



## Article

# Emerging Urban Forests: Opportunities for Promoting the Wild Side of the Urban Green Infrastructure

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**Abstract:** Many cities aim to increase urban forest cover to benefit residents through the provision of ecosystem services and to promote biodiversity. As a complement to traditional forest plantings, we address opportunities associated with “emerging urban forests” (i.e., spontaneously developing forests in cities) for urban biodiversity conservation. We quantified the area of successional forests and analyzed the species richness of native and alien plants and of invertebrates (carabid beetles, spiders) in emerging forests dominated by alien or native trees, including *Robinia pseudoacacia*, *Acer platanoides*, and *Betula pendula*. Emerging urban forests were revealed as shared habitats of native and alien species. Native species richness was not profoundly affected by the alien (co-)dominance of the canopy. Instead, native and alien plant species richnesses were positively related. Numbers of endangered plants and invertebrates did not differ between native- and alien-dominated forest patches. Patterns of tree regeneration indicate different successional trajectories for novel forest types. We conclude that these forests (i) provide habitats for native and alien species, including some endangered species, (ii) allow city dwellers to experience wild urban nature, and (iii) support arguments for adapting forests to dynamic urban environments. Integrating emerging urban forests into the urban green infrastructure is a promising pathway to sustainable cities and can complement traditional restoration or greening approaches.

**Keywords:** biodiversity conservation; cemeteries; endangered species; invasive tree species; plant invasions; passive restoration; rewilding; secondary succession; urban woodland; urban wilderness

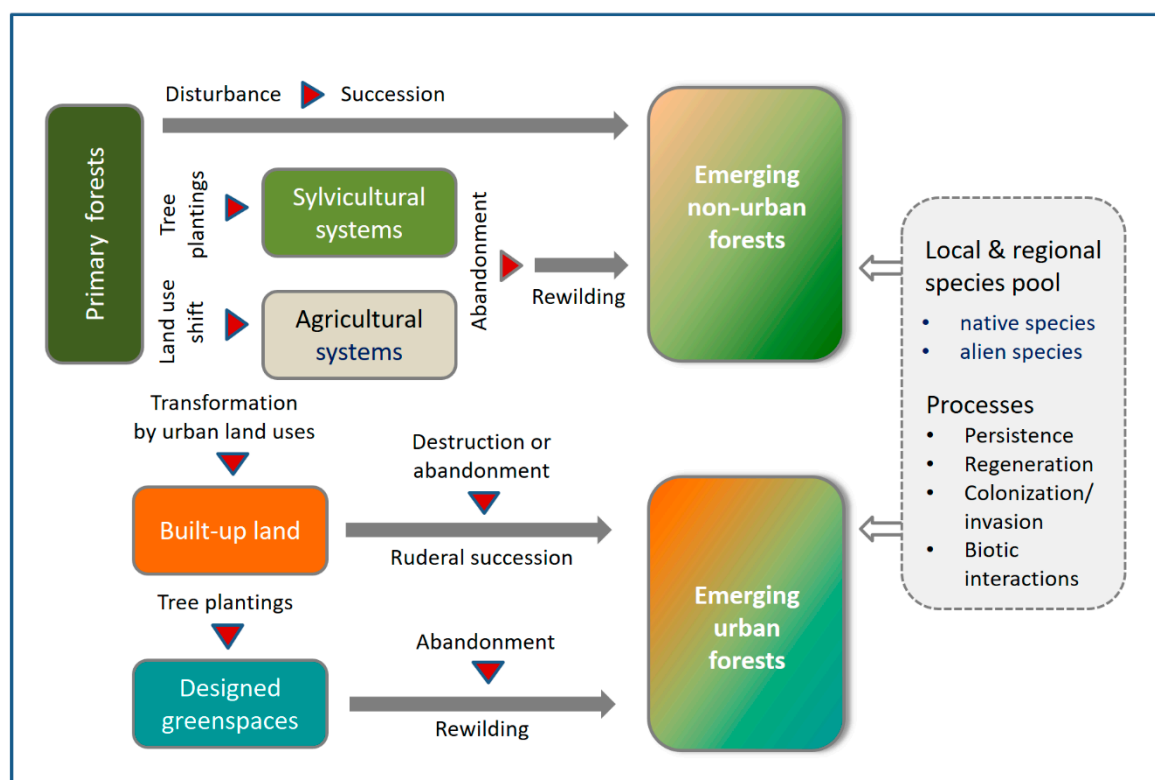
## 1. Introduction

The pressure on forests around cities is increasing in many parts of the world, with urban growth and intensified land use as key drivers [1–3]. As a consequence, forest patches within cities are of increasing importance for biodiversity conservation [4,5] and are highly valued by urban dwellers due to their contribution to liveable cities and the wealth of associated ecosystem services they bring [6–9]. Complementing the urban green infrastructure with new forests is thus a timely challenge for cities around the globe [8,10–12].

Yet forest patches in cities differ considerably in terms of their origin and the way in which humans have shaped their development [10,13,14] and could thus contribute differently to urban biodiversity conservation. A traditional conservation focus is on natural forest remnants that many cities encompass within their borders, including in tropical [15,16], temperate [17,18], and boreal regions [19,20]. Natural

remnants in cities provide habitats for species of conservation concern [21–24], but have often been lost, transformed or fragmented due to urban development [5,10,25].

Creating new forests by planting trees in cities is well established in restoration ecology, e.g., [26–29], ranging from near-natural sites at the urban fringe, e.g., [30,31], to anthropogenically altered sites [32–34]. Yet such tree plantings and related maintenance require the allocation of considerable resources and do not always yield satisfying results, e.g., when continued maintenance is necessary [31,35]. It may thus be useful to consider complementary pathways towards establishing new forests in cities. We focus here on “emerging urban forests” as forests that evolve on urban sites through natural processes (e.g., colonization, and succession). Generally, emerging forests have been defined as secondary, or successional forests, developing in response to severe disturbance or abandonment of previous land use as illustrated in Figure 1 [36–39].



**Figure 1.** Pathways to emerging forests in non-urban (above) and urban environments (below). Red triangles indicate major drivers of change. Grey arrows illustrate successional processes that may start from either open land subsequent to major disturbance events or abandonment of land-use. Rewilding covers successional processes within a matrix of existing vegetation, in response to a decrease or cessation in management.

In cities, emerging forests can result from different development paths. The first pathway is the colonization of previously cleared or abandoned urban-industrial land, indicated as ruderal succession in Figure 1. Outcomes of ruderal succession series have been reported for a range of urban-industrial land-use types [40–44], including vacant lots [33,45–47], transportation corridors [48,49], post-industrial sites [38,43,50–52], and landfills [53,54]. A second, less acknowledged pathway towards emerging urban forests is spontaneous rewilding of designed greenspaces. This is a parallel to rural landscapes where forests evolve in response to decreased (or ceased) agrarian land use [36,55], sylvicultural management [56,57] (Figure 1), or the abandonment of villages and farmsteads [58,59]. Although rewilding is likely a common process in many urban greenspaces, resulting wild woods have been mostly reported for old cemeteries in Europe, e.g., [60–63]. As an exception, Pregitzer et al. [64] recently reported successional forests in urban parks in New York City.

We expected that different types of emerging forests in cities harbor different species assemblages due to filtering in terms of divergent seed sources and environmental conditions. While the species composition in successional forests mainly results from colonization from adjacent seed sources, previously planted ornamentals and co-occurring wild species provide additional seed sources in rewilded green spaces. Moreover, succession in rewilded greenspaces starts from developed soils with an increased nutrient availability, whereas ruderal soils have different features, which have been shown to affect biodiversity patterns [42,48,65].

Making use of successional processes is established practice in restoration ecology [66–68] and is often referred to as “passive restoration” [55]. Since the beginning of this century, rewilding has been a hot topic in ecosystem management and biodiversity conservation [55,69] and is also attracting increasing attention in cities [51,70,71]. However, since cities are hotspots for alien plant species, there are concerns that introduced species could have a negative impact on native species in urban forest patches [13,26,27,72–75].

Indeed, historical analyses of urban floras have revealed a steep increase in numbers of alien woody species [76–78]. Wild-growing alien species contributed, for example, 16% to Berlin’s woody flora in 1800 but 67% in 1990 [79]. Remnant forest patches in cities harbor more alien species than in non-urban environments [80], with the higher numbers of alien species due to edge effects [81]. Moreover, alien species can dominate successional forests on urban land as was shown first for Berlin [40,82] and beyond, e.g., [45,83]. Whether emerging urban forests provide habitats for native plant and animal species—despite the generally high occurrence of alien species in cities—is understudied though.

The degree to which alien species are drivers or passengers of change [84] in urban environments likely depends on the characteristics of the dominant species and the particular ecosystem types [85]. Yet there is limited evidence about the role of emerging urban forests in large cities and their domination by native or alien tree species. Moreover, comparative analyses of diversity patterns of different types of successional forests in cities are rare; but see [49,86,87].

Here we analyze biodiversity patterns of emerging urban forests within the city of Berlin, Germany, at two spatial scales. At the city scale, we quantified the area of successional forests on open land (i.e., outside designed greenspaces) and the dominant tree species. Given the high propagule pressure of introduced woody species as a typical urban feature [79,88–90], we expected that most of these forest patches would be dominated by alien tree species.

At the community scale, we analyzed how the alien vs. native status of dominant tree species related to diversity patterns of plants and invertebrates in the ground layer. Our data set included (i) successional forests on previously open land and (ii) rewilded tree stands on old cemeteries. The latter are a prominent example of rewilded urban greenspace and are increasingly important in European cities due to changing burial practices [91]. As a consequence, parts of many cemeteries in Berlin are no longer used for burials, and natural processes have been allowed to proceed with limited management interference.

We hypothesized a negative relationship between native species richness in the ground layer and alien dominance in the canopy and thus expected native species richness to decrease from (i) plots dominated by a common native tree species (*Betula pendula*; [92]) to (ii) plots covered by a mixture of native and alien tree species (native *Acer platanoides*, alien *A. pseudoplatanus*; [93]) to (iii) plots dominated by *Robinia pseudoacacia*, a North American tree species that modifies associated plant assemblages due to nitrogen fixation [94,95].

We adopted a multi-taxon approach to compare responses of vascular plants and two groups of invertebrates (carabid beetles and spiders) to the dominant tree species because (i) different groups of taxa perform differently in early stages of forest succession [96] and (ii) alien dominance in plant species might affect higher trophic levels if introduced species provide less suitable resources for animal species [97,98]. Since endangered species are important indicators of the conservation value of habitats, we tested whether their number differed across forest types.

In detail, we addressed two main research questions at the landscape scale: (1) how important are successional forests that have emerged on previously open land in Berlin (in terms of total area, patch number, patch size)? and (2) to what extent are these forests dominated by native or alien tree species or a mixture of the two?

Addressing the community scale, we further asked: (3) do emerging urban forests that are dominated by native vs. alien tree species differ (a) in terms of plant and invertebrate richness (total, alien, native species, and endangered species), and (b) in the composition of their species assemblages? and (4) is the number of alien plant species in the ground and shrub layers of emerging urban forests negatively related to native plant species richness?

## 2. Methods

### 2.1. Study Region and Study System

Berlin is Germany's largest city with 3.6 million inhabitants within a total area of 891.1 km<sup>2</sup>. While 48% of the land within the administrative borders of the city is built-up areas and another 10.9% streets, 41.1% of the city is represented by green or blue spaces. These include forests (17.5%), lakes and rivers (6%), parks and other greenspaces [99].

Natural forest remnants on the prevailing sandy soils are dominated by oaks (*Quercus robur*, *Q. petraea*) and Scots pine (*Pinus sylvestris*), but many of these stands have been replaced by intensively managed plantations; forest remnants on wet soils are dominated by alder (*Alnus glutinosa* [82]). Important native pioneer trees are *Betula pendula*, *Populus tremula*, *Salix caprea*, and *Sorbus aucuparia* [100], which are abundant on forest sites and also on vacant urban land [41,79]. The most frequent non-native tree species in Berlin include *Robinia pseudoacacia*, *Prunus serotina*, *Acer negundo*, *Quercus rubra*, and *Ailanthus altissima* [79]. Two maple species (*Acer platanoides*, *A. pseudoplatanus*) were rare in Berlin up to the end of the 19th century, but are among the most abundant tree species today due to frequent plantings in forests, urban greenspaces, and along streets [101]. While *A. platanoides* is considered native to Berlin, *A. pseudoplatanus* is listed as an alien species [93].

Due to destruction during World War II and delayed urban development until the German reunification in 1989, a considerable amount of vacant land remained within the city and was recolonized through natural succession. At the beginning of the 1980s, 142 sites of spontaneously vegetated vacant land with a total area of 550 ha and covering 1.2% of the total area of (then West) Berlin had been mapped as "Stadtbrachen" [102]. While some of these areas remained as wild urban woodland, others were integrated into urban parks or were re-built as Berlin began growing again [103–105].

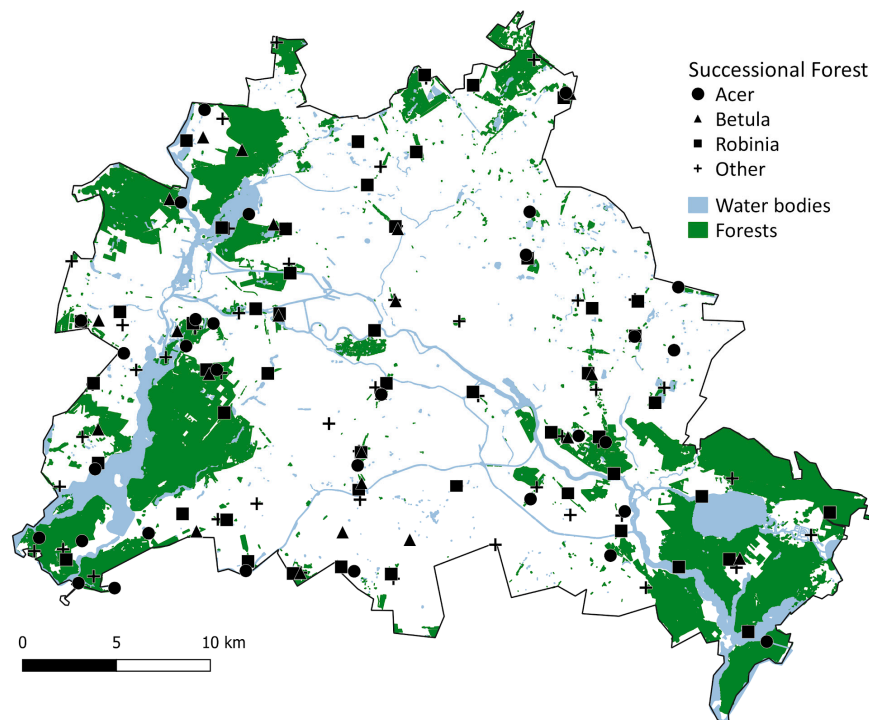
Forest succession on vacant land in Berlin has been described since the 1960s, based on field studies (synthesis by [40,54,82]) and experimental studies [106,107]. A few studies have analyzed invertebrates in successional forests on vacant land [108,109] and on a rewilded cemetery [62].

Cemeteries in Berlin are appropriate models for studying successional processes in tree-dominated greenspaces as most have been designed in a park style, with tree allées, tree clumps, and individual trees. Berlin has 220 cemeteries within its administrative borders, covering 1125 ha in total [99]. In a pioneer study, Graf [110] reported 690 wild-growing plant species from 42 cemeteries with a total size of 297 ha; 13.5% were tree species. Due to changes in burial practices, a considerable amount of Berlin's cemeteries are not used anymore, resulting in significantly decreased management or abandonment. Therefore, 290 ha (28%) of Berlin's cemetery area are planned to be converted to public green spaces or some other use.

Most of the wild parts of cemeteries are dominated by *A. platanoides*, *A. pseudoplatanus*, or a combination of the two maple species, as demonstrated in studies of the Jewish cemetery in Weißensee [62,109] and in other greenspaces [111,112].

## 2.2. Analyses at the Landscape Scale

To respond to the first research question, we used the biotope map of Berlin [99] to determine the dominant tree species of the successional forest patches that have emerged on open land within Berlin (i.e., outside formal greenspaces and forest areas). We differentiated among forest patches dominated by the following species: *Betula pendula*, *Populus tremula*, *Robinia pseudoacacia*, *Populus × canadensis*, *Acer* spp. as well as an additional category (“other”) when there was no data about the dominant species (Figure 2). This selection of species corresponds to the differentiation of biotope types in Berlin’s biotope map. For each type of successional forest, we calculated patch number and size with the field calculator in QGIS [113].



**Figure 2.** Locations of 516 patches of successional forests in Berlin, based on Berlin’s biotope map [99], that were analyzed at the landscape scale. The symbols indicate different forest types, dominated by different tree species according to Berlin’s biotope map. The number of visible symbols is lower than total patch number due to overlapping symbols. Please note that rewilded forests in greenspaces are not shown here.

## 2.3. Analyses at the Community Scale

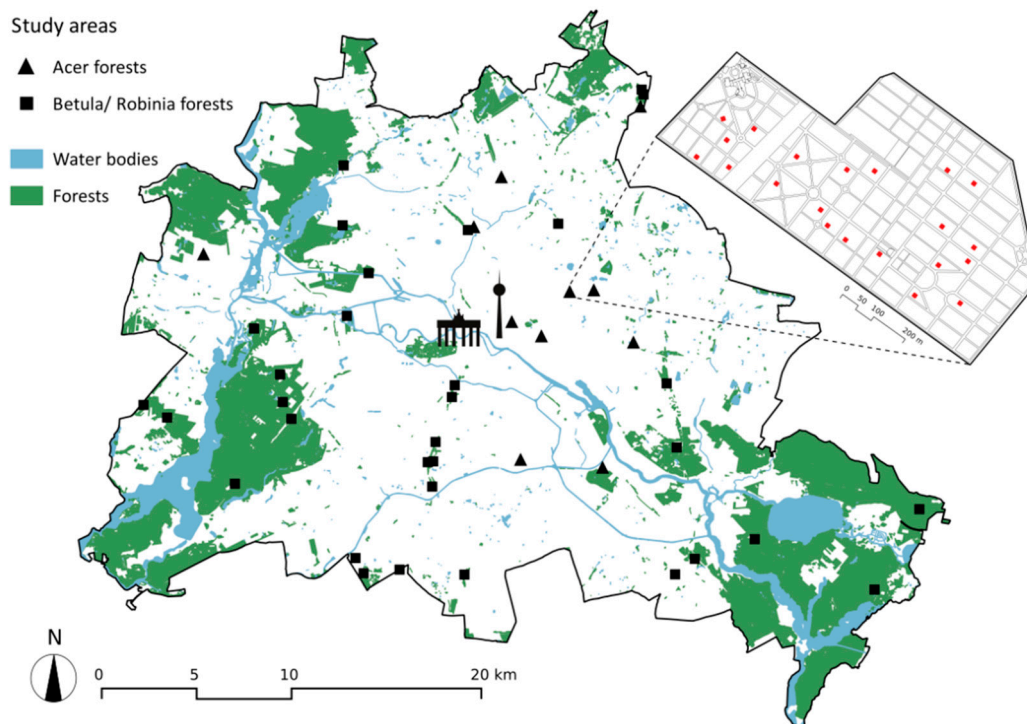
To respond to the second research question of whether the patches were dominated by native species, alien species, or a combination of the two, we compared species assemblages of three types of emerging forests that are all common in Berlin: (i) native *B. pendula* stands, (ii) *Acer* stands that are dominated by the native *A. platanoides* or the alien *A. pseudoplatanus* or a mixture of both, and (iii) stands of the alien *R. pseudoacacia*.

We used data from a plot-based sampling of the three forest types for vascular plants and two groups of ground-dwelling arthropods (carabid beetles, spiders; see Table 1 for details on data sources). While vascular plants are a standard group in urban biodiversity studies [114], the two less commonly studied invertebrate groups are suitable indicator species due to pronounced habitat preferences in urban habitats in general (e.g., [115–117]) and urban forests in particular (e.g., [118]).

All vascular plant species were recorded in 119 plots, each 10 m × 10 m, which were distributed across Berlin (Figure 3). For the *Acer*-dominated forest type, we analyzed 30 plots from wild parts of ten Christian cemeteries. We further included data from 21 plots that had been sampled in rewilded parts



of a large (39 ha) 19th-century Jewish cemetery [62,109]. For stands dominated either by *B. pendula* or *R. pseudoacacia* we re-analyzed data from a previous study [49]. In this study, 34 pairs of woodland patches had been selected based on the biotope map of Berlin, with one patch dominated by *B. pendula* and the other by *R. pseudoacacia*. These pairs were separated by at least 1000 m to avoid spatial autocorrelation. Within each patch of the woodland pairs, a study plot was randomly located. A minimum distance of 20 m was kept between plots to avoid neighboring effects.



**Figure 3.** Location of the forest patches within Berlin that were analyzed at the community scale. Triangles represent *Acer* forests on rewilded cemeteries, and squares represent *Betula* and *Robinia* forest patches, resulting from ruderal succession. Water bodies are shown in blue and forest areas in green. One area, the Weißensee Jewish cemetery, is shown at a larger scale to illustrate the distribution of the 10 m × 10 m plots (red squares) for vegetation and invertebrate sampling. The icons indicate the city center of Berlin.

The vegetation data were stored and tabulated with the software TURBOVEG for Windows [119]. The differentiation between native and non-native species followed [93]. The group of native species was merged with the group of archaeophytes (pre-1492 introductions), while the group of non-native species included neophytes (post-1492 introductions).

For carabid beetles and spiders, we used data from 41 plots that were a subset of the vegetation plots (Table 1). For the *Acer* stands, we analyzed data from the Jewish cemetery [62,109]. For *Betula* and *Robinia* stands, we re-analyzed data from [87], who had sampled invertebrates in a set of ten woodland pairs. For each pair, one patch was dominated by *B. pendula* and the other by *R. pseudoacacia* (more than 90% coverage each). Both taxa were sampled using three uncovered and randomly installed pitfall traps keeping a minimum distance of 5 m between them. Pitfall traps were 500 mL white plastic cups (9 cm diameter, 12 cm depth) filled with a 4% formalin-detergent solution (125 mL). Both sampling periods lasted two months, and emptying was done twice at four-week intervals. Finally, we identified carabid beetles and spiders to species level using standard determination keys for carabids [120] and spiders [121–123]. In contrast to vascular plants, carabid beetles and spiders were not assigned to either natives or non-natives since the percentage of non-native species in both groups is very low in Berlin [124,125].

As species of conservation concern, we addressed endangered species listed in the regional Red Lists for Berlin for plants [126], spiders [125] and carabids [124].

**Table 1.** Information about study areas, plots, and sampling methods for vascular plants and invertebrates (carabid beetles and spiders) for forests dominated by *Acer*, *Robinia* or *Betula*.

	<i>Acer</i> Forests		<i>Betula</i> and <i>Robinia</i> Forests
Vascular Plants			
Study area	Weißensee Jewish cemetery	10 Christian cemeteries	Successional forests across Berlin
Data source	[62,109]	This study	[49]
Number of plots	21	30	Paired plots, 34 dominated by <i>Betula pendula</i> , 34 dominated by <i>Robinia pseudacacia</i> (68 in total)
Plot size	10 m × 10 m	10 m × 10 m	10 m × 10 m
Plot selection	Random selection with Hawth's Analysis Tools for ArcGis	Random selection with Hawth's Analysis Tools for ArcGis and Random Points tool in QGIS	Random selection
Recording time	April–May 2013 [127]	April–May 2013; May–June 2015 [127]	May–July 2010 [128]
Abundance estimation method	transformation of values into percentages for statistical analyses	transformation of values into percentages for statistical analyses	transformation of values into percentages for statistical analyses
Invertebrates			
Study area	Weißensee Jewish cemetery		Successional forests across Berlin
Data source	[62,109]		[87]
Number of plots	21		20
Recording time	24 April–25 June 2013		1 May–30 June 2012

## 2.4. Statistical Analyses

### 2.4.1. Landscape Scale

We tested for differences in the patch sizes among *Betula*, *Acer*, and *Robinia* forests by means of a Kruskal–Wallis rank sum test with the package ‘stats’ in R 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria) [129]. This is a non-parametric analysis that tests the null hypothesis that two or more samples from a dependent variable belong to the same distribution [130]. We used the size of the different forest patches as the dependent variable and the type of forest as the independent variable to test the validity of the null hypothesis that all forests have similar patch sizes.

### 2.4.2. Community Scale

We tested differences in species richness and number of species of conservation concern among the three forest types for vascular plants and invertebrates (summed data from three pitfall traps and carabid beetles and spiders). Differences in origin (native vs. non-native) were tested only for vascular plants. Prior to statistical analysis, normal distribution of data and homogeneity of variance were checked using Shapiro–Wilk and Fligner–Killeen tests. If normal distribution and homogeneity of variance were not met, data were log-transformed. Afterwards, we tested for differences using a one-way ANOVA, and pairwise comparisons were made with Holm–Sidak post-hoc tests.

To analyze community structure of vascular plants, carabid beetles, and spiders, we ran non-metric multidimensional scaling (NMDS) using the VEGAN package [131]. Before analyses, the relative abundances of 28 carabid, 63 spider, and 148 vascular plant species were square-root transformed. NMDS is an iterative ordination method that places samples in a k-dimensional space using the ranked distances among them. The scaling was based on the Bray–Curtis dissimilarity matrix of taxa. In search of a stable solution for a three-dimensional model, 100 random starts were used. To test if woodland type (*Acer*, *Betula*, and *Robinia*) and woodland origin (rewilded and successional) affected species compositions of vascular plants and invertebrates, we performed a permutational multivariate ANOVA (command ‘adonis’ in R package ‘vegan’) with 10,000 permutations.

The relationship between number of neophytes and number of native plant species was tested using linear regression analysis for each forest type after checking for normality of data distribution using the Shapiro–Wilk test.

All statistical analyses were performed using the software environment R 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria) [129].

### 3. Results

#### 3.1. Successional Forests at the Landscape Scale

Analyzing the biotope map of Berlin revealed 516 patches of successional forests, with a total area of 337.6 ha (Table 2). About 39% of patches were clearly dominated by alien tree species, and most of these by *R. pseudoacacia*. Sixteen percent of forest patches were dominated by native tree species, most prominently by *Betula pendula*. For a large group of patches (44%), the database did not allow the identification of dominant native or non-native tree species. About a third of these patches were dominated by trees of the genus *Acer*, thus including both native (*A. platanoides*) and alien (*A. pseudoplatanus* and *A. negundo*) species. The size of *Betula*, *Acer*, and *Robinia* forest patches did not differ significantly ( $p = 0.49$ , Kruskal–Wallis rank sum test).

**Table 2.** Successional forests emerging on open land in Berlin. Patch number, average patch size, and total area are given for forests dominated by native or alien tree species. The category “undefined” includes mixed native/alien *Acer* forests and other forest patches that had not been further specified in Berlin’s biotope mapping.

Dominant Trees	Patch Number	Average Patch Size (ha)	Total Area (ha)
Native species			
<i>Betula pendula</i>	64 (12.4%)	0.4536	29.0 (8.6%)
<i>Populus tremula</i>	20 (3.9%)	0.2778	5.6 (1.7%)
Total native	84 (16.3%)	0.4118	34.6 (10.3%)
Alien species			
<i>Robinia pseudoacacia</i>	173 (33.5%)	0.5842	101.1 (29.9%)
<i>Populus × canadensis</i>	30 (5.8%)	0.3656	11.0 (3.3%)
Total alien	203 (39.3%)	0.5518	112.0 (33.2%)
Undefined			
<i>Acer</i> spp.	78 (15.1%)	0.6229	48.6 (14.4%)
Other species	151 (29.3%)	0.9430	142.4 (42.2%)
Total undefined	229 (44.4%)	0.8340	191.0 (56.6%)
Total	516 (100%)	0.6543	337.6 (100%)

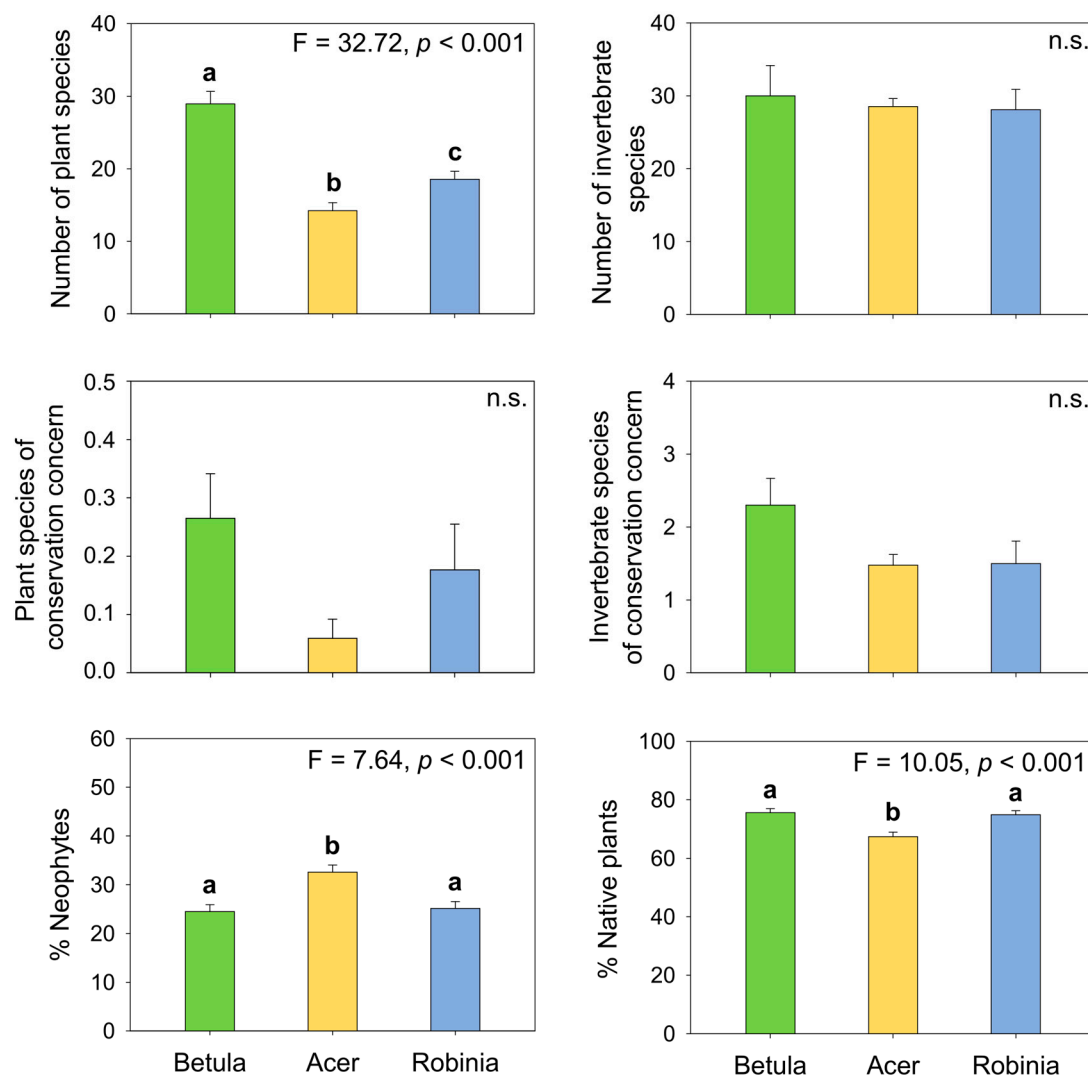
#### 3.2. Biodiversity Patterns at the Community Scale

##### 3.2.1. Biodiversity Measures across Forest Types

Numbers of plant species differed significantly among the three forest types ( $F = 32.72$ ,  $p < 0.001$ , one-way ANOVA) (Figure 4). *Betula* forests had more species compared to *Robinia* and *Acer* forests



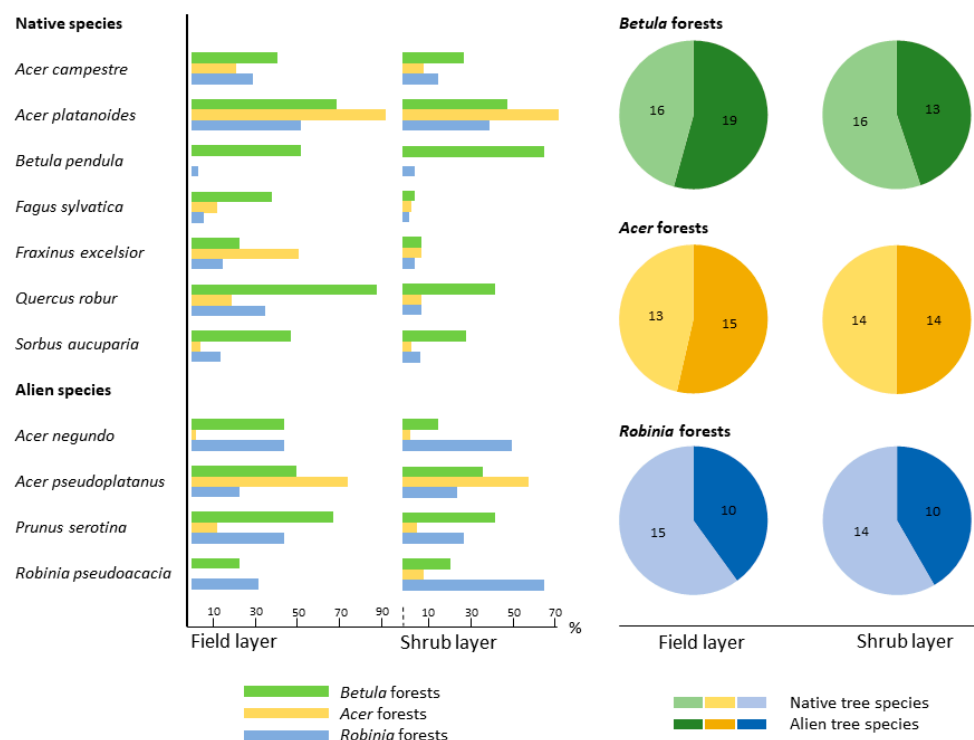
(Figure 3). Numbers of plant species of conservation concern did not differ significantly among forest types. However, because of a generally low frequency of these species in all forest types, this diversity measure varied greatly between stands due to a large number of zero values. Therefore, non-significant differences between the forest types may predominantly be attributed to this variation. Percentage of neophytes was significantly higher in *Acer* forests, while *Betula* and *Robinia* forests harbored the same percentage of neophytes ( $F = 7.64, p < 0.001$ , one-way ANOVA). Consequently, *Acer* forests had the lowest percentage of natives ( $F = 10.05, p < 0.001$ , one-way ANOVA). Numbers of invertebrate species and of species of conservation concern did not differ significantly among forest types.



**Figure 4.** Differences in the mean number of plant species per plot were significant among the three forest types ( $F = 32.72, p < 0.001$ , one-way ANOVA), whereas number of invertebrates as well as number of species of conservation concern (i.e., red-listed species) did not differ. Percentage of neophytes ( $F = 7.64, p < 0.001$ , one-way ANOVA) and natives ( $F = 10.05, p < 0.001$ , one-way ANOVA) differed significantly among forest types with *Acer* forests showing the highest percentage of neophytes and the lowest percentage of natives. Small letters indicate results of Holm-Sidak post-hoc tests ( $p < 0.05$ ) with different letters indicating significant differences in pairwise comparisons.

A total of 45 tree species were able to colonize the emerging forests (Figure 5), including—combined for the ground and shrub layers—18 native and 27 alien tree species. Tree species richness was similar in the two layers, both for native species (17–18 species) and for alien species (21–23), with some

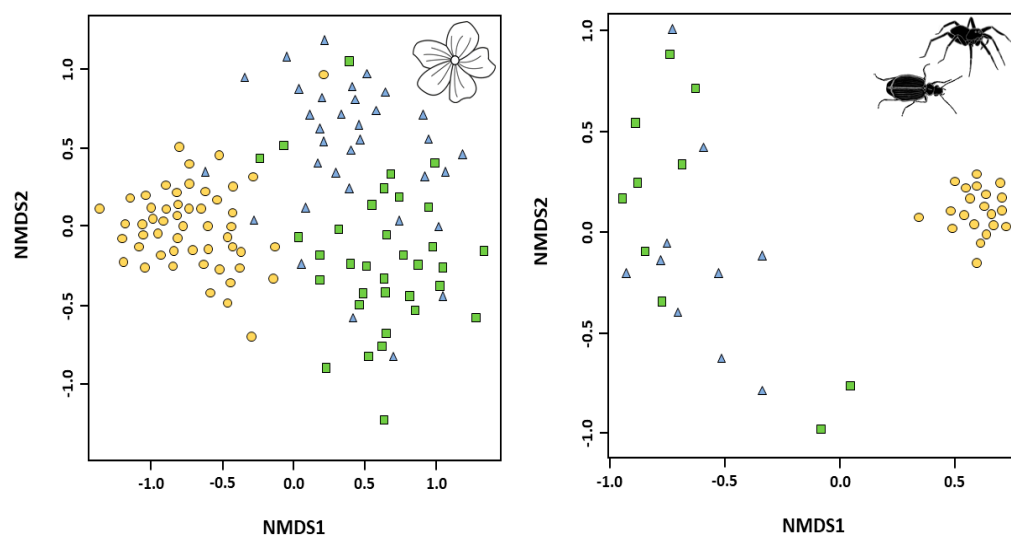
differences among forest types (see pie charts in Figure 5). The ground layer of the alien *Robinia* forest patches, for example, harbored a higher share of native tree species than the native *Betula* forests.



**Figure 5.** Colonization of the ground and shrub layer of three types of emerging urban forests by native and alien tree species. The pie charts show the total numbers of alien (darker colors) and native (lighter colors) tree species in the ground and shrub layer of each forest type. The columns illustrate the percentage of plots of each forest type in which the given species was found in the ground layer or the shrub layer. Species with a frequency of >30% in at least one forest type are shown (*Betula*:  $n = 34$  plots, *Acer*:  $n = 51$ , *Robinia*:  $n = 34$ ).

### 3.2.2. Species Assemblages across Forest Types

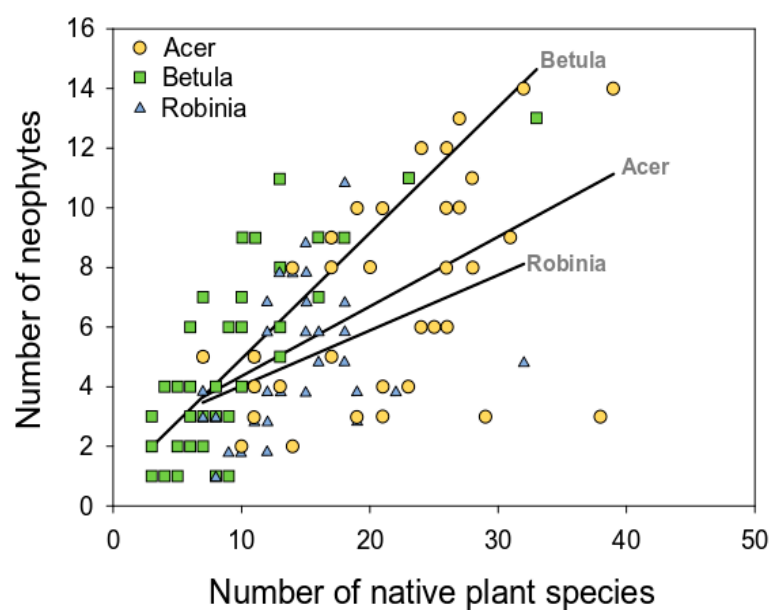
The NMDS revealed that all three forest types harbored distinct vascular plant species communities (Figure 6), and consequently the permutational MANOVA showed that species distribution was affected by forest type ( $F = 18.0$ ,  $df = 2$ ,  $R^2 = 0.24$ ,  $p < 0.001$ ) and forest origin ( $F = 33.9$ ,  $df = 1$ ,  $R^2 = 0.22$ ,  $p < 0.001$ ). Regarding invertebrates, similar patterns and effects could be detected although species compositions of *Betula* and *Robinia* forests were more similar, and *Acer* forests were clearly distinct. Both forest type ( $F = 12.4$ ,  $df = 2$ ,  $R^2 = 0.40$ ,  $p < 0.001$ ) and forest origin ( $F = 23.0$ ,  $df = 1$ ,  $R^2 = 0.37$ ,  $p < 0.001$ ) again significantly affected species distribution of carabid beetles and spiders.



**Figure 6.** Community structure of emerging urban forests in Berlin for plant species (left) and invertebrates (spiders and carabid beetles; right). Graphical representation of the non-metric multidimensional scaling (NMDS; explanations: green square = *Betula* forest, yellow circle = *Acer* forest, and blue triangle = *Robinia* forest). Species composition of vascular plants (dimensions = 3, stress = 0.17) was significantly affected by forest type ( $F = 18.0$ ,  $df = 2$ ,  $R^2 = 0.24$ ,  $p < 0.001$ , permutational multivariate analysis of variance) and forest origin ( $F = 33.9$ ,  $df = 1$ ,  $R^2 = 0.22$ ,  $p < 0.001$ ), which was also true for species composition of invertebrates (dimensions = 3, stress = 0.10) (forest type:  $F = 12.4$ ,  $df = 2$ ,  $R^2 = 0.40$ ,  $p < 0.001$ ; forest origin:  $F = 23.0$ ,  $df = 1$ ,  $R^2 = 0.37$ ,  $p < 0.001$ ).

### 3.2.3. Relation between Native and Alien Plant Richness

Numbers of neophytes significantly increased with increasing number of native plants in all forest types (Figure 7), with the steepest rise of neophytes in *Betula* forests ( $t = 3.3$ ,  $p = 0.002$ ) compared to *Acer* ( $t = 8.8$ ,  $p < 0.001$ ) and *Robinia* ( $t = 2.4$ ,  $p = 0.02$ ) stands.



**Figure 7.** Positive relationship between richness in alien plant species (neophytes) and native plant species in three types of urban emerging forests; linear regression for *Betula* forests ( $t = 3.3$ ,  $p = 0.002$ ), *Acer* forests ( $t = 8.8$ ,  $p < 0.001$ ), and *Robinia* forests ( $t = 2.4$ ,  $p = 0.02$ ).

#### 4. Discussion

Novel urban environments such as vacant lots, abandoned industrial areas, and transportation corridors have increasingly received attention as habitats of plant and animal species, with many studies focused on early or intermediate succession stages [42,132,133]. Here we addressed emerging urban forests as tree-dominated vegetation that could result from different processes such as ruderal succession on previously open urban land or rewilding of greenspaces. While the importance of spontaneously regenerating alien tree species in urban environments is well known, e.g., [12,13,79,83,88], this is likely the first study that unravels how the dominance of alien compared to native tree species in the canopy of wild forest patches relates to biodiversity patterns of multiple taxonomic groups. We were further able to relate the responses of species of conservation concern to the different forest types since Red Lists of endangered plants, spiders, and carabids were available for Berlin.

In the following, we discussed our results on (i) the alien vs. native dominance of successional urban forests at the landscape scale and (ii) biodiversity patterns at the community scale for three types of emerging forests, and (iii) draw conclusions on the role of emerging forests for developing the urban green infrastructure.

##### 4.1. Successional Forests at the Landscape Scale

Our study indicates that the emergence of successional forests by “passive restoration” [55], i.e., self-organized community assembly, makes a notable contribution to Berlin’s green infrastructure. Our analyses revealed that the total area of successional forests in Berlin (338 ha) was greater than the area covered by Berlin’s central park, the Tiergarten (210 ha). Moreover, the high number of 516 forest patches and their dispersion throughout the city (Figure 2) were expected to support ecosystems services and access to wild urban nature also in areas that lack a sufficient provision of formal green spaces.

We expected an alien dominance of successional forests in Berlin as the propagule pressure resulting from extensive plantings of non-native trees in urban environments is a well-established predictor of biological invasions [134,135]. This hypothesis was only partially confirmed by our analyses. Forest patches dominated by a single alien tree species indeed made up a larger share than native-dominated patches, but by no means exclusively. A considerable number of patches were also dominated by native trees. The highest number of forest patches, however, was the “undefined” category, which could not be divided into native or alien species due to methodological constraints (i.e., missing differentiation in the Berlin Biotope Map). This impedes a final assessment of the quantitative significance of native vs. alien tree species as both groups are represented by the *Acer* forest type and in the “other” category. Previous studies revealed *Acer* forests as dominated by the native *A. platanoides*, alien congeners (*A. pseudoplatanus* and *A. negundo*), or mixtures of these species [101,111,112]. Other dominant tree species of successional forests in Berlin include native *Salix* and *Populus* species [54] and the alien *Ailanthus altissima* [136].

The most important successional forest types dominated by a single species were alien *Robinia* and native *Betula* forests. Communities of these species have been described since the 1960s for Berlin and beyond [94,95], starting with studies on early successional stages on post-war rubble soils [137] and later covering a broader range of sites, e.g., within transportation corridors (see early synthesis in [40,82]. While many previous studies on urban successional forests largely relied on measures of abundance, e.g., [45,79,138], but see [46,64], our analysis adds insights into the relative importance of different tree species as dominants of successional forests in terms of covered area at the city scale.

Stands of the most important alien tree species, *R. pseudoacacia*, accounted for about three times the area of the most important native tree species, *B. pendula*. However, patch size—which is important for a range of habitat functions for plants [139] and animals [140]—did not differ significantly among forest types.

Comparing results from Berlin with other studies on successional forests suggests that cities in different biogeographic regions share some dominant tree species, including *A. platanoides*,

*R. pseudoacacia*, and *A. altissima*, as shown for a Mediterranean city [45] and for temperate North American cities [13,46,64,83]. Whether the shared dominance of the same tree species in different cities will lead to a biotic homogenization of urban successional forests deserves further comparative studies on a global scale.

#### 4.2. Biodiversity Patterns at the Community Scale

Our multi-taxonomic study demonstrated clear differences in species assemblages of forest types but did not consistently confirm the expected negative relationship between alien tree dominance and (native) species richness across plant and invertebrate species (Figure 4). The current species assemblages as well as the future development of the forests, indicated by tree recruitment patterns, suggest emerging urban forests in Berlin as novel forest types and shared habitats of native and alien species.

##### 4.2.1. Total, Native, and Alien Richness

Cities are hotspots of alien species, and this phenomenon has been addressed in very different ways: as a threat to native biodiversity, e.g., [75] or as a sign of adaptation to novel urban conditions, e.g., [141]. Since the dominance of alien trees in the canopy of emerging urban forests decreased from *Robinia* to *Acer* to *Betula* forests, we could test for related effects on the total, native, and alien species richness, and on the community structure of the three forest types.

For invertebrates, species richness did not differ significantly among forest types. As there were no alien spider or carabid species in our study, results demonstrate the absence of negative effects of a dominant alien—and invasive—tree species (i.e., *Robinia*) on native invertebrates. This adds evidence to neutral effects of invasive plants on animal species, which has been demonstrated before for spiders. In a previous insect study, however, negative effects prevailed [97], likely due to the inclusion of herbivorous insects that usually rely more on resources of native plant species than do other functional groups [97], but see [142].

For plants, patches of the native *Betula pendula* showed the highest total species richness, while stands of the alien *Robinia* harbored significantly fewer plant species, as shown previously [49]. It is likely that the capacity of *Robinia* to increase nitrogen availability for associated species [94,143] promotes a less diverse suite of competitive, N-demanding ruderal species [94,144], resulting in a lower plant species richness in the understory compared to native *Betula* stands [49].

Surprisingly, the mixed native/alien *Acer* forests had significantly fewer plant species in total and more alien species than both the alien *Robinia* and the native *Betula* stands. The lower species richness is likely an effect of resource availability as light is usually limited in the ground layer of *Acer* stands, resulting in a limited number of shade-tolerant species in the understory [138]. Correspondingly in its alien range in North America, stands of *A. platanoides* had fewer plant species than native forest communities [145]. The higher numbers of alien species in the *Acer* forests in this study can be explained by their emergence in rewilded greenspaces. Here, community assembly descends not only from colonization from adjacent seed sources—as in the other successional forests—but also involves previously planted ornamentals and extant wild species. In fact, escaped ornamentals play an important role in the flora of cemeteries, as shown for Berlin [62,110], and correspondingly in *Acer* forests that emerge on burial grounds.

As *Robinia* profoundly changes habitat conditions due to its nitrogen-fixing capacity, this species might be hypothesized to induce an “invasional meltdown” [146] by facilitating other introduced species below its canopy. Correspondingly, Von Holle et al. [147] reported higher numbers of alien species in *Robinia* stands compared to native forest patches, which led the authors to address *Robinia* stands as “islands of invasion” in nutrient-poor native forest systems. Yet previous testing for the invasional meltdown hypothesis has led to ambiguous results and little support at the community level [148]. The absence of significant differences between numbers of alien species in alien *Robinia* vs. native *Betula* stands in our study does not support the invasional meltdown hypothesis. This contrasts



with a study on the same invasive tree species in a rural North American setting [147] and highlights the need to consider the context dependence in assessing invasion impacts [149,150]. In our study, the high propagule pressure of alien species in Berlin obviously translates to a considerable but not dominating share of alien species of about 25% across all forest types. Indeed, propagule pressure has been found to better predict invasion success in urban tree stands than resource availability (and competitors) in the understory vegetation [151]. Native species generally prevailed in the understory forest assemblages with shares of about 75% in *Betula* and *Robinia* forests and 65% in *Acer* forests.

Interestingly, increased numbers of alien plant species in the plots were not related to a decrease in native richness. Numbers of native and alien plant species were instead significantly positively related—consistently across all forest types (Figure 7). This result matches the “the rich-get-richer” phenomenon, which has largely been reported at broader spatial scales [152–154]. Correspondingly, urban biodiversity studies have revealed urban ecosystems harboring a wealth of both native and alien species [23,155,156]. Dyderski et al. [78], for example, found a positive relationship between richness of alien and native tree species in remnants of riparian forests. Yet at finer spatial scales as in our study, negative associations between native and alien richness often, but not exclusively prevail, e.g., due to a higher importance of biotic interactions compared to niche heterogeneity at higher spatial scales [154]. Given the high variability of the alien-native patterns across scales, ecosystems, and regions, Fridley et al. [154] conclude that broad generalizations are poorly supported by scientific evidence. Our study highlights emerging urban forests in Berlin as shared habitats of alien and native species where drivers of species richness such as proximity to seed sources and availability of environmental resources shaped native and alien richness in a similar way.

The idea that the high representation of alien species in urban floras generally translates to a threat to native species thus finds no support for emerging urban forests in Berlin. Given the context dependence of invasion impacts [149], these results cannot be generalized for other regions. In North American cities, for example, highly competitive alien vine species can decrease species richness and tree regenerations considerably [64,157]. Such contrasting results from different regions highlight the need to consider context dependence of ecological effects in invasion assessments [150]. Gaertner et al. [158] argue for differentiating strategies for managing alien species in urban environments between species that have been classified as invasive or non-invasive. *Robinia*, as one of the dominant species of emerging urban forests in Berlin, has been generally classified as invasive due to negative impacts that had mostly been reported for grasslands and other (semi)open vegetation types [94,95]. Since our study does not provide evidence of deleterious effects of *Robinia* on the native diversity of emerging forests compared to other dominant tree species, we argued for assessing alien species based on their demonstrated effects in the specific environmental context. This requires context-dependent decisions for managing—or even conserving—*Robinia* forests as proposed by [159].

#### 4.2.2. Community Structure

The species composition of ruderal succession stages usually diverges from succession series on non-urban sites [37]. Our study revealed the role of the dominant tree species in further modulating species assemblages and successional trends in urban emerging forests. The NMDS (Figure 6) showed that the community structures of plant and invertebrates were significantly related to forest type (*Betula* vs. *Robinia* vs. *Acer*) and forests origin (successional vs. rewilded). This was most obvious for plant species. For invertebrates, patches of rewilded *Acer* forests were clearly separated from the two types of successional forests. As a future direction, effects of forest origin (rewilded vs. successional) should be untangled from effects related to the identity of the dominant tree species, based on a larger data set. Results of this study indicate that community composition is determined by factors beyond species richness. Correspondingly, a North American study on regenerated forest patches differentiated communities as dominated by either native or alien tree species [13].

The differentiation of species assemblages is likely driven by habitat filtering due to the identity of the dominant tree species and associated differences in vegetation structure. *Betula* stands are generally

light, whereas *Robinia* stands have a light canopy but a dense shrub layer; *Acer* stands usually present a closed canopy and a dense shrub layer. Moreover, as described above, N-availability for plants is enhanced in *Robinia* stands due to N<sub>2</sub>-fixation, which facilitates the establishment of other species in the understory compared to other forest types [95,160].

Structural differences between forest stands usually translate to different biodiversity patterns of animal species (e.g., [161,162] for birds). In an Australian study, the volume of the understory vegetation was an important predictor for species richness in different groups of animals [163]. In our study, however, it was not species richness but community structure of invertebrates that differed among forest types. Correspondingly, Hejda et al. [144] found conspicuous differences in species composition but not species richness of three taxonomic groups in *Robinia* forests compared to native forests. Despite a considerable share of alien species, the emerging forests harbored different sets of associated plant and invertebrate species. This confirms corresponding results for plant communities of *Robinia* and *Betula* stands in the same study region about 25–50 years ago [137,164] and indicates that a conversion of community structure in the course of succession is missing thus far.

#### 4.2.3. Successional Trends

A large number of both native and alien tree species were able to establish in the ground and shrub layers of the emerging urban forests, with differing patterns across forest types (Figure 5). Contrary to many expectations of recruitment limitations in native woody species in urban regions [165], there was no lack in the regeneration of native tree species from urban seed sources. The recruitment of native and alien trees can indicate the future development of the emerging forest types.

The dominant tree species of the canopy were also common in the shrub layer of the respective forest types, but for *B. pendula* and *R. pseudoacacia* this was less true in the ground layer. The latter is likely due to the high demands for light in these species [151] and might indicate a future change of dominance in the upper vegetation layers. The high frequency of trees typical of native oak-pine forests (*Quercus robur* and *Sorbus aucuparia*) indicates a development of *Betula* stands towards this type of native forest vegetation, which prevails on nutrient-poor sandy soils of the post-glacial landscape around Berlin [166]. Yet other species that are atypical of native oak-pine forests were frequently found in the *Betula* stands, including the native *A. platanooides* and the alien *A. pseudoplatanus* and, surprisingly, the native *Fagus sylvatica*. These species indicate enhanced nutrient availability, a common feature of urban environments [167]. Correspondingly, the enormous increase in abundance of *Acer* species in Berlin during the last 150 years has been explained as an urbanization effect, due to nitrogen influx from urban sources [79,101]. We thus concluded that emerging forests that are currently dominated by the native pioneer tree *B. pendula* would approach late successional native forest vegetation, yet with novel species combinations that include both native and alien *Acer* species and a mixture of native and alien plants in the ground layer as well.

The high frequency of *Acer* species in all vegetation layers of the *Acer* forests indicates that this novel forest type will persist for a longer time in rewilded greenspaces. Predictions for the *Robinia* forests are less clear. A fast decay of *Robinia* forests had been predicted in the 1960s, reflecting the pioneer character of this species in its native North American range [137]. Indeed, pioneer stands in the Appalachians are being replaced within a period of less than 30 years, mainly due to damaging stem borers and the presence of highly competitive late successional tree species [168]. In Berlin, however, 40-year-old stands were still vigorous around 1990, indicating that the life span of *Robinia* in Europe can be longer than in its native range, likely due to the absence of herbivore pressure [164]. Today, i.e., another 30 years later, several large *Robinia* stems have been noted dying off in emerging forests (pers. observation). Still, *Robinia* is able to grow root sprouts below its canopy [169]. The question remains, however, whether these sprouts can take over in the future to prolong the dominance of *Robinia* in emerging forests. A further confounding parameter is the potential shading out of the light-demanding *Robinia* by *Acer* species. Shade-tolerant *Acer* species are frequent in *Robinia* (and *Betula*) forests (Figure 5). However, whether these saplings will outcompete the less shade-tolerant

*Robinia* in the future—and analogously the *Quercus* species in the *Betula* forests—is an open question as well. The growth of *Acer* species may be constrained by drought stress on many urban sites such as derelict railway areas. This might result in a co-dominance of *Robinia* and *Acer* species in more mature forest patches too.

Overall, these results suggest that community assembly in emerging forests of Berlin has resulted in different forest types with a distinct community structure and a large suite of juvenile tree species. The latter indicates different trajectories to more mature forests but with uncertainties about the direction and speed of future development. *Acer* forests in rewilded greenspaces will likely persist for a longer time, and changes in dominance patterns will likely occur faster in *Betula* stands than in *Robinia* stands.

The (co-)dominance of alien tree species in the canopy of *Robinia* and *Acer* forests resulted in distinct plant and invertebrate species assemblages. The native *Betula* forests also harbored a considerable share of alien species. Berlin's emerging urban forests thus represent novel urban ecosystems with regard to both dimensions of novel ecosystems [170]: novel environmental conditions (i.e., the anthropogenic sites) and novel assemblages of alien and native species. Beyond alien plant species, some native tree species also contribute to novel species assemblages. Most prominently, *A. platanoides*, a formerly rare species of the pristine forest vegetation, currently is and will remain abundant in all forest types, including the native *Betula* forests.

The co-existence of alien and native species in urban emerging forests seems to be a global phenomenon that extends beyond Berlin. Stewart et al. [88] suggested that native forest regeneration in cities of New Zealand may proceed by involving mixtures of alien and native woody species; this has also been demonstrated for successional forests on abandoned land in Puerto Rico [38,171]. These novel forest types will continue to differ from native forests in the future while still providing habitats for a number of native and alien species that are well adapted to urban conditions.

#### 4.2.4. Endangered Species

Despite a sharp increase in urban biodiversity studies, Shwartz et al. [172] conclude in their meta-analysis that the contribution of cities to biodiversity conservation has not yet been sufficiently demonstrated. One reason is that biodiversity conservation can not necessarily be described simply in terms of species richness and numbers of native species, e.g., due to different relevance of common versus rare or endangered species. Recent studies have shown that cities can also host a considerable number of endangered species, e.g., [173]. This is true of novel urban ecosystems as well, as shown for Berlin [23,174] and beyond [42]. Our study contributes insights into the role of alien- vs. native-dominated emerging forests for endangered species of different taxonomic groups since Red Lists of endangered plants, spiders, and carabid beetles were available for the city of Berlin.

The emerging forest types harbored a limited set of species of conservation concern. While on average each forest patch harbored 1–2 endangered invertebrate species, an endangered plant species was only found in about 1 out of 10 patches. Accordingly, Planchuelo et al. [174] revealed a significantly lower probability of occurrence of highly endangered plant species in forests that had been classified as novel ecosystems. In contrast, natural forest remnants harbored the highest number of populations of highly endangered plant species. The scarcity of endangered plant species in the emerging forests of Berlin can likely be explained in two ways. First, rare habitat specialists of open ecosystems can be lost during early- and mid-successional transitions to tree-dominated vegetation [65,132]. Second, dispersal may be limited in many endangered plant species [175], especially in ancient forest species [176,177], preventing them from colonizing young emerging forests. Correspondingly, forest species of carabid beetles are largely confined to the urban fringe of European cities [115]. In the same vein, many invertebrate taxa of an urban forest remnant in New Zealand were not able to colonize other forest stands [24].

From a species protection perspective, the emerging forest patches support some habitat functions for endangered species of plants, spiders, and carabids. The number of species of conservation

interest could increase over time as shown for other secondary forests [176]. Since we could not detect any effect of the introduction status of the dominant tree species on the occurrence of endangered species—consistently among plants and invertebrates (Figure 4)—our study indicates that it is not alien dominance in the canopy but rather other environmental parameters that limited the establishment of endangered species across all forest types.

## 5. Conclusions on the Role of Emerging Forests for Urban Green Infrastructure

Endangered species are important indicators of the conservation value of their habitats but do not represent the total range of targets of biodiversity conservation [178]. Particularly in an urban context, goals of biodiversity conservation should also include the role of urban nature for liveable environments for urban dwellers [179]. It is thus necessary to include a range of socially and ecologically based goals when discussing the role of emerging urban forests for developing the urban green infrastructure. Based on previous work [10,141,179–182], we here highlighted six ways in which emerging forests can contribute to developing biodiverse and liveable cities:

1. Preserve native biodiversity and populations of endangered species. All types of emerging urban forests harbored a considerable number of native plant and invertebrate species—despite a considerable share of alien species. Their role as habitat for endangered species was limited but may increase with time. Yet most likely, the emerging urban forests will not be able to approach natural forest remains in the near future. This strongly supports the well-established aim of placing the highest priority on protecting natural forest remnants in cities, e.g., [21], and indicates as well some opportunities for native species in novel urban settings.
2. Create ecological networks with stepping stones or corridors for plants and animals. While ecological network functions were not studied here, emerging urban forests likely support ecological networks by providing forest patches dispersed over the urban fabric that may be used as stepping stones for birds and other animals [42,140]. Since the alien *Robinia* forests harbored similar numbers of (endangered) invertebrates as the other forest types, they also contribute to ecological networks, e.g., for pollinators [183] or at higher trophic levels [95,144].
3. Facilitate and elucidate the adaptation of ecological systems to urbanization and other environmental pressures. Urbanization as a major driver of change in the Anthropocene period affects all components of urban ecosystems [184]. In consequence, novel urban ecosystems arise and support the understanding of how species assembly responds to a combination of novel environmental drivers in urban settings [141,185]. Allowing emerging forests to develop without intervening in the diversity patterns of alien and native species will provide insights into the adaptation of forest systems to changing urban environments, including interactions with climate change effects; and will allow conclusions to be drawn on the resilience of species and communities to urban pressures, and selection of suitable native or alien species for urban greenspaces.
4. Re-connect people with nature and support experience of natural elements. The diversity of both species assemblages and structural features of emerging urban forests and their adjacency to urban residents create manifold opportunities to experience natural elements and their dynamics in the neighborhood. This is an important service in times of decreasing experience in nature [186], with anticipated positive feedbacks to people's willingness to protect biodiversity [187], and a strong argument for conserving emerging forests close to places where people live [188].
5. Enhance wilderness in cities. Since wilderness areas significantly decline at a global scale [2], the aim of promoting wilderness areas in urban environments—complementing the highly managed ecosystems in public and private greenspaces—is on the urban agenda [70]. Emerging urban forests represent a kind of “novel urban wilderness,” with species assemblages contrasting with the “ancient wilderness” of natural forest remnants but similarly shaped by natural processes [104]. While ancient wilderness areas are usually located at the urban fringe, emerging

urban forests are often integrated into the urban fabric and thus can support access to wilderness in the daily life of urban residents.

6. Provide ecosystem services for urban people. There is increasing evidence of positive feedback between biodiversity and the provision of ecosystem services in cities [189]. Emerging forests in particular, including abundant alien tree species, have been shown to provide a range of regulating ecosystem services on vacant land [44,46]. Moreover, they constitute informal greenspaces [190] supporting manifold social uses and cultural services [191–193]. Importantly, these ecosystem services are being delivered without the use of resources to produce plants and carry out landscaping and maintenance; thus they have a low CO<sub>2</sub> footprint. Integrating emerging forests into the urban green infrastructure therefore also contributes to both climate change mitigation and adaptation.

Although there are many reasons for integrating emerging urban forests into the green infrastructure of cities, some important challenges remain. Studies on the extent to which people value wild vegetation on urban vacant lots have yielded ambiguous results. While some studies revealed prevailing positive valuations of wild vegetation in urban settings [9,71], other studies showed that people preferred open succession stages over woody stages [194,195]. This is likely related to concerns about safety and to general cross-cultural preferences for semi-open scenery [196]. Moreover, rubbish and other signs of neglect may reduce the acceptance of emerging urban forests, necessitating “orderly frames” to improve public perception [191,197]. As with spontaneous vegetation in general [198–200], integrating emerging urban forests into urban green systems thus often requires planning, design interventions, and management to mitigate risks and enhance the opportunities that this novel type of urban woodland offers for the development of biodiverse and liveable green cities. The successful integration of emerging forests in newly established formal parks and greenways in Berlin [103–105], the post-industrial landscape of the Ruhr region [50] and beyond, e.g., [201], illustrates promising perspectives for enhancing the wild side of urban green infrastructure.

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