The ecological role of Fraxinus for species diversity in floodplain forests

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The ecological role of *Fraxinus* for species diversity in floodplain forests

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Author Contributions: PH originally formulated the idea. AF and PH conceived the experiments. AF carried out the fogging experiments and sorted the samples. PS identified most of the beetle species, assigned the species to their feeding guilds, provided autecological knowledge and was involved in the analysis. TM developed the mathematical models. TM and AF performed the statistical analyses. AF wrote the MS in consultation with all authors. All authors contributed to the MS and provided editorial advice.

Abstract

To assess how different tree species contribute to overall diversity and system function, we sampled 99 trees by fogging in Elbe floodplain forests and collected 182,179 arthropods, of which 25,861 (14.2%) were beetles. Ninety percent of all beetle individuals and 65% of the beetle species were associated with the canopy. Beetles of the herb and soil layer contributed 35% to canopy richness, but represented only 8% of all individuals. Beetle communities differed significantly in diversity, structure and functional composition between tree species, suggesting different roles in maintaining diversity. Two types of communities could be distinguished: 1) those with high proportions of specialists that formed a predictable framework, characterised by high alpha diversity and low within-beta diversity such as those on *Quercus robur* and *Ulmus laevis*, and 2) those on *Fraxinus excelsior* with predominantly non-specific beetles, characterised by high alpha and high beta diversity. We found that the distribution of the most abundant zoophagous and second most abundant phytophagous guilds in the beetle- and ordinal communities was similar for all trees but differed significantly between tree species. This suggests strong top-down control of herbivore populations. These results indicate that a comprehensive assessment of tree canopy diversity is necessary and overdue to understand the ecological processes that ensure the functioning of forest ecosystems and the provision of ecological services.

Key Words: canopy arthropods, climate change, diversity maintenance, guild composition, top-down control

Introduction

In temperate forests, diversity is greatest in the soil, on the ground and in the canopy, with the taxa present differing significantly in frequency distribution and functional importance (Floren et al. 2022b; Nielsen 2019). While studies of soil communities have intensified in recent years, e.g. (Philippot et al. 2023), little effort has been made to develop a top-down approach to understanding the functional significance of the entire canopy fauna across all taxa. This is surprising given the richness and abundance of arthropods in the canopy and the significant relationship between biodiversity and ecosystem function (Floren and Schmidl 2008; Kristensen et al. 2020). It is all the more incomprehensible as the technical conditions for collecting arthropods (Lowman et al. 2012) and efficient molecular methods for identifying highly diverse taxa such as Diptera, parasitic Hymenoptera or Acari have greatly improved in recent years (Macher et al. 2023). Despite the numerous ecological functions that arthropods perform, little is known how important different tree species are for maintaining species diversity and system processes (Swart et al. 2020). Although this should be of particular relevance to forestry, interest in the canopy is mainly focused on pest species e.g. (Binkley 2021; Franklin et al. 2018).

The late recognition of the canopy as a habitat for a rich biocoenosis was mainly due to the difficulty of access. Despite some early studies (Southwood 1961), it was the fogging investigations in the rainforests of Panama by T. Erwin that focused attention on canopy diversity (Erwin 1982), leading many years later to a greater interest in canopy research in temperate forests (Floren and Schmidl 2008; Moran and Southwood 1982; Ozanne et al. 2000; Stork et al. 1997; Thunes et al. 2003). Fogging is the only method to date that can be used to sample arboreal arthropod communities in an unbiased way, as it collects free-living arthropods in approximately the same numbers as they occur in the trees (Floren et al. 2022a). Determining the frequency distribution of all taxa and their species also allows all specimens to be assigned to their feeding guild and thus to analyse their functional significance.

The aim of our work is to highlight the importance of different tree species for maintaining biodiversity and system functioning. We use data from a recent fogging study that aimed at assessing the impact of the neophyte tree *Fraxinus pennsylvanica* on biodiversity (Floren et al. 2022a). Several

77 deciduous trees were fogged in a floodplain forest of the Middle Elbe Biosphere Reserve in Germany,
78 including *Q. robur*, *U. laevis, F. pennsylvanica, F. excelsior* and *T. cordata*. Usually, the number of
79 arthropods associated with a particular tree species is used to assess the importance of a tree species
80 for biodiversity (Ammer 1991; Brändle and Brandl 2001; Kennedy and Southwood 1984; Southwood
81 1961). All these studies report maximum richness for *Q. robur*, which is therefore considered most
82 important for biodiversity and its conservation (Mölder et al. 2019). Here we test whether this is also
83 true for whole beetle communities, such as those obtained by fogging. Communities are characterised
84 by their alpha and beta diversity for standardised comparison. In a further step, we estimate how many
85 of these beetles find suitable habitat conditions in the trees and are likely to use them regularly. We
86 then contrast these with the tourist beetles from the herb and soil layer and ask how much they
87 contribute to community diversity.
88 In order to gain a more detailed insight into the mechanisms of canopy community assembly, we
89 focus on phytophagous and tree-specific xylobiont beetles, as there is sufficient autecological data on
90 host-tree adaptation available. We ask, how beetle communities on *Q. robur* and *U. laevis*, with their
91 many specialists, differ from *T. cordata* and *Fraxinus*, for which only few specialists are known
92 (Hultberg et al. 2020). We test the hypothesis that their communities have higher proportions of non-
93 specific species including tourists from other trees and from the herb and soil layer and investigate
94 how this affects guild composition. Assessments of individual taxa provide only a very specific insight
95 into the importance of the canopy fauna. However, the true functional importance of the canopy fauna
96 only becomes apparent when entire communities are analysed. We therefore calculated the
97 composition of guilds across all recorded taxa, which we use as a proxy for function and the ability to
98 provide ecosystem services, such as herbivore population control (Gardarin et al. 2018; Gontijo et al.
99 2015). This also allows us to estimate the extent to which Coleoptera are representative of the
100 community as a whole.
101
102 **Materials and Methods**
103 **Study area**

Field work was carried out in the hardwood floodplain forests of the Middle Elbe Biosphere Reserve in Germany in 2017 (S-Figure 1). The annual precipitation is 550 mm, whilst the mean July temperature 18 °C. A total of 99 trees were fogged at several sites in Saalberghau and Steckby-Lödderitzer Forst (51°51,32 N, 12°12,05 E and 51°53,28.2 N, 11°59,49.5 E). These were 30 *Fraxinus excelsior*, 30 *F. pennsylvanica*, a neophyte hat grows in high density in the area, 21 *Quercus robur*, 12 *Ulmus laevis* and 6 *Tilia cordata* trees (Tab. 1). The study areas showed the greatest possible similarity in the external conditions. All field work was carried out from the end of May to mid-June.

Fogging

Arthropods were collected by insecticide knockdown (fogging), which is highly effective for quantitative sampling of tree-specific communities of mobile arthropods (Floren et al. 2022b). Only natural pyrethrum was used as insecticide, which is highly specific to arthropods, destroyed in direct sunlight within hours and does not leave persistent substances in the trees. The fogging takes only a few minutes and is limited to a narrow radius around the studied tree. Tree-specific samples were assured by exactly positioning the collecting sheets beneath the tree crown projection area thereby excluding arthropods from neighbouring trees. Foggings were carried out early in the morning or in the evening when there was little wind. Arthropods that dropped into the collecting sheets two hours following fogging were collected and conserved in 80% ethanol. For more details on the method see (Floren 2010; Floren et al. 2022a).

Ordinal communities

Due to sample losses the arthropods of 72 fogged trees were fully assigned to their feeding guilds. For most taxa guild assignment was unambiguous but for Coleoptera and Heteroptera, which comprise different feeding guilds, assignment is based on species identifications done by specialists. Guild assessment could not be achieved for the Diptera. The following feeding guilds were distinguished: phytophages comprised chewers and sap-suckers. Lepidoptera were mainly present as caterpillars and very few adults were collected. Zoophages mainly include Araneae, Coleoptera, Heteroptera (Hemiptera) and all parasitoid Hymenoptera. Ants were collected in low numbers and considered

zoophages. Xylophages (xyl) and mycetophages (myc) were mainly represented by beetles. The remaining guilds were saprophages (sap) and epiphyll-grazers (grazer). Here, we focus on the “major taxa”, which are defined by their frequency distribution and constancy in the trees (Floren et al. 2022b). They include Diptera, Hemiptera (Homoptera and Heteroptera), Hymenoptera, Coleoptera, Psocoptera, Lepidoptera and Araneae. All other arthropods were included in the group 'Others'.

Composition of beetle communities

All phytophagous beetles and all tree-specific xylobiont beetles were chosen for a detailed analysis. Phytophages were separated between stenophagous specialists (oligo- and monophagous beetles) and polyphagous generalists. The zoophagous *Archarius pyrrhoceras* (Curculionidae) previously *Curculio pyrrhoceras*, which is specialised on *Q. robur* was also included in the analysis. The larvae develop in the galls of the wasp *Cynips quercusfolii* (Cynipidae) and consume the gall tissue as well as the wasp larvae (Kopelke 1983). In addition to the tree-specific phytophages, beetles that had entered a crown of another tree species (“tree tourists”) were also treated separately. Due to insufficient ecological knowledge on host-tree associations, no other beetles were included in the analysis. This group of canopy-associated species was contrasted with all beetles from the herb and soil layer ("ground tourists").

Statistics

Statistical analyses were performed using the software R version 4.3.2 (R Core Team 2023) and the packages of the Bioconductor project (Marini et al. 2020). Individual- and sample-based rarefaction curves were computed using the iNEXT package (Hsieh et al. 2022). In addition, rarified Shannon accumulation curves were calculated with the Rarefy package (Thouverai et al. 2023). Robust non-metric multidimensional scaling (NMDS) was used to represent beta diversity (Jaccard index) between beetle communities as implemented in R-package vegan (Oksanen et al. 2022). For an adequate stress value, we choose k=4 dimensions. To better illustrate the differences between tree species, we have drawn polygons representing the hulls of predefined samples. To robust this visualization we show the hull of samples after deleting the outer hull of the considered sampling. The influence of girth in breast

height of trees (Gbh) and tree species (Tree) on the beta diversity (Jaccard index) was modelled by a PERMANOVA as implemented in the adonis function in the vegan package (McArdle and Anderson 2001): beta diversity ~ Gbh + Tree + s(WE) + s(NS), where b-splines (s()) on the geographical coordinates were used to adjust for spatial autocorrelation. The significance of the factors was derived by a permutation-based statistical test based on 9,999 permutations. We applied a post-hoc test on the factor Tree and corrected the associated p-values for multiple testing (Martinez 2017).

To further analyse community composition for "associated beetles", "tree tourists" and "ground tourists", relative proportions per tree species were visualised as barplots, separately for individuals and species. Here and throughout the manuscript we tested for significance of proportional differences between groups by using logistic regression as implemented in the framework of general additive models (GAM); R package "mgcv" (Wood 2017), referring to associated and tourist beetles, singletons and feeding guilds. In case of overdispersion family = "quasibinomial" was selected; if no overdispersion was detected, family = "binomial" was chosen. All tree related significance levels are based on models adjusting for tree girth in breast height (GBH) and spatial autocorrelation based on the same model as in case of the PERMANOVA model. Beetle guild composition and ordinal guild composition was displayed as boxplots and tested by the same GAM as described above. The associated Tukey post-hoc tests were performed using the R package "emmeans" (Lenth 2024). We assumed p-values to be weakly significant if $p < 0.05$ (*), significant if $p < 0.01$ (**) and strongly significant if $p < 0.001$ (***). All p-values were adjusted for multiple testing using the method of Benjamini and Hochberg (Benjamini and Hochberg 1995).

Results

Beetle communities

From all 99 fogging samples 182,179 arthropods were collected, of which 25,861 (14.2%) were beetles sorted to 519 beetle species (Tab. 1). Most species were collected from *F. excelsior* (337 species) followed by *Q. robur* (305 species), while numbers of individuals were highest on *Q. robur* and *U. laevis*. Zoophages dominated both in species number (191 species; 36.8%) and abundance (11,314 individuals; 43.8%), with the exception of *U. laevis*, where few phytophagous species reached

188 maximum abundance, statistically affecting the proportions of the other groups. Phytophages had the
189 second highest number of species (116 species, 22.4%) and abundance (8,629 individuals, 33.4%).
190 Although only six *T. cordata* trees could be fogged, the ranking was consistent with the other trees.
191 Mycetophages, xylophages and saprophages provided between 3% and 13% of all beetles. The
192 xylobiont beetles, which include several feeding guilds, contributed 208 species (40.1%) and 12,509
193 individuals (48.4%).
194 **Table 1:**
195 Individual and sample-based rarefaction curves (Fig. 1 A, B) recorded highest diversity on *F.*
196 *excelsior*, that exceeded the diversity on *Q. robur*. The number of species on *F. pennsylvanica* was
197 identical to that on *Q. robur* in the same subsample of individuals. High diversity on *Fraxinus* was
198 caused by many rare and the absence of abundant species. As proven by sample-based rarefaction, *Q.*
199 *robur*, *F. exelsior* and *U. laevis* sampled highest numbers of new species with every fogging. Due to
200 the pronounced dominance hierarchy on *U. laevis* and *Q. robur*, beetle diversity was lower compared
201 to *F. excelsior*, as shown by rarified Shannon curves (Fig. 1 C). *T. cordata* followed in third place.
202 NMDS ordination of Jaccard diversity showed high overlap between *F. excelsior* and *F.*
203 *pennsylvanica* and a clear separation of *Q. robur* and *U. laevis*, which overlapped little (Fig 1D). *T.*
204 *cordata* was not clustered uniformly but was closest to *F. pennsylvanica*. PERMANOVA, corrected
205 for spatial autocorrelation, confirms significant differences in beta diversity between tree species (S-
206 Tab. 1). The factor “Tree Species” is highly significant ($p < 0.001$) and explained most of the variance.
207 Beta diversity differed significantly between trees, except for *T. cordata*, including both *F. excelsior*
208 and *F. pennsylvanica* (Fig 4D).
209 **Figure 1:**
210
211 **Community composition**
212 Based on the results of all trees fogged, we found that 65.2% of all beetle species (339 of 519 species)
213 and 91,8% of all beetle individuals (23,726 of 25,861 individuals) had a close relationship with the
214 canopy due to their habitat requirements. Beetles from the herb and ground layer ("tourist ground")
215 represented 180 species (34.8%) but only 2,110 individuals (8.2%), of which 63 species and 716

individuals were phytophages, and 73 species in 339 individuals were zoophages. Only few xylobiont beetles had entered the canopy from the herb and ground layer.

In a further step we defined a subset of tree-specific phytophagous and xylobiont species for which sufficient autecological knowledge is available to correlate the compositional differences to tree species (see Methods part for model details). This can lead to different assignments for different tree species, e.g. *Archarius pyrrhoceras* (Curculionidae) is adapted to *Q. robur*, where it was found in 89 specimens and assigned to the “associated” group, but to *U. laevis*, where it occurred in 6 specimens, it was assigned as a "tree tourist". The selected subset, on which the compositional analysis is based, represent 259 species (42.7%) and 11,044 individuals (49.9%), including 54 phytophages in 7,911 individuals and 33 xylobiont species in 1,925 individuals.

The most striking difference was found between *Fraxinus* and the other tree species. Beetle communities on *Fraxinus* showed no significant differences in relative proportions between all groups (“associated”, “tourist tree” and “tourist ground” beetles, Fig. 2, S-Fig. 2-3). In contrast, *Q. robur* and *U. laevis* were dominated by associated beetles (on average 81,2%), most of which were stenophagous specialists, with tourists from other trees or the herb and ground layer contributing little to the overall composition. In contrast, *Fraxinus* communities had significantly fewer associated beetles, on average 27.6%. “Ground tourists” peaked on *T. cordata,* but this was due to one species, *Meligethes aeneus* (Nitidulidae), which was collected from one tree with 248 specimens. Only two phytophagous specialists were collected in low numbers from the ash trees. These were *Lignyodes enucleator* (Curculionidae), collected from *F. excelsior* in 158 individuals, but also mainly from one tree. Two individuals of *Stereonychus fraxini* (Curculionidae) were collected from all 30 *F. pennsylvanica* trees. No specialist species was found on *T. cordata*. The "gap" left by the small number of phytophagous specialists was filled by tree-specific xylobiont beetles, which represented 47.7%. In contrast, their proportion was 84.8% on *Q. robur* and *U. laevis*. “Ground tourists” contributed on average 59.0% to all tree species (Fig. 2B). Significant differences were found only between both *F. excelsior* and *F. pennsylvanica* compared to *Q. robur* and between *U. laevis* and *Q. robur* (S-Tab. 3). The data showed also significant differences in the distribution of singletons (Fig. 2 C). Highest proportions per tree were recorded on both *Fraxinus* species, which differed not significantly between each other (Fig. 2 C,

S-Tab. 4). The occurrence of singletons on *Fraxinus* was highly significantly associated with the number of "tourist ground" beetles but not with any other factor (Fig. 2 D, S-Tab. 5).

Figure 2:

Guild composition of beetle communities

To characterise the functional importance of the arboreal beetle communities we used guild composition as surrogate measure. Overall, communities differed significantly in guild composition (Fig. 3). Zoophages dominated on all trees, with highest proportions on *F. pennsylvanica* (67.7%) and *F. excelsior* (55.9%). The ash trees had also significantly lower proportions of phytophages than the other trees (S-Tab. 6). Mycetophages were the third largest feeding guild, representing on average less than 20% of species per tree. Guild proportions on *U. laevis* were strongly influenced by the mass occurrence of phytophages mainly due to the chrysomelid *Luperus saxonicus*, while high numbers of xylophages were caused by *Magdalis armigera* (Curculionidae). Saprophages were lowest in abundance but reached highest proportions on *Fraxinus*. *F. excelsior* and *F. pennsylvanica*, and *Q. robur* and *T. cordata*, showed the highest correspondence in guild composition.

Figure 3:

Guild composition of ordinal communities

We use beetle guild composition as a measure of community function. The question is whether this is a beetle-specific or a general pattern. To test this, we now focus on the ordinal composition across all taxa. Zoophages together with parasitic Hymenoptera dominated at the ordinal level, representing on average 60% of all arthropods, with a maximum of 77% on *F. pennsylvanica* and a minimum of 43% on *T. cordata* (Fig. 4). Within the predator guild, parasitoids were most abundant, followed by the zoophagous Heteroptera, Coleoptera and Araneae. Phytophagous arthropods followed in second rank (S-Tab. 8). Most abundant were Hemiptera and Coleoptera, while Lepidoptera caterpillars represented only between 2.4% and 3.9% of phytophages (S-Fig. 2). Proportions of sap-suckers were at maximum on *T. cordata*, while beetle chewers dominated on *U. laevis*. Almost all arthropods in the mycetophagous and xylophagous guilds were beetles. Grazers were the third most common guild on

the ordinal level. As with saprophages, their proportions did not differ between trees. Mycetophages represented comparatively small proportions in all communities, ranging from 0.9% on *F. excelsior* to 3.3% on *Q. robur*. As in the previous analyses, *F. excelsior* and *F. pennsylvanica* differed not significantly in the guild composition.

Figure 4:

Discussion

Tree canopies as a missing link in forest research

It is now widely recognised that trees host highly diverse and abundant arthropod communities (Floren and Schmidl 2008; Stork et al. 1997). Their importance in maintaining ecosystem processes and functions is slowly being recognised but is still little considered in forestry, e.g. (Binkley 2021; Franklin et al. 2018). Canopy communities are unique in their taxonomic composition and function. They are clearly separated from the airspace, herb layer and soil layer, but are in constant exchange and strongly influence each other (Bardgett and Wardle 2010; Kristensen et al. 2020; Ozanne et al. 2003; Swart et al. 2020). This is also indicated by the fact that most larval stages of arboreal arthropods develop in the soil. From a conservation point of view, tree canopies are also underestimated as habitats or refuges for rare species, species classified as threatened in the Red Lists or species new to science (Floren et al. 2021; Hultberg et al. 2020; Thunes et al. 2021).

Using one of the largest fogging datasets in temperate latitudes, we show that tree species vary not only in diversity but in their importance for maintaining biodiversity. Fogging is highly effective in collecting free-living canopy arthropods in a tree-specific way. This is supported by our finding that 65% of all fogged beetle species and 92% of all fogged beetle individuals were adapted to the canopy, where their habitat requirements are met. They include all xylobiont beetles, tree-specific phytophages and a remaining fraction of mostly unspecific zoophagous, mycetophagous and saprophagous beetles. In contrast, tourist beetles from the herb and soil layer accounted for 35% of all species, but only for 8% of all beetle individuals, indicating a substantial contribution to the arboreal diversity but little influence on guild composition and associated effects on food webs. Some 'tourist ground' species collected in higher abundance may indicate a stronger relationship with the canopy, but this remains to

300 be verified. Examples are *Meligethes aeneus* (Nitidulidae, 287 individuals) or *Aphthona euphorbiae*
301 (Chrysomelidae, 80 individuals), compare (Sprick and Floren 2007).
302 From a forestry perspective, canopy biodiversity has long been considered unnecessary, as forest
303 management ensured efficient economic use. This is changing with climate change, which is forcing a
304 fundamental transformation of forests and management practices to control pests and invasive species
305 and to secure economic sustainability and ecosystem services (Bongers et al. 2021; Harvey et al. 2023;
306 Prade and Coyle 2023).
307
308 **Species Diversity**
309 The differences between beetle communities go far beyond the tree-specific specialists that have
310 received the most attention so far (Brändle and Brandl 2001; Southwood 1961). Surprisingly, beetle
311 communities on both *Fraxinus* species, and especially *F. excelsior,* showed higher alpha diversity than
312 those on *Q. robur* and *U. laevis,* while all tree species differed significantly from each other in beta
313 diversity. In contrast to the few specialists, a large number of facultatively associated species are
314 reported from ash (Hultberg et al. 2020).
315 Our data suggest a previously unrecognised importance of native *F. excelsior* in maintaining
316 biodiversity, but further research is needed to verify whether they describe a general pattern. This
317 would include analysing other forest types, e.g. *Hordelymo-* or *Carici-Fagetum* on calcareous ground,
318 where *Fraxinus* occurs in greater abundance due to its high physiological plasticity (Lévesque et al.
319 2023). In contrast to *Q. robur* and *U. laevis*, only six specimens of *T. cordata* were sampled, which
320 proved insufficient for a reliable diversity analysis, as the high variability within the beetle
321 communities prevents a clear assignment to either the *Q. robur*-*U. laevis* or the *Fraxinus* group. This
322 study illustrates that significant tree-specific differences in alpha- and beta diversity can be identified
323 on the basis of at least twelve foggings.
324 The great importance particularly of *Quercus* for biodiversity has been extensively studied and often
325 emphasised (Mölder et al. 2019; Thunes et al. 2021). Here, we focus on *Fraxinus*. While *F. excelsior*
326 is considered a keystone species from a forest ecological perspective (Hultberg et al. 2020;
327 Langenbruch et al. 2012; Pautasso et al. 2013), its importance for the conservation of arthropod

328 biodiversity remains speculative, although they undoubtedly contribute to maintaining a high level of
329 biodiversity. Phytophagous specialists were characteristic on oaks and elms but were only fogged from
330 few ash trees. Two monophagous species from ash, *Lignyodes enucleator* and *Stereonychus fraxini*
331 (Curculionidae) were rare. *S. fraxini* was only collected in two individuals from two *F. pennsylvanica*,
332 where this normally common species feeds on young ash in the shrub layer (PS, own observation). *L.*
333 *enucleator* was found only on one collecting site and only on *F. excelsior*, where it develops in the
334 fruit stands.
335 The variable number of phytophagous specialists among trees in Central Europe may be explained
336 by the diversity of a tree genus in the Tertiary after the Eocene-Oligocene extinction event 34 million
337 years ago (Sprick and Floren 2008). The low historical importance of *Fraxinus* and *T. cordata*
338 correlates well with the low number of specialists. However, not only did we sample few specialist
339 *Fraxinus* species, but we also found few polyphagous beetles, particularly of the genera *Polydrusus*
340 and *Phyllobius*. This may be caused by specific phytochemicals and their mixtures in ash, such as
341 certain flavonoids, phenolic acids, bitter compounds, coumarins and triterpenes (Hegnauer 1969),
342 which primarily act as a defence against predators. In addition to phytophagous beetles, 23 tree-
343 specific xylobionts were sampled in 2,201 individuals. While Scolytinae (Curculionidae) cannot be
344 quantified by fogging because they live in tree trunks and show pronounced swarming phases,
345 xylobiont beetles, which move freely on leaves and branches, were well represented in the fogging
346 samples and evenly distributed among the trees. Examples were species of the genera *Agrilus*,
347 *Dasytes*, *Magdalis*, *Euglenes* or *Lissodema* that were collected from the canopy sometimes in
348 hundreds of specimens (Floren et al. 2022b; Leroy et al. 2022).
349
350 **Community composition**
351 Compositional differences in beetle communities were correlated to tree species by using a subset of
352 phytophagous and xylobiont beetles. Together with "ground tourists" the data represented 43% of all
353 individuals and 50% of all species. The inclusion of zoophagous, mycetophagous and saprophagous
354 species was prevented by insufficient autecological knowledge. On *Q. robur* and *U. laevis* tree-
355 specific beetles formed the basic framework of structurally similar communities. They were

complemented by tourist beetles from other trees, most of which were also specialists. A proportional dominance of specialist beetles was also recorded for *F. excelsior*, but this was a side-effect of the overall low abundance of phytophages. Even the ash specialist, *L. enucleator*, which was collected at only one site, was consistent with the dominance of specialists. Specialist dominance is consistent with the assumption that they outcompete polyphagous species in their optimal habitats because they use resources more efficiently (Büchi and Vuilleumier 2014). However, this is in contrast with the low numbers of specialists and polyphagous beetles on *Fraxinus* and their complete absence on *T. cordata*. As discussed above, this is more likely due to historical and phytochemical effects.

The "gap" left by the lack of phytophagous specialists was filled by tree-specific xylobionts and low abundant tourist beetles. But what explains the significantly higher proportions of singletons on ash trees and the significant association of singletons with beetles in the herb and soil layer (Fig. 2 C, D)? One possible explanation is that greater canopy openness which allows more light through, creating a more favourable microclimate for arthropods (Seibold et al. 2016) and also offering escape from enemies, reproduction or dispersal (Gardarin et al. 2018). This effect is not limited to the canopy, but also extends to the herb and soil layers, where the more favourable microclimate in combination with the highly decomposable ash leaves should also increase the abundance of arthropods, more of which will then reach the canopy. In general, however, the extent to which arthropod communities are influenced by plant traits, such as habitat availability or microclimatic changes, remains poorly understood (Gardarin et al. 2018). From a faunistic point of view, the ecological importance of *Fraxinus* could therefore be seen in the increase of canopy heterogeneity, which promotes high species coexistence and functional diversity (Swart et al. 2020; Wildermuth et al. 2024).

The structure and frequency distribution of the beetle communities resembles the core-transient framework, according to which communities are composed of locally adapted, abundant core species with strong habitat connectivity and less abundant transient species with weak habitat connectivity (Jenkins et al. 2018; Umaña et al. 2017). Accordingly, communities on *Q. robur* and *U. laevis* show some similarity to more predictable core communities, which were characterised by high alpha- but low beta diversity. This classification does not fit communities with mainly transient species, such as those on *Fraxinus*, which form rather unpredictable assemblages with high alpha- and high beta

384 diversity, with species for which it is not clear why they prefer a particular environment. However,
385 this also indicates that the lack of autecological knowledge is a major difficulty in categorising core
386 and transitional species.
387
388 **Functional importance of canopy communities**
389 In a recent study in temperate forests we have shown that eight main taxa form the basic structure of
390 canopy communities (Floren et al. 2022b), with Diptera dominating as the most species-rich and
391 functionally diverse group (S-Tab. 8). The largest differences in guild composition were found
392 between trees with strong core communities, such as *Q. robur* and *U. laevis*, and those with no or
393 weak core communities, such as *Fraxinus* and *T. cordata* and was particularly evident in zoophages
394 and phytophages (Fig. 4). These differences were confirmed by the ordinal guild composition, raising
395 the question of the influence of beetles on the overall composition. It turned out that the contribution
396 of beetles varied both between tree species and between guilds. The influence on the zoophage guild
397 was strongest on *Q. robur* (32%) and *T. cordata* (43%). However, due to the higher abundance of a
398 few phytophagous species, beetles represented 51% of the phytophages on *U. laevis*, but less than 20%
399 on the other trees.
400 Contrary to our expectation of primary consumer dominance, zoophages dominated all trees (Fig. 4),
401 suggesting that canopy arthropods are crucial in controlling herbivores and pest species. High predator
402 diversity and abundance favours top-down regulation of herbivore populations (Gardarin et al. 2018;
403 Staab and Schuldt 2020; Stemmelen et al. 2022) and high predation pressure is often associated with
404 high levels of system stability (Macfadyen et al. 2009). The predator effect becomes much more
405 apparent when the usually less specialised zoophages are considered together with the often highly
406 specialised parasitoid Hymenoptera (Gontijo et al. 2015). High predator diversity is supported by a
407 high degree of habitat heterogeneity, such as that found in the hardwood floodplain forests studied.
408 Our data show also that guild composition on *Fraxinus* was diametrically different compared to the
409 other tree species, with zoophages reaching maximum dominance and phytophages collected in lowest
410 numbers. The finding of predator dominance contrast with a recent study by Mottl and co-workers,
411 who investigated guild composition of canopy arthropods along a latitudinal gradient, but who found

412 no evidence of top-down regulation, but rather bottom-up limitation (Mottl et al. 2020). However, the
413 authors used a completely different sampling method (manual sampling of felled trees) and limited
414 their analysis to a few groups of phytophages and zoophages (caterpillars and leaf miners vs. spiders
415 and ants). This greatly limits comparability.
416 Phytophages were represented mainly by Hemiptera and Coleoptera, while caterpillars, which have
417 been described as the "cornerstone" of the canopy community (Leroy 2022), never represented more
418 than 4%, not even on oaks. Our data indicate that the great ecological impact attributed to this group is
419 based on a generalisation of locally limited mass occurrences and their sometimes disastrous effects
420 (Floren et al. 2022b). The third largest guild were grazers, mainly Psocoptera, which can reach highest
421 abundance within an individual community (Baz 2004; Floren et al. 2022b; Thunes et al. 2003). Most
422 arboreal psocopterans are found on the bark surface where they feed on algae and lichens, while leaf-
423 inhabiting species feed primarily on small leaf fungi. However, the impact of their functional
424 contribution is still largely unknown. The remaining xylophages, mycetophages and saprophages
425 made up less than 2% of the total communities on all trees (median 1.4%), suggesting a low
426 importance when considering trophic relationships.
427
428 **The ecological role of *F. pennsylvanica***
429 After our study in the floodplain forests 2017, *F. excelsior* died in large numbers following drought
430 and ash dieback, accompanied by high abundances of ash-specific bark beetles of the genus *Hylesinus*
431 (Scolytinae, Curculionidae), as this was clearly visible in the severely damaged bark. At the same
432 time, oak trees began to die on a large scale. These changes are mainly seen as a consequence of
433 climate change (Hart et al. 2014; Jactel et al. 2021), which have triggered unpredictable forest
434 dynamics (Floren et al. 2022a). This is also an indication of the problems that forestry will face in the
435 future for species-rich mixed forests.
436 It is likely that the neophyte *F. pennsylvanica*, which has not yet been affected by tree mortality to
437 the same extent as *F. excelsior*, will play a greater role in the forest as it shares many characteristics
438 with the native ash tree, even if it remains uncertain to what extent it can replace the ecological role of
439 *F. excelsior*. For a full discussion see (Floren et al. 2022a). In addition to drought-induced dieback and

ash dieback, another threat is the rapidly spreading of the emerald ash borer, *Agrilus planipennis* (Buprestidae) in Europe, which has caused mass mortality of native ash species in eastern North America (Hultberg et al. 2020; Prade and Coyle 2023). This means that all options must be considered to prevent such scenarios, including accepting the presence of *F. pennsylvanica*.

Conclusion

High abundance, high species- and functional diversity, high exchange and interaction of the canopy with the atmosphere, the herb- and the soil layer and the rhizosphere provide increasing evidence of the importance of arboreal communities for forest function and the provision of ecosystem services. We are only just beginning to recognise this complexity and how much ecosystem processes are affected. Differences in species- and functional diversity as well as in guild composition between tree species also indicate different ecological roles for maintaining diversity, with *Fraxinus* as a striking example. These results emphasise the need for a holistic approach to canopy research that finally considers all taxa to quantify the importance of the canopy, as this lack of knowledge is now proving to be an obstacle to mitigating the effects of climate change.

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Kopetz (female *Malthodes*/Cantharidae), W. Rücker (several Latridiidae). Voucher specimens are deposited in the collection of A. Floren.

Conflict of Interest: The authors declare that they have no conflict of interest.

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Table 1: Collecting efficiency and characterisation of beetle communities showed the greatest differences in diversity and composition between *Fraxinus* and the other trees.

Figure 1: A) Individual-based rarefaction curves show highest beetle diversity on *F. excelsior*, but sample-based rarefaction curves show that alpha diversity increases most with each fogged tree in *Q. robur*. The legend depicts tree species in different colours with the number of foggings per tree in brackets; Fe = *F. excelsior*, Fp = *F. pennsylvanica*, Qr = *Q. robur*, Ul = *U. laevis*, Tc = *T. cordata*. **C)** Rarefied Shannon diversities reflect differences in the evenness of beetle abundance distributions per tree species. **D)** Non-metric multidimensional scaling (NMDS) based on the Jaccard beta diversity separates beetle communities on *Fraxinus* from those on *Q. robur* and *U. laevis*, which were also largely separated. *T. cordata* was closest to *F. pennsylvanica*. Polygons visualise differences in beta diversity. The p-value refers to the factor "Tree Species", which was the most significant factor in a PERMANOVA ($p < 0.001$, S-Tab. 1). **E)** The post-hoc tests between trees showed significant differences between tree species except for *T. cordata*.

Figure 2: Barplots reveal significant compositional differences between tree species for both individuals **A)** and species **B).** Differences in relative proportions of associated beetles ("Assoc"), "TouristGround" and "TouristTree" between *Fraxinus* and the other tree species suggest differences in community assembly mechanisms (models S-Tabs. 2, 3). **C)** Proportion of singletons per tree were significantly higher on *Fraxinus* than on *Q. robur*, *U. laevis* and *T. cordata*. **D)** Negative binomial regression model adjusted for girth in breast height and spatial autocorrelation found a strong significant association between the number of singletons per tree and the number of "TouristGround" species (S-Tab. 4).

Figure 3: A) Guild composition of beetle communities presented as box plots for the most frequent guilds showed strong significant differences between tree species. Each dot represents the percentage of each beetle guild per tree. The trees were dominated by zoophages except for *U. laevis*, where phytophages were most abundant. **B)** A heatmap summarises proportional values and counts (in brackets) for all guilds and trees. The colour code indicates high (red) and low (green) proportions. **C)** Post-hoc-tests for the factor Tree species. For the whole model see (S-Tab. 6). Fe = *F. excelsio*r, Fp = *F. pennsylvanica*, Qr = *Q. robur* , Tc = *T. cordata*, Ul = *U. laevis.* Number of foggings in brackets. Zoo = zoophages; phy = phytophages, myc = mycetophages, xyl = xylophages, sap = saprophages.

Figure 4: A) Ordinal level: Guild composition of entire arthropod communities (excluding Diptera), presented as box plots for the most frequent guilds. Each dot represents the percentage of each arthropod guild per tree. Differences were most striking between *Fraxinus* and the other trees, with zoophages always dominating, followed by phytophages in second place. **B)** A heatmap summarises proportional values and counts (in brackets) for all guilds and trees. The colour code indicates high (red) and low (green) proportions. Number of foggings in brackets. **C)** Post-hoc-tests based on GAMs. For more details see (S-Tab. 7). Fe = *F. excel*sior, Fp = *F. pennsylvanica*, Qr = *Q. robur* , Tc = *T. cordata*, Ul = *U. l*aevis. Zoo = zoophages; phy = phytophages, myc = mycetophages, xyl = xylophages, sap = saprophages.

668 **Table 1:**

	Total	*F. excelsior*	*F. pennsylvanica*	*Q. robur*	*U. laevis*	*T. cordata*
Trees fogged	99	30	30	21	12	6
Species	519	337	279	305	215	131
Individuals	25861	3584	5228	7391	8298	1360
Zoophages Individuals	11314 (43.8%)	2003 (55.9%)	3537 (67.7%)	3524 (47.4%)	1546 (18.6%)	704 (51.8%)
Zoophages Species	191 (36.8%)	124 (36.8%)	107 (38.4%)	113 (37.0%)	72 (33.5%)	57 (43.5%)
Phytophages Individuals	8629 (33.4%)	601 (16.8%)	478 (9.1%)	1817 (24.6%)	5323 (64.2%)	410 (30.1%)
Phytophages Species	116 (22.4%)	67 (19.9%)	57 (20.4%)	75 (24.6%)	50 (23.3%)	27 (20.6%)
Xylobiont beetles						
Individuals	12509 (48.4%)	2176 (60.7%)	3859 (73.8%)	3577 (48.4%)	2159 (26%)	738 (54.3%)
Species	208 (40.0%)	146 (43.3%)	123 (44.1%)	125 (41.0%)	96 (44.7%))	55 (42.0%)

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670

Figure 1:

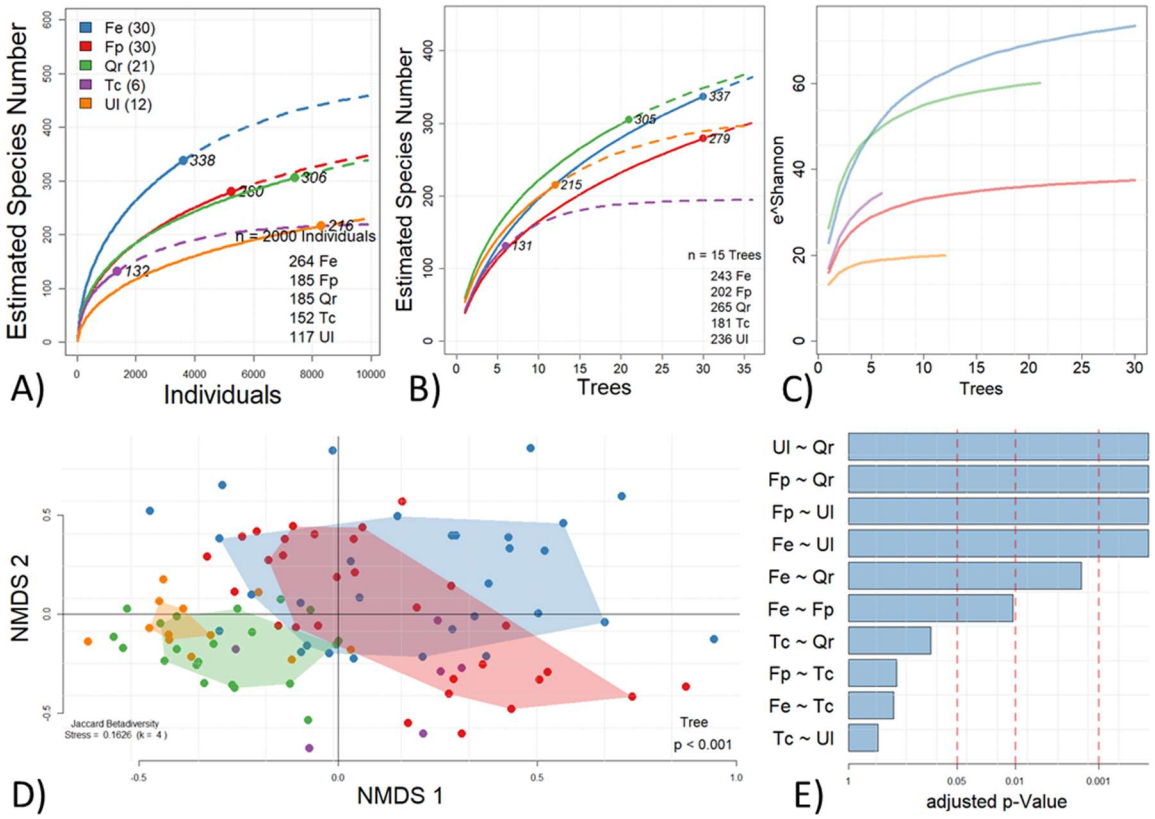
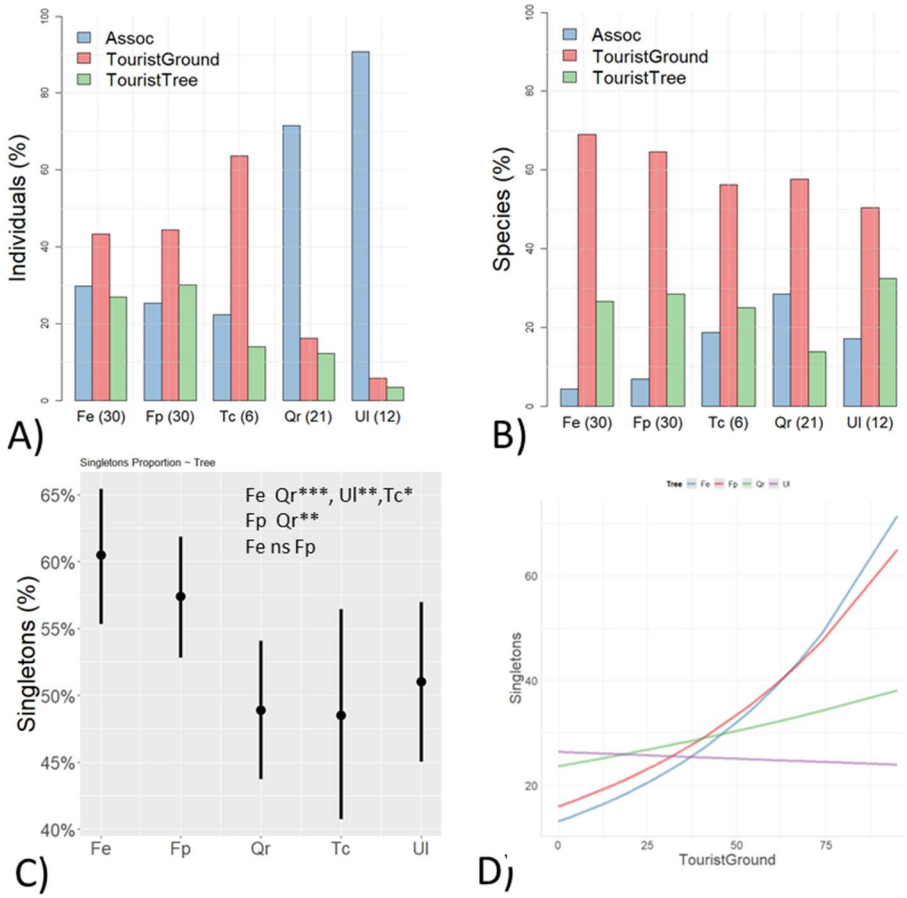
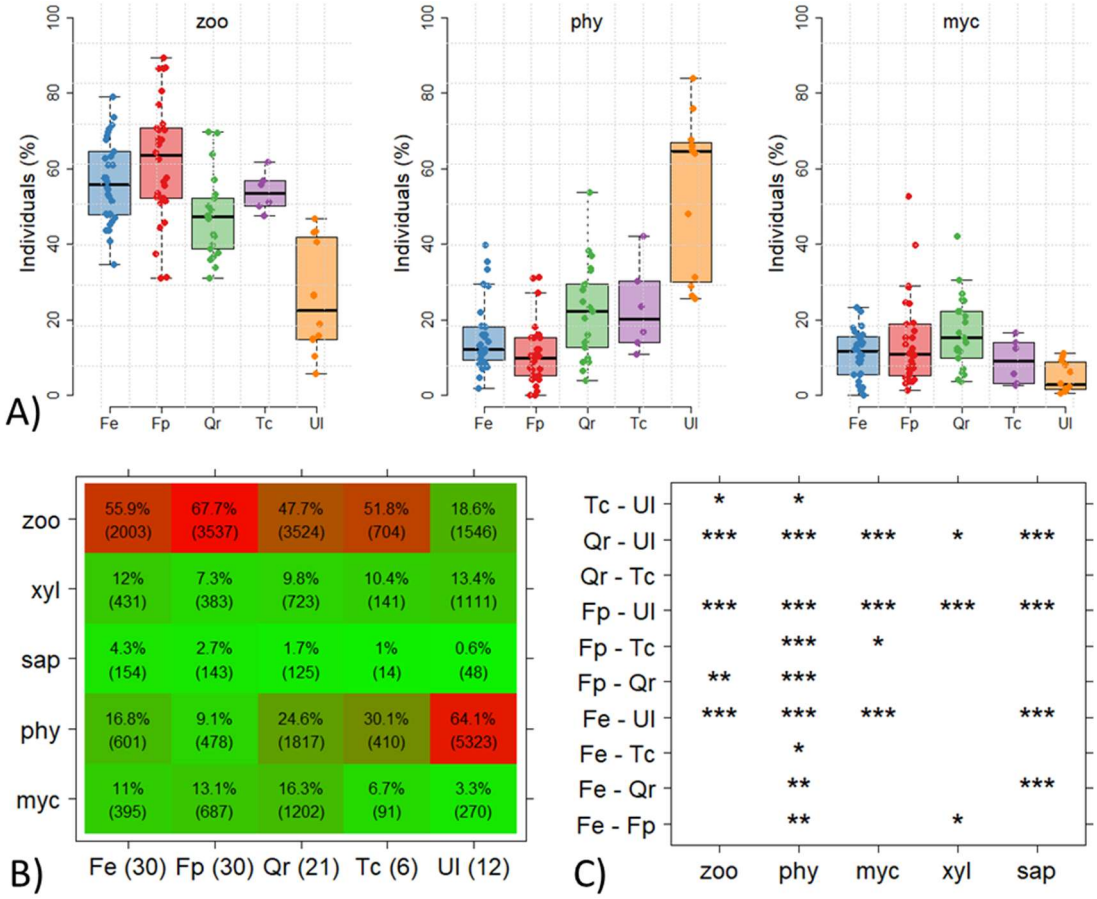

Fe (30)
Fp (30)
Qr (21)
Tc (6)
Ul (12)
Estimated Species Number
Individuals
338
260
306
216
132
n = 2000 Individuals
264 Fe
185 Fp
185 Qr
152 Tc
117 Ul
A)
Trees
337
305
279
215
131
n = 15 Trees
243 Fe
202 Fp
265 Qr
181 Tc
236 Ul
B)
e^Shannon
C)
NMDS 1
NMDS 2
Jaccard Betadiversity
Stress = 0.1626 (k = 4)
Tree
p < 0.001
D)
Ul ~ Qr
Fp ~ Qr
Fp ~ Ul
Fe ~ Ul
Fe ~ Qr
Fe ~ Fp
Tc ~ Qr
Fp ~ Tc
Fe ~ Tc
Tc ~ Ul
adjusted p-Value
E)

Figure 2:


Assoc
TouristGround
TouristTree
Individuals (%)
Fe (30)
Fp (30)
Tc (6)
Qr (21)
Ul (12)
A)
Species (%)
B)
Singletons Proportion ~ Tree
Fe Qr***, Ul**,Tc*
Fp Qr**
Fe ns Fp
Singletons (%)
C)
Singletons
TouristGround
D)

677 **Figure 3:**



678

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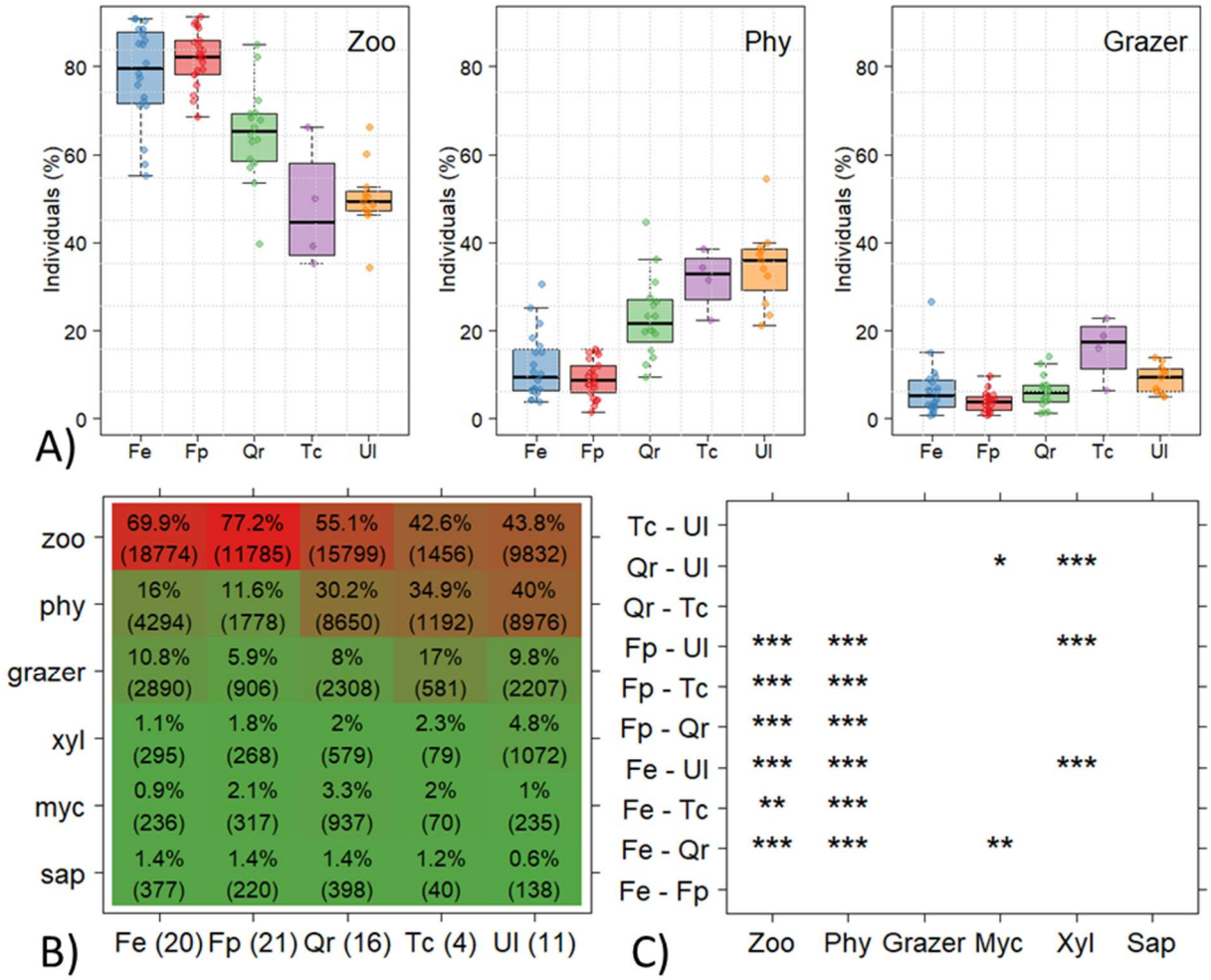
Figure 4:


Zoo
Phy
Grazer
Individuals (%)
0
20
40
60
80
Fe
Fp
Qr
Tc
Ul
A)
zoo
phy
grazer
xyl
myc
sap
69.9% (18774)
77.2% (11785)
55.1% (15799)
42.6% (1456)
43.8% (9832)
16% (4294)
11.6% (1778)
30.2% (8650)
34.9% (1192)
40% (8976)
10.8% (2890)
5.9% (906)
8% (2308)
17% (581)
9.8% (2207)
1.1% (295)
1.8% (268)
2% (579)
2.3% (79)
4.8% (1072)
0.9% (236)
2.1% (317)
3.3% (937)
2% (70)
1% (235)
1.4% (377)
1.4% (220)
1.4% (398)
1.2% (40)
0.6% (138)
Fe (20)
Fp (21)
Qr (16)
Tc (4)
Ul (11)
B)
Tc - Ul
Qr - Ul
Qr - Tc
Fp - Ul
Fp - Tc
Fp - Qr
Fe - Ul
Fe - Tc
Fe - Qr
Fe - Fp
Zoo
Phy
Grazer
Myc
Xyl
Sap
C)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterialMSFraxinus.pdf