentally, that is, manipulating irrigation while keeping unchanged forest composition, that increasing drought in tree monocultures results in altered carabid diversity, here the loss of predatory species. This confirms the more general results on the combined effect of climate change and intensive land management in the loss of insect species (Outhwaite et al., 2022). Our results obtained in a tree diversity experiment, controlling both tree species richness and composition, are also consistent

with recent studies showing that faunal diversity, in this case of carabid beetles, is often higher in mixed forests than in pure forests. The two factors combined in the same experimental set-up finally make it possible to show that increasing the diversity of pine forests by association with a broadleaved species is a promising way to compensate for the loss of specific and functional diversity of carabid beetles in a context of worsening drought conditions. The main process at work seems to be a diversification of food resources and shelters. It would now be interesting to study whether the same diversity effects apply to other taxonomic groups, especially the soil fauna which probably suffers the most from increased drought (Gillespie et al., 2020). Many carabid beetles being omnivorous or polyphagous, it would also be of great functional interest to assess whether the increase in their diversity in mixed coniferous and broadleaved forests better support diverse ecosystem functions. This would provide further evidence that diversifying plantation forests is a relevant approach to ensure their multifunctionality and improve their resilience to climate change disturbances (Messier et al., 2022).

AUTHOR CONTRIBUTIONS

Séverin Jouveau: Data curation (lead); investigation (lead); methodology (lead); resources (equal); software (equal); validation (equal); visualization (equal); writing – original draft (lead). **Charlotte**

Poeydebat: Data curation (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Bastien Castagneyrol:** Data curation (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Inge van Halder:** Data curation (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Hervé Jactel:** Conceptualization (lead); data curation (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Data INRAE at <https://data.inrae.fr>.

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SUPPORTING INFORMATION

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

Supporting Information Table S1 Taxonomy, authority, species code, total activity-density per species, species body length mean, wing morphology, habitat specialisation, diet and life stage(s) at which the species overwinters (larva, imago or both)

Supporting Information Table S2 Authors (Literature cited), Carabid beetle species code, Trait and their values (and categories) included in this study.

Supporting Information Table S2 Reference

Supporting Information Table S3 Summary of the mixed-effect models averaging coefficient testing the effects of understorey diversity, tree composition and irrigation on all carabid community response variables (only models with $\Delta AICc < 2$ that were selected for averaging are shown). b is the coefficient, $ci.lb$ and $ci.ub$ are Lower and upper 95% confidence intervals respectively. The acronyms TREE_COMP, and SDI_UNDER stand for tree composition in the plot and Shannon diversity (in log base 10) of understorey vegetation, respectively

Supporting Information Table S4 Summary of the mixed-effect models testing the effects of understorey diversity, tree composition and irrigation on all carabid community response variables (only models with $\Delta AICc < 2$ that were selected for averaging are shown). The acronyms TREE_COMP, and SDI_UNDER stand for tree composition in the plot and Shannon diversity (in log base 10) of understorey vegetation, respectively.

Supporting Information Figure S1 Ombrothermic diagram with total monthly precipitations (*blue solid line*) and average temperatures (*red dashed line*) from January 2015 to December 2017 in (A) control blocks and (B) irrigated blocks, which includes the additional precipitation (3 mm per night) when irrigation is active (on average early May to late September). Temperature scale is set to 2 mm/°C, and values above the 100 mm black line are scaled to 20 mm/°C (Walter and Lieth, 1967). When temperature is two times greater than precipitation, there is an arid period (*orange*). Data are from the local INRAE weather station at Cestas Pierroton (44.742°N to 0.782°E), less than 2 km from the experimental site. (Extract from Maxwell, 2021)

Supporting Information Figure S2 Height in 2016 of *Pinus pinaster* (Pp box plot in red), *Betula pendula* (Bp box plot in green), Oaks species, *Quercus robur* (Qrob Box plot in blue), *Q. ilex* (Qilex Box plot in darkblue) and *Q. pyrenaica* (Qpyr Box plot in purple) and understorey (UNDER Box plot in yellow). Box plots represent mean (black dots), median, 5% and 95% percentiles. Red dashed line is the mean of understorey height in 2016.

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