Article

The Impact of the Neophyte Tree *Fraxinus pennsylvanica* [Marshall] on Beetle Diversity under Climate Change

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Abstract: We studied the impact of the neophyte tree *Fraxinus pennsylvanica* on the diversity of beetles in floodplain forests along the river Elbe in Germany in 2016, 2017 and in 2020, where 80% of all *Fraxinus excelsior* trees had died following severe droughts. Beetles were collected by insecticidal knock-down from 121 trees (64 *F. excelsior* and 57 *F. pennsylvanica*) and identified to 547 species in 15,214 specimens. The trees sampled in 2016 and 2017 showed no signs of drought stress or ash dieback and serve as a reference for the comparison with the 2020 fauna. The data proved that *F. excelsior* harbours the most diverse beetle community, which differed also significantly in guild composition from *F. pennsylvanica*. Triggered by extremely dry and long summer seasons, the 2020 ash dieback had profound and forest-wide impacts. Several endangered, red-listed beetle species of Saxonia Anhalt had increased in numbers and became secondary pests on *F. excelsior*. Diversity decreased whilst numbers of xylobionts increased on all trees, reaching 78% on *F. excelsior*. Proportions of xylobionts remained constant on *F. pennsylvanica*. Phytophages were almost absent from all trees, but mycetophages increased on *F. pennsylvanica*. Our data suggest that as a result of the dieback of *F. excelsior* the neophyte *F. pennsylvanica* might become a rescue species for the European Ash fauna, as it provides the second-best habitat. We show how difficult it is to assess the dynamics and the ecological impact of neophytes, especially under conditions similar to those projected by climate change models. The diversity and abundance of canopy arthropods demonstrates their importance in understanding forest functions and maintenance of ecosystem services, illustrating that their consideration is essential for forest adaptation to climate change.

Keywords: forest conversion; neophyte trees; ash dieback; beetle communities; ecosystem function

1. Introduction

Predictions of the effects of climate change assume that forests in Germany will be strongly affected in the future, particularly by shifts in tree species composition, drought, fire, extreme weather conditions and gradations of pest species and pathogens [1–3]. Forestry is reacting to this by converting commercial forest stands into structurally heterogeneous mixed forests which are thought to be more robust [4–6]. In addition, drought-resistant tree species from different regions of Europe are being considered for cultivation [3]. The introduction of neophyte trees is referred to as assisted colonisation, which is considered to merely accelerate the process of natural recolonisation [7]. In addition, tree species from separated regions of the world are also assessed for their suitability as supplementary trees. Measures such as the conversion of forests to mixed stands and the cultivation of neophytes are intended to ensure future economic viability and to mitigate the risks of climate change [3,4]; however, the introduction of neophytes poses great risks to our native biodiversity and its ecosystem services, which is why they are subjected to

comprehensive risk analyses [8,9]. Still, such studies rarely involve canopy arthropods and if they do, they are mainly concerned with trees that are already cultivated, such as *Pseudotsuga menziesii* Mirb. or *Quercus rubra* L. [10–13].

The canopy of temperate forest trees harbour a diverse and abundant arthropod fauna [14]. Arthropods are key components in the provision, regulation, and dynamics of many ecosystem services, such as pollination, decomposition or regulating population dynamics of potential pest species [15,16]. The high numbers in the canopy best emphasise their ecological relevance, but there is still far too little information available on how canopy arthropods are linked to ecosystem services; however, this also raises the question of why the canopy fauna plays only a minor role in the discussion of how to adapt forests to the projected changes due to climate change [3]. One reason for this might be that there are no standardised metrics to assess the multifunctional impact of the canopy fauna on an ecosystem level and to define their role in maintaining ecosystem function and services [15–17]. Such standardisation would also be useful, for example, for comparing forest types or to assess the impact of forest management and neophytes on native biodiversity.

Our comparative investigation of the canopy communities on *F. pennsylvanica* [Marshall] and the native ash tree *F. excelsior* L. should be seen in this context. *F. excelsior* is considered a foundation species that defines much of the structure of a community by creating locally stable conditions for other species [18,19]. We examine canopy beetle communities from *F. pennsylvanica* and *F. excelsior* using proportions of generalists and specialists and the composition of feeding guilds as a proxy for their impact. The severe droughts in 2018 and also 2019 in combination with the ash pathogen *Hymenoscyphus fraxineus* [T. Kowalski] resulted in a large-scale dieback of *F. excelsior* trees in 2020, of which more than 80% of all fully grown trees were affected [pers. com. H. Panach, Biosphere Reserve Mittelelbe]. Due to higher tolerance to the ash dieback, the neophyte *F. pennsylvanica* showed only little effects [20]. This particular situation allows us to relate the effects of extreme droughts to the effects of the neophyte *F. pennsylvanica* on the arthropod fauna. In particular, our study aims to answer (1) How beetle diversity and guild composition differs between *F. excelsior* and *F. pennsylvanica*; (2) How ash dieback affects beetle communities on both *F. excelsior* and *F. pennsylvanica*? (3) What role do canopy beetles play during forest adaptation to climate change?

2. Materials and Methods

Field work was conducted in the hardwood floodplain forests of the biosphere reserve Mittel-Elbe in 2016, 2017, and 2020 (Figure 1A). The 2016 and 2017 investigations were independent of those in 2020 and were carried out as part of a biodiversity monitoring program. The annual precipitation is 550 mm, whilst the mean July temperature 18 °C. Research was carried out at several sites in the nature reserves Saalberghau and Steckby-Lödderitzer Forst (51°51′32 N, 12°12′05 E–51°53′28.2 N, 11°59′49.5 E). The study areas showed the greatest possible similarity in the external conditions, which also referred to the soil types, which are fluvisol or gley-fluvisol. The last strong summer flood was documented in 2013, whilst the water levels in the following years were very low.

A total of 121 trees were fogged, 64 *F. excelsior* and 57 *F. pennsylvanica*. The number of foggings per tree species and year is given in Table 1. All field work was carried out from the end of May to mid-June. The difference in the number of foggings per tree species in 2016 and 2017 is due to the different availability of suitable trees in the field. In 2020, we were allowed to sample beetles from seven fully grown trees of both *F. excelsior* and *F. pennsylvanica*. From all trees, we measured height, girth in breast height (gbh) and leaf cover (proportion against the sky). All trees chosen for the study were vital and showed no sign of drought stress or of the fungal pathogen. The neophyte Red Ash *F. pennsylvanica* is highly tolerant to flooding and was planted in the last century for timber production [21]. Due to its high dispersal potential, it is found in high density in some areas and has been classified as an invasive species with potential negative impacts on regional

biodiversity [22], but this assessment was neither supported by our findings (Floren own data) nor by a botanic and forestry survey (Albrecht et al., unpublished report).
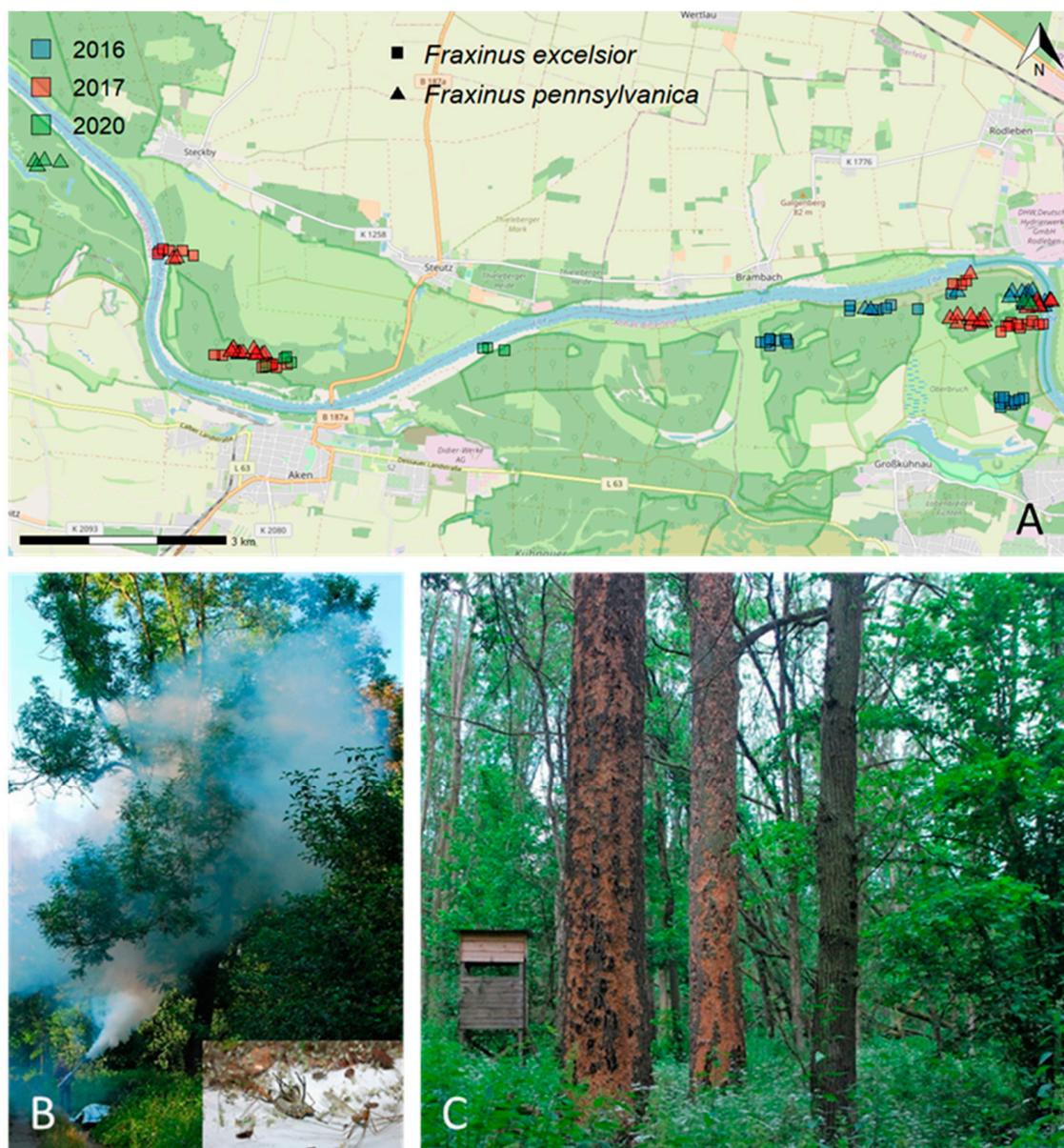

Figure 1. (**A**) Study sites in the hardwood forests of the nature conservation areas Saalberghau (East) and Steckby-Lödderitzer Forst (West) along the Elbe near Dessau in 2016, 2017 and 2020. Trees are distinguished by colours and jittered for better visibility. *F. excelsior* is marked as square, *F. pennsylvanica* as a triangle. (**B**) The fogging of an ash tree. The warm fog rises up into the canopy. All arthropods that dropped into the collecting sheets two hours following fogging were collected (inlay Figure). (**C**) As a result of drought and ash dieback, most *F. excelsior* trees had died in 2020. Following a mass development of the ash bark beetle *Hylesinus fraxini* (Curculionidae, Scolytinae), woodpeckers subsequently destroyed the bark of dead *F. excelsior* trees (Fotos A. Floren).

Table 1. Summary statistics for all beetles and after assignment to feeding guilds. Feeding guilds refer to xylobiont beetles; Fe = *F. excelsior*, Fp = *F. pennsylvanica*.

	Fe: 2016	Fe: 2017	Fe: 2020	Fp: 2016	Fp: 2017	Fp: 2020
Samples	27	30	7	20	30	7
Individuals	1892	3584	829	2135	5228	1546
Species	235	337	106	171	279	145
Singletons	98	134	54	77	109	61
Singletons (%)	41.7	39.8	50.9	45.0	39.1	42.1
Mean Exp Shannon	19	22	14	13	16	23
Nr. of phytophages	269	605	49	169	481	63
% phy of all beetles	14.2	16.9	5.9	7.9	9.2	4.1
Nr. of xylobiont beetles	950	2177	646	1492	3859	1101
% xyl. of all beetles	50.2	60.7	77.9	69.9	73.8	71.2
Feeding guilds of xylobiont beetles						
Xylophages	189	431	501	102	383	212
- (%)	19.9	19.8	77.6	6.8	9.9	19.3
Zoophages	682	1494	122	577	2997	617
(%)	71.8	68.6	18.9	38.7	77.7	56.0
Mycetophages	53	145	20	790	398	262
(%)	5.6	6.7	3.1	52.9	10.3	23.8
Saprophages	26	107	3	23	81	10
(%)	2.7	4.9	0.5	1.5	2.1	0.9

2.1. Insecticidal Knock-Down (Fogging)

Insecticidal knock-down is a highly effective method to collect ectophytic, free-living canopy arthropods in a quantitative and tree specific way [23]. In order to keep the impact on the ecosystem as low as possible, we used only natural pyrethrum in a concentration of around 1%, diluted in highly purified white oil. Natural pyrethrum is highly specific to arthropods and destroyed in direct sunlight within hours. It does not leave harmful substances in the trees. The fogging of an individual tree takes only a few minutes and depends on the weather conditions. The warm fog rises into the canopy and up into the air where it quickly dilutes. Depending on the local weather conditions, the effect of the insecticide is limited to a narrow radius of about 50 m around the examined tree in the direction in which the fog drifts. Tree specific samples can be obtained by exactly positioning the collecting sheets beneath the study tree crown projection area, thus excluding arthropods from neighbouring trees. Foggings were carried out early in the morning or in the evening when there was little air movement. All arthropods that dropped into the collecting sheets 2 h after fogging were collected and conserved in 80% ethanol.

2.2. Beetle Identification and Guild Assignment

All beetles were sorted from the fogging samples, identified to species and assigned to their feeding guilds by specialists following [24,25]. In addition, all xylobiont (saproxylic) beetles were combined into one group which comprise different feeding guilds. The following feeding guilds were distinguished: phytophages (phy), zoophages (zoo), xylophages (xyl), saprophages (sap) and mycetophages (myc).

2.3. Statistics

Statistical analyses were performed in the statistical framework R (R Development Core Team 2021) using the packages 'vegan' [26], 'lme4' [27] and packages of the Bioconductor project [28]. The map of the study area was created with the R packages rosm [29] and prettymapr [30]. We used the package iNEXT [31] to perform coverage-based rarefaction on Hill numbers with extrapolation of accumulation curves to test for completeness of sampling and to compare diversities between trees in the smallest subsample size. Based on standardised values, we model the Shannon diversity by a negative binomial generalized linear model (GLM) with the following variables: Year, Treespecies, Year:Treespecies, GBH,

Leaf.cover, TreeHeight and WestEast. Year is modelled as a categorial factor with three levels 2016, 2017 and 2020. Factor TreeSpecies as a categorial factor with two levels, *F. excelsior* and *F. pennsylvanica* whilst Treespecies:Year denotes the corresponding interaction term. The tree specific factor Girth at Breath Height (GBH), LeafCover and TreeHeight are modelled as numeric factors. Due to the WestEast extension of the sampling area, we add the geographical coordinates as a numerical factor. The optimal model was chosen by the Bayesian Information Criterion (BIC) as implemented in the stepAIC function from the MASS package [32]. The optimal model is: ShannonDiversity ~ Year + TreeSpecies + Year:TreeSpecies. For this and the following models the marginal effects of the interaction term "Year * TreeSpecies" is visualised as implemented in the R package sjPlot [33]. Guild composition is modelled by logistic regression. Due to overdispersion, we applied the logistic regression with the quasibinomial family. As for these models, no AIC or BIC is defined, we iteratively compare models using analysis of variance based on a quasi F ratio, dropping the least non-significant term from the model. Visualisation of the fitted coefficient and the associated interaction terms is based on the package sjPlot. The colour code of the coefficient matrix indicates the magnitude of the coefficient, whilst NAs indicate parameters not included in the optimal model. Zeros indicate not significant parameters but are present in the optimal model.

3. Results

The number of beetle species and beetle frequencies varied greatly between *F. excelsior* and *F. pennsylvanica* in 2016 and 2017, indicating high dynamics of the canopy communities. Species and Shannon diversity were higher on *F. excelsior* than on *F. pennsylvanica* but more beetle individuals were collected from *F. pennsylvanica* (Table 1). 2020 marks a sharp break in respect to diversity and was accompanied by significant changes in the functional composition, as illustrated by the absence of phytophagous beetles and the proportional increase of xylobiont beetles. On *F. excelsior*, xylobionts represented 77.9% of all beetles. Of all xylobionts, the xylophages alone made up 77.6%. This was mainly at the expense of zoophagous and mycetophagous beetles. On *F. pennsylvanica*, on the other hand, zoophages and mycetophages accounted for almost 80% of the xylobiont beetles. Saprophages were found in 2020 with only a few individuals.

How sampling effort determines species diversity is shown by rarefaction statistic (Figure 2). In 2016, 2017 species numbers and diversity were higher on *F. excelsior* compared to *F. pennsylvanica*, for both individual- and sample-based rarefaction curves. How much the beetle communities had changed in 2020 is illustrated by the accumulation curves which did no longer distinguish *F. excelsior* and *F. pennsylvanica*. Remarkably, the sample-based curves had reversed between *Fraxinus* species, proving that *F. excelsior* sampled only a few new beetle species with every new fogging (compare inlay tables). This demonstrates the strong influence of ash dieback on beetle communities.

Standardised diversity of beetle communities was calculated as rarefied Shannon diversity (Figure 3) showing a significant but reversed trend for *F. excelsior* and *F. pennsylvanica* between years (Kruskal-Test, $p > 0.001$). Whilst alpha diversity on *F. excelsior* reached the lowest value in 2020, it was maximum on *F. pennsylvanica*. Diversity differed not significantly for both *F. excelsior* and *F. pennsylvanica* between 2016 and 2017 (Wilcox.tests, n.s.) which distinguishes the communities of these two years from 2020. The extent to which beetle communities had changed in 2020 is also demonstrated by the fact that formerly common species avoided *F. excelsior* and were mainly collected by *F. pennsylvanica* (Figure S1). Exceptions were the two specialists *Agrilus convexicollis* (Buprestidae) which was frequently collected from both tree species and *Tetrops starkii* (Cerambycidae), which was collected only in a few specimens on *F. excelsior*.
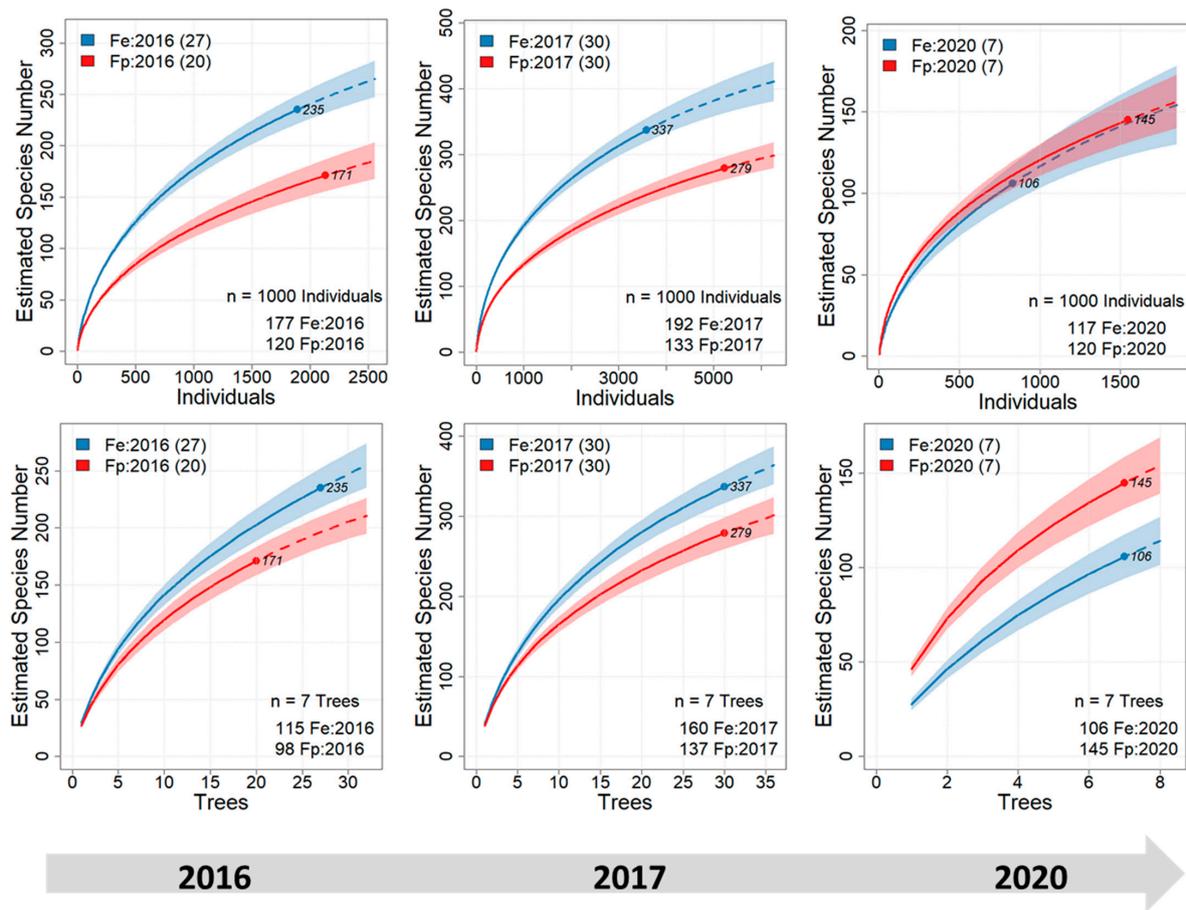
Figure 2. Individual- and sample-based rarefaction curves for all beetles collected by insecticidal knock-down from *F. excelsior* (Fe) and *F. pennsylvanica* (Fp) in a floodplain forest of the region Mittelelbe (Germany) in 2016, 2017 and 2020. Number of foggings per tree species and year in brackets. The accumulation curves document high diversity in 2016 and 2017 and a sharp decline in 2020 after a large-scale dieback of *F. excelsior* trees. *F. pennslyvanica* was hardly affected. This also resulted in a reversal of the sample-based accumulation curves. Inlay tables provide standardised diversity measures computed on the smallest subsample in common, namely 1000 beetles for the individual-based rarefaction curves and 7 fogged trees for the sample-based rarefaction curves.
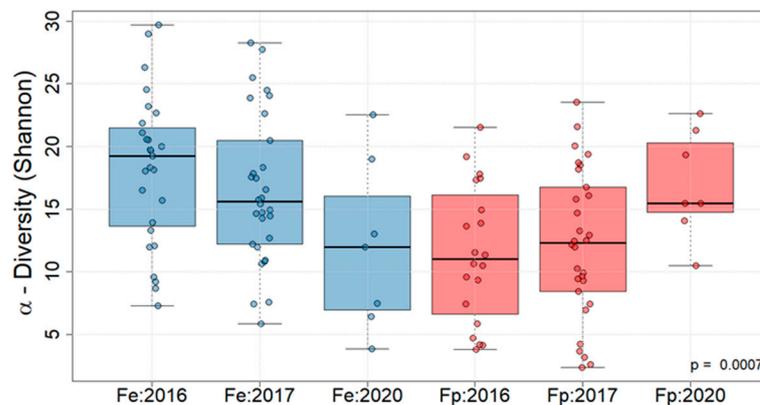

Figure 3. Rarefied Shannon Diversity of canopy beetles collected from *F. excelsior* (Fe, blue) and *F. pennsylvanica* (Fp, red) showed reversed trends during the study years. Calculations were carried out for a subsample of 50 specimens per tree.

The dynamic of alpha diversity raises the question to what extent also the functional composition is affected. This is shown by the fitted marginal interaction effects of each guild (Figure 4). Overall, there were more xylobiont beetles and mycetophages on *F. pennsylvanica*, but proportions of phytophages, zoophages and saprophages were higher on *F. excelsior*. All parameters showed strong deviations in 2020 compared to the previous years, following the large-scale dieback of European Ash. This is reflected by significant interaction term Treespecies:Year. Proportions of specialist species increased highly significantly on *F. excelsior* (coefficient = 1.72; IA-term, $p < 0.001$), whilst phytophages strongly declined on all trees. Remarkably, xylobiont beetles increased significantly over years on *F. excelsior*, where xylobionts accounted for almost 80% of all beetles (Table 1). Their proportion remained stable at a high level on *F. pennsylvanica*. The increase in *F. excelsior* was mainly caused by xylophagous beetles, which also accounted for almost 80% of all xylobionts, whilst zoophages, mycetophages and saprophages were downregulated.
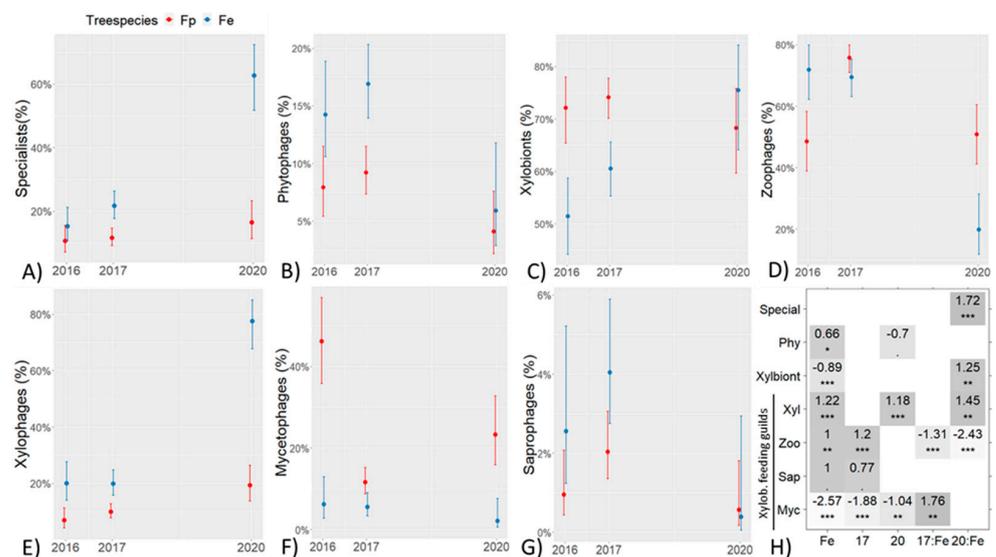

Figure 4. Modelling the dynamics of the arboreal beetle communities on *F. excelsior* (Fe, blue) and *F. pennsylvanica* (Fp, red) shows how proportions of specialists (**A**), phytophages (**B**), xylobiont beetles (**C**) and their feeding guilds (**D**–**G**) changed over years. (**H**) The coefficient matrix summarizes the modelling results, where the columns reflect the contrasts: Fe = Fp–Fe, 17 = 2017–2016, 20 = 2020–2016. The last two columns refer to the interaction terms Year*Treespecies relative to the year 2016 reflecting the differences in years and tree species.

4. Discussion

As a result of climate change, extreme weather events will increase, raising concerns that forest ecosystems may collapse [34]. Droughts, in particular, are predicted to occur more often and in greater severity under climate change. We use the drought in 2018 and 2019 [35] to illustrate the consequences for forest diversity, using canopy beetles as an example. Whether this is due to a direct consequence of climate change is irrelevant to our work. As a result of the drought, most of the European Ash trees died in the Elbe floodplain forests. The large-scale dieback of trees all over Germany increases the pressure on forestry to transform forests into mixed stands in order to secure profitability and other ecosystem services for the future including pollination, seed dispersal, resistance to storms, pest regulation or carbon sequestration to name just a few [3,16,17,36,37]. Here, we also address the ecological role of neophytes, which are considered by foresters to play an important role in forest adaptation to climate change [3,4,38].

Thus far, the huge amount of canopy arthropods has been excluded from this discussion. This is primarily due to a lack of awareness of their importance in maintaining ecosystem functioning [15,17]. Assessing the functional relevance of canopy arthropods

requires intrinsic knowledge of the overall diversity and the interactions among functional groups—knowledge which is still very limited [2,15,39]. In addition, causal biodiversity-functioning relationships cannot simply be inferred from monitoring data alone but require manipulative experiments [40,41]. Such experiments are difficult to conduct in the field, particularly when canopy arthropods are involved. The dieback of European Ash in the floodplain forests studied comes very close to a knock-out experiment, offering the possibility to study in the field the consequences of the loss of this abundant foundation species and particularly, whether the associated ash fauna is able to adapt to the neophyte *F. pennsylvanica*.

4.1. How Do Beetle Communities Differ between F. excelsior and F. pennsylvanica?

Studies on the impact of the *F. pennsylvanica* on biodiversity before the severe drought years documented a highly diverse beetle fauna on both *F. excelsior* and *F. pennsylvanica* (Table 1). Whilst the assessment of *F. pennsylvanica* as an invasive species was based primarily on assumed effects on plant diversity [22] recent work casts doubt on this assessment (Albrecht et al. unpublished report). Moreover, only minor effects on the arthropod fauna were found (Floren own data). However, this point is not important for this work.

However, despite large differences in the number of beetles collected in 2016 and 2017 (Table 1), diversity was consistently higher on the native *F. excelsior* which differed also in functional composition (Figure 4). Adjusting the data for spatio-temporal and tree-specific effects confirmed that more xylobiont beetles occurred on *F. pennsylvanica*, whilst phytophagous beetles were more frequent on *F. pennsylvanica*. The high proportion of xylobionts is remarkable, because trees of *F. excelsior* had fewer deadwood in the canopy than *F. pennsylvanica*. The community level differences provide a simple example of the impact of neophytes on biodiversity and guild composition. As we show below, the assessment of the impact of neophytes on biodiversity depends, as so often, on the overall ecological situation [41,42].

One measure that describes the importance of neophytes as a habitat for the native fauna is their ability to harbour adopted specialist species; however, only comparatively few specialists are known to occur on *Fraxinus* [43,44], which hampers the interpretation of this measure. There are just three phytophagous specialists, and all were collected in low abundance, *Lytta vesicatoria* (Meloidae), *Stereonychus fraxini* and *Lignyodes enucleator* (Curculionidae), although they all have the potential to occur in large numbers and become local pests [45,46]. The increased occurrence of generalists illustrates the effect of neophytes on the native fauna and has also been found in the North American *Acer negundo* [L.] in the floodplain forest of the river Donau compared to the native *Acer campestris* [L.] [47]. Similar to *F. pennsylvanica*, *A. negundo* was introduced more than 100 years ago and had an accordingly long time to co-evolve with the arthropod fauna. The question of how neophytes alter community diversity in the long term and how this impact the provisioning of ecosystem services is still completely unknown.

4.2. How Does Ash Dieback Affect Beetle Communities?

As a result of ash dieback, the arboreal beetle communities collapsed, completely affecting the biodiversity of the whole forest and not just of individual trees (Floren own data). Structural changes in beetle communities were particularly striking on *F. excelsior* where xylobionts were found to represent nearly 80% of all beetles in 2020, whilst phytophages were largely absent. A few red-listed species, *Agrilus convexocillis* and *Tetrops starkii* (both category 2 in Saxonia Anhalt) were collected in high numbers and became secondary pests [48]. Common species avoided *F. excelsior* and were instead captured in high abundance from *F. pennsylvanica*. Only *T. starkii* had a strong preference for *F. excelsior*. Overall, more specialists were found on *F. excelsior*. The differences in beetle communities cannot be explained by differences in tree vitality. All trees chosen for fogging were in a good condition and without visible damage from the fungi pathogen that causes ash dieback. That

F. excelsior was overall much more affected may reflect differences in secondary compounds, but this has not yet been confirmed. The search for more resistant ash trees is currently being intensified in many countries aiming to save *F. excelsior* from local extinction [49]; however, our results cast doubt on the ability of the ash fauna to use resistant ash trees in the same way as non-resistant trees.

4.3. Fraxinus pennsylvanica—Invasive Species or Rescue Species?

Ash dieback illustrates how complex the effects of extreme weather conditions on biodiversity are and gives an example of how climate change may affect forests in the future. Apparently, *F. pennsylvanica* is more resistant to drought and less susceptible to the fungal pathogen that causes ash dieback [20]. Because *F. pennsylvanica* and *F. excelsior* are members of the same genus, and the Oleaceae are protected from arthropod attack by effective secondary compounds, it is very likely that the ash fauna will use the neophyte as an alternate host if it becomes locally extinct. This could make *F. pennsylvanica* a rescue species for native ash species which can probably not survive on other trees [18]. Taking the predictions of climate change seriously, the loss of biodiversity must be considered severe, as it is also likely to reduce the resilience of forests to climate extremes [16]. This is true for both plants and, most likely, also for canopy arthropods. Neither the dieback of *F. excelsior*, nor the impact on arthropod diversity, or the potential importance of *F. pennsylvanica* had been predicted. Should *F. pennylvanica* actually prove to be a rescue species, this would entail another, non-biological problem, namely that the conservation status of protected areas is increasingly measured by the presence of invasive alien species per se [42], and this could result in lesser financial allocations—which in turn affect the treatment of neophytes in the field.

4.4. What Ecological Role Do Canopy Beetle Communities Play during Forest Adaptation to Climate Change?

According to official forestry statements, commercial forests should consist of at least three tree species in stable mixtures in the future, including neophyte trees which should be planted where management objectives cannot be achieved with locally occurring species [3]; however, what appropriate tree mixes are and in what proportions tree species should be cultivated remains an open question. Recently, it has been shown that the choice and the mixture of tree species are of great importance for the diversity and stability of forest stands [16,50]. Furthermore, plant diversity is a driver of species richness of herbivores, predators and parasitoids [6,51] suggesting that changes in the functional composition can have major impacts on forest dynamics. The successful establishment of mixed forests requires intrinsic knowledge of the involvement of biodiversity in ecosystem functioning; this knowledge is not available for canopy arthropods which undoubtedly add a new dimension of complexity to this already complex system.

To the present day, no overall survey of the canopy arthropod fauna has been carried out, nor is there an assessment of their ecological importance. For this reason, we are using beetles as a representative example and show how insufficient the canopy is still studied. This can be illustrated by the large proportion of 23% of endangered, red-listed species that were collected from trees of the Elbe floodplain forests [52]. Research in recent years has proven the relationship between diversity and ecosystem function [16]. This highlights the importance of the highly diverse canopy arthropod communities as a major player. One of the most compelling examples demonstrating the functional importance of canopy arthropods is the calamities of pest species. Climate change facilitates the distribution of pest species, allowing them to expand into new ranges [2,53,54]. Bark beetles (*Scolytinae*) attacking conifers are among the best-known examples [55]; they can cause extensive tree mortality through coordinated mass attacks, whilst their effects on important ecosystem services such as carbon storage, nutrient cycling, and water provisioning are highly variable depending on the structure, composition, and spatial patterns of the vegetation [55].

Deciduous trees can also be damaged by bark beetles and eventually die. This occurred to *F. excelsior* trees which had experienced a long-lasting summer drought [35] and which were vulnerable to insect attack, mainly by *Hylesinus* bark beetles, *H. oleiperda* in particular (Figure 1). In addition to such direct infestations, arthropods also act as vectors of fungi and other plant pathogens [56]. The decrease in diversity and the significant changes in guild composition point to a fundamental restructuring of the canopy communities [18]. The loss of a foundation tree, such as *F. excelsior*, certainly has the potential to unleash cascading effects [57]. That drought-resistant neophytes offer a solution in this highly complex and poorly understood system is questionable. Several studies have shown that the probability increases that neophyte trees become invasive or create opportunities for native insects to become pests [42,54]; this is likely to be true for some of the secondary pest species of *Fraxinus*. Given the importance of biodiversity in providing ecosystem services and their sustainable use [16], it would be very important to further investigate the trajectories that floodplain forests follow in their regeneration.

5. Conclusions

Investigating the impact of the neophyte *F. pennsylvanica* on beetle diversity following the large-scale dieback of the European Ash *F. excelsior* showed that many beetle species switched to *F. pennsylvanica*. The American Red ash, which is closely related to the European Ash, might therefore become a rescue species for the ash associated fauna; however, as neophytes are not adapted to the endemic fauna, their introduction usually poses a potential threat to the native biodiversity. This applies also to the planned cultivation of drought-resistant neophytes, which are expected to make forests more resilient to drought and other impacts of climate change. The presented data suggest that the effects on biodiversity and the maintenance of ecosystem services by neophytes cannot be predicted at the current level of knowledge.

idae). Voucher specimens are deposited in the collection of A. Floren. We also thank three reviewers for commenting on the manuscript.

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