Tree species diversity can amplify forest microclimate offsets

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Abstract

1. Macroclimate warming is affecting ecosystems worldwide. Tree canopies, however, can significantly buffer temperature fluctuations, giving rise to lower maximum temperatures, higher minimum temperatures and enhanced water availability below the canopy. These microclimate offsets have the potential to help mitigating the effects of macroclimate warming on forest biodiversity and functioning. Forest ecosystem offsets have been well-studied, but much less is known about how offsets are modulated by individual tree species and species diversity and mixing.
2. We installed temperature and air humidity loggers in a multi-site tree diversity experiment to quantify the role of tree species richness and composition on below-canopy offsets and investigate mechanisms underlying the biodiversity effects.
3. Forest offsets highly depended on tree species identity and diversity. Not only monocultures of larch (*L. eurolepis*) and Douglas fir (*P. menziesii*) had a high performance for thermal buffering, but also mixtures with species such as birch (*B. pendula*) and pine (*P. sylvestris*).
4. Diversity effects were only detected in the more developed forest stands. In these stands, characterized by a high basal area, we detected a 0.4°C decrease in summertime maximum temperature offset per tree species added to the mixture. However, the mechanisms behind this effect (complementarity vs selection) were contrasting among sites.
5. Synthesis and applications. Our findings can inform the optimal design of tree plantations in the face of climate change and have therefore important implications for minimizing climate-change impacts on below-canopy biodiversity and functioning. Although tree species diversity affected microclimate offsetting in different ways, increasing species richness could help to mitigate below-canopy warming.

Key-words: biodiversity, microclimate, climate change, forest, soil temperatures, understorey

1. Introduction

Our planet is warming significantly, affecting ecosystems worldwide. Forests, however, can buffer macroclimate temperature and humidity changes below the canopy (De Frenne & Verheyen, 2016; Williams et al., 2017; Zellweger et al., 2020). Both evapotranspiration and redistributions of wind and radiation in a forest's canopy give rise to lower maximum temperatures and higher minimum temperatures near the forest floor. Moreover, lower temperature due to below-canopy shading leads to higher air relative humidity (RH) in forests, assuming constant air water content (Von Arx et al., 2013). As such, forests can act as "protective blankets", as refugia for heat-sensitive species (Bertrand et al., 2011; Bramer et al., 2018; Castaño et al., 2018; De Frenne et al., 2013, 2019). In the face of climate change, quantifying microclimates has become more important than ever before (De Frenne et al., 2019; De Frenne & Verheyen, 2016).

Forest microclimates and the effects of forest structure have been studied since the beginning of the 20th century (Cole & Geiger, 1951). More recently, the study of forest microclimates has regained attention because of climate change and new insights on its magnitude, drivers and consequences (De Frenne et al., 2019; Zellweger et al., 2019). These studies, for example, found that the offset of within-forest temperatures (calculated as the difference between below-canopy and free-air temperatures; De Frenne et al., 2021) ranges between -4.1 ± 0.5 and 1.1 ± 0.2 °C compared to macroclimate maximum and minimum temperatures (De Frenne et al., 2019), offsets that are of greater magnitude than the global warming of land and ocean temperatures over the past century (~0.85 °C), and greater than the warming of regional surface temperatures following deforestation (usually <1 °C). Despite its significance, the thermal insulating function of forest canopies has been neglected in biodiversity-ecosystem functioning research so far, especially compared to other functions such as biomass production, carbon drawdown or nutrient cycling (Gamfeldt et al., 2013; Joly et al., 2017; Ratcliffe et al., 2017; Tilman et al., 2001). We thus do not know to what extent forest microclimate offsets are different in monocultures vs in forests with an increasing number of tree species.

Biodiversity can improve ecosystem functioning in communities via two mechanisms. First, if mixtures do better than expected based on the relative abundance and the performance of its constituent species in

75 monocultures, this is due to 'niche differentiation' in terms of resource partitioning, facilitation or diversity-
76 dependent effects, and this is referred to as complementarity effects (Turnbull et al., 2013). Second, more
77 diverse communities are more likely to contain high-performing species, which can also generate a positive
78 biodiversity effect on ecosystem functioning in case they dominate the community; this is referred to as
79 selection effects (Baeten et al., 2013; Loreau & Hector, 2001; Van de Peer et al., 2018; Van Der Plas et al.,
80 2016). Complementarity among crowns in canopy space affects light interception and use, and relates to
81 patterns of stem biomass overyielding, which increases with greater crown complementarity (Williams et al.,
82 2017). We can thus hypothesise that both mechanisms lead to a positive relationship between tree species
83 diversity and below-canopy temperature offsets.

84 Here we investigate these biodiversity effects based on data collected in a large-scale, multisite tree species
85 diversity experiment in Belgium (Verheyen et al., 2013, 2016), that allows disentangling complementarity
86 and selection effects. Within all experimental sites, we deployed 192 microclimate sensors continuously
87 monitoring air and soil temperatures and air vapour pressure deficits (VPD). Based on these data, we then
88 compare microclimatic conditions among plots that differ in tree species richness. We sought to test (1) if
89 microclimate buffering depends on the tree species present in the overstorey; (2) whether tree species
90 diversity effects play a role in microclimate buffering; (3) which mechanism are responsible for these effects
91 (selection vs complementarity), and (4) if higher tree species richness can amplify microclimate offsetting.

92

93 **2. Materials and methods**

94 2.1. Study area

95 We performed our study in a large-scale, multisite tree diversity experiment in Belgium, western Europe
96 (FORBIO), that included ten key tree species of European forests (Verheyen et al., 2013, 2016). Plots were
97 planted as monocultures and mixtures (1 up to 4 species), distributed across three research sites in
98 contrasting macroclimates in Belgium for a total of 120 plots and 89,000 trees: Gedinne (Ge), an upland site
99 with a continental climate, Hechtel-Eksel (H-E), a lowland site on sandy soils with a continental climate, and

Zedelgem (Ze), a lowland site 15 km from the North Sea with an oceanic climate. For more details on the site's macroclimate see supplementary information Figure S1 and Table S1.

The first site, Ge, is located in the south of Belgium, in the Ardennes and consists of two blocks c. 2 km apart, Gouverneurs (49°59'N 4°59'E) and Gribelle (49°60'N 4°59'E). The climate in the Ge site is colder and wetter (mean annual temperature = 10.4°C, air relative humidity = 84.5%) compared to the climate of the other two sites. The Ze site (51°9'N 3°7'E) and H-E site (51°10'N 5°19'E) are both located in the northern part of Belgium. However, the climate in the Ze site (mean annual temperature = 12.1°C, air relative humidity = 83.7%) is milder and less continental than that in the H-E site (mean annual temperature = 11.7°C, air relative humidity = 78.7%), with higher temperatures in summer and lower temperatures in winter (see also Table S1).

The three sites all have a similar experimental design, with a pool of five species in each site, each species occurring in the same frequency. Each site comprises 40 plots spread across two blocks in each of the three sites, including ten monoculture plots (two plots per species composition, one in each block) and 30 mixture plots (ten for each tree species diversity level of 2, 3 and 4). In this study, only the monoculture plots and the 2- and 4-species mixtures were considered, so that 15 treatments were selected, including five monocultures, five four-species combinations and five two-species combinations (being a random selection of all possible two-species combinations) in each site and block, resulting in a selection of 90 (15 x 2 x 3) plots across all research sites (Figure S2 and Table S2). All trees were planted in 2010 (Ge and Ze) and 2012 (H-E) as 2- or 3-year old seedlings on a 1.5 m x 1.5 m grid (planting density of 4,444 trees/ha) and were thus 10-13 years old at the time of our measurements.

2.2. Microclimate

We installed Lascar Easylog EL-USB-1 and Lascar Easylog EL-USB-2 sensors in all selected plots, at a location representative for the plots' tree species composition (e.g. exactly at the crossing point of 4 groups of 3 x 3 trees of different tree species in the four-species mixtures), to monitor microclimates in the soil (temperature) and air (temperature and relative humidity), respectively. Air temperature loggers were attached to a wooden pole at a height of 1.0 meter and protected against solar radiation by a custom-made radiation shield. The radiation shields were oriented towards the north. Soil temperature loggers were buried at a depth of 5

cm, 10 cm away from the wooden poles. Besides the sensors below the trees, we also installed two sensors well away from trees at each site to monitor the open-air non-forest climate. This resulted in a total of 96 measurement locations (3 sites x 2 blocks x [5 monocultures + 5 two-species mixtures + 5 four-species mixtures + 1 reference]) and thus 192 sensors (air and soil temperatures monitored at each location). All sensors collected data for a complete year from March 2019 to March 2020 with a temporal resolution of one hour.

Hourly VPD was calculated as the difference between the saturated (P_{sat}) and the effective air pressure (P_{air}), calculated based on hourly air temperature T (°C) and hourly air relative humidity RH (%) (Barrass, 1974; Davis et al., 2019; Von Arx et al., 2013):

$$P_{sat} = 0.6112 * \exp((17.62 * T)/(T + 243.12))$$

$$P_{air} = P_{sat} * \mathrm{RH}/100$$

$$VPD = P_{sat} - P_{air}$$

Offsets were calculated as the difference between below-canopy and free-air temperatures and VPDs. We first summarized our hourly observations into daily statistics, focusing on maximum and minimum daily values. Next, we calculated daily offset values based on these daily maximum and minimum values measured both in the forest and the open field plots.

2.3. Forest structure

Tree height and diameters at breast height (DBH) were measured on each sensor's 16 neighbouring trees. Tree height was measured with a vertex clinometer and DBH with a calliper at 1.30 m above the ground. Measurement of tree height and DBH occurred in March 2020. Subsequently, basal area (BA, $m^2\ ha^{-1}$) of individual species was calculated based on these DBH measurements. Canopy cover was measured at exactly the same location as the temperature loggers with a spherical densiometer (Depauw et al., 2020; Lemmon, 1956). The measurements of canopy cover were performed in August 2019, to represent canopy conditions in the growing season.

2.4. Diversity effects

To gain more insights into diversity effects and the possible ecological mechanisms, we here apply the partitioning approach developed by Loreau and Hector (2001). This methodology first of all quantifies the net diversity effect (EN), as the difference between observed functioning (e.g. yield or biomass production, but in this case air temperature and VPD offsets) in mixtures and the expected values calculated from the monocultures of its component species (weighted by abundance). Subsequently, the methodology allows to attribute this net effect (EN) to either complementarity (EC) or selection effects (ES) (Loreau M. & Hector. A., 2001; Van de Peer et al., 2018; Van Der Plas et al., 2016).

To calculate these effects in our study, we calculated expected microclimate offsets in two ways. First, by assuming that effects of species on microclimate offsetting are proportional to their basal area, and hence assuming that complementarity effects are absent (EF_{exp1}). Next, by assuming that effects of species on microclimate offsetting are proportional to their abundance only, hence assuming that both complementarity and selection effects are absent (EF_{exp2}):

$$EF_{exp1} = \sum_{i=1}^{s} RYO_i * M_i^{-1} * F_i$$

$$EF_{exp2} = \sum_{i=1}^{s} RYE_i * N_i^{-1} * F_i$$

Where S represents the species richness present in the plots, RYO_i is the observed abundance of species i (based on basal area), M_i the basal area of species i grown in monoculture, F_i the thermal offset in a monoculture of species i, RYE_i is the expected abundance (number of trees planted) of species i in the mixture, N_i the number of trees planted in the monoculture of species i. Based on these terms, diversity effects were then calculated as (Loreau M. & Hector. A., 2001; Van Der Plas et al., 2016):

$$EC = EF_{obs} - EF_{exp1}$$

$$ES = EF_{exp1} - EF_{exp2}$$

$$EN = EC + ES$$

2.5. Data analyses

To analyse species identity effects on microclimate offsetting, linear mixed-effects models (LMMs) were adopted, without fixed predictor variables (intercept only) but with 'block | plot' as nested random terms, to take into account the hierarchical nature of our design. To account for temporal autocorrelation of microclimate data (Koenig & Liebhold, 2016; Ruel & Ayres, 1999), we incorporated the corAR1(form=~Day) variance structure (Zuur et al., 2007), to test whether the value of microclimate offsetting was significantly different from zero. We applied the *lme* function of the *nlme*-package to fit our models (Zuur et al., 2007). Similar analyses were applied to test whether diversity effects (EN, EC and ES) were significantly different from zero.

Next, we assessed whether tree species richness can explain variation in the magnitude of microclimate offsetting (T and VPD). We fitted LMMs with species richness (1, 2, or 4) as a fixed predictor and 'block | plot' as random-effect terms and the corAR1(form=~Day) variance structure, again to account for temporal autocorrelation, using restricted maximum likelihood in the *lme* function from the *nlme*-package (Zuur et al., 2007). To test whether a model with species richness performed significantly better than the baseline intercept-only model, we additionally performed χ^2-tests. Goodness-of-fit was determined by calculating marginal and conditional R^2 values using the *r.squaredGLMM* function in the *MuMIn*-package (Bartón, 2014).

Similar analyses were performed to assess whether basal area and canopy cover depended on species richness, i.e. to see whether increasing tree species diversity led to a denser forest structure, potentially explaining our findings related to microclimate offsets. We again fitted LMMs with species richness (1, 2, or 4) as a fixed predictor and '1| block' as random intercept (here plot was not needed since there were no repeated measurements per plot). All analyses were performed in R version 3.4.44a.

3. Results

The maximum (T_{max}) and minimum (T_{min}) temperature offsets were highly dependent on the tree species present in the overstorey. Cooling was most pronounced for T_{max} offsets in summer and warming of T_{min} offsets in winter at the Ge site. Cooling for offsets were highest in stands dominated by *Larix eurolepis* (-5.56

± 1.5 °C; Mean ± SD) and *Pseudotsuga menziesii* (-5.25 ± 1.8 °C) at the upland site (Ge). High thermal cooling was also detected below canopies of birch (*B. pendula*) and pine (*P. sylvestris*) at both the H-E and Ze site in both monocultures and mixtures. The highest cooling occurred within mixtures of *P. menziesii* and *P. sylvestris* (-2.22 ± 1.0 °C) at the H-E site, and monocultures of *P. sylvestris* (-5.61 ± 1.5 °C) at the Ze site, respectively (mixed-effects models: $P < 0.05$; Figure 1; Table S3). For summertime soil temperature offsets, we detected a consistent cooling across our three research sites, with on average -2.91 °C and -1.96 °C for maximum and minimum soil temperatures; these are reported in supplementary information Figure S5.

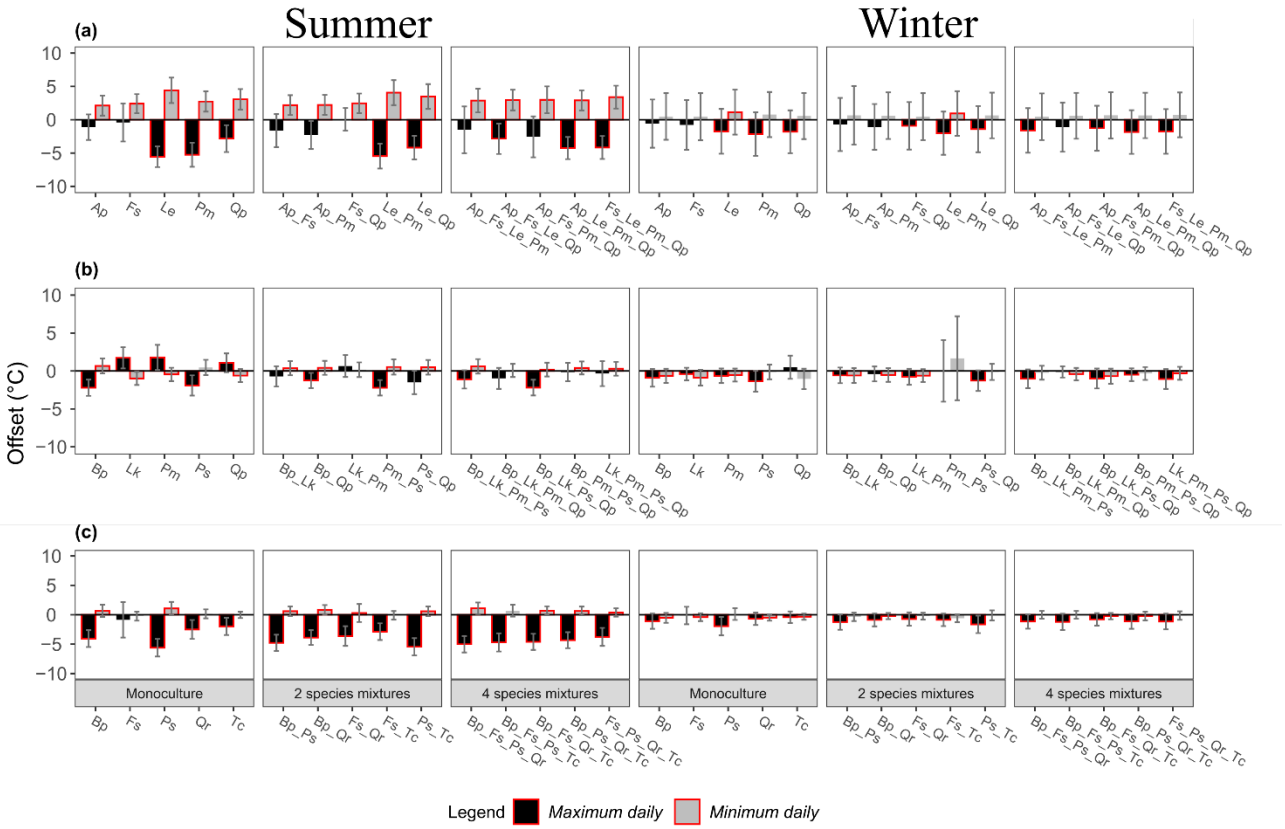


Figure 1 Air temperature offsets in both monoculture and mixture plots. Bars display air temperature offset (T_{max} and T_{min}) in summer (left) and winter (right) in Gedinne (a), Hechtel Eksel (b) and Zedelgem (c). Intercept-only mixed-effects model with '*block* | *Plot*' as nested random term, and corAR1(form=~Day) as variance structure to account for temporal autocorrelation, were applied to test whether air temperature offsets in varying forest stands were significantly different from zero. Red outer lines of bars indicate that the intercept was significantly different from zero, with $P < 0.05$. Full statistical results are reported in supplementary information Table S3.

VPD offsets were largely consistent with those reported for temperature offsets. Maximum and minimum VPD were generally lower in both summer and winter within forests compared to free-air VPD, which indicates moister conditions in the forest compared to the open. These offsets were most pronounced in stands of *Pseudotsuga menziesii* (-1.09 ± 0.5 kPa; Mean ± SD) and *Larix eurolepis* (-1.01 ± 0.4 kPa; mixed-effects models: all $P < 0.05$; Figure 2, Table S4). The largest VPD offsets subsequently occurred within stands of mixtures of *L. eurolepis* and *P. menziesii* (-1.09 ± 0.5 kPa) at the upland site (Ge). In H-E, presence of pine always resulted in a large VPD offset, e.g. as in combinations of *P. sylvestris* and *P. menziesii* (-0.56 ± 0.3 kPa), and mixtures of *B. pendula, L. kaempferi, Q. petraea, and P. sylvestris* (-0.52 ± 0.3 kPa). In Ze, *P. sylvestris* and *B. pendula* exhibited the highest offsets, with the largest offset for summertime VPD_{max} in monocultures of *P. sylvestris* (-1.04 ± 0.43 kPa), followed by mixed *P. sylvestris* and *T. cordata* (-0.96 ± 0.40 kPa) and *P. sylvestris* and *B. pendula* (-0.89 ± 0.38 kPa; mixed-effects models: $P < 0.05$; Figure 2, Table S4).

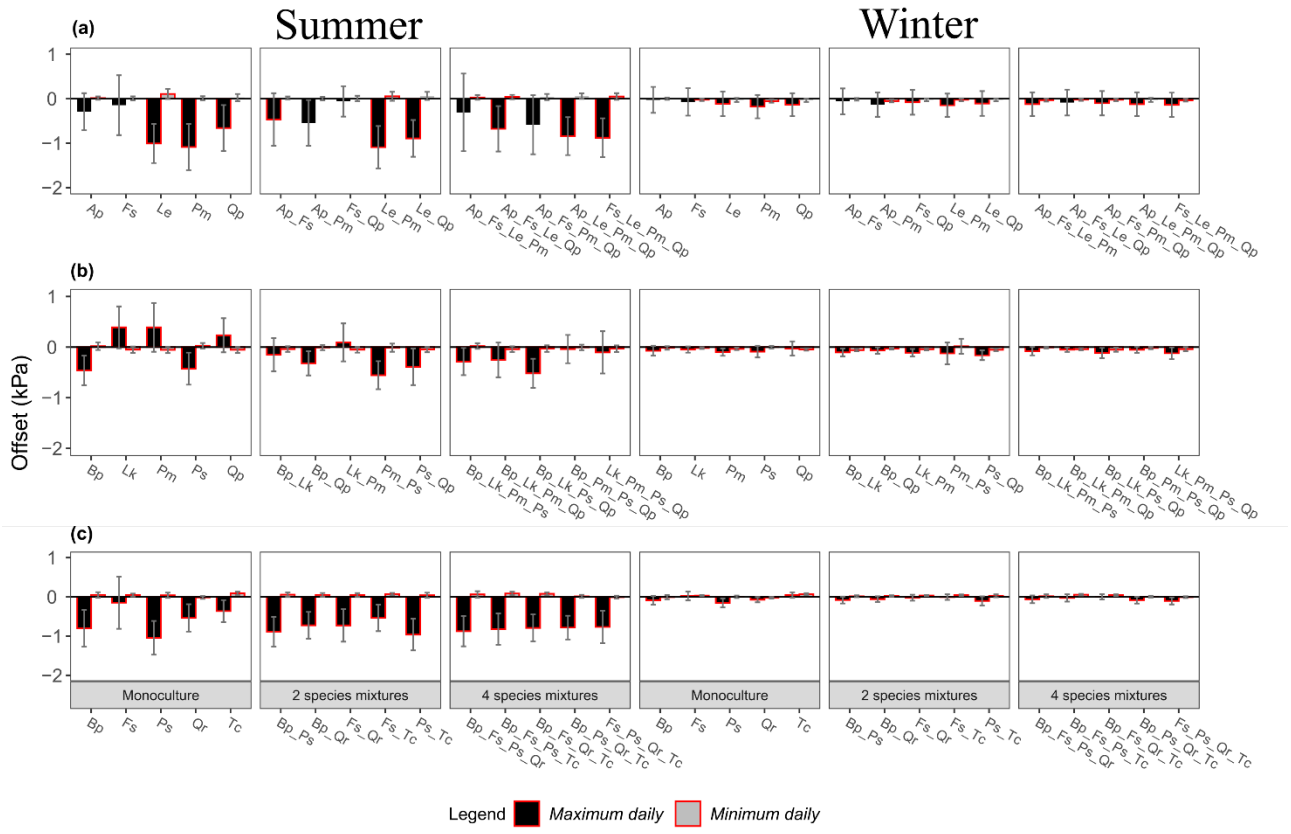


Figure 2 VPD offsets in both monoculture and mixture plots. Bars display VPD offset (VPD_{max} and VPD_{min}) in summer (left) and winter (right) in Gedinne (a), Hechtel Eksel (b) and Zedelgem (c). Intercept-only mixed-effects model with '*block* | *Plot*' as nested random

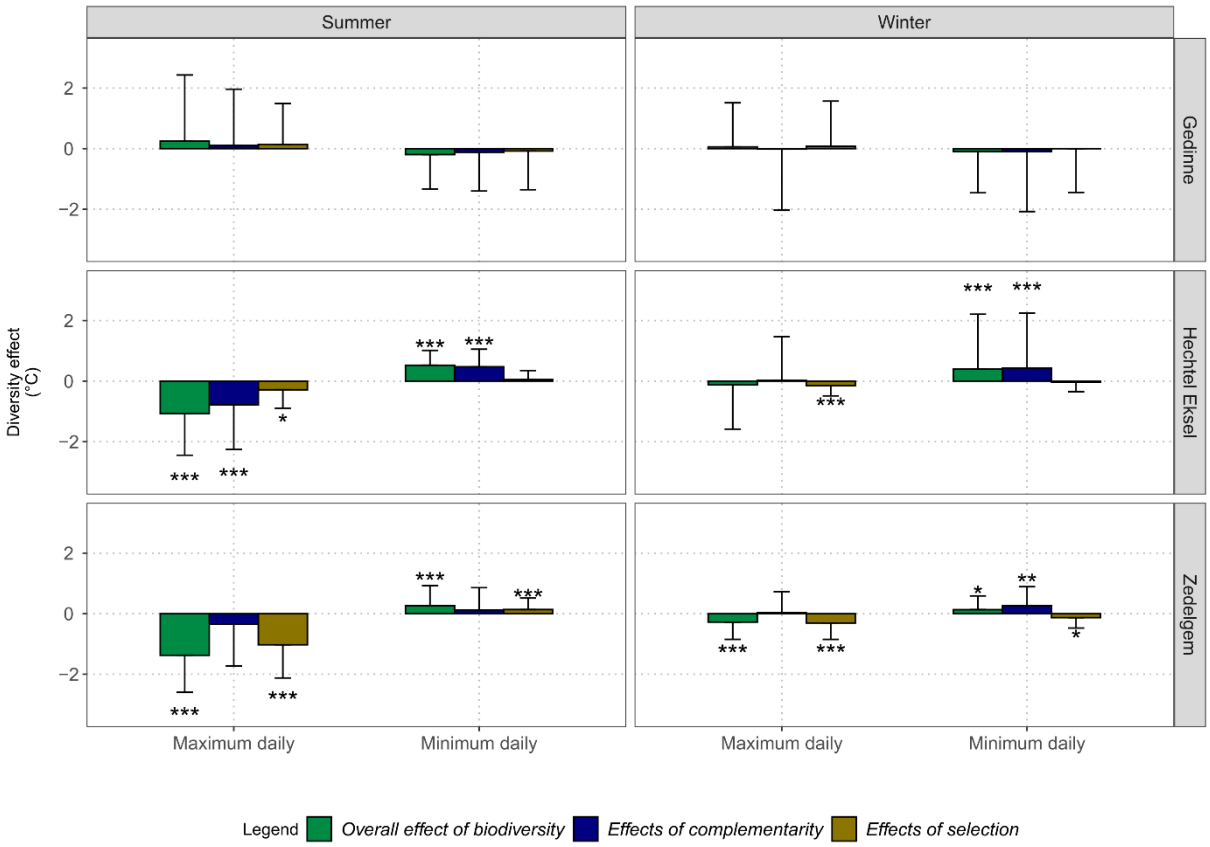


Figure 3 Tree species diversity effects (overall, and separated into complementarity and selection) on air temperature offsets. Diversity effects are based on the methodology of Loreau and Hector (2001), and here analysed with intercept-only mixed-effects models with *block* | *plot* as nested random term, and corAR1(form=~Day) as variance structure to account for temporal autocorrelation. Bars denote which specific diversity effects are responsible for maximum (T_{max}) and minimum (T_{min}) temperature offsets. Full statistical results are reported in supplementary information Table S8. *P < 0.05; **P < 0.01; ***P < 0.001.

term, and corAR1(form=~Day) as variance structure to account for temporal autocorrelation, were applied to test whether VPD offsets in varying forest stands were significantly different from zero. Red outer lines of bars indicate that the intercept was significantly different from zero, with P < 0.05. Full statistical results are reported in supplementary information Table S4.

We detect, in general, negative net diversity effects for maximum temperature offsets and positive net diversity effects for minimum temperature offsets. However, the contribution of selection and complementarity effects to this overall biodiversity effect differed among sites (Figure 3, Table S8). In general, complementarity effects were found to be dominant at the H-E site, while selection effects were dominant at Ze site. No diversity effects were detected at the Ge site.

Although net diversity effects were often not significantly different from zero for VPD offsets, we observed similar differences in the importance of complementarity and selection effects in Ze and H-E site as found for

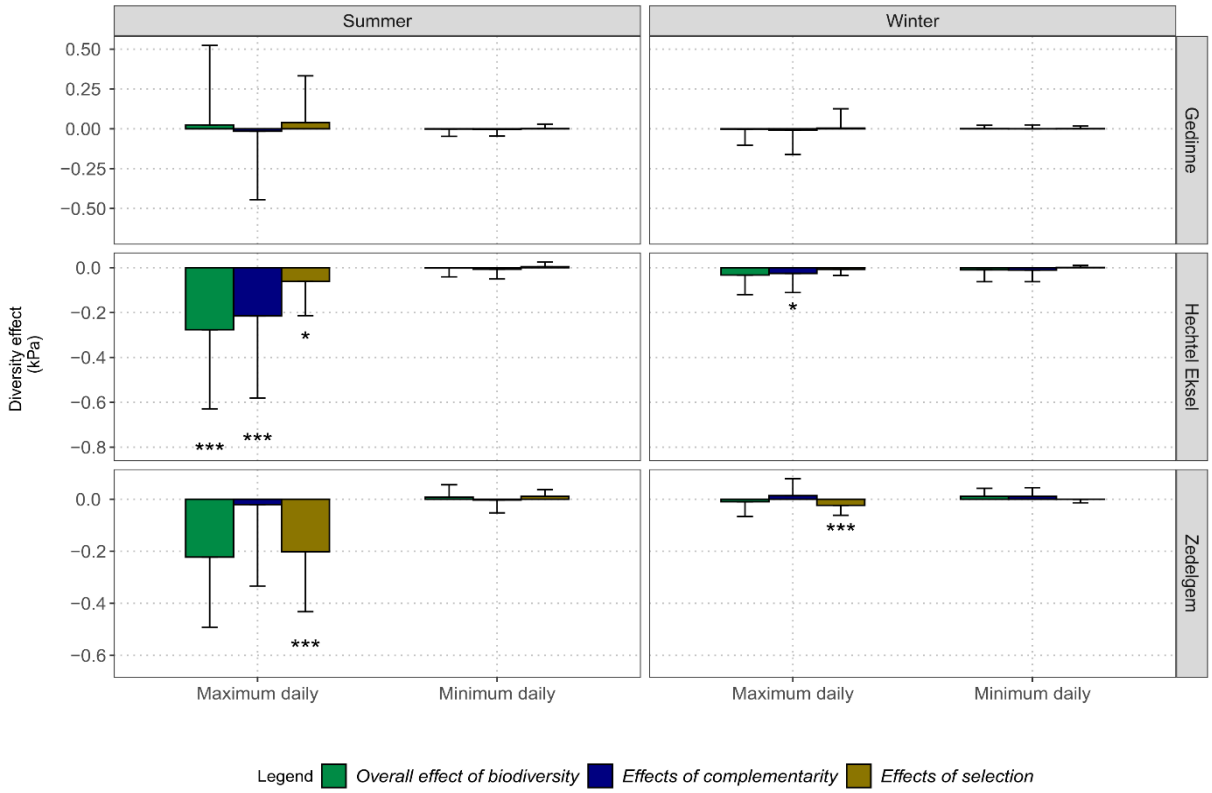


Figure 4 Tree species diversity effects (overall, and separated into complementarity and selection) on VPD offsets. Diversity effects are based on the methodology of Loreau and Hector (2001), and here analysed with intercept-only mixed-effects models with *block | plot* as nested random term, and corAR1(form=~Day) as variance structure to account for temporal autocorrelation. Bars denote which specific diversity effects are responsible for maximum (VPD_{max}) and minimum (VPD_{min}) VPD offsets. Full statistical results are reported in supplementary information Table S9. *P < 0.05; **P < 0.01; ***P < 0.001.

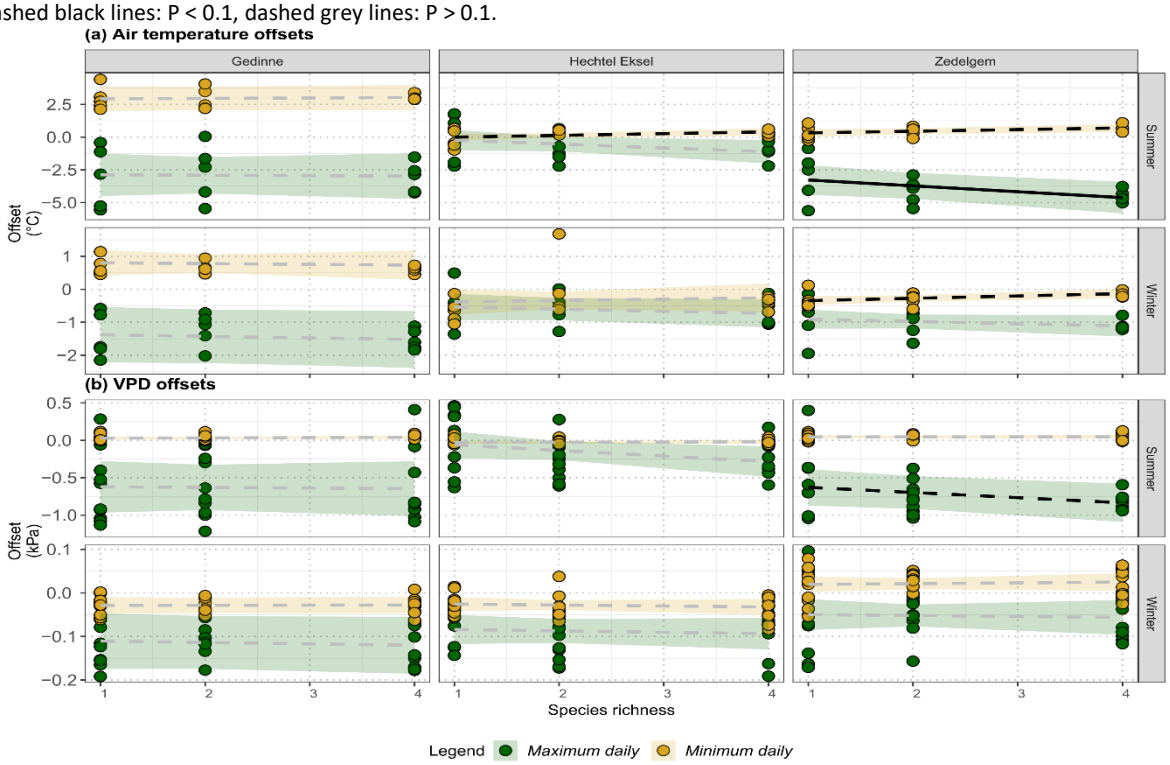
239 temperature offsets (Figure 4, Table S9). Again, complementarity effects were found to be dominant at H-E,
240 while selection effects were dominant at Ze site. Again, no diversity effect was found in Ge site.

241

242 Our data show both decreasing (for maximum temperature) and increasing (for minimum temperature)
243 offsets with species richness (Figure 5a, Table S10). These trends were rather weak, but found to be
244 significant for summertime maximum temperature offsets in Ze, with a 0.4°C decrease in offset per tree
245 species added to the mixture. Similar but only marginally significant trends were detected for minimum
246 temperatures in winter at H-E and for minimum temperature offsets in both seasons at Ze.

247 VPD offsets did either not respond to species richness or decreased only slightly with species richness (Figure
248 5b, Table S10). We only detected a marginally significant decrease in VPD offset with increasing species
249 richness during the summer season at Ze site.

Figure 5 Tree species diversity effect on air temperature offsets (a) and VPD offsets (b). Lines represent fitted mixed-effects models with *'Species richness*' as fixed-effect, *'Block | Plot'* as nested random term, and corAR1(form=~Day) as variance structure to account for temporal autocorrelation. Offsets were always calculated as the difference between microclimate variables inside forests minus those recorded outside the forest. Full statistical results are reported in supplementary information Table S10. Solid black lines: $P < 0.05$, dashed black lines: $P < 0.1$, dashed grey lines: $P > 0.1$.



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Canopy cover significantly increased with species richness in the Ze site (Figure 6, Table S11; mixed-effects models: 4.34 % / SR, P<0.01) and marginally significantly increased in the H-E site (mixed-effects models: 6.95 % / SR, P<0.1). No significant trend was found in the Ge site. No significant diversity effects were detected in terms of basal area; we only found a marginally significant increasing trends with species richness in the Ze site (mixed-effects models: 1.65 m^2 ha^{-1} SR^{-1}, P<0. 1).

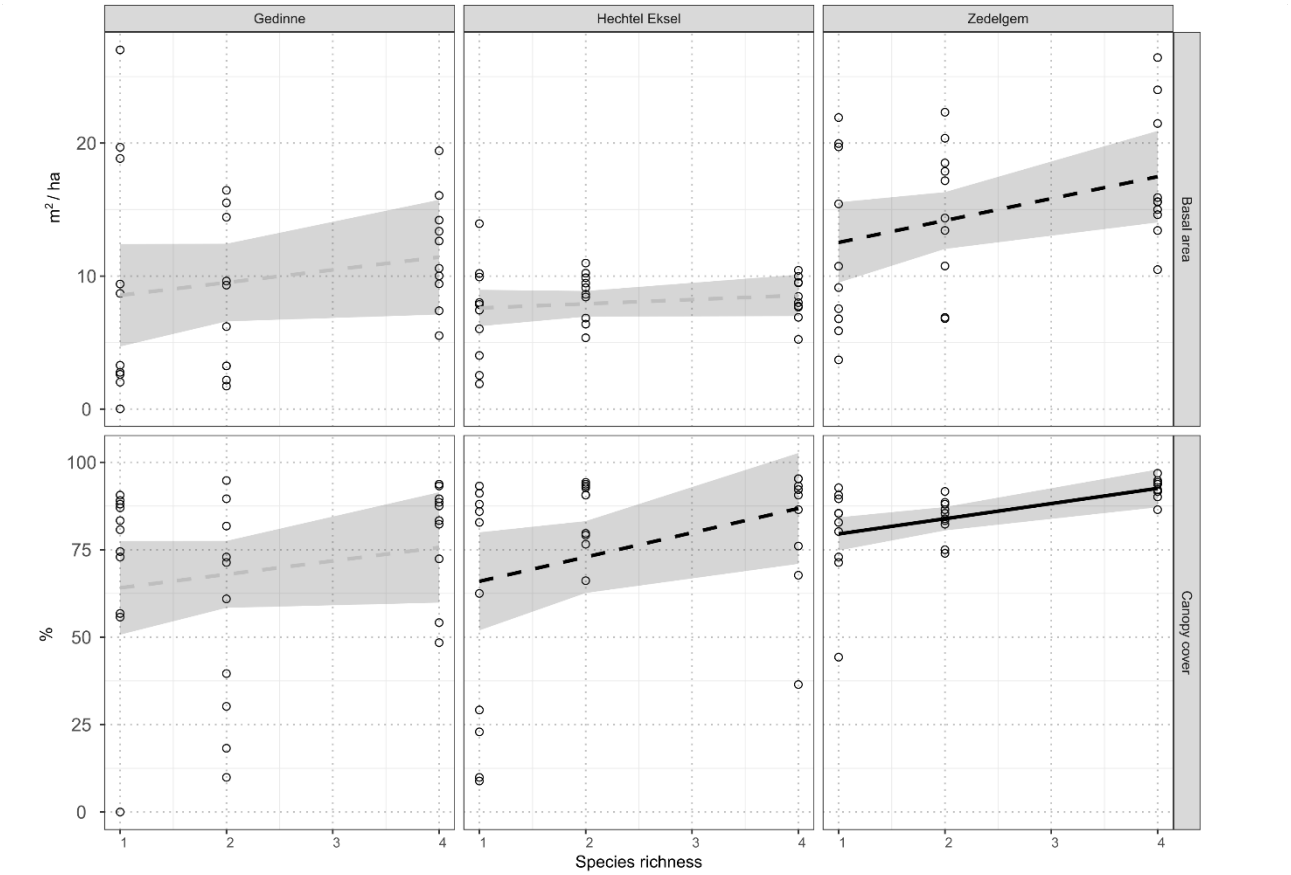

Figure 6 Tree species diversity effects on basal area and canopy cover. The lines showed the prediction of basal area based on mixed-effects models with 'species richness' as fixed effect and 'Block' as a random-effect term. Full statistical results are reported in supplementary information Table S11. Solid black lines: P < 0.05, dashed black lines: P < 0.1, dashed grey lines: P > 0.1.

4. Discussion

We here obtained mean below-canopy air temperature offsets of -1.8 ± 2.6 °C (Mean ± SD) and +0.6 °C ± 2.1 °C for summertime maximum and wintertime minimum daily temperatures, respectively. These values are in agreement with global mean offsets: De Frenne *et al.* (2019), for example, reported that maximum and minimum air temperature below the forest canopy is, on average 4.1 ± 0.5 °C cooler and 1.1 ± 0.2 °C warmer than the macroclimate. In another study focusing on mature temperate deciduous forests across Europe, Zellweger et al. (2019) detected offsets of −2.1 (−3.7 to 1.4) and 0.4 °C (−1.2 to 2.0), for maximum summer temperature and minimum winter temperature, respectively. The fact that these offset values reported in mature forests are close to those we found in young experimental forests, suggests that the buffering capacity of a forest is not always strongly affected by forest age and can approach its maximum offsets shortly after planting.

The mean offset values we detected differed considerably depending on the site. Microclimate offsets are thus context dependent, potentially driven by differences in regional climatic conditions, distance to the nearest coast and differences in stand structure (Zellweger et al., 2019). We indeed found that microclimate offsets were negatively correlated with macroclimate (Figure S14), with the most pronounced cooling of air temperature extremes in the research site with the highest open-field mean annual temperature (mean of maximum temperature offset of -2.3 °C in Ze). In addition to the effect of macroclimate on microclimate offsetting, our results also showed the importance of stand structural attributes for microclimate buffering, with increased buffering in stands with higher basal area (Figure S15). Our findings thus evidence that forests play an important role in the microclimate buffering, which can help for mitigating warming temperatures and improving water availability in the face of climate change (Bertrand et al., 2011; Bramer et al., 2018; Davis et al., 2019; De Frenne & Verheyen, 2016; Frey et al., 2016).

Tree species identity affected microclimate offsets via trees' functional traits. The highest offsets (both air temperature and VPD offsets) were detected in stands composed of relative fast-growing species, characterised by a high basal area and canopy cover (Table S16 and S17). For instance, in Ge, not only

286 monocultures of *L. eurolepis* and *P. menziesii* had a high thermal buffering capacity, but also mixtures with
287 species such as *B. pendula* and *P. sylvestris* in the H-E and Ze site (Table S16 and S17), indicating high species
288 identity effects for microclimate offsetting.

289 In addition to tree species identity effects, also diversity effects were detected. The underlying drivers, being
290 either selection or complementarity effects, however, differed depending on the research site. In Ge, net
291 diversity effects were only observed in 12.5% of the mixtures, for both temperature and VPD offsetting
292 (Figure S6 and S7). Among the few mixtures with significant net diversity effects, most of them are larger
293 than expected based on monoculture offsets. Only in mixtures of *F. sylvatica* and *Q. petraea* offsets were
294 smaller than expected which can be explained by their similarities in terms of phenology and morphology,
295 leading to higher interspecific than intraspecific competition for nutrients and light. No overall net diversity
296 effect was detected in Ge, which may be attributable to slow growth of some species at that cold location
297 (e.g. basal area of maple and beech are currently both below 3 m^2/ha; Figure S12) and could not form
298 considerable differences in canopy architecture in mixtures (Cardinale et al., 2007; Tilman et al., 2001; Van
299 de Peer et al., 2018). Given that diversity effects on stand biomass have been reported to increase linearly
300 through time (Tatsumi, 2020), we can expect that diversity effects on microclimate offsetting will increase
301 with tree age.

302 In H-E, net diversity effects were observed in 50% and 30% of the mixtures, for both temperature and VPD
303 offsetting (Figure S6 and S7). Our additive partitioning approach revealed that these diversity effects were
304 mainly driven by complementarity effects (Figure 3, Figure 4). We also detected overyielding of basal area,
305 the mechanisms behind this increased productivity, as well as the increased productivity itself, might explain
306 higher thermal buffering in mixed stands. A more efficient crown packing, for example, can increase both
307 overstorey productivity and thermal buffering, by optimising photosynthesis, the filtering of incoming
308 radiation and evapotranspiration at the canopy scale (Zellweger et al., 2019). Unfortunately, our study does
309 not allow to disentangle the individual importance of these drivers for thermal buffering in mixed stands. In
310 Ze, the net diversity effect was observed in 50% of the mixtures, for both temperature and VPD offsetting.
311 Selection effects were found to be the driving force. This was mostly due to overyielding of *B. pendula*, with

c. 0.34 cm^2 basal area increase per tree in mixtures (Figure S13), which might have amplified microclimate offsetting in mixtures at Ze.

Our final question was whether increasing tree species richness can amplify the buffering capacity of a forest, in the same way species richness can increase productivity (Morin et al., 2011). In our study, however, effects of tree species richness on microclimate offsets are contrasting among research sites. Only in Ze, a significant increasing trend with species richness was found in summertime for T_{max} offsetting. As we detected similar trends between basal area and species richness, again being only significant for the Ze site, we expect that the higher buffering capacity with higher species richness can be explained by overyielding of high-performing species in mixtures, which mainly occurred for *B. pendula* in Ze. Therefore, we can conclude that species richness effects on microclimate offsetting were rather weak and highly context-dependent. However, the fact that we detected this effect only in Ze and not in Ge and HE, both sites with a lower BA, might also suggest that this effect can increase with tree age and stand maturity.

In sum, we here show that microclimate offsets highly depend on tree species identity and diversity. The next step will be to incorporate tree species diversity effects into the fine-scale spatial modelling of below-canopy temperatures for achieving better predictions about the impact of future climate change on forest biodiversity and function. Our research underpins that higher tree species diversity can indeed amplify thermal offsets. Forest managers and policy makers can exploit such thermal offset diversity effects as a regulating service when developing mitigation and adaptation plans to mediate forest microclimates. This might especially be relevant for afforestation and reforestation projects that aim to quickly create a typical forest microclimate on currently treeless habitats such as former arable lands or clear-cut areas.

Authors' contribution statement

SZ, KV, PDF and DL conceived and designed research. SZ led the data collection, data analysis and writing.

337 **Data accessibility**

338 Data will be made available upon request.

339 **Conflict of interest**

340 The authors have no conflicts of interest to declare.

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