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Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests

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Abstract

Aim: The tinder fungus *Fomes fomentarius* is a pivotal wood decomposer in European beech *Fagus sylvatica* forests. The fungus, however, has regionally declined due to centuries of logging. To unravel biogeographical drivers of arthropod communities associated with this fungus, we investigated how space, climate and habitat amount structure alpha and beta diversity of arthropod communities in fruitbodies of *F. fomentarius*.

Location: Temperate zone of Europe.

Taxon: Arthropods.

Methods: We reared arthropods from fruitbodies sampled from 61 sites throughout the range of European beech and identified 13 orders taxonomically or by metabarcoding. We estimated the total number of species occurring in fruitbodies of *F. fomentarius* in European beech forests using the Chao2 estimator and determined the relative importance of space, climate and habitat amount by hierarchical partitioning for alpha diversity and generalized dissimilarity models for beta diversity. A subset of fungi samples was sequenced for identification of the fungus' genetic structure.

Results: The total number of arthropod species occurring in fruitbodies of *F. fomentarius* across European beech forests was estimated to be 600. Alpha diversity increased with increasing fruitbody biomass; it decreased with increasing longitude, temperature and latitude. Beta diversity was mainly composed by turnover. Patterns of beta diversity were only weakly linked to space and the overall explanatory power was low. We could distinguish two genotypes of *F. fomentarius*, which showed no spatial structuring.

Main conclusion: *Fomes fomentarius* hosts a large number of arthropods in European beech forests. The low biogeographical and climatic structure of the communities suggests that fruitbodies represent a habitat that offers similar conditions across large gradients of climate and space, but are characterized by high local variability in community composition and colonized by species with high dispersal ability. For European beech forests, retention of trees with *F. fomentarius* and promoting its recolonization where it had declined seems a promising conservation strategy.

KEYWORDS

dead wood, *Fagus sylvatica*, *Fomes fomentarius*, insects, invertebrates, restoration, saproxylic, sporocarp

1 | INTRODUCTION

Most parts of the temperate zone of Europe—from the Iberian Peninsula to the Black Sea and from southern Italy to southern Sweden—are naturally covered by forests dominated by European beech *Fagus sylvatica* (Figure 1). These forests, however, have declined over recent centuries due to deforestation until around 1800, and since then due to conversion to conifer-dominated (*Pinus*

sylvestris, Picea abies) plantations (Dirkx, 1998; Schelhaas, Nabuurs, & Schuck, 2003). Historic deforestation and degradation have recently been reinforced by large-scale clear-cutting of old-growth beech forests in regions that, until recently, were rather unaffected (e.g., in the Carpathians; Vanonckelen & Van Rompaey, 2015; Mikoláš et al., 2017). Since the distribution of European beech is restricted to the temperate zone of Europe, the EU has acknowledged its global responsibility by listing several types of beech forest as Natura 2000

habitats (Council of the European Union,). Furthermore, some of the last natural or almost natural European beech forests are part of the UNESCO World Heritage "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe" (http://whc.unesco.org/en/list/1133). Despite these commitments to conserving biodiversity in European beech forests, our understanding of large-scale drivers of biodiversity in beech forests remains limited, hampering systematic conservation planning, given prevalent area conflicts (Ammer et al., 2018; Kouki, Hyvärinen, Lappalainen, Martikainen, & Similä, 2012; Margules & Pressey, 2000).

The species pool of organisms associated with European beech forests can be expected to be structured across large spatial scales reflecting different underlying mechanisms. European beech was one of the last tree species to recolonize central and northern Europe from its major refugia in southern Europe after the last glaciation and is still expanding its range towards the north and east (Magri, 2008). Understorey plant diversity in European beech forests reflects this history and is determined by distance to the nearest known major refuge (Jiménez-Alfaro et al., 2018; Willner, Pietro, & Bergmeier, 2009). In addition, populations of European beech may also have persisted in microrefugia in central Europe (Robin, Nadeau, Grootes, Bork, & Nelle, 2016). Due to its high competitiveness and

climate tolerance, European beech covers a wide range of climatic conditions (Figure 1; Brunet, Fritz, & Richnau, 2010), which might structure communities (Heilmann-Clausen et al., 2014). Towards its ecological range limits, increasing presence of other tree species and arthropods associated to these trees (Brändle & Brandl, 2001) may further influence the regional species pool.

These natural drivers of community structure in beech forests interact with anthropogenic factors. Forest clearing and forest management have been more intense in western than in eastern Europe resulting in a gradient of habitat loss of natural beech forest and consequently fragmentation of these forests from east–west (Abrego, Bässler, Christensen, & Heilmann-Clausen, 2015; Kaplan, Krumhardt, & Zimmermann, 2009; Larsson, 2001). Many specialist species for old-growth beech forests have thus become rarer or locally extinct in western Europe and can today only be found in eastern Europe (Eckelt et al., ; Speight, 1989).

On smaller spatial scales, species communities can be affected by the regional climate acting as environmental filter as shown for wood-inhabiting beetles and fungi in beech forests (Bässler, Müller, Dziock, & Brandl, 2010; Müller et al., 2012) and minute tree-fungus beetles in fruitbodies (Reibnitz, 1999). Moreover, not only large-scale gradients of anthropogenic pressure can influence communities in
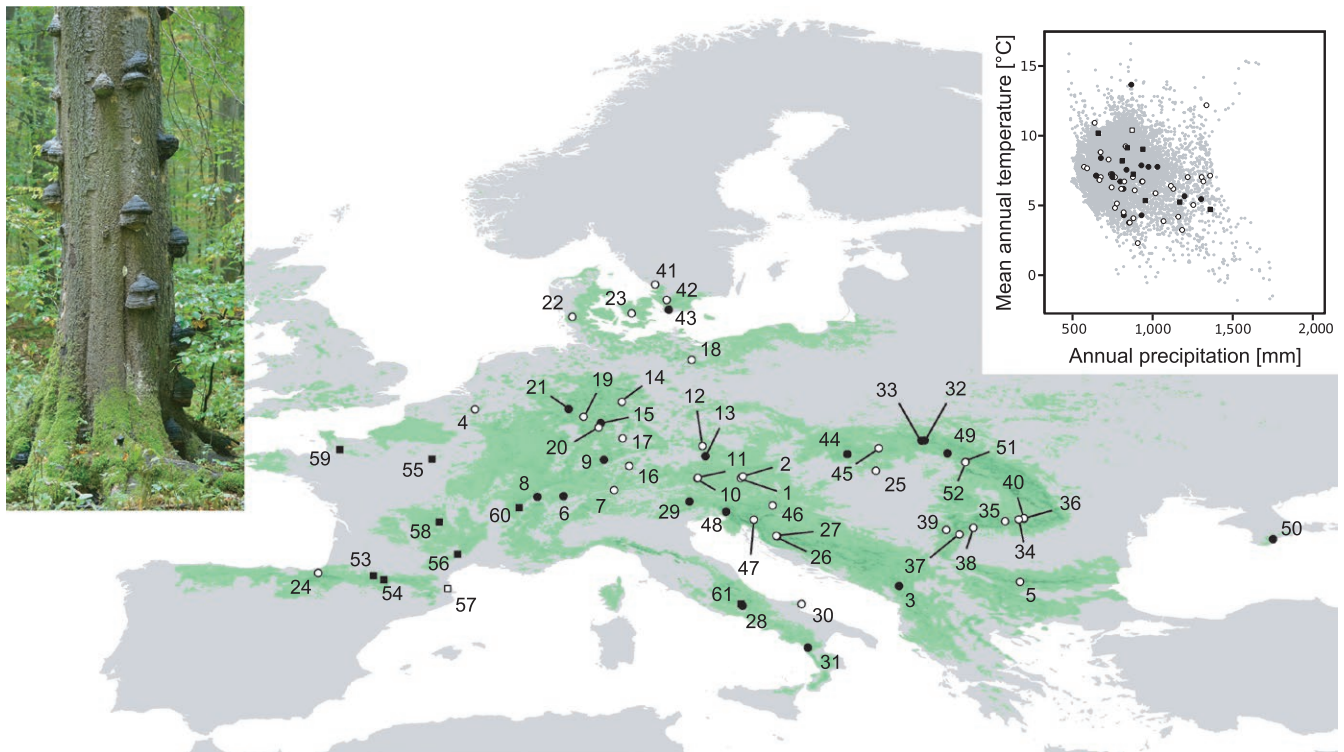

FIGURE 1 Map of the 61 sampling sites of this study. The green area depicts the predicted current distribution of European beech *Fagus sylvatica* (Brus et al.., 2011). The numbers in the map correspond to the study site ID in supporting information Appendix S2 and Appendix S3: Table S3.1. Circles indicate the 52 study sites for which data on all arthropods were available; squares indicate the nine sites for which only beetle data were available and which are part of the analyses in Supporting information Appendix S4. Black filling indicates sites with active forest management and white filling indicates unmanaged sites. Left inset: A typical example of a European beech tree with fruitbodies of *Fomes fomentarius*. Photograph by Thomas Stephan. Right inset: Mean annual temperature and annual precipitation of all study sites (filled circles and squares (see above)) and 10,000 randomly sampled points in the distribution of F. *sylvatica* representing the climate space where beech-dominated forests are occurring

beech forests but also the amount of available habitat at local and landscape scales (Fahrig, 2013; Seibold et al., 2017) and the connectivity of habitat patches (Abrego et al., 2015; Nordén et al., 2018; Rukke, 2000).

Fungi are the main biotic agents of wood decomposition and their mycelia and fruitbodies are an important food for many arthropods as they contain higher concentrations of nutrients stored in a more accessible form than in undecayed wood (Filipiak, Sobczyk, & Weiner, 2016; Merrill & Cowling, 1966; Stokland, Siitonen, & Jonsson, 2012). In particular, fungal fruitbodies, especially polypores, serve as habitat for many fungicolous arthropod species (Schigel, 2012). Studies of the diversity and composition of fungicolous arthropod communities have so far been restricted to local and regional scales, and generally indicate that many arthropod species are host-specific (Jonsell & Nordlander, 2004; Komonen, 2001). Occurrence and abundance of fungicolous arthropod species on single trees and forest stands depend on habitat availability (Rukke, 2000). At the regional scale, turnover in species composition has been found to be high among fungal host species, but low among sites across host species (Komonen, 2001). So far, no study has investigated diversity patterns of fungicolous arthropods at continental scales (Schigel, 2012).

The tinder fungus *Fomes fomentarius* is one of the main decomposers of wood in many beech forests in Europe. However, *F. fomentarius* has a much larger range than European beech covering the temperate and boreal zones of Europe, Asia and North America. Outside beech forests, it occurs especially in riparian and boreal forests on *Betula*, *Populus*, *Alnus* or other hardwood trees (Matthewman & Pielou, 1971; Reibnitz, 1999; Rukke, 2000). As a white-rot fungus, it can efficiently break down lignocellulose and contributes to the death of weakened living trees, thus promoting natural forest dynamics (Butin, 1989). Its fruitbodies and the created dead wood are habitat for many arthropod species (Schigel, 2012). Their community composition is largely affected by the physical conditions of the fruitbodies which change with ongoing decomposition (Dajoz, 1966; Reibnitz, 1999; Thunes & Willassen, 1997). Thus, in order to capture the whole local community occurring in *F. fomentarius* different stages of decomposition have to be taken into account (Graves, 1960).

Trees colonized by the fungus have been suggested as a focal habitat for biodiversity conservation in beech forests (Larrieu et al., 2018; Müller, 2005). However, due to centuries of logging and direct persecution for phytosanitary reasons, populations of this fungus have declined or became locally extinct in many areas (Vandekerkhove et al., 2011; Zytynska et al., 2018). To guide conservation planning and strategies in European beech forests, such as the selection of areas to be set aside for conservation (Bouget, Parmain, & Gilg, 2014) or for active restoration by dead wood enrichment (Dörfler, Gossner, Müller, & Weisser, 2017), it is necessary to understand how arthropod communities—which represent the largest fraction of animal biodiversity in forests—are biogeographically structured.

In this study, we reared arthropods from fruitbody samples of *F. fomentarius* across the whole distributional range of European beech. Our aims were to estimate alpha and beta diversity of arthropods in fruitbodies of *F. fomentarius* and to disentangle the effects of post-glacial recolonization of its host tree, macro-climate, anthropogenic pressure and habitat amount on diversity patterns. Specifically, we expected (a) decreasing alpha diversity and increasing nestedness with latitude due to the recolonization history of beech, (b) decreasing alpha diversity and increasing nestedness from east-west due to the anthropogenic land use history, (c) increasing turnover with increasing differences in macro-climatic conditions across both latitudinal and longitudinal space, and (d) increasing alpha diversity with increasing habitat amount at local and landscape scales.

2 | METHODS

2.1 | Collection of *Fomes fomentarius* fruitbodies

We collected fruitbodies from 61 beech-dominated forest sites across the distributional range of *F. sylvatica* (Figure 1) between June and August 2013. These sites were chosen to cover the natural distribution of *F. sylvatica*, as well as the full range of climatic conditions within this area (Figure 1). We were not able to include sites from some parts of the distributional range, for example southern England, where *F. fomentarius* is almost absent for historical reasons (Abrego, Christensen, Bässler, & Ainsworth, 2017). Sites were located in unmanaged (36) and managed forests (25); both management categories were evenly distributed across Europe (Figure 1).

For arthropod rearing, we collected 10 fruitbodies of *F. fomentarius* per site following a standardized protocol. Assemblages inhabiting fruitbodies of bracket fungi change with ongoing fruitbody decomposition. Therefore, we sampled fruitbodies at different successional stages of decay. At each site, sampling included fruitbodies attached to wood that had just recently died and were still moist (3 to 4 fruitbodies) and fruitbodies that had been dead for a longer time (6 to 7 fruitbodies). The latter were either dry when still attached to wood (3 to 4 fruitbodies) or wet when lying on the ground (3 to 4 fruitbodies). This sampling protocol aimed at covering most of the available habitat heterogeneity represented by the fruitbodies. The total volume sampled per site ranged between 0.2 and 21.7 kg (mean: 2.7 kg) and did not represent the local availability of fruitbodies as transportation and rearing logistics restricted the sampled volume.

In addition, we collected samples of living fruitbodies to analyse the genetic structure within the population of *F. fomentarius* in Europe. From these samples, we applied a microwave-based method to extract DNA (Dörnte & Kües, 2013) and amplified sequences for the internal transcribed spacer (ITS) region and the elongation factor α (efa) gene by touchdown PCR (for details, see Supporting information Appendix S1).

2.2 | Arthropod rearing

To rear arthropods, all fruitbodies of the same site (from now on called "sample") were put into a cardboard box (25 cm × 25 cm × 50 cm) in an unheated well-ventilated storage room with a seasonal

temperature regime. A transparent collecting jar was attached to each box and filled with 90% ethanol to collect arthropods attracted to light. Collecting jars were emptied every two months and arthropods inside the boxes were collected by hand. Rearing was carried out for 12 months for each sample.

2.3 | Arthropod identification and classification

Reared arthropod specimens were stored in ethanol and beetles were determined to species level by taxonomists. The remaining fauna was identified by metabarcoding using next-generation sequencing carried out by Advanced Identification Methods GmbH (Munich, Germany; for details, see Supporting information Appendix S1). Arthropod sequences were matched against the publicly available DNA barcode library within the Barcode of Life (BOLD—v4.boldsystems.org; Ratnasingham & Hebert, 2007). Laboratory problems impeded the use of next-generation sequencing for samples from nine sites (Figure 1).

We considered all species that were reared from fruitbody samples, including species that use hollow fruitbodies as shelter or develop at the interface between fruitbodies and white-rotten wood. However, since this includes species that do not interact directly with the fruitbody, we additionally analysed the data excluding these species. Based on literature, we classified species or genera that are known to feed directly on the fungal tissue or exclusively prey upon mycetophagous species as "fungi specialists" (Supporting information Appendix S2); and we classified all species according to their trophic level as consumers (i.e., species that feed on non-animal tissue), predators (i.e., species that feed on animal tissue) or parasitoids (i.e., species that develop on or within single host organisms and ultimately kill their host).

2.4 | Environmental predictor variables

Coordinates of each site were recorded in the field using handheld GPS devices (Supporting information Appendix S3, Table S3.1). We extracted data on all 19 bioclimatic variables for each site from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Since bioclimatic variables are often correlated, we performed a principal component analysis on the correlation matrix for temperature and precipitation variables separately (i.e., temperature: BIO 1 – 11; precipitation: BIO 12 – 19). The first two principal components explained most of the variation in both datasets (temperature: 75%; precipitation: 91%; Supporting information Appendix S3, Table S3.2) and were subsequently used as a proxy for bioclimatic conditions at the sites. The first principal components represented a gradient in mean temperature or precipitation with high values indicating sites with overall high temperature or sums of precipitation, respectively. The second principal components represented a gradient in seasonality with high values for sites displaying high temperature or precipitation seasonality, respectively.

To obtain a proxy for landscape-scale habitat amount and anthropogenic pressure, we calculated the proportion of forest cover surrounding the sites for radii from 100 to 5,000 m (100-m steps). Forest cover within a radius of 700 m around sites had the highest independent effect on alpha diversity, and thus, this radius was chosen for further analyses (Supporting information Appendix S3, Figure S3.1). We used data based on Landsat satellite images from the database on Global Forest Change (Hansen et al., 2013), which is available with a spatial resolution of approximately 25 metres per pixel, with values ranging from 0 to 100 per pixel encoding the proportion of canopy closure for all vegetation taller than 5 m in height. To evaluate the role of sample size (as a proxy for local habitat amount) for alpha and beta diversity, we recorded the total dry weight of fruitbodies per sample after 12 months of rearing. Proportions of forest cover were logit-transformed and sample size was $\log_e$-transformed.

2.5 | Statistical analyses

All statistical analyses were carried out using *R* version 3.3.2 (R Core Team, 2016). The main analyses included beetles identified taxonomically and all other arthropods identified by metabarcoding and were thus restricted to the 52 sites for which metabarcoding data were available. Additional analyses were conducted for beetle data from all 61 sites with beetle abundances (see Supporting information Appendices S4 and S5).

To estimate the overall species pool, we calculated the Chao2 estimator, as implemented in the *vegan* package version 2.4–3 (Oksanen et al., 2018). The Chao2 estimate is a function of species occurring once or twice in the dataset and offers robust lower bound estimation for species richness based on incidences under the assumption that rare species have similar detection probabilities (Chao, 1987). Calculations were based on data for all species and separately for fungi specialists and each trophic guild (i.e., consumer, predator and parasitoid) on the 52 sites. In addition, we used the rarefaction–extrapolation framework based on species incidences across all sites (Chao et al., 2014). We used Hill number of the orders 0 (species richness), 1 (the exponential of Shannon's entropy) and 2 (the inverse of Simpson's concentration) to analyse the diversity of rare and common species within one framework. We used 999 replicated bootstraps to calculate confidence intervals around the species-accumulation curves using the *iNEXT* package (Hsieh, Ma, & Chao, 2016).

Alpha diversity was calculated as the number of species per site. To estimate the relative importance of the predictor variables, we performed hierarchical partitioning—as implemented in the *hier.part* package version 1.0–4 (Walsh & Mac Nally, 2013)—based on generalized linear models. For the generalized linear models, we chose a quasipoisson error distribution and a log-link function in order to account for frequently observed overdispersion in models of count data. Please note that alternatively choosing models including an observation-level random effect or models with a negative-binomial error distribution did not alter the main results. The models included alpha diversity as the dependent variable and space (latitude, longitude), climate (mean temperature, temperature seasonality, mean precipitation, precipitation seasonality) and habitat amount (forest

cover, sample size) as predictor variable sets. All calculations were performed separately for all species, fungi specialists and each trophic guild on the 52 sites.

Beta diversity was calculated as the Sørensen dissimilarity among all 52 sites using presence–absence information. The community composition of all species and fungi specialists was visualized using non-metric multidimensional scaling (NMDS). Subsequently, we fitted the environmental vectors of space, climate and habitat amount to the resulting ordination as implemented in the *envfit* function using the *vegan* package. In addition, we performed an analysis of similarity in order to test for group differences in community composition among managed and unmanaged sites, as well as among biogeographical regions again using *vegan* (see Supporting information Appendix S3 for further details). Furthermore, we decomposed beta diversity in its turnover and nestedness components based on the Sørensen index family as implemented in *betapart* (Baselga, Orme, Villeger, Bortoli, & Leprieur, 2017). The turnover component represents beta diversity introduced by the replacement of species between sites, while the nestedness component represents the beta diversity introduced by the removal/gain of species between sites. To estimate the relative importance of the predictor variables (latitude, longitude, mean temperature, temperature seasonality, mean precipitation, precipitation seasonality, forest cover and sample size) for beta diversity, we calculated generalized dissimilarity models (GDMs) as implemented in the *gdm* package (Manion et al., 2017) for total beta diversity, and turnover and nestedness components separately. GDMs allow the analysis of spatial patterns of community composition across large regions under consideration of nonlinear relationships between dissimilarity in community composition along environmental gradients (Ferrier, Manion, Elith, & Richardson, 2007). All GDMs were calculated using the default of three I-splines. The calculated coefficient for each of the three I-splines represents the rate of change along a third of the gradient of the environmental predictor when keeping all other predictors constant (i.e., high values of the first I-spline indicate a high rate of change along the first third of the gradient). We estimated the relative contribution of each predictor set as the difference in explained deviation between a model containing all predictor sets and a model from which this predictor set was removed (Legendre & Legendre, 1998; Maestri, Shenbrot, & Krasnov, 2017). All calculations were again performed separately for all species, fungi specialists and each trophic guild on the 52 sites.

Data for beetles including abundances were available for all 61 sites; we thus conducted similar analyses for this group as for all arthropods (see Supporting information Appendices S4 and S5). These analyses considered the influence of increasing numbers of individuals on alpha diversity and the effect of space, climate and habitat amount on abundance-based dissimilarities of the beetle communities. Here, we used Bray–Curtis dissimilarities and decomposed it into the two components based on balanced variation in abundance (i.e., individuals of some species at a site are substituted by equal numbers of individuals at another site) and dissimilarity introduced by abundance gradients (i.e., individuals are lost without substitution from one site to the other; Baselga, 2013).
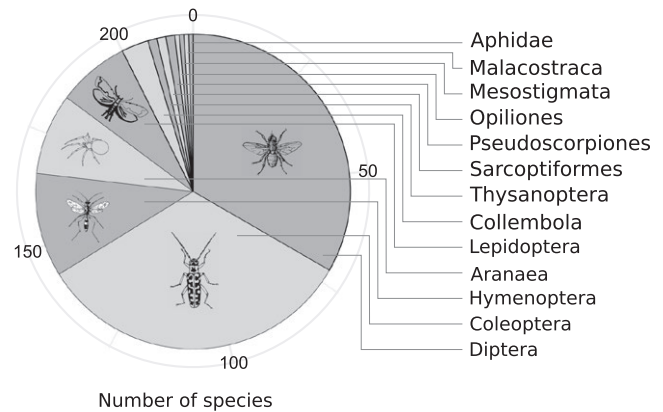
FIGURE 2 Pie chart of the proportion of species from different arthropod orders reared from fruitbodies of *Fomes fomentarius* from 52 beech-dominated forest sites across Europe. The overall number of determined species was 216

3 | RESULTS

In total, we identified 216 arthropod species emerging from fruitbodies of *F. fomentarius* from 52 sites. Species belonged to 13 orders, with highest species richness found in Diptera (*n* = 72) and Coleoptera (*n* = 71; Figure 2; Supporting information Appendix S2). The majority of taxa (*n* = 179) could be assigned to species by the taxonomist or by alignment of operational taxonomic units (OTUs; see Supporting information Appendix S1) with existing databases. The remaining 37 OTUs not assigned to a species were mostly members of the Cecidomyiidae (Diptera), for which barcodes were not available in the databases. We identified 74 species as fungi specialists. Concerning trophic guilds, we classified 131 species as consumers, 68 species as predators and 17 species as parasitoids. Genetic analysis of *F. fomentarius* samples revealed two genotypes that were previously identified as possible sympatric cryptic species (termed genotype "A" and "B"; Judova, Dubikova, Gaperova, Gaper, & Pristas, 2012). However, intraspecific genetic variation among sites was very low and genotype B occurred only at five of our sites widely spread over the sampling area (Supporting information Appendix S1).

Chao2 estimators indicated an overall species pool of 587 (SE =103) for all species, 249 (SE =181) for fungi specialists, 402 (SE =104) for consumers, 163 (SE =43) for predators and 42 (SE =24) for parasitoids associated with *F. fomentarius* in European beech forests. The observed effective number of typical species (q = 1) was 87, while the observed effective number of dominant species (q = 2) was 44 (Supporting information Appendix S3, Figure S3.3). Many of the dominant species were consumers, such as beetles of the family Ciidae, the Tenebrionidae *Bolitophagus reticulatus*, the micro-moth *Scardia boletella* and Cecidomyiidae sp.3 (Figure 3). The most frequent parasitoids were the hymenopterans *Astichus* spp. and a scuttle fly (Phoridae). Beetles included four species considered to be "primeval forest relicts" (Eckelt et al.,), namely *Bolitophagus interruptus*, *Bolitochara lucida*, *Teredus cylindricus* and *Philothermus evanescens*, which were each found at one site (Slovenia, France, southern Italy and Sweden, respectively).
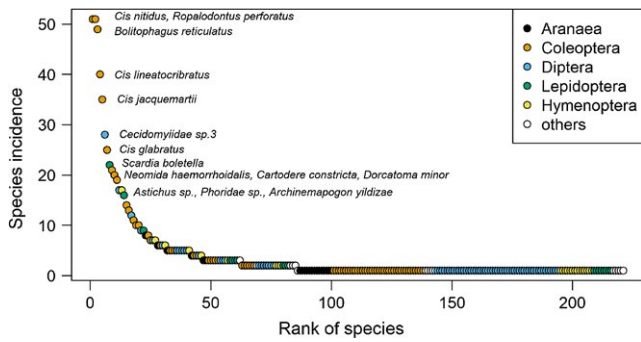
FIGURE 3 Rank-incidence plot of all 216 arthropod species reared from fruitbodies of *Fomes fomentarius* from 52 beech-dominated forest sites across Europe

Considering all arthropods, the mean species number per site was 16 (SE =6) with the lowest number (six species) found in the German Wetterau and the highest number (36 species) located in Abruzzo, Italy. In the quasipoisson models, our predictor variables explained 20% of the deviance in alpha diversity for all species and 26% for the fungi specialists (Figure 4). The explained deviance decreased from consumers (22%) to predators (16%) and parasitoids (6%) correlated to the number of species of the trophic guilds (Table 1). According to hierarchical partitioning, habitat amount, that is forest cover and sample size, explained most of the deviance in our models (Figure 4). Alpha diversity of all species, fungi specialists, consumers and predators increased with increasing sample size (Table 1, Figure 5a) and that of consumers also increased with increasing forest cover. Moreover, alpha diversity of all species, fungi specialists and consumers decreased with increasing longitude and that of fungi specialists also decreased with latitude. Alpha diversity of fungi specialists and consumers additionally decreased with increasing mean temperature and precipitation (Table 1). Most effects, however, were only marginally significant (Table 1).

Ordination of the community composition of all species as well as fungi specialists revealed large differences in community composition across our study sites (Supporting information Appendix S3: Figure S3.2). Except for a significant effect of sample size on the community composition of all species ($r^2 = 0.13$, $p < 0.05$), environmental variables were not significantly correlated with the axes of the NMDS (Supporting information Appendix S3; Figure S3.2 A & D). In addition, we found no differences in community composition among managed and unmanaged sites, as well as among biogeographical regions (Supporting information Appendix S3: Figure S3.2). The largest proportion of dissimilarity was due to turnover, rather than nestedness for all species (98%), fungi specialists (96%) and all trophic guilds (consumer: 97%; predator: 99%; parasitoids: 97%). The proportion of deviance explained by GDMs was below 15% for overall beta diversity, nestedness and turnover in all groups (Figure 4). For all species, we found a marginally significant increase of dissimilarity introduced by nestedness with increasing longitudinal distance between sites (Table 2). No single predictor had a significant effect on beta diversity of fungi specialists and consumer species (Supporting information Appendix S3, Table S3.4 & Table S3.5). Dissimilarity in latitudinal distance had a significant positive effect on the overall beta diversity as well as on the turnover component for predators and parasitoids (Supporting information Appendix S3, Table S3.6 and Table S3.7). Additionally, we found a significant increase in overall beta diversity as well as in dissimilarity due to turnover with increasing dissimilarity of sample size for predators.

Our analyses for beetles from all 61 sites included abundance data for 123 species (Supporting information Appendix S5). Here, alpha diversity was strongly affected by sample size (Figure 5; Supporting information Appendix S4, Table S4.1). The number of beetle species increased with fungal sample size as the range in sample size was considerably higher across all 61 sites (Figure 5b) than across the subset of 52 sites (Figure 5a). Beetle community composition was
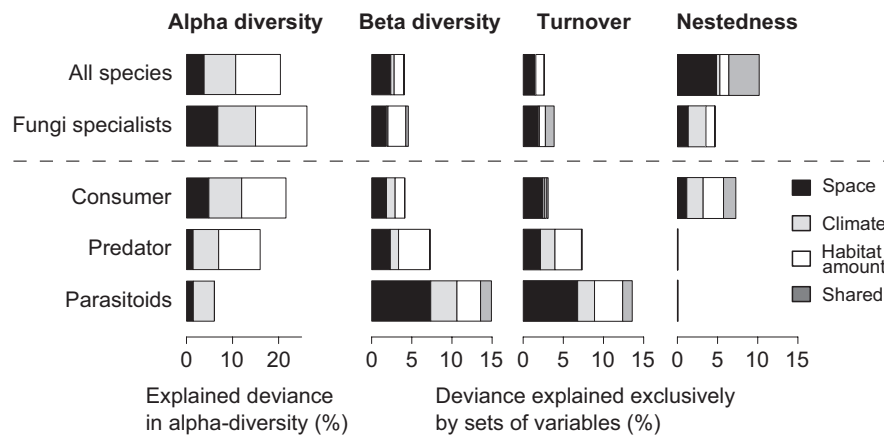
FIGURE 4 Relative contribution of predictor sets in explained deviance of alpha and beta diversity and its components turnover and nestedness. Alpha diversity was modelled using generalized linear models and the relative contribution is based on hierarchical partitioning. Beta diversity is based on presence–absence data and its components were modelled using generalized dissimilarity models and the relative contribution was calculated as the "pure" effect of the predictor set on the overall explained deviance of the model. All analyses were conducted for all species and fungi specialists separately and for the trophic levels consumer, predator and parasitoids. Bar colours represent the predictor sets with space in black, climate in light grey, habitat amount in white and the deviance shared by the predictors in dark grey

TABLE 1 Z-values and explained deviance of generalized linear models (quasipoisson family) with the number of species of all species or within guilds as response variables. Significant effects are indicated by bold typesetting. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see Methods section)

Predictor set	Predictor	All species	Fungi specialists	Consumer	Predator	Parasitoids
Space	Latitude	−1.36	**−1.98**[**]	**−1.70**[**]	−0.08	−0.93
	Longitude	**−1.77**[**]	**−2.12**[*]	**−1.82**[**]	−1.08	−0.34
Climate	Temperature (PC1)	**−1.72**[**]	**−1.90**[**]	**−1.92**[**]	−0.48	−1.00
	Temperature (PC2)	−0.82	−0.79	−0.43	−1.24	0.31
	Precipitation (PC1)	−1.41	−1.30	−1.57	−0.68	−0.01
	Precipitation (PC2)	−0.31	0.13	−0.45	0.74	−1.49
Habitat amount	Forest cover	1.26	0.94	1.45	0.13	−0.13
	Sample size	**1.75**[**]	**2.20**[*]	1.55	**2.20**[*]	0.17
Explained deviance		0.20	0.26	0.22	0.16	0.06

Note. [a]Significance levels: [*]$p < 0.05$, [**]$p < 0.1$
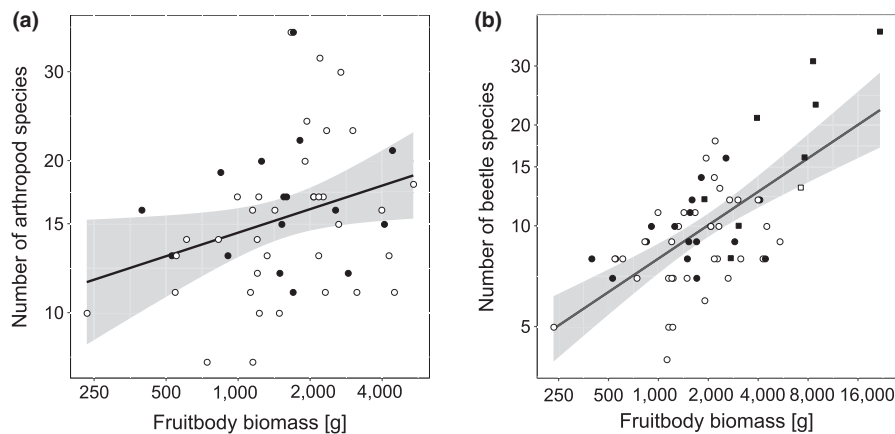
FIGURE 5 Relationship between (a) the number of arthropod species per fruitbody sample and sample size, that is the total weight of the 10 sporocarps sampled, of 52 sites and (b) the number of beetle species per fruitbody sample and sample size including all 61 sites. Circles indicate the 52 study sites for which data on all arthropods were available; squares indicate nine sites for which only beetle data were available and which are part of the analyses in Supporting information Appendix S4. Black filling indicates sites with active forest management, white filling indicates unmanaged sites. A simple regression line and confidence interval are shown. Axes are log-transformed

affected by dissimilarity in sample size and longitude. Here, beetle communities showed increased rates of turnover and balanced changes of abundances with longitude and increased rates of nestedness and abundance gradients with sample size. Our models for all beetle species explained up to 59% of the deviance in alpha diversity, 34% in Sørensen dissimilarity and 19% in Bray–Curtis dissimilarity (Supporting information Appendix S4, Table S4.1; Figure S4.1). Variables linked to habitat amount consistently explained most of the deviance in models of species richness, overall community composition and community dissimilarity due to nestedness, while variables linked to spatial distance explained most of the deviance due to species turnover (Supporting information Appendix S4).

4 | DISCUSSION

Overall, our results indicate that fruitbodies of *F. fomentarius* form an important micro-habitat in European beech forests, hosting a rich fauna (estimated ~600 arthropod species). However, the arthropod communities included about 30 dominant species which occurred at most sites across Europe and can be considered typical for fruitbodies of *F. fomentarius*. Moreover, there was a large number of species that use *F. fomentarius* fruitbodies occasionally. The latter group includes fungicolous species using a wider range of fungal hosts (e.g., *Bolitophagus interruptus*, Coleoptera, which is more common on *Ischnoderma* spp.), species that feed on white-rotten wood (e.g., *Corymbia scutellata*, Coleoptera) or fungal mycelia and species that use cavities inside fruitbodies simply for shelter (e.g., *Amaurobius fenestralis*, Aranaea) or that benefit from arthropod prey (e.g., *Plegaderus dissectus*, Coleoptera). Alpha diversity increased with sample size and decreased with longitude, latitude and temperature. Despite the large extent covered in our study (approx. 1,800 km in latitude and 3,000 km in longitude), beta diversity—which was characterized by high turnover—was not structured by drivers associated with space, the biogeography of *F. sylvatica* and habitat amount. Moreover, increasing nestedness and decreasing

TABLE 2 Coefficients of three I-splines (i.e., 1, 2 and 3) from the GDM of overall beta diversity, turnover and nestedness of all arthropod species. Significant (*p* < 0.05) or marginally significant (*p* < 0.1) *P*-values for the I-splines of the predictor variables after 999 permutations are indicated by bold typesetting PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see Methods section)

Response matrix	Predictor set	Predictor	I-spline 1	2	3	Sum of coefficients	*P*
Overall beta	Space	Latitude	0.155	0.007	0.003	0.165	0.11
		Longitude	0	0.067	0	0.067	0.42
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0.017	0	0	0.017	0.68
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0.061	0	0	0.061	0.35
	Habitat amount	Forest cover	0	0.016	0	0.016	0.73
		Sample size	0.12	0	0	0.12	0.24
Turnover	Space	Latitude	0.116	0	0.054	0.170	0.24
		Longitude	0	0	0.082	0.082	0.46
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0.004	0	0.030	0.034	0.65
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0	0	0	0	0.99
	Habitat amount	Forest cover	0	0.018	0.001	0.019	0.73
		Sample size	0.121	0	0	0.121	0.25
Nestedness	Space	Latitude	0.001	0	0	0.001	0.70
		Longitude	**0.132**	**0**	**0**	**0.132**	**0.07**
	Climate	Temperature (PC1)	0.013	0	0	0.013	0.51
		Temperature (PC2)	0	0	0	0	0.98
		Precipitation (PC1)	0.010	0	0	0.010	0.57
		Precipitation (PC2)	0.018	0	0	0.018	0.47
	Habitat amount	Forest cover	0.05	0	0	0.05	0.27
		Sample size	0	0	0	0	0.97

alpha diversity towards the east follow not the continental gradient of increasing land use intensity from the Carpathians to western Europe.

Post-glacial dispersal lags have been identified as one of the driving mechanisms causing patterns of alpha and beta diversity across Europe in plants, insects and vertebrates (Pinkert et al., 2018; Svenning, Fløjgaard, & Baselga, 2011; Svenning, Normand, & Skov, 2008). In contrast, beta diversity of saproxylic beetles was shown to be higher between sites than between elevational zones and bioregions (Müller et al., 2012). We found only a weak decrease in alpha diversity of fungi specialists with latitude and no significant effect of latitudinal distance on beta diversity of all arthropods and the trophic guilds in *F. fomentarius* fruitbodies. Only predatory species showed an increased rate in turnover with increasing latitudinal distance: the rate of change in species composition was highest at low latitudes (Supporting information Appendix S3, Table S3.6). There are several potential explanations as to why post-glacial recolonization of the main host tree species appears to be of minor relevance for communities of arthropods occurring in *F. fomentarius* fruitbodies.

For instance, species associated with fungal fruitbodies in general display high dispersal abilities (Komonen & Müller, 2018). Flight mill experiments showed a dispersal ability of *Neomida haemorrhoidalis* and *Bolitophagus reticulatus* (both Coleoptera; body length: 6 – 8 mm and 6 – 7.5 mm, respectively; Wagner & Gosik, 2016) of >30 km and >100 km, respectively (Jonsson, 2003). Additionally, there is evidence that the genetic distance of fungivores does not increase with geographic distance, indicating the absence of dispersal limitation (Kobayashi & Sota, 2016). Another possible explanation is that although European beech is the main host of *F. fomentarius* in temperate Europe today, other hosts that recolonized Europe much earlier—such as birch—are also frequently used (Judova et al., 2012). If *F. fomentarius* recolonized Europe with the latter tree species, its arthropods may have had more time for recolonization and thus post-glacial dispersal lags are less likely to be important. Last, if microrefugia of European beech also occurred in central Europe (Robin et al., 2016), recolonization pathways may be complex and not well described by latitude used as a proxy for distance to major refugia in southern Europe.

A gradient of decreasing anthropogenic pressure from western to eastern Europe explains why many specialist species of old-growth forests have become rare or extinct in western Europe (Eckelt et al., ; Ódor et al., 2006; Speight, 1989). We thus expected to find an increase of fungicolous arthropod alpha diversity with increasing longitude, but in fact we observed a weak decrease. Additionally, we found a marginally significant increase in compositional dissimilarity due to nestedness with increasing longitudinal distance of the overall arthropod community. However, the rate of change in composition due to nestedness was highest at low longitudes, while explanatory power was low and nestedness did not account for more than 4% of compositional dissimilarity (Table 2). For beetles, we found an increased rate in turnover and balanced changes of abundance at the lower end of the longitudinal gradient (Supporting information Appendix S4, Table S4.4). In parallel to the gradient of historic anthropogenic pressure, there is an east–west climatic gradient from oceanic towards more continental climates, which is shown by a moderate correlation between climate variables and longitude (Supporting information Appendix S3, Table S3.3). Both decreasing alpha diversity and increasing nestedness with increasing longitude as well as increased beetle turnover at low longitudes are inconsistent with the expected effect of historic anthropogenic pressure, but may also be explained by a milder climate in the west. However, we have to point out that we were not able to collect *F. fomentarius* samples in the westernmost regions (e.g., England) due to the rarity of fruitbodies of *F. fomentarius*. Moreover, many of our sites, also in western Europe, were located in unmanaged forests (Figure 1) and although forest management had no effect on overall community composition (Supporting information Appendix S3, Figure S3.2), the gradient of anthropogenic pressure may be less pronounced across our sites than at a landscape scale.

Environmental filtering by climatic drivers is often an important mechanism structuring communities (Cadotte & Tucker, 2017; Kraft et al., 2015), including dead wood-associated insects and fungi (Bässler et al., 2010; Müller et al., 2012; Seibold et al., 2016). Being poikilothermic, arthropods generally benefit from higher temperatures (Schowalter, 2006). However, we found a marginally significant negative effect of temperature on alpha diversity. One possible explanation is that fruitbodies are drier and thus less suitable for some species in warmer climates. However, in general beta diversity was not affected by dissimilarity in climatic conditions. This suggests that climate is of minor importance for arthropods associated with *F. fomentarius* despite considerable variability in climatic conditions within our sampling range (Figure 1).

The amount of available habitat is one of the fundamental drivers of biodiversity (Fahrig, 2013; MacArthur & Wilson, 1967). In Europe, human activities over millennia have reduced the forests and features of old-growth stands (overmature and dead trees), which has led to a decline of many saproxylic insects (Seibold et al., 2015). Forest cover is only a coarse proxy for the amount of habitat available to species associated with dead wood or fruitbodies of *F. fomentarius*, as the amount of their actual habitat—dead wood or fruitbodies of *F. fomentarius*, respectively—can vary considerably

within beech forests depending, for example, on current forest management (Abrego et al., 2015; Bässler, Ernst, Cadotte, Heibl, & Müller, 2014). This was also reflected by the time needed to find ten fruitbodies of *F. fomentarius* in the present study, which ranged from minutes to days. Nevertheless, we found the number of consumers among fungicolous arthropods and fungi specialists among beetles to increase with forest cover (700 m radius around sites). Consistent with results of earlier studies that found a positive effect of fruitbody availability on fungicolous beetle diversity at regional scales (Araujo, Komonen, & Lopes-Andrade, 2015; Rukke, 2000), we found the number of arthropod species to increase with increasing fruitbody biomass. Although our measure of fruitbody biomass did not reflect the abundance of *F. fomentarius* at the sites, based on our results covering a range of fruitbody biomass from 0.4 to 21.7 kg and earlier findings at regional scales (Araujo et al., 2015; Rukke, 2000), we expect more fungicolous arthropod species in forests with more fruitbodies of *F. fomentarius*.

For beetles, sample size strongly affected the number of species even when accounting for abundance, which suggests that habitat heterogeneity increases with fruitbody biomass (Supporting information Appendix S4, Table S4.1). Here, larger samples seem to provide more different habitat niches, for example through different stages of decomposition within and among fruitbodies (Dajoz et al., 1966) similarly as shown for coarse woody debris (Seibold et al., 2016). Concerning community composition, only the total beta diversity and turnover component of predatory arthropods were affected by sample size. However, abundance-based dissimilarity in community composition of beetles was affected by longitude and sample size. Here, dissimilarity due to abundance gradients (analogous to nestedness) increased with sample size. Overall, this indicates that local habitat amount is an important driver of alpha diversity of fungicolous arthropod communities and, at least for fungicolous beetle communities, an important driver of beta diversity.

Based on the ITS region, Judova et al. (2012) have suggested that populations of *F. fomentarius* are comprised of two sympatric cryptic species; this has been confirmed by Pristas, Gaperova, Gaper, and Judova (2013) using the efa gene. One genotype, termed genotype A, has been suggested to be prevalent on European beech while the other, termed genotype B, is additionally found on other host species (Judova et al., 2012). Our genetic analysis of *F. fomentarius* supports this, as all but 5 of 36 of our samples—all sampled from European beech—belonged to genotype A. Nevertheless, the occurrence of genotype B on European beech in the Pyrenees, southern Italy, Belgium and Denmark is a noteworthy result (Supporting information Appendix S1). The low intraspecific variation among sites rendered an analysis of the inhabiting arthropod community based on genetic differences fruitless. Further studies are needed to test the hypothesis that *F. fomentarius* of genotype B hosts arthropod communities different from genotype A.

In our analyses, we incorporated variables which are known to be strong drivers of large-scale differences in community composition (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; Soininen,

Lennon, & Hillebrand, 2007; Zellweger, Roth, Bugmann, & Bollmann, 2017). Furthermore, we accounted for differences in habitat specialization and trophic level, forest management intensity and biogeographical regions and even considered the genetic properties of the fruitbodies. Nevertheless, while our models explained considerable proportions of variation in alpha diversity most of the variation in the community composition of arthropods occurring in fruitbodies of *F. fomentarius* remained unexplained. Although explaining the full variation in community composition was beyond the scope of this study, these results appear surprising. We suggest three directions for future studies. First, future studies investigating the community composition of arthropods occurring in fruitbodies of bracket fungi should focus on factors driving community composition at local scales. This may include the amount of fruitbodies at the site and landscape scale which represent habitat availability and may affect population dynamics via increased dispersal success and rescue effects given sufficient patch connectivity (Gonzalez, 2005; Snäll & Jonsson, 2001; Venier & Fahrig, 1996). Furthermore, studies could investigate the effects of microclimate as mediated by canopy openness and forest successional stage, which were shown to generate large differences in community composition in saproxylic organisms (Hilmers et al., 2018; Seibold et al., 2016). Second, further studies need to include arthropod communities in fruitbodies of *F. fomentarius* on other host tree species, such as *Betula* spp. or *Populus* spp., and investigate potential alternative post-glacial recolonization routes. Third, to better understand scale-dependency of community turnover, future studies could cover the whole range of *F. fomentarius* including North America and East Asia. For instance, the Tenebrionidae *Bolitophagus reticulatus* is a ubiquitous species in *F. fomentarius* from Europe to Korea (Jung, Kim, & Kim, 2007), but is completely replaced by its relative *Bolitotherus cornutus* in North America (Matthewman & Pielou, 1971), indicating that there might be a stronger biogeographical structuring of the community at such larger scales.

Our results showed that fruitbodies of a single fungus *F. fomentarius* provide habitat to a high number of arthropods, thereby contributing considerably to biodiversity in European beech forests. Considering the responsibility of European countries to protect biodiversity in this ecosystem, we recommend making the promotion of bracket fungi as *F. fomentarius* an integrated goal of forest conservation strategies in European beech forests. The weak biogeographical structuring and high turnover of communities between sites suggest that a prioritization of certain regions within Europe is of minor importance with regard to arthropod communities in *F. fomentarius*. Instead, we recommend that conservation should range from the protection of forests where *F. fomentarius* is highly abundant and inhabited by Europe-wide rare arthropod species (e.g., in the Carpathian Mountains), to the retention of individual habitat trees and dead wood with fruitbodies of the species from harvesting and salvage logging (including unintentional destruction by logging machinery) throughout Europe, and to the reintroduction of the species to regions (e.g., in western Europe) where it has become extinct and relict populations are lacking (for

methods see Abrego et al., 2016). The example of the region of Flanders, Belgium, shows that *F. fomentarius* is able to recolonize areas where it was formerly extinct from a few relict populations if beech dead wood and habitat trees are retained (Vandekerkhove et al., 2011). Furthermore, many fungicolous arthropods are able to track *F. fomentarius* populations recolonizing suitable habitats due to their high dispersal ability (Vandekerkhove et al., 2011; Zytynska et al., 2018). In addition to positive effects on species associated with its fruitbodies, promoting *F. fomentarius* will potentially help to restore fundamental ecosystem processes and natural forest dynamics in beech forests as it is the primary decomposer of beech wood and an important agent of tree senescence and death. Species associated with broadleaf dead wood and sunny conditions in forests may also benefit from gaps created when beech trees are killed by *F. fomentarius*. As *F. fomentarius* provides habitat, shapes further habitat characteristics and drives ecosystem processes, it can be considered a keystone modifier or ecosystem engineer in European beech forests (Mills, Soule, & Doak, 1993).

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