

Contrasting effects of tree origin and urbanization on invertebrate abundance and tree phenology

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Abstract. The ongoing wide-scale introduction of nonnative plants across the world may negatively influence native invertebrate fauna, due to a lack of coevolved traits related to the novel plants, e.g., unique phytochemicals or shifted phenology. Nonnative plants, specifically trees, are common in urban environments, areas that already pose novel habitats to plants and wildlife through a wide array of anthropogenic factors. For example, impervious surfaces contribute to increased ambient temperatures, the so-called urban heat island effect (UHI), which can affect local plant phenology. Yet, few studies have simultaneously studied the effects of urbanization and tree species origin on urban invertebrate communities. We measured the city-level UHI and phenology of nine native and seven nonnative tree species in five city-center parks in southern Sweden, as well as four common native species in a rural control forest. We quantified the abundance of invertebrates on a subset of native and nonnative tree species through shake sampling, sticky traps, and frass collection. In the urban environment, nonnative trees hosted significantly fewer invertebrates compared to native trees. Furthermore, the nonnative trees had a delayed phenology compared to native species, while the peak of caterpillars associated with the subset of trees surveyed for this measure was significantly earlier compared to that of the native species studied. The effect of tree species origin on urban invertebrate abundance was of a greater magnitude (effect size) than the effect of urbanization on invertebrate abundance in native tree hosts. Hence, the results indicate that the impact of nonnative vegetation may be a stronger driver of invertebrate declines in urban areas than other factors. As the effect of species origin on tree phenology was at a level comparable to the urban effect, increasing prevalence of nonnative vegetation can potentially obscure effects of urbanization on phenology in large-scale studies, as well as induce mismatches to invertebrate populations. Since parks harbor a large proportion of urban biodiversity, native trees play a crucial role in such habitats and should not be considered replaceable by nonnative species in terms of conservation value.

Key words: *exotic plants; nonnative trees; plant phenology; temperate region; trophic levels; urban green spaces; urban heat island.*

INTRODUCTION

Across the globe, nonnative plant species make up a significant proportion of the vegetation in urban environments (Aronson et al. 2014). These introduced species often have different traits compared to natives of the same taxa, such as altered phenology and novel phytochemical composition (Cappuccino and Arnason 2006, Shustack et al. 2009). Nonnative plants in urban systems have been found to host lower invertebrate biodiversity and abundance compared to native species (Burghardt et al. 2009, 2010, Faeth et al. 2011, Burghardt and Tallamy 2015, Narango et al. 2018, Padovani et al. 2020, Tallamy et al. 2021, Berthon et al. 2021). Plants play a

crucial role in urban ecosystems, for example through temperature regulation and pollution reduction (Janhäll 2015, Willis and Petrokofsky 2017, Ziter et al. 2019), in addition to sustaining and modulating local animal diversity and abundance (Faeth et al. 2011, Beninde et al. 2015). In temperate regions of the Northern Hemisphere, nonnative plants, particularly trees, are often advocated in urban green space planning, since they can be more tolerant than locally native species to the harsh conditions in urban environments, i.e., dry soils and elevated temperatures (Sjöman et al. 2016). Factors such as aesthetics, commercial accessibility and presumed ease of maintenance are also driving the use of nonnatives (Avolio et al. 2018). Hence, there is a need for more knowledge on the possible effects on complex trophic interactions from the introduction of nonnative plant species in urban environments (Dale and Frank 2018). Especially so in relation to sustainable urban planning

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and consequences that may affect ecosystem services linked to environmental health, as well as climate adaptation and biodiversity conservation (Faeth et al. 2011, Stevenson et al. 2020).

In general, the time since introduction of a new plant species has been found to be positively correlated to the arthropod abundance and diversity that it hosts, meaning that nonnative plants introduced earlier support higher insect abundance than more recent introductions (Brändle et al. 2008, Padovani et al. 2020). Furthermore, nonnative plants closely related to local species (congeneric species) generally host more invertebrates both in terms of abundance and diversity compared to less closely related nonnatives (Burghardt et al. 2010, Burghardt and Tallamy 2015, Padovani et al. 2020). This suggests that the difference in invertebrate abundance and diversity hosted by nonnative and native vegetation can be explained by a lack of coevolutionary history, which shapes relations between many pollinators and herbivores and their host plants (Ehrlich and Raven 1964). However, it has been suggested that nonnative plants may create novel habitats for invertebrates and could therefore increase diversity on a regional level. For example, Padovani et al. (2020) showed that novel nonnative plants were associated with a distinct arthropod fauna, rather than a subset of the species found on native plants. On the other hand, Burghardt and Tallamy (2015) found the opposite pattern: invertebrates found on novel nonnative plants were not host specific, but generalists found on native plants as well. In both studies, nonnative plants also hosted significantly lower abundances of invertebrates in addition to an overall lower diversity (Burghardt and Tallamy 2015, Padovani et al. 2020). Other studies have similarly found that invertebrates linked to nonnative plants typically are generalists rather than specialists (Brändle et al. 2008). Even on nonnative congeners, the abundance of specialist arthropod species can be five times lower than on closely related native plants (Burghardt et al. 2010). The lower abundance of invertebrates associated with nonnative vegetation has been found to carry negative effects to higher trophic levels, such as lowering the diversity and breeding attempts of birds (Burghardt et al. 2009, Narango et al. 2017, 2018).

In urban ecosystems, vegetation is one of the primary biotic components actively and directly managed by humans, making its effects on higher trophic levels highly relevant (Faeth et al. 2011). Nonnative vegetation is closely connected to human activity, with continuing introductions for horticulture into gardens, suburbs, and cities on a global and massive scale (Richardson and Rejmánek 2011, van Kleunen et al. 2015). Currently, nonnative species make up over a quarter of plants found in cities across the world, habitats that may already be particularly unfavorable to invertebrates (Aronson et al. 2014, Piano et al. 2020). Previous research studying how nonnative plants affect higher trophic levels have done so either in suburban gardens

or experimentally (e.g., Burghardt et al. 2009, Burghardt and Tallamy 2015, Narango et al. 2018). Less attention has been given to the effects on invertebrate abundance and diversity of specific plant species and plant composition across both urban and rural environments. The few detailed studies comparing urban and rural habitats that do exist often focus on native plants only, and do not account for the unique effects of nonnative species (e.g., Meineke et al. 2013, Kozlov et al. 2017, Seress et al. 2018), thus leaving out a large part of the urban tree canopy. This is especially true for habitats in northern Europe.

Urbanization is currently altering ecosystems around the world at a rapid pace and through a wide array of factors (Grimm et al. 2008, Seto et al. 2012). One important aspect is the urban heat island effect (UHI): the local increase in ambient temperature within a city. An UHI can be caused by several factors, including increased short wavelength light absorption and decreased net evaporation (Oke 1978). The UHI, together with other local changes in the abiotic environment such as artificial light at night, carry direct implications to the urban ecosystem and can result in altered phenology of urban plants, e.g., earlier bud burst and longer growing season in temperate cities (Roetzer et al. 2000, Neil and Wu 2006, Dallimer et al. 2016, Li et al. 2017, 2019, Brelsford and Robson 2018, Wohlfahrt et al. 2019). These factors can also affect arthropod populations directly (Owens et al. 2020) and potentially cause a phenological mismatch between arthropods and host plants (Fisogni et al. 2020). For Lepidoptera caterpillars, a mismatched emergence by only a few days can have detrimental effects at a population level, as leaves quickly decrease in water and nitrogen content, while defense compound levels increase simultaneously (van Asch and Visser 2007). Furthermore, a phenological mismatch can be amplified at higher trophic levels, such as insectivorous birds, affecting the ecosystem from the bottom up (Both et al. 2009).

Here, we studied the phenology of 16 nonnative and native tree species in five centrally located city parks in southern Sweden, together with a rural comparison of the most commonly occurring native species, to investigate the effects from both urbanization and tree species origin. We measured ambient temperature to quantify the UHI on a city level. In addition, we measured the abundance of caterpillars, flying insects and tree-dwelling invertebrates on a subset of the tree species, in order to investigate the potential effect of plant species origin and urbanization on higher trophic levels. We expected to find an UHI effect with higher ambient temperature in the urban environment and an advanced phenology in terms of bud burst of urban trees. Nonnative species were hypothesized to have a delayed phenology compared to native species, as most introduced trees in the study region originate from comparatively southern latitudes. Nonnative trees were also hypothesized to host a generally lower invertebrate abundance compared

to native species. Similarly, we expected tree individuals situated within the urban environment to host a lower invertebrate abundance than those in the rural area.

METHODS

Study sites

The urban environment was located in the city of Malmö (55°35'24" N 12°59'19" E; Fig. 1) in southern Sweden, the third largest city in Sweden with over 300,000 inhabitants (SCB 2020). The sites consisted of five parks in the central part of the city, ranging 3–45 ha in size and characterized by a mixture of tree species (both native and nonnative), amenity grass, ponds, and urban infrastructure such as paths, paved roads, light posts, and buildings. The rural location was situated in the nature reserve of Skrylle (55°41'16" N 13°21'36" E, Fig. 1), 26 km northeast of Malmö. The trees studied were all located within a 120-ha deciduous forested area of the reserve dominated by European beech (*Fagus sylvatica*), silver birch (*Betula pendula*), and common oak (*Quercus robur*), with some patches of European spruce (*Picea abies*) together with smaller pastures and gravel roads.

Selection of tree species and sample sizes

In the urban environment, we used a georeferenced tree database of publicly managed areas provided by the City of Malmö's Streets and Parks department to select tree species. We compiled lists of the most common native and nonnative species in Malmö's parks, and from these we selected (1) nine native species common to the study region both in the rural study site and in the urban parks and (2) seven recently introduced and/or not yet naturalized nonnative species, popular in urban landscaping design (Table 1). Through this method, we could select nonnative species based on occurrence in

the urban environment in a relatively standardized way, compared to choosing species on a more arbitrary basis of perceived occurrence or traits. Here, we define nonnative plants as species introduced to Sweden after the 13th century (Essl et al. 2018). We aimed at sampling a selection of species representing a wide range of plant families common in the city and present in as many of the five parks as possible. However, in some cases, not all species were present in all parks, see Appendix S1: Table S1. Apart from Turkey oak (*Quercus cerris*), none of the nonnative species belonged to genera whose native range span over our study region. For the rural control, we selected four common deciduous species present both in the urban area and in the nature reserve of Skrylle (Table 1).

In total, 73 tree individuals belonging to 16 species (nine native and seven nonnative) were surveyed for phenology in the urban environment, while 39 individuals belonging to four native species were included in the urban/rural comparison (see Appendix S1: Table S1). A subset of these were sampled for invertebrates through shake sampling and sticky traps (see Methods: Invertebrate collection): 38 individuals belonging to nine species (five native and four nonnative) were included (Fig. 2a). In the urban/rural comparison, a total of 35 individuals belonging to four native species were sampled using these methods (Fig. 2b). For frass sampling (see Methods: Frass collection), we included 25 individuals belonging to five species (three native and two nonnative) in the urban environment. In the urban/rural comparison, 30 individuals belonging to three native species were included. Not all species were sampled for each method due to logistic constraints (time and/or height of canopy).

Where applicable, the same tree individuals were surveyed for both phenology and invertebrates with the exception of tree of heaven (*Ailanthus altissima*) and goat willow (*Salix caprea*), where some individuals were excluded from invertebrate sampling due to the height of

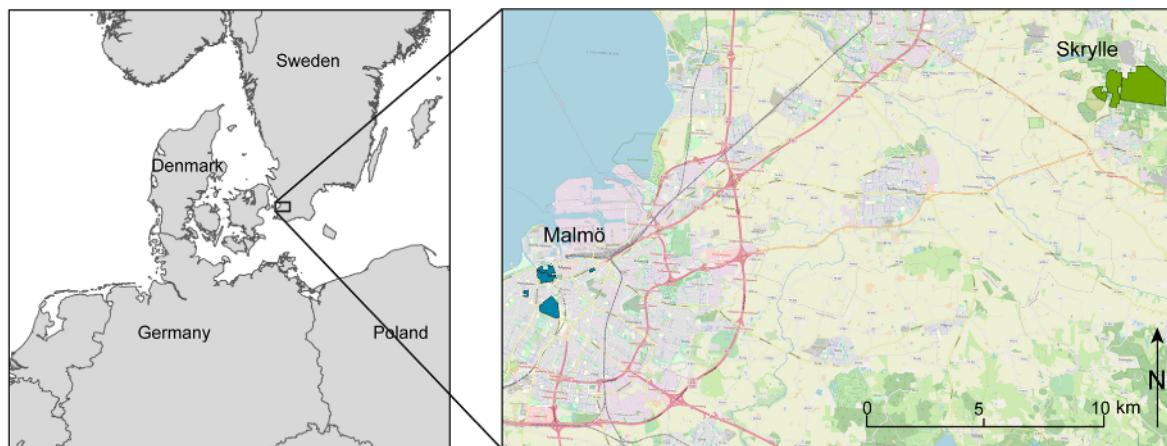


FIG. 1. Map of study locations. The urban site consisted of five centrally located parks of varying size, within the south Swedish city of Malmö. The rural site was located within the nature reserve of Skrylle, situated 26 km northeast of Malmö.

TABLE 1. Tree species included in the study and their local abundance.

Species	Trivial name	Origin	Presence (urban/rural)	Proportion of urban park assemblage (%)
<i>Acer platanoides</i>	Norway maple	native	urban	0.8
<i>Betula pendula</i>	silver birch	native	urban and rural	4.5
<i>Crataegus monogyna</i>	common hawthorn	native	urban	3.0
<i>Fagus sylvatica</i>	European beech	native	urban and rural	41.8
<i>Prunus avium</i>	wild cherry	native	urban	0.3
<i>Quercus robur</i>	common oak	native	urban and rural	3.0
<i>Salix caprea</i>	goat willow	native	urban and rural	0.2
<i>Sorbus intermedia</i>	Swedish whitebeam	native	urban	0.2
<i>Tilia × europaea</i>	common linden	native	urban	1.7
<i>Ailanthus altissima</i>	tree of heaven	nonnative	urban	0.2
<i>Ginkgo biloba</i>	ginkgo	nonnative	urban	0.3
<i>Gleditsia triacanthos</i>	honey locust	nonnative	urban	0.6
<i>Platanus × hispanica</i>	London plane	nonnative	urban	0.7
<i>Pterocarya fraxinifolia</i>	Caucasian wingnut	nonnative	urban	0.9
<i>Quercus cerris</i>	turkey oak	nonnative	urban	0.4
<i>Robinia pseudoacacia</i>	black locust	nonnative	urban	0.4

Notes: Tree species were selected based on their local abundance and use in urban landscaping. In total, nine native and seven nonnative trees were included in the study. Species occurring in the area prior to the 13th century were considered to be native. Non-native species accounted for 23% of the total tree assemblage of the parks study, representing 73% of all species present. Note that while coniferous species were not considered for sampling, they are included in the total park assemblage percentage.

the canopy (see Appendix S1: Table S1). Tree individuals were chosen to be of a similar size of canopy and age across all species. According to the tree database, the local average age of the urban park trees were around 80 yr, while the local average age of the trees in the nature reserve of Skrylle was approximately 70–80 yr, based on municipality maintenance plans. For the urban trees, individuals were selected so that no significant age difference was present depending on origin. Spatially, trees were chosen to be as evenly distributed across the sites as possible, avoiding local and/or edge effects (Fig. 2a,b). In the rural environment, trees in densely forested areas were avoided to better mirror the open configuration of the urban parks and to match the level of canopy cover.

Tree phenology

For all selected species, we surveyed the phenology of tree individuals by recording the day number (i.e., number of days from 31 March) of bud burst, basing the definition and methodology on protocols from Meier et al. (2009). A tree individual was considered to have reached bud burst when at least 50% of the leaf had emerged from at least 50% of all visible buds. Regular phenology checks were carried out from 18 March until all individuals had reached bud burst on 9 May 2019, at intervals of no more than 2 d between each check.

Invertebrate collection

We used two direct methods to quantify the abundance (number of individuals) of invertebrates on host

trees: shake sampling and sticky traps. Both methods were used on the same tree individuals and repeated three times per individual, with one sample per week, over a 3-week period from 26 May to 15 June 2019. As we aimed to investigate the role of nonnative trees in the urban ecosystem, the sampling period was chosen to encompass the general peak abundance of caterpillars, which is subsequently an important period for local bird species relying on this food source during breeding (Naef-Daenzer et al. 2000, Visser et al. 2006).

The shake sampling followed a protocol based on Majer et al. (1996), where a representative branch was chosen and manually shaken 10 times in rapid succession. The same branch was used for all three sampling occasions. Dislodged invertebrates would fall onto a white cloth bed sheet (approximately 1.5 × 2.5 m) placed beneath the branch and were immediately counted and, following a rudimentary identification on site, determined to the closest taxonomic group possible. The tree dwelling invertebrates were later tallied into the three major functional groups: spiders, aphids, and caterpillars. The latter category was composed of insect larvae but was dominated by lepidopteran larvae. With the exception of a low number of ants, which were disregarded, these three groups accounted for all identified invertebrates in the samples. A few single individuals of winged invertebrates, such as beetles, may have escaped before sampling, given the height of the trees. Shake sampling was performed on days with calm winds (5 or lower on the Beaufort wind force scale) and no rain. We collected flying insects with sticky traps, using commercially available “fly paper” (Flyson Flytube, 32 × 10 cm; Pharmaxim AB, Helsingborg, Sweden) placed 3 m

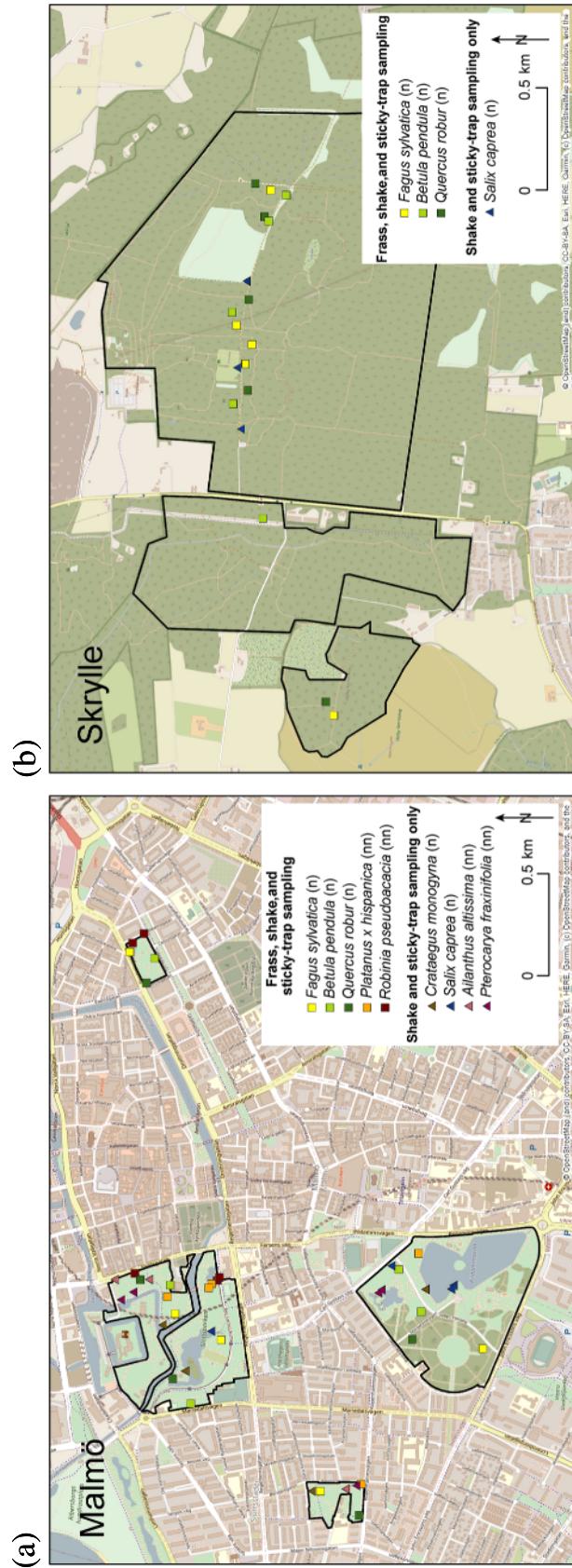


FIG. 2. (a, b). Maps showing trees sampled for invertebrates. Maps of the trees sampled for frass and invertebrates and their dispersion across (a) the urban parks and (b) the rural environment. Squares denote species sampled with all methods, while triangles denote species sampled only by sticky traps and shake-sampling. Tree species origin is noted in parenthesis: (n) denotes native species, while (nm) denotes nonnative species. Colors indicate specific tree species. See *Methods* for details.

above ground level close to the trunk of the tree on the same day that shake sampling took place, on a separate branch. Each trap was left up for 24 h, after which all flying insects were counted. The few individuals of non-flying insects or other invertebrates caught (e.g., caterpillars or spiders) were excluded. The collection of flying insects was conducted on the same tree individuals as the shake sampling, with the exception of one London plane (*Platanus × hispanica*), which could not be sampled for flying insects due to canopy height.

Frass collection

The abundance of caterpillars was further indirectly measured using frass fall collectors. Selection of tree species to be surveyed for frass fall was based on occurrence, canopy structure, and overall size (see Appendix S1: Table S1). Frass, the feces of larvae, is collected as it drops from the canopy of trees and gives an accurate and standardized measure of the local caterpillar abundance (Liebhold and Elkinton 1988, Tinbergen and Dietz 1994). Here, we used large plastic funnels (25 cm in diameter) fitted with permeable fabric at the mouth to collect frass. Each collector was hung under the canopy, 1 m from the trunk and 3 m from the ground. Frass was collected from 17 April to 18 June 2019 and each collector was emptied at intervals with a maximum of 3 d in between, with 17 frass samples collected per tree individual. The samples were manually sorted to remove debris using a compound microscope with 8× magnification to identify the frass, then dried at 40°C for 24 h and subsequently weighed. Thereafter, we calculated the frass fall as grams of frass per square meter per day (Visser et al. 2006).

Temperature data

In order to document the ambient temperature in the two environments, 13 temperature loggers (iButton Thermochron 8K, accuracy of $\pm 0.063^\circ\text{C}$; Maxim Integrated Products, San Jose, CA, USA) were placed in each site (rural and urban), on representative trees and shaded from direct sunlight (see Appendix S2: Fig. S1). Ambient temperature was logged every 60 min, from 31 March to 16 June 2019. One of the rural loggers failed throughout the study period and thus did not provide data.

Statistical analyses

All statistical analysis was conducted using R version 3.5.2 (R Core Team 2018).

Generalized linear models (GLMs) and generalized linear mixed models (GLMMs), using the *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017), were used to analyze the effects of environment (urban/rural) and tree species' origin (native/nonnative) on bud burst, tree dwelling invertebrate abundance,

flying insect abundance, frass peak date, and total frass amount over the sampling period. In addition, we tested the difference between the environments in ambient temperature using a GLMM. We verified model assumptions (normality of model residuals and variance homogeneity) by inspecting model residuals and checked for over-dispersion and outliers using the function *testResiduals* of the *Dharma* package (Hartig 2020). When a response variable did not show equal variances, we corrected for this by modeling individual variance and adding it as weights, using the *varIdent* function of the *nlme* package (Zuur et al. 2009). Distributions were selected to best match the type of data: Poisson distribution was assumed for count data and Gaussian for continuous variables, but in one case count data was log-transformed in order to be analyzed using functions requiring Gaussian distribution (*gls* function, *nlme* package), to enable the correction of variance heterogeneity as specified above. *P* values were obtained with function *Anova* (package *car*) on final models using Type III Wald chi-square tests, with degrees of freedom estimated using the Satterthwaite method. For all GLMMs, random factors were estimated as positive.

We analyzed if timing of bud burst (day number) depended on environment type (urban/rural), using a GLM (Gaussian distribution) with environment, tree species and the interaction term between tree species and environment included as fixed factors. To analyze the effect of tree species' origin on bud burst in urban parks, we used a GLMM (Gaussian distribution) with origin as a fixed factor and species and park as random intercepts to account for the nonindependence of tree individual of the same species and from the same park. We analyzed the effects of environment on tree dwelling invertebrate abundance with a GLM, with invertebrate abundance (number of individuals) pooled over the three sampling occasions as response variable and environment, tree species and their interaction as fixed factors. The nonsignificant interaction between environment and tree species was removed from the final model. A quasi-Poisson distribution was used to account for overdispersion of the data. A GLMM (Poisson distribution) was used to analyze the effects of tree origin on tree dwelling invertebrate abundance in urban parks, with tree species and park as random intercepts.

The sticky-trapped flying insects were pooled from the three sampling occasions per tree, prior to analysis. To analyze if flying insect abundance depended on environment, we first used a GLM with number of individuals as a response variable, and environment type (urban/rural), tree species, and their interaction as fixed factors. However, inspection of model residuals showed that variance was not equal between environments. We therefore constructed a generalized least squares model (GLS, *nlme* package) with individual variance modeled as weights to account for this, since the GLM function does not have the *varIdent* function to easily create and apply such weights. The *anova* function was used,

together with F statistics, to generate P values. The model was run with a Gaussian distribution and log-transformed data, as GLS cannot take a Poisson distribution. For the effect of tree origin in flying insect abundance, we analyzed the urban data with a GLMM (Poisson distribution), assigning tree origin as fixed factor, and species and park as random intercepts.

The peak day of frass fall was defined as the sampling day with the highest mass value for each of the sampled trees. Data was analyzed with a GLM (Gaussian distribution) with the corresponding day number (days from 31 March) as response variable, environment type, tree species, and their interaction as fixed factors. The interaction was nonsignificant and therefore removed. To analyze the effect of tree species origin on frass peaks in urban parks, we used a GLMM with origin as a fixed factor and tree species and park as random intercepts, specifying a Gaussian distribution. To calculate total frass amount during the sampling period, all samples per tree individual throughout the period were pooled. We used a GLM (Gaussian distribution) to analyze differences of environment types on frass fall amount, with environment, tree species, and their interaction as fixed factors. As frass amount is an indirect measure that could be influenced by tree size, we initially included the tree diameter at breast height (DBH) as a fixed factor. DBH was subsequently removed as it proved nonsignificant and did not influence the results qualitatively, in order to simplify the model. The interaction was also nonsignificant and removed. To analyze the effect of tree

origin on frass fall amount in urban parks, we used a GLMM (Gaussian distribution) with species origin as fixed factor and tree species and park as random intercepts. The DBH was initially added and then removed as above. Both models analyzing frass amount were run with and without three outliers of extreme values originating from one large, rural oak. However, this did not change the results qualitatively and we present the results without the outliers for both models. To analyze the UHI, daily mean temperature was calculated for each iButton temperature logger and a GLMM was constructed, with temperature ($^{\circ}\text{C}$) as response variable, environment (urban/rural), day number, and their interaction as fixed factors, and logger ID as random factor intercept. The interaction proved non-significant and was removed from the final model. Estimated marginal means and their contrasts were calculated for all models using the *emmeans* package (Lenth 2021).

Hedges' g standardized unbiased effect size (Hedges and Olkin 1985) was calculated for all response variables in models where both tree origin and environment were tested, using the *esc_mean_sd* function (*esc* package). The effect size is a measure of the magnitude of the quantitative difference (i.e., biological effect) between the groups, and was used to descriptively compare the standardized differences depending on origin and environment (Nakagawa and Cuthill 2007, Kelley and Preacher 2012). An effect size value of 0.5 can be considered to indicate a medium effect and a value of 0.8 or above a large effect (Cohen 1992).

TABLE 2. Results of statistical analysis on environmental effects.

Response variable	Estimate	SE	χ^2	F	df	P	Hedges' g
Bud burst (day number), $N = 39$							
Environment (urban/rural)	-6.140	± 0.833	10.058		1,31	0.002	-1.257
Species			46.600		3,31	<0.001	
Environment \times species			8.584		3,31	0.035	
Abundance of tree-dwelling invertebrates (number), $N = 35$							
Environment (urban/rural)	1.390	± 1.750	0.632		1,30	0.427	0.252
Species			7.826		3,30	0.050	
Environment \times species			1.510		3,27	0.680	
Abundance of flying insects (number), $N = 35$							
Environment (urban/rural)	0.685	± 0.197		8.223	1,27	0.008	0.881
Species				1.123	3,27	0.357	
Environment \times species				3.171	3,27	0.040	
Frass peak day (day number), $N = 30$							
Environment (urban/rural)	-2.424	± 3.515	0.475		1,27	0.491	-0.250
Species			10.959		2,27	0.004	
Environment \times species			2.461		2,25	0.292	
Frass abundance (g), $N = 30$							
Environment (urban/rural)	-0.037	± 0.152	0.136		1,26	0.712	-0.032
Species			14.288		2,26	<0.001	
Environment \times species			0.286		2,24	0.867	

Notes: The output of all statistical models, including Hedges' g standardized unbiased effect size, model estimates and the corresponding standard error (SE) for tests of environmental effects (urban and rural environment). N denotes total sample in each model and df are from model tests (*Anova* and *anova* functions). Positive values of model estimates and Hedges' g indicate higher values for the urban site compared to the rural, while negative values indicate the opposite. Estimates are the contrasts of estimated marginal means. Significant results ($P < 0.05$) are shown in boldface type.

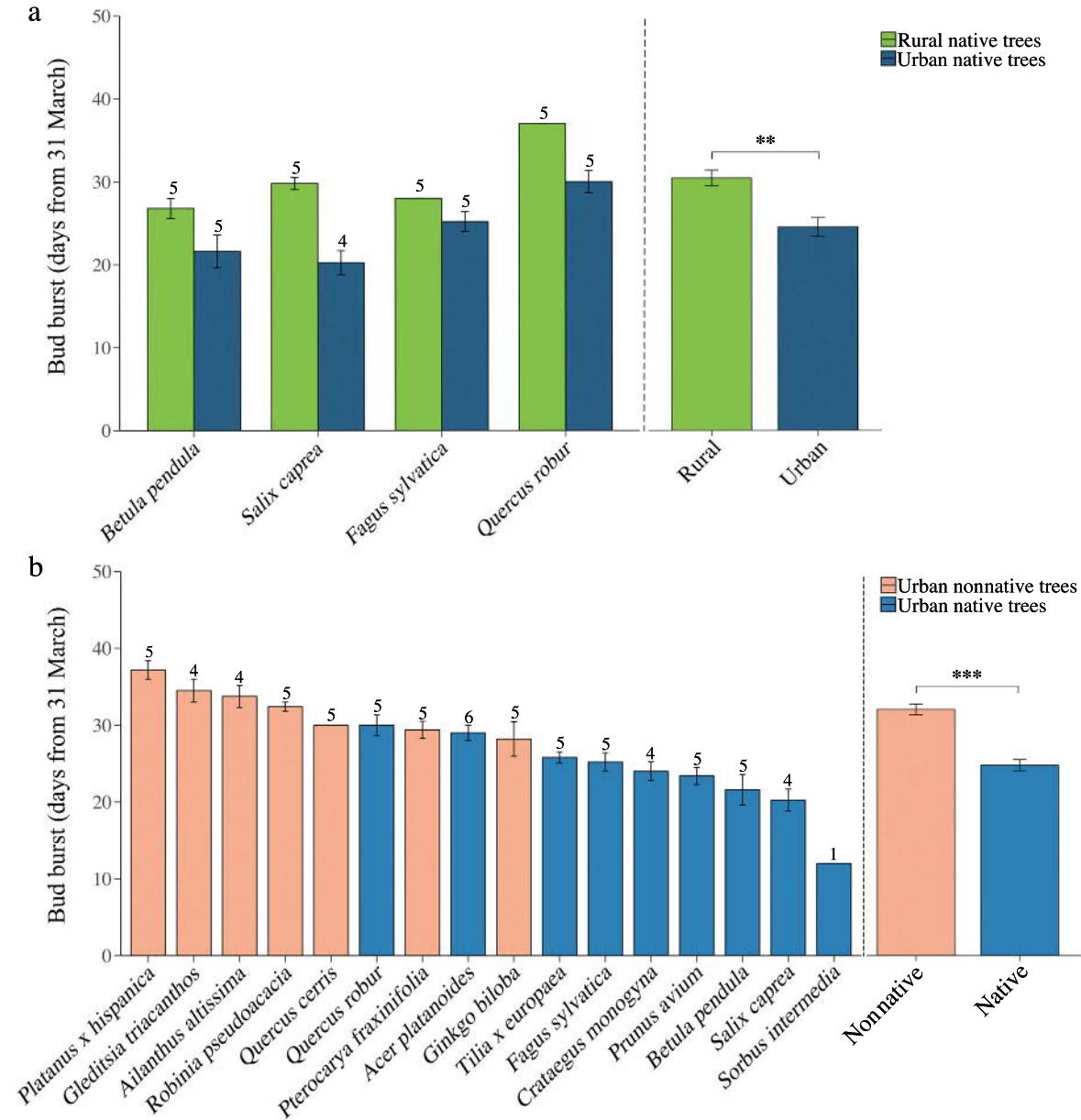


FIG. 3. The phenology of native and nonnative tree species. Day number (days from 31 March) of bud burst for tree species depending on (a) environment (urban/rural) and (b) species origin (native/nonnative). The two right-most bars in panels a and b show mean values for per group (native/nonnative). Significance levels are indicated by asterisks (** $P = 0.01-0.001$, *** $P < 0.001$). The bars show mean \pm SE of raw data; numbers above the error bars denote the number of tree individuals surveyed per species. Note that for *Quercus cerris* and rural *Fagus sylvatica* and *Quercus robur* no error bar is visible as all individuals were recorded to have reached bud burst on the same day, respectively. For Swedish whitebeam (*Sorbus intermedia*), only one individual was surveyed due to a lack of mature, representative individuals.

RESULTS

An analysis of the local tree data base of publicly managed areas revealed that of the 5,521 trees situated within the five city parks studied, nonnative species accounted for 23% of all tree individuals, varying between 12% and 46% in the parks. In terms of unique species, nonnative trees accounted for 73% of the total

157 species found within the parks, varying between 58% and 70%. The 16 species included in our study represented 59% of all tree individuals present in the parks. Out of the 114 nonnative species present, the seven included in the study accounted for 16% of the nonnative tree abundance. The nine native species accounted for 73% of the total native abundance, consisting of a total of 36 species. Note that seven species in the tree

TABLE 3. Results of statistical analysis on origin effects.

Response variable	Estimate	SE	χ^2	df	<i>P</i>	Hedges' <i>g</i>
Bud burst (day number), <i>N</i> = 73						
Origin (nonnative/native)	8.000	±1.788	20.014	1,68	<0.001	1.666
Abundance of tree-dwelling invertebrates (number), <i>N</i> = 38						
Origin (nonnative/native)	-7.780	±2.470	15.381	1,34	<0.001	-1.372
Abundance of flying insects (number), <i>N</i> = 37						
Origin (nonnative/native)	-27.300	±11.200	7.817	1,33	0.005	-0.947
Frass peak day (day number), <i>N</i> = 25						
Origin (nonnative/native)	-9.933	±3.399	8.542	1,20	0.003	-1.252
Frass abundance (g), <i>N</i> = 25						
Origin (nonnative/native)	-0.118	±0.147	0.650	1,20	0.420	-0.130

Notes: The output of all statistical models, including Hedges' *g* standardized unbiased effect size, model estimates and the corresponding SE for tests of tree species origin effects (only urban environment). *N* denotes total sample in each model and df are from model tests (*Anova* and *anova* functions). Positive values of model estimates and Hedges' *g* indicate higher values for nonnative trees compared to native, while negative values indicate the opposite. Estimates are the contrasts of estimated marginal means. Significant results are shown in boldface type.

data base were only classified to a family level and their origin could therefore not be determined. Additionally, given the heterogeneity of urban green space stewardship and management (Aronson et al. 2017), while this analysis encompasses the full park tree composition, the city-wide occurrence of these tree species may vary.

Bud burst occurred significantly earlier in the urban environment compared to the rural one, with an average difference of 6.1 ± 0.83 d (estimated marginal mean \pm SE) between the native species occurring in both environments (Table 2). A significant interaction between environment and species was also found, with common oak (7.0 ± 1.34) and goat willow (9.6 ± 1.44) showing stronger responses than silver birch (5.2 ± 1.99) and European beech (2.8 ± 1.20). Species also differed in bud burst compared to each other, with silver birch being the earliest and common oak the latest (Fig. 3a). Within the urban environment, trees with a nonnative origin were significantly later to reach bud burst compared to native species (Table 3; Fig. 3b), with an average difference of 8.0 ± 1.79 d.

In total, 514 tree-dwelling invertebrate individuals were collected through shake sampling and 2,374 flying insects were caught using sticky traps. For tree-dwelling invertebrate abundance measured by shake sampling, no significant difference could be found between native trees in the urban and rural environments (Table 2). However, the native tree species sampled across the two environments differed significantly in tree dwelling invertebrate abundance, with birch having the highest numbers (14.7 ± 1.92) and oak the lowest (8.1 ± 1.42), while European beech and goat willow had intermediate levels (10.8 ± 1.64 and 10.9 ± 2.36 , respectively) (Fig. 4a). Furthermore, flying insect abundance measured with sticky traps, showed a significant interaction between environment and tree species, with the three species birch (41.4 ± 21.00), goat willow (125.7 ± 87.00), and beech (31.4 ± 15.68) showing larger differences between environments, with higher levels of insect abundance in the urban environment, while common

oak (-2.2 ± 8.37) did not show any difference. Flying insect abundance was also higher in the urban environment in general (Fig. 4b), while tree species by itself did not show a significant effect on flying insect abundance (Table 2). The origin of the urban trees proved to have a significant effect on the local invertebrate abundance, which was higher on native host trees compared to nonnative ones, both for tree dwelling invertebrates (Fig. 4c) and flying insects (Fig. 4d), with an average difference of 7.8 ± 2.47 tree dwelling invertebrates and 27.3 ± 11.20 flying insects.

The peak day of frass did not differ between urban and rural environments for the subset of native species sampled at both sites (Fig. 5a), but it did differ depending on tree species, with common oak on average peaking on day number 49.4 ± 2.95 , European beech on day 42.3 ± 3.09 and birch being the earliest with an average peak recorded on day number 35 ± 3.09 , counted from 31 March. A similar relationship was found in terms of frass amount, where environment type did not have a significant effect, while tree species differed strongly. Common oak had a higher frass fall (0.796 ± 0.091 $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) compared to that of European beech (0.381 ± 0.088 $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and silver birch (0.413 ± 0.091 $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). Within the urban environment, frass peak date varied between the nonnative species sampled (London plane and black locust) and the native (common oak, silver birch, and European beech), with the two nonnative host trees peaking on average 9.9 ± 3.40 d prior to the three native hosts (Fig. 5b). In terms of frass amount, species' origin did not have a significant effect.

We observed a significant UHI effect, consisting of a $1.4^\circ \pm 0.13^\circ\text{C}$ higher average daily temperature in the urban environment compared to the rural one (Appendix S2: Fig. S2). The temperature differed depending on date, but no significant interaction between environment and date was found (Table 4).

In all cases, tree species origin (native/nonnative) had higher absolute values of Hedges' *g* than the

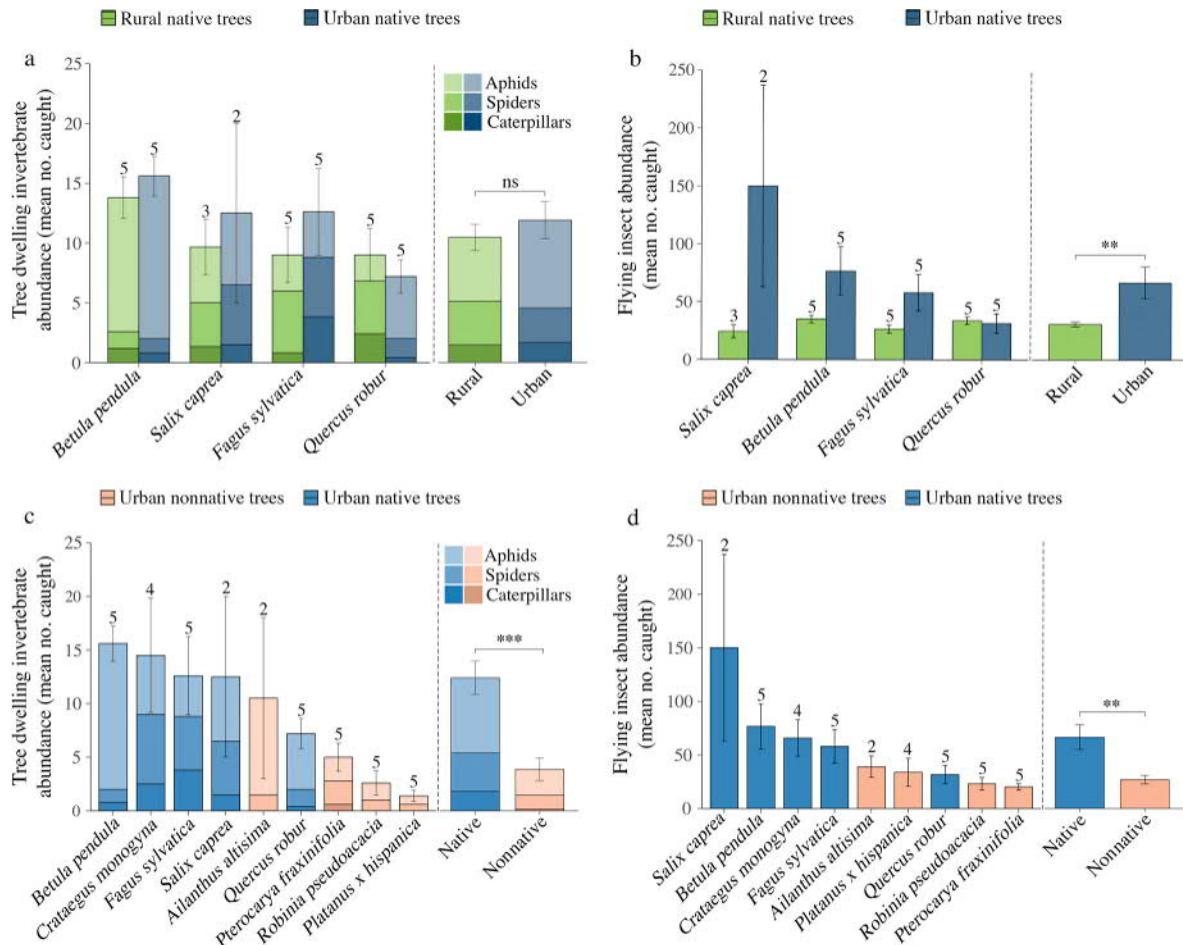


FIG. 4. Invertebrate abundance hosted by native and nonnative trees. The mean abundance (number of individuals caught) of invertebrates per tree species of (a) tree-dwelling invertebrates measured by shake sampling on urban and rural native trees, (b) flying insects caught by sticky-traps on urban and rural native trees, (c) tree-dwelling invertebrates depending on origin (native/nonnative urban trees), and (d) flying insects depending on site (native/nonnative urban trees). The two right most bars in each figure show mean values of all tree species combined per group. The differently shaded fields in panels a and c indicate the ratio of the three major taxonomic groups represented. Note that the caterpillar category contains larvae of some insect species outside of the Lepidoptera order (see *Methods* for details). Significance levels are indicated by asterisks (ns, not significant; ** $P = 0.01$ – 0.001 , *** $P < 0.001$). The bars show mean \pm SE of raw data; numbers above the error bars denote the number of tree individuals sampled per species.

corresponding effect of environment (urban/rural), indicating a stronger biological effect caused by species origin (Fig. 6). Notably, in all cases where both factors (origin/environment) were statistically significant for the same response variable, they showed opposite patterns, e.g., while urban areas had advanced bud burst, nonnative species showed a delayed bud burst. All statistically significant effects corresponded to a strong biological effect ($g > 0.8$), with bud burst depending on origin showing the strongest effect ($g = 1.666$).

DISCUSSION

Both urban environments and nonnative plant origin may cause altered phenology and decreased abundance of invertebrates, with possible consequences on both

biodiversity per se and ecosystem health (Dale and Frank 2018, Berthon et al. 2021). Here, we used several measures of invertebrate abundance in an urban environment in order to assess the effects of commonly planted nonnative trees on higher trophic levels within a city. In addition, for a subset of native species, we measured the invertebrate abundance in a rural forested control area to assess the impact of urbanization. We included temperature measures to assess the UHI effect on a city level, and phenology surveys to investigate differences depending on both environment and origin.

Lower abundance of invertebrates in nonnative trees

Tree dwelling invertebrates were on average three times more abundant on native tree species compared to

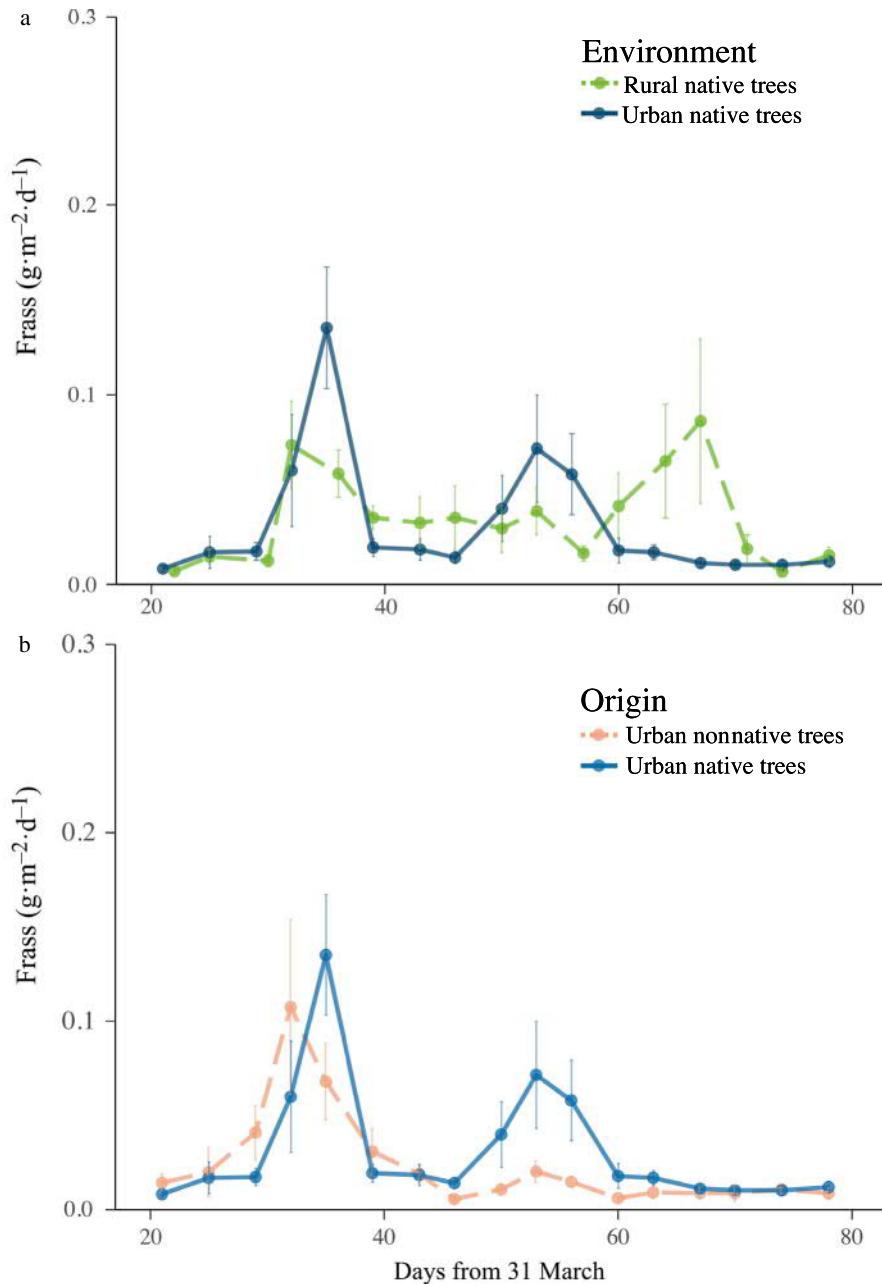


FIG. 5. Temporal changes in caterpillar abundance measured as frass fall. The amount of frass was measured from mid-April to mid-June (here in days from 31 March) from (a) three native tree species occurring in both the rural and urban sites (30 individuals total) and (b) three native and two nonnative species (25 individuals total) within the urban environment. The bars show mean \pm SE of raw data.

nonnative tree species within the five urban parks surveyed. Flying insects showed the same relationship and were more than twice as abundant on native tree species compared to nonnative ones. These results are in line with our expectations and previous studies finding a negative effect of nonnative plant species on invertebrate abundance (e.g., Burghardt et al. 2010, Narango et al. 2018) and show that this also applies to an urban Scandinavian environment. This response from local

herbivores and pollinators likely arises from the lack of coevolution with nonnative host plants, through novel phytochemical defense compounds, lack of cues, and potential phenological mismatches disrupting trophic relationships (Ehrlich and Raven 1964, Cappuccino and Arnason 2006, Bukovinszky et al. 2017). The lower abundances of tree dwelling invertebrates in nonnative tree species reported here appeared to be consistent across invertebrate groups, including spiders. However,

TABLE 4. Results of statistical analysis on temperature differences.

Response variable	Estimate	SE	χ^2	df	<i>P</i>
Temperature (°C), <i>N</i> = 1950					
Environment (urban/rural)	1.357	±0.134	102.42	1,1945	<0.001
Day number			2708.09	1,1945	<0.001
Environment × day number			2.342	1,1944	0.126

Notes: The output of the statistical model, including model estimate and the corresponding SE for the test of the urban heat island (UHI) effect. *N* denotes total sample in each model and *df* are from model tests (*Anova* and *anova* functions). Positive values of model estimates indicate higher values for the urban site compared to the rural. The estimate is the contrast of estimated marginal means. Significant results are shown in boldface type.

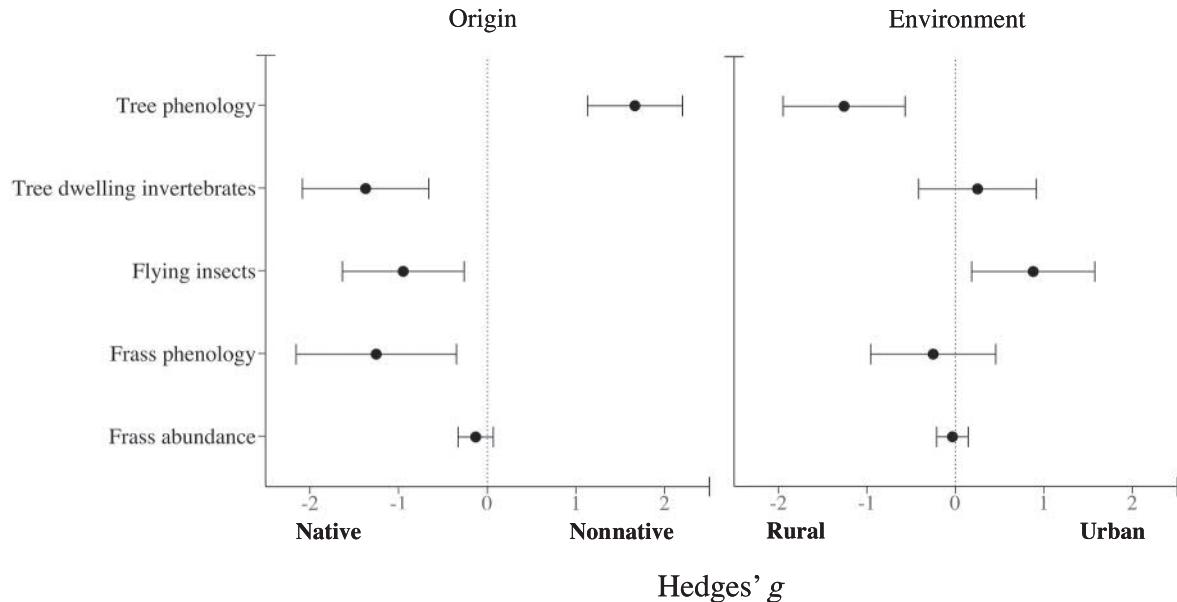


FIG. 6. The effect size for main factors. Hedges' *g* standardized unbiased effect size for main factors on all variables tested for both environment and origin. Positive values indicate higher values for the urban site compared to the rural, and higher values for nonnative trees compared to native, while negative values indicate the opposite. Horizontal bars display 95% confidence intervals.

this could not be explicitly tested, given the relatively limited sample sizes per group. While spiders are likely not directly affected by tree species origin, the lower local abundance of available prey may carry effects to higher trophic levels, such as spiders. Although the shake sampling found caterpillars to be very rare on nonnative trees, the frass fall collectors revealed no overall difference in caterpillar abundance between nonnative and native tree hosts. This discrepancy could potentially be explained by a larger subset of nonnative species being sampled by shake sampling than for frass or, more likely, it could be a consequence of tree species phenology, see Discussion: Phenological differences and large UHI effect.

Similar invertebrate abundance on native trees across environments

In contrast to our prediction, there was no apparent negative impact from urbanization on invertebrate

abundance, as the native trees hosted similar amounts of tree-dwelling invertebrates in the urban and rural environments and had a similar caterpillar abundance estimated from frass fall. However, we found an interaction between tree species and environment for flying insects, with three of the four species (silver birch, European beech, and goat willow) showing higher abundances in the urban environment, while one species (common oak) showed no such difference. As we did not classify the flying insects in terms of species, we cannot tell if these differences were driven by one, or a few, common species. However, as the literature is rather consistent in terms of invertebrate diversity being lower within cities (e.g., Faeth et al. 2011, Piano et al. 2020), the "urban exploiter scenario" i.e., one or a few numerous species driving the pattern, is a plausible explanation. On a superficial basis, urban samples did appear to be dominated by one or a few species belonging to the family Culicidae (i.e., mosquitoes). Three of the five parks contain bodies of water, which could specifically increase the local abundance of

flying insects, such as Culicidae (Bentley and Day 1989). Studies have also shown that the increased temperature of cities can drive the abundance of herbivorous invertebrates in so-called “pest outbreaks” (Meineke et al. 2013, Dale and Frank 2018). Local increase of such species may have the potential to mask other negative urban effects on overall invertebrate abundance, at least on native trees.

Strong effects of tree origin in comparison to urbanization

Our findings indicate that nonnative tree species have a larger negative impact on invertebrate fauna than the urban environment per se, as revealed from the lack of major differences across environments for the native host trees and the generally larger effect sizes found for species origin, compared to environment. This suggests that nonnative vegetation, which is common in urban environments (in this case, 23% of the overall park tree assembly), may be an important underlying factor causing a general decline of invertebrates in urban environments. There are several other factors as to why invertebrate abundance may be lower in urban environments, such as artificial night light (Owens et al. 2020) and air pollution (Thimmegowda et al. 2020), yet in the present study these seem to be of less importance than vegetation composition. Furthermore, given that the urban vegetation differs in species composition to rural comparisons (van Kleunen et al. 2015), studies of urban effects on invertebrates could potentially be confounded by the effects of vegetation composition, specifically through the disproportionate dominance of nonnative plants in urban ecosystems. However, it is important to note that using the abundance of invertebrates to assess the impact of urbanization on biodiversity does not show the full picture, as abundance itself may partly be driven by a few urban exploiter species, and because cities typically have been founded in areas with naturally high productivity (Faeth et al. 2011, Meineke et al. 2013). Complementary studies, focusing on effects of tree origin on invertebrate community composition, are therefore much needed. Even so, abundance of invertebrates plays an important role, especially in the perspective of ecosystem function and bottom-up effects on higher trophic levels, such as insectivorous birds (e.g., Narango et al. 2018).

Phenological differences and large UHI effect

Our study focused on a single city of a relatively small size (300 000 inhabitants), paired with a single forest site. Certain urban effects, such as the UHI, are expected to be stronger in larger cities (Manoli et al. 2019). Therefore, the observed UHI effect was of a surprisingly large magnitude, averaging 1.4°C throughout the measuring period, given the city’s size and that all temperature loggers were located within forested parts of parks. In comparison, European cities with over 1 million inhabitants

have an average UHI effect of 2.0°C (Peng et al. 2012). Given the observed UHI effect, it was not surprising to find earlier bud burst of the native trees in the warmer urban environment. Interestingly, we also found a significant difference between native and nonnative species within the city, with nonnative species being on average 8 d later to reach bud burst compared to native species. Again, this difference was larger in magnitude than the one observed for native trees across the urban and rural environment (6 d difference). Other studies have found varying patterns in phenology between native and nonnative urban vegetation, e.g., Shustack et al. (2009) found that species nonnative to North America had an earlier phenology, although this was to a large extent driven by a single plant species (*Lonicera maackii*) native to temperate western Asia. Assuming that the phenology of plants is determined by temperature and day length, our results are not necessarily contradictory to those of Shustack et al. (2009), as the shift in phenology of nonnatives likely is caused by a difference in climate between the species’ native range and that of the environment it is introduced into. For example, both the black locust (*Robinia pseudoacacia*) and honey locust (*Gleditsia triacanthos*) originate from eastern and central United States, at comparatively southern latitudes to our study area. Moving a southern species north is likely to result in delayed phenological events compared to local native species, which are adapted to shorter day lengths and/or lower temperature and may require lower thresholds of these cues in order to reach bud burst (Ghelardini et al. 2006, Linkosalo and Lechowicz 2006). Given the wide variety of origin of urban trees, this likely leads to a large heterogeneity in phenology, depending on local species composition.

Large-scale studies of urban plant phenology have had trouble identifying general urban effects on the onset of the growing season across cities, something that has been hypothesized to be caused by differences in vegetation composition and region (e.g., Dallimer et al. 2016, Li et al. 2019). Our results show that the origin of species can indeed affect phenology at a level comparable to the urban effect itself, possibly masking general effects of urban environments. Surprisingly however, the phenology of caterpillars (measured as the peak of frass fall) was earlier on the two nonnative tree species compared to the three native species within the urban environment. Although we only sampled five species for frass, and are thus limited in the conclusions we can draw, some interesting observations can be made: (1) the peak of frass on the two nonnative species sampled (London plane and black locust) occurred a few days before they reached full bud burst and (2) this peak is close in time to the two early native species sampled (silver birch and European beech). Although further research is required, a potential explanation could be that caterpillars emerge mismatched to the phenology of nonnative trees, following cues better matching the phenology of their native host species, such as silver birch or

European beech. The definition of bud burst used here requires over 50% of buds to burst, meaning that some leaves are available for caterpillars before trees reach full bud burst. Still, while the native species peaked in frass fall 1–2 weeks after bud burst, London plane and black locust peaked 5 and 2 d prior, respectively, suggesting a phenological mismatch. An alternative hypothesis is that caterpillars have a low assimilation rate of the nonnative leaves, potentially only being able to process the youngest leaves, resulting in high egestion followed by a premature death (Feeny 1970, Cappuccino and Arnason 2006, van Asch and Visser 2007). However, the present study is limited to a relatively narrow time window and selection of species and more in-depth studies of the specific caterpillar species, their life history, and the possibly novel defense compounds they encounter are needed to reveal underlying mechanisms. The potential explanations proposed here are only speculative given the lack of such information. Regardless of cause, the early frass peak explains the apparent contradictory results of a lack of difference in terms of caterpillar biomass (frass), and significantly lower caterpillar abundance from shake sampling. The shake sampling took place after the early frass peak in order to cover the generally larger peak of common oak (see *Methods*), which has been found to modulate breeding bird species relying on caterpillar as a food source for nestlings (Naef-Daenzer et al. 2000, Visser et al. 2006). The results therefore also suggest that, despite a lack of difference in overall frass amount, the nonnative species sampled likely have a low value as a food source for local breeding birds, which is in line with prior studies (Burghardt et al. 2009, Narango et al. 2018). Indeed, Great Tits (*Parus major*) breeding in the parks were, in the year the study took place, generally not matched to the frass peaks of the two nonnative tree species sampled (J. K. Jensen et al., *unpublished data*). Thus, not only can nonnative trees carry direct negative effects on higher trophic levels, but they may also induce a potential mismatch through their delayed phenology. Such mismatches have been suggested to take place in urban environments (Fisogni et al. 2020) and nonnative vegetation could specifically contribute.

Future directions and limitations

The present study was carried out to include some of the most common native and nonnative tree species and cover the phenologically important period of bud burst, which carries effects to higher trophic levels (Visser et al. 2006, van Asch and Visser 2007). However, it is important to note that population-level effects may change over the season and that the number of tree species and time window of our sampling is limited in this aspect. Although the use of multiple sampling techniques adds robustness to the assessment, this study can therefore not answer if or how the effects of urbanization and tree origin will continue over the season and through events such as flowering and fruiting. Similarly, phenological

events can vary between years. Future studies including a wider temporal sample, both within and across years, are needed to confirm the generality of the pattern observed here and, ideally, nonnative trees in rural environments should be included as a comparison. Because nonnative trees are often used particularly in urban settings, the latter may be difficult to achieve, as only small trees can be purchased and planted in an experimental design. Still, the effect sizes found (Fig. 6), suggest that the influence of tree origin has strong effects within the frame of the current study period and region. As the effects of urbanization are known to vary between regions (Li et al. 2019), it is important to note that the results represent only one city and one corresponding rural site in northern Europe. Future studies including multiple cities and incorporating urbanization indices could add more detail and inference to our novel comparison of urbanization and origin effects.

Implications for urban greening

Urbanization is projected to increase rapidly and a quarter of urban plant species are already nonnative worldwide (Aronson et al. 2014, United Nations 2018). As vegetation management is one of the few impactful and direct ways to manage urban nature, the implications of adding nonnative species to urban ecosystems, especially in large quantities, should be taken into careful consideration (Faeth et al. 2011, Berthon et al. 2021). Our results show that a selection of commonly used nonnative tree species have a shifted phenology and host a significantly lower invertebrate abundance compared to native species during a time period critical to breeding of insectivorous birds. Both these factors thus likely have negative effects on higher trophic levels, especially since nonnative species make up a large portion of urban trees (van Kleunen et al. 2015). Furthermore, the magnitude of the effect of tree species origin was similar to or larger than the overall urban effect sizes, in terms of both phenology and invertebrate abundance.

Nonnative species are often grouped together, yet their effects on local fauna may be species specific, e.g., in relation to how closely related nonnative species are to native species and time since their introduction (Brändle et al. 2008, Burghardt and Tallamy 2015), as well as to the specific resources they provide (Berthon et al. 2021). The same is true for native plants, where some keystone species or genera support biodiversity and ecological interactions to a higher degree than others (Narango et al. 2020). Although we did observe large differences between the studied tree species, the general effect of origin was still clear. Therefore, adhering to the precautionary principle, selecting native species for urban greening could be considered a simple rule of thumb, in particular, in green spaces where conservation or enhancement of biodiversity is a specific target (Berthon et al. 2021).

It is important to acknowledge that urban trees contribute to an array of ecosystem services other than

habitat for biodiversity, such as regulation of local temperature and air quality (Janhäll 2015, Ziter et al. 2019). Certain locations in the urban environment, e.g., streetscapes, are especially harsh and native species may struggle to establish and survive there (Sjöman et al. 2016). Therefore, nonnative tree species in Europe contribute to improve several aspects of the urban environment by providing a healthy canopy (Willis and Petrokofsky 2017, Riley et al. 2018). However, urban parks are generally much more benign environments and parks specifically harbor a large part of urban biodiversity (Nielsen et al. 2014). Therefore, a focus on retaining or increasing the proportion of native vegetation in parks and other green spaces will be crucial to secure future urban biodiversity and related ecosystem service, such as pollination, pest control, recreation, and nature experience for urban residents. As recent research has highlighted the differential contribution among native genera to critical ecological interactions (Narango et al. 2020), a promising development would be to use more detailed information on the functions of plant genera and/or species, and their potential contribution to urban ecosystem restoration and biodiversity conservation. Achieving this will require improved collaboration and understanding between researchers and practitioners in fields such as urban and plant ecology and green space design and management.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2491/full>

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Data (Jensen et al. 2021) are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.05qfttf32>