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Non-Native, Non-Naturalised Plants Suffer Less Herbivory Than Native Plants Across European Botanical Gardens

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ABSTRACT

Aim: The enemy release hypothesis states that the invasion success of non-native species is partly due to their escape from natural enemies, e.g., herbivores. Large-scale studies of herbivory using multiple species across multiple sites are needed to test the generality of herbivory release in non-native plants.

Location: Europe.

Methods: We carried out leaf-herbivory surveys from 2007 to 2021 in 15 botanical gardens ranging in latitude from 47°N (Switzerland) to 63°N (Norway) to investigate how herbivory levels differed between (i) native and non-native species, and (ii) native and non-naturalised or naturalised species.

Results: Overall, we found that herbivory levels were lower on non-native than native species. In addition, we found that non-naturalised plants suffered less herbivory than natives and that naturalised plants showed similar levels of herbivory to native plants.

Main Conclusions: We find broad support for lower herbivory of non-native plant species compared to natives. However, the stronger reduction in herbivory for non-naturalised plants suggests that herbivore release may be transient and less pronounced for naturalised non-native species that have become abundant and integrated into resident communities. This has implications for the management of naturalised non-native plants, which are performing well in their non-native ranges despite suffering comparable herbivory levels to native species.

1 | Introduction

Plants make up a large proportion of invasive species, and their impacts on native ecosystems include changing vegetation structure (Bezemer, Harvey, and Cronin 2014), altering soil properties (Weidenhamer and Callaway 2010) and affecting local hydrological processes (Weidlich et al. 2020). It is therefore important to understand the factors that limit the invasion success of non-native plants. The role of natural enemies has been widely studied because plant interactions with other organisms, such as herbivores, can influence the invasion success (Elton 1958; Huang et al. 2012; van der Putten et al. 2005). One of the key hypotheses investigated is the enemy release hypothesis, which states that the success of invasive species is in part due to the loss of their natural enemies in the new region (Darwin 1859; Keane and Crawley 2002). This hypothesis has received mixed support (Baso et al. 2024; Heger and Jeschke 2014; Qi et al. 2019; Siemann, Rogers, and Dewalt 2006) and may depend on factors such as the proximity of the invasive population to its native range (e.g., Tabassum and Leishman 2018). Tests of the enemy release hypothesis were often limited in terms of the number of species considered (e.g., Harvey et al. 2013; Lakeman-Fraser and Ewers 2013) and do not always compare natives with both non-native species that are naturalised and those that are not (van Kleunen et al. 2010). If reduced enemy damage, such as herbivory, is beneficial to naturalisation of non-native plants, we would expect naturalised non-native plants to suffer less leaf herbivory than both native and non-naturalised non-native plants.

Botanical gardens are a convenient study system for investigating general differences between native and non-native plants (e.g., Razanajatovo et al. 2015). Botanical gardens currently house around 30% of all plant species (Mounce, Smith, and Brockington 2017) and have long been used for scientific research (Donaldson 2009) and plant conservation (Pullaiah and Galbraith 2023). The distribution of botanical gardens around the world makes it possible to test hypotheses in multiple locations, which is useful for determining if trends exist on a broad scale or are dependent on local factors. Botanical gardens are also relevant in the field of invasion ecology because they have contributed to the introduction of invasive plant species around the world, including half of the world's most invasive species according to the IUCN (Boudjelas et al. 2000; Hulme 2011). At least 93% of the global naturalised alien flora is grown in botanical gardens globally (van Kleunen et al. 2018).

To assess the generality of herbivore release in non-native plants, we carried out leaf-herbivory surveys of 2752 species in 15 European botanical gardens to address the following questions: (i) Do non-native plants suffer less herbivory than natives across botanical gardens? (ii) Do naturalised non-native plants suffer less herbivory than natives and non-naturalised non-natives? To address these questions, we created statistical models within each botanical garden to observe the differences between non-native (or non-naturalised and naturalised) and native herbivory. Due to the wide variety in plant sizes, we included plant height in our analysis to account for the potential for larger plants to attract more herbivores (Rudgers and Whitney 2006). We carried out a meta-analysis using the subsequent effect sizes from each garden to observe differences in herbivory across all gardens. We then repeated analyses after excluding non-native plant species with native ranges in Europe, to rule out potential effects of close biogeographic origin and native range uncertainty of the European non-native plants.

2 | Materials and Methods

2.1 | Garden Surveys

Surveys were carried out in the years 2007–2021 in 15 botanical gardens across Europe (Table S1; this and all subsequent supporting figures and tables can be found in Appendix S1), each during the summer; for a summary of methods see Figure 1. The botanical gardens spanned a latitudinal range from 46.95°N (Bern, Switzerland) to 63.45°N (Trondheim, Norway; Figure 2), and an elevational range of 5 m (Bremen) to 530 m (Bern; Table S1). Herein, individual surveys will be referred to by the botanical garden's location (Table S1). In each garden, as many species as possible (94–982 spp.) were randomly surveyed in the time available, with an effort to include a good proportion of native species. This approach was recommended by van Kleunen et al. (2014), who suggested that a greater number of species is preferable for generalised ecological studies than more frequent sampling of fewer species. Only plants growing outside were selected, as herbivores might not have had access to plants growing in greenhouses.

The following information was documented for each surveyed species: species name and family; status or origin (native, non-native to the respective country); plant growth form (grass, herb, shrub, tree, cactus); plant phenological stage (vegetative, flowering, fruiting); plant height (cm; measured with a measuring tape if less than 200 cm, estimated if greater than 200 cm); ground area covered by plant (cm^2); level of herbivory (see below). Plant height was included to account for the potentially confounding effect of plant height on herbivory levels, where larger plants may be more conspicuous and therefore more attractive to herbivores, though we acknowledge that other traits (such as leaf toughness) are likely to play a role in herbivory interaction once plant-herbivore contact has been made. The following databases were used to determine the native status of each species: the Online Atlas of British and Irish Flora (2022) for species in the UK; the Norwegian Biodiversity Information Centre (2020) for species in Norway; and Euro+Med (2006) for species surveyed in mainland Europe. Tree or shrub growth form was confirmed by checking Plants of the World (POWO 2022). There

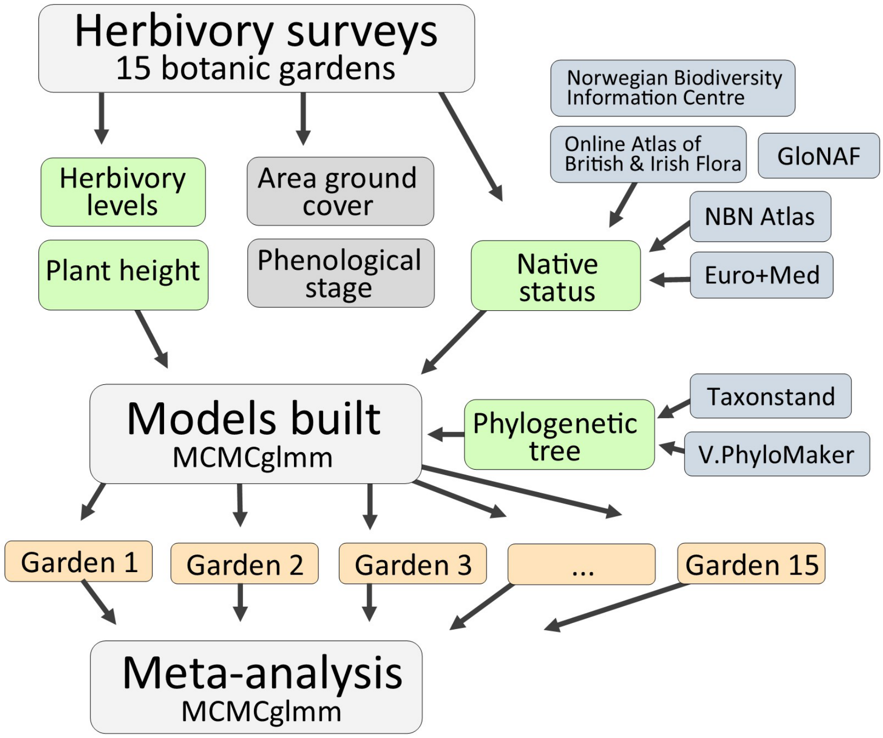

FIGURE 1 | Summary of survey and data analysis methods. Green boxes represent model input data, grey boxes represent surveyed information which was not used in models, and blue boxes represent sources of information/tools used.

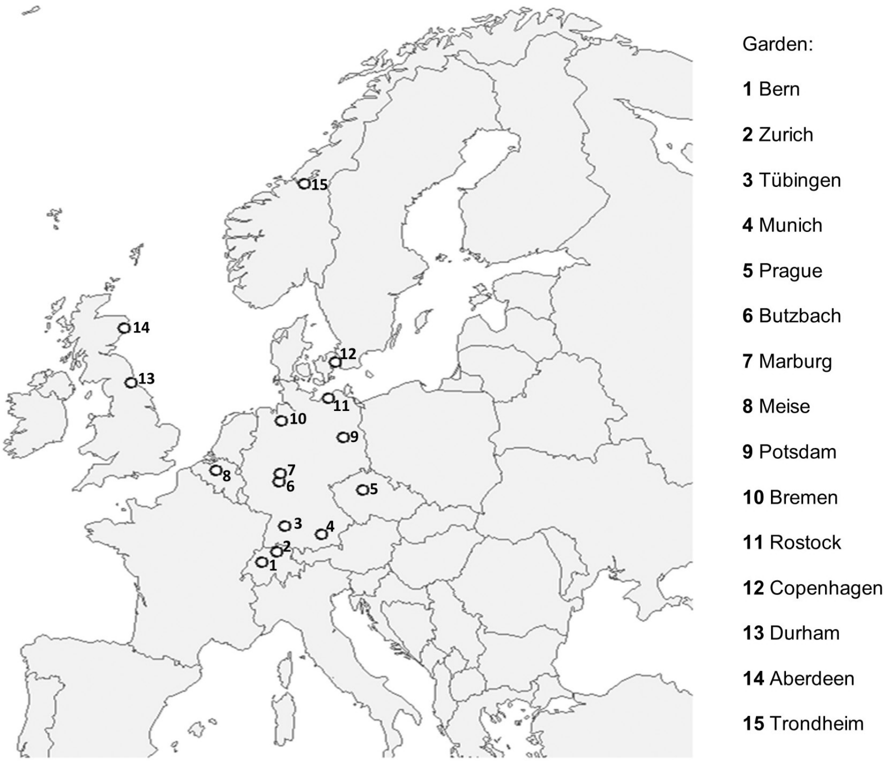

FIGURE 2 | Locations of the European botanical gardens used for surveys of herbivory in native and non-native plants.

were three methods employed to record the level of leaf herbivory. In Durham and Aberdeen, herbivory was measured as the proportion of a subset of leaves with herbivory damage, categorised into chewing, leaf mining or galling. The subset of leaves was chosen by randomly selecting two stems or branches (or one-quarter of leaves for rosette plants) and counting the total number of leaves, then counting the number of leaves with each damage type. If two stems or branches contained <10 leaves, more stems or branches were selected until the total number of leaves >10. In Trondheim, a similar method was applied but instead of sub-setting two stems or branches, 10 leaves were randomly chosen and the proportion of damage was recorded. For the other 12 gardens, herbivory was measured as the estimated percentage chewing leaf damage on the entire plant (Table S1). In 13 gardens, generally only one observation was made per species, but in Aberdeen and Durham an average of three observations were made per species.

A total of 5986 observations were made of 2752 species across all surveys. Some species were investigated in multiple gardens, but the vast majority of species (1796) were investigated in only a single garden (Figure S1). The common ivy *Hedera helix* was the most frequently investigated species, surveyed in 10 gardens. The most common growth form was herbs, making up 64% of all observations, followed by shrubs (21% observations), and trees (15% observations). In each group except grasses, there was a greater number of non-native than native species (Figure S2). There were only seven observations of cacti in total, all of which were non-native. The species surveyed belonged to 191 plant families. The most frequently surveyed were Rosaceae with 568 observations, followed by Asteraceae and Lamiaceae with 499 and 262 observations, respectively (Figure S3; for full list of families see File S1).

Generally, a higher number of non-native than native species were surveyed in each botanical garden, with the exception of Butzbach, Prague and Rostock. There was also a greater number of non-naturalised than naturalised species in all gardens (Figure 3 and Table S2). In surveys where different damage types were recorded (Durham, Aberdeen and Trondheim), the most common damage type was chewing, which was found in 75.7% of observations, followed by leaf mining (7.6% of observations) and galling (only 2.1% of observations; Figure S4). Mean herbivory levels and associated deviations for each garden can be found in Table S1.

2.2 | Phylogenetic Data

All species names were harmonised according to The Plant List using the R package 'Taxonstand' (Cayuela et al. 2012). Species, genus and family names from The Plant List were then used to create phylogenetic trees for each individual garden with the package 'V.PhyloMaker' (Jin and Qian 2019). These phylogenetic trees were incorporated into the models outlined below.

2.3 | Investigating Herbivore Release

Markov chain Monte Carlo generalised linear mixed models (MCMCglmms) were built using the R package 'MCMCglmm' (Hadfield 2010) to test for differences in herbivory between native and non-native species (henceforth referred to as 'herbivory models'). These models were chosen as they can analyse non-normally distributed data, complex effects (e.g., treating species as a random effect (see below) despite some species only occurring once in the data) and can incorporate phylogenetic trees to account for phylogenetic relatedness between species. MCMCglmms were carried out for each botanical garden individually due to the different sampling methods used. Only leaf-chewing was analysed, since this was recorded across all gardens whereas other forms of herbivory were only recorded in Durham, Aberdeen and Trondheim.

Native status was treated as a fixed effect. For each garden, one model was created with native status categorised as 'native' or 'non-native' (two levels) and a second model with 'native' species, and non-native species split into 'non-naturalised' and 'naturalised' (three levels). Here, we use 'non-naturalised' to refer to a non-native species that has not become established in its non-native range. These more specific categorisations were achieved using the Global Naturalised Alien Flora dataset (GloNAF; van Kleunen et al. 2019) and the National Biodiversity Network (NBN Atlas 2022) databases to determine the naturalisation status of non-native species. If a non-native species was not documented by these databases as being naturalised in the botanical garden's country, it was classified as 'non-naturalised'.

We included the measured plant height (cm) as a covariate to account for the potential for plant size to affect herbivore attraction to the plant. However, the conclusions were unaffected when we did not include plant height in the model; summaries of meta-analyses without plant height are presented at the end of Appendix S1 (Table S13). Phylogenetic trees specific to the garden in question (created using 'V.Phylomaker'; Jin and Qian 2019—see above) were treated as random effects. Species names were also chosen as random effects; although most species only had one observation per garden there were a few instances where multiple observations were made, and in Durham and Aberdeen an average of three observations were made per garden. Models where non-native status was split into non-naturalised and naturalised were repeated using non-naturalised species as baseline to allow for a direct comparison between these and naturalised species.

The priors and number of iterations used varied for each garden model and were altered to optimise model mixing; an uninformative prior was used where possible, but an expanded prior was necessary for twelve of the 15 gardens. Priors were chosen by inspecting iteration chains and posterior distributions of parameter estimates for good mixing and expected distributions. The number of iterations used was 400,000–800,000, with a burn-in of 20,000 and a thinning interval of 100 for all gardens (Table S3). The priors and iterations were consistent for each of the two models created per garden; for full model summaries see Tables S4–S6.

2.4 | Meta-Analysis Across Botanical Gardens

To investigate herbivory on native and non-native plants across all gardens, we extracted garden model effect sizes and associated errors and analysed them in a meta-analytical framework. 'MCMCglmm' (Hadfield 2010) was used to conduct meta-analyses. We used 500,000 iterations with an expanded prior to estimate the overall mean difference in herbivory between native plants and (i) non-native, (ii) non-naturalised and (iii) naturalised plants as intercept models (Table S7). A meta-analysis was also carried out separately to determine the difference between herbivory on non-naturalised and naturalised species across all gardens (Table S7), as the general meta-analysis only showed the trend for the difference between herbivory on

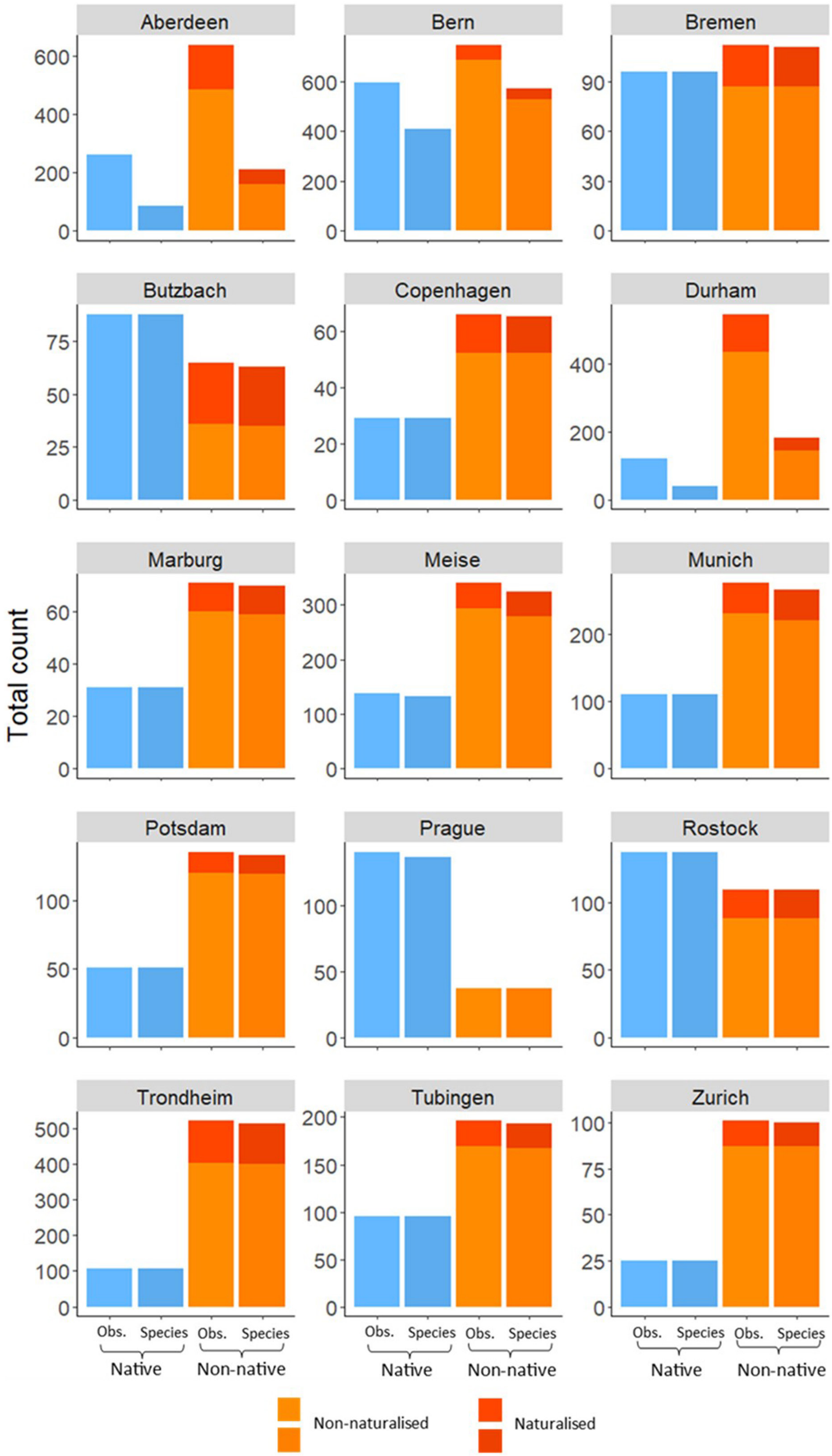

FIGURE 3 | The number of observations (Obs.) made in each garden compared to the number of species surveyed split into native and non-native species. Note different y-axis scales for each garden.

native and non-naturalised or native and naturalised species. Analyses were repeated using only data from 2007 to 2009 surveys to determine whether sampling method or surveying time period (e.g., Meineke et al. 2019) affected the observed results (Table S8); this was not repeated for 2021 data as there were only three gardens surveyed in this time period and therefore insufficient data for a meta-analysis.

2.5 | Investigating the Effect of Non-Native Species' Native Range

The level of leaf herbivory suffered by non-native plants may depend on their biogeographic origins: non-native plants that are geographically more distant from their native range may be more likely to escape herbivore enemies and suffer less herbivory (e.g., Tabassum and Leishman 2018). To assess whether the results of our study were influenced by non-native species' biogeographic origin, we repeated the above analyses using all native species but only non-native species whose native ranges are outside Europe. In addition, non-native plants that originate from somewhere in Europe might experience less enemy release than those with a native range that does not include Europe, and constraining the data by excluding species native to Europe allowed us to avoid this potential effect. We used the R package 'rWCVP' (Brown et al. 2023), which connects to the World Checklist of Vascular Plants (WCVP; Govaerts 2022), to obtain information about species' native ranges. Any species that was native to any country within Europe, including European Russia, was discarded. This left us with 4895 observations across all 15 gardens (for a full breakdown of sample and species numbers see Table S2). Using this subset of species, we repeated the analysis for the individual gardens (Tables S9–S11) and the meta-analysis across all gardens (Table S12). All data manipulation and analyses were carried out in R version 3.6.1 (R Core Team 2019).

3 | Results

3.1 | Do Non-Native Plants Suffer Less Herbivory Than Natives Across All Botanical Gardens?

The following results are deemed significant if credible intervals (CIs) calculated by the MCMCglmms do not cross 0. This corresponds with a pMCMC value < 0.05. Two analyses were carried out to investigate differences in leaf herbivory levels between native and non-native species. First, non-native species were treated as a single group and second, non-native species were split into two groups 'non-naturalised' and 'naturalised'. The meta-analysis across all gardens showed strong evidence of lower herbivory levels on non-native plants compared to natives (pMCMC = 0.004; Table 1a and Figure 4). When investigating herbivory levels on natives compared with those on non-naturalised and naturalised species, non-naturalised species showed lower herbivory than natives (pMCMC = 0.002), but there was only very weak evidence for lower herbivory on naturalised species (pMCMC = 0.099; Table 1b,c and Figure 4). Herbivory levels between non-naturalised and naturalised plants were similar (pMCMC = 0.399; Table 1d). For full meta-analysis summaries see Table S7.

TABLE 1 | Results of meta-analyses using 'MCMCglmm' to investigate, across 15 botanical gardens, the differences in herbivory between (a) non-native and native species, (b) non-naturalised and native non-native species, (c) naturalised and native non-native species, and (d) non-naturalised and naturalised non-native species. Bold pMCMC values indicate significant results (<0.05) where the 95% CI (credible interval) does not cross 0; for full summary see Table S7.

	Posterior mean (95% CI)	pMCMC
(a) Non-native versus native herbivory		
Intercept	−0.17 (−0.27 to −0.06)	**0.004**
(b) Non-naturalised versus native herbivory		
Intercept	−0.18 (−0.28 to −0.08)	**0.002**
(c) Naturalised versus native herbivory		
Intercept	−0.11 (−0.25 to 0.03)	0.099
(d) Non-naturalised versus naturalised herbivory		
Intercept	0.04 (−0.06 to 0.12)	0.399

These results were broadly unchanged for both the repeated analyses using only data from 2007 to 2009 (Table S8) and using the subset of data where non-native species with native ranges within Europe were removed (see Figure S6 and Tables S9–S12).

3.2 | Herbivory Differences of Individual Gardens

The models comparing native vs. non-native species revealed strong evidence for lower herbivory levels on non-native species in four of the 15 gardens (Butzbach, Durham, Munich, Potsdam; pMCMC < 0.05; Figure S5). Weaker evidence for the same trend was observed in a further four gardens (Bern, Bremen, Prague, Trondheim; pMCMC < 0.10). There was no evidence for greater herbivory levels on non-native species in any garden (Table S4). The models comparing native vs. non-naturalised and naturalised species revealed strong evidence of lower herbivory on non-naturalised species in three gardens (Butzbach, Durham, Trondheim) and on naturalised species in two gardens (Butzbach and Durham; pMCMC < 0.05) than on native species. Weaker evidence for lower herbivory on non-naturalised species was found in five gardens (Bern, Bremen, Munich, Potsdam, Prague) and for lower herbivory on naturalised species in three gardens (Meise, Munich, Tübingen; pMCMC < 0.10). There was no evidence of higher herbivory levels on non-naturalised or naturalised species compared to natives in any gardens. Differences in herbivory between non-naturalised and naturalised species were only observed in Trondheim, where naturalised species had higher levels of herbivory than non-naturalised species, but evidence for this was weak (pMCMC = 0.075; Figure 4, Figure S5, and Tables S5 and S6).

For the repeated analyses using only non-native species with native ranges outside Europe, individual garden models showed that there was strong evidence of lower herbivory on non-native species than native species for five gardens (Aberdeen, Bern, Butzbach, Durham, Potsdam; pMCMC < 0.05; Figure S6a

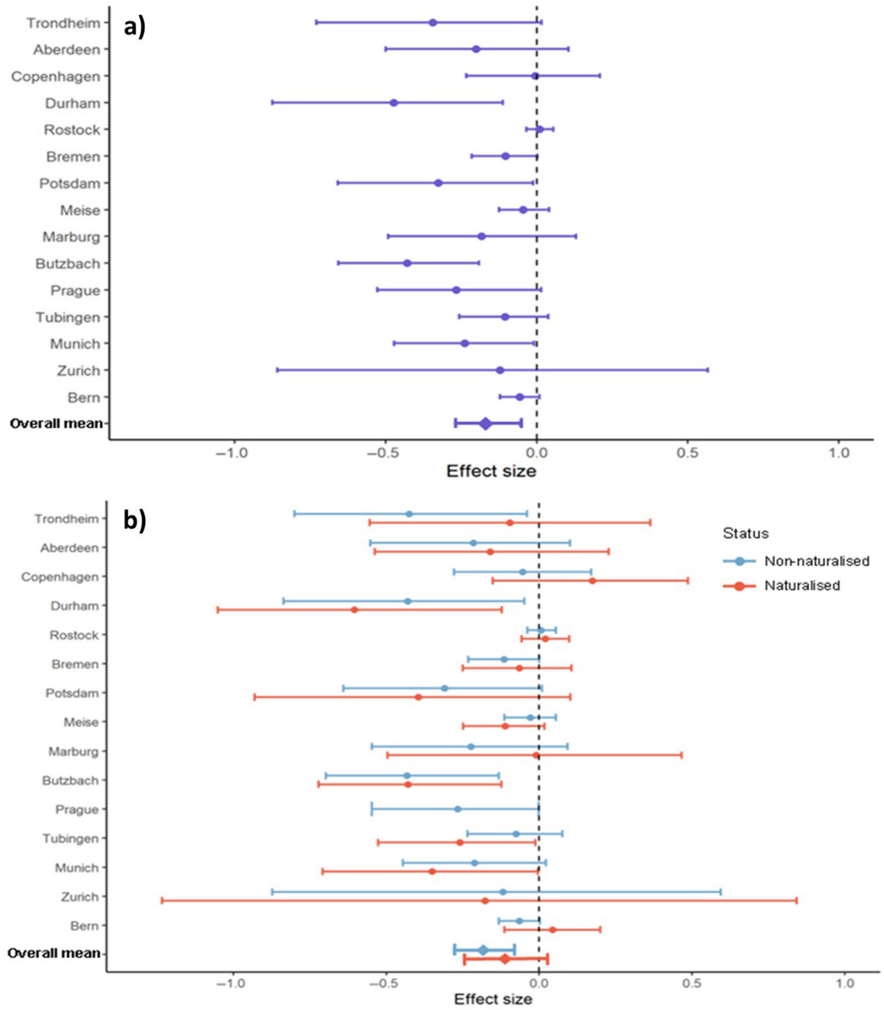

FIGURE 4 | Effect sizes of MCMCglmms for 15 botanical garden surveys comparing herbivory levels on (a) native and non-native plant species and (b) native and non-native plant species [split into non-naturalised (blue) and naturalised (red)]; ± 95% credible interval (CI). Prague did not contain any naturalised species. Overall means in bold show mean effect sizes across all gardens ± 95% CI: (a) non-native species herbivory (pMCMC = 0.005, CI did not cross 0); (b) non-naturalised species herbivory (pMCMC = 0.001; CI did not cross 0) and naturalised species herbivory (pMCMC = 0.08; CI crossed 0). Mean effect sizes were calculated using a meta-analysis with MCMCglmm. Negative effect indicates lower herbivory levels on non-native species and positive effect indicates higher herbivory levels on non-native species. Gardens are listed by latitude from most northern (Trondheim) to most southern (Bern).

and Table S9) and weaker evidence for a further three gardens (Meise, Munich, Prague; $p < 0.10$). There was lower herbivory on non-naturalised species in three gardens (Aberdeen, Butzbach, Potsdam), with weaker evidence of this same trend in a further four gardens (Bern, Bremen, Durham, Prague), and lower herbivory on naturalised species in five gardens (Aberdeen, Butzbach, Meise, Munich, Tübingen; Figure S6b and Table S10) with weaker evidence in one garden (Prague). There was weak evidence that herbivory on naturalised species was higher than natives in one garden (Copenhagen). When herbivory of non-naturalised species was compared to herbivory of naturalised species, there was only weak evidence that herbivory was lower on naturalised species in one garden (Tübingen; Table S11).

Plant height was included as a covariate to account for the potentially confounding effects of plant size on herbivory levels. Height was found to affect herbivory levels in six gardens, five of which (Bremen, Copenhagen, Durham, Marburg, Trondheim) showed that taller plants had greater levels of herbivory and one of which (Aberdeen) showed that taller plants had lower levels of herbivory.

4 | Discussion

4.1 | Herbivory on Native and Non-Native Plants

The overall lower levels of leaf herbivory on non-native than native species across all gardens supports the idea that enemy release is a general phenomenon occurring at multiple locations across Europe, although some gardens showed no significant differences in herbivory levels between native and non-native species. We found an overall difference in herbivory both when using the entire dataset and when restricting the non-natives to non-European species, which shows that inclusion of non-native species from biogeographic regions closer to the observation sites did not dilute the observed herbivore release. Evidence for the generality of enemy release was also found in meta-analyses carried out by Liu and Stiling (2006) and Xu et al. (2021), who combined data from multiple datasets and reported overall lower levels of herbivory on non-native than native species. However, to our knowledge this is the first study to collect directly comparable data across multiple sites to investigate herbivore release.

Reduced herbivory levels were observed on the non-naturalised subset of non-native plants, and it is therefore likely that these species have moved outside the range of their native herbivores. Enemy release can depend on several factors. For example, generalist herbivores are more likely to eat non-native plants than specialist herbivores (Brian and Catford 2023), so enemy release may be more likely to occur when there are a greater number of specialist herbivores in the non-native range. Non-native plants may also suffer greater levels of herbivory if they are more closely related to native species (Harvey et al. 2013). However, we incorporated phylogenetic trees in our statistical models so either (i) the non-naturalised non-native species in this study are not closely related to the native species generally, or (ii) phylogenetic relatedness has not affected the reduction in herbivory on non-native species.

While non-naturalised species showed overall lower levels of herbivory than natives, this was not observed for naturalised species. As naturalised species are more abundant in the local community, they may have accumulated more herbivores than non-naturalised species to which native herbivores have not yet adapted. However, it is uncertain whether this means that there was a greater abundance of the same herbivore at naturalised plants or a greater number of herbivore species. Time since introduction has been linked to enemy release; for example, Santamaría et al. (2022) found that the invasive algae *Caulerpa cylindracea* benefitted from enemy release initially but within a decade was highly consumed by the dominant native herbivorous fish *Sarpa salpa*. If we assume that naturalised species are more likely to have been introduced longer ago (Mbobo et al. 2022), these results agree with our finding that naturalised species had higher herbivory levels than non-naturalised species. Similarly, Gruntman et al. (2017) reported that older non-native populations of *Impatiens glandulifera* suffered herbivory levels comparable to that of native populations. Several other studies, however, detected lower herbivory on naturalised than non-naturalised species (Cappuccino and Carpenter 2005; Huang et al. 2020; Jogesh, Carpenter, and Cappuccino 2008). One explanation for such a trend is that reduced herbivory contributes to the naturalisation of species (Huang et al. 2020). However, we suggest that our results could be due to the higher abundance of naturalised species. Although fewer naturalised species were surveyed, there are likely to be a greater number of individual plants available as they are generally more widespread than non-naturalised plants which cannot form self-sustaining populations (Divíšek et al. 2018). Therefore, herbivores may recognise naturalised plants more readily as food sources.

The two opposing trends of lower levels of herbivory on either naturalised species (Cappuccino and Carpenter 2005; Huang et al. 2020; Jogesh, Carpenter, and Cappuccino 2008) or non-naturalised species (this study) call for further research to shed light on the interactions between non-native plants and herbivores in the invaded communities. In particular, the potential influence of species abundance and time since introduction need to be investigated to determine the mechanisms behind the differences in herbivory levels in relation to naturalisation status.

4.2 | Implications for Non-Native Species Management

Our results have implications for the management of non-native species. Although our study took place within botanical gardens, where plant spread would be tightly controlled, gardens contribute large numbers of invasive species globally (Boudjelas et al. 2000; Hulme 2011). Determining which factors may influence species' success is therefore important even if these species have not yet 'escaped' the gardens where they are currently controlled. In our study, we have found support for herbivory release of non-naturalised non-native species. However, naturalised non-native plants, which have become self-sustaining in their non-native range and are therefore more likely to become invasive (Richardson et al. 2000), suffer similar herbivory levels to native species. This suggests that herbivory, which may limit the success of some plants (Darwin 1859; Keane and Crawley 2002), has either increased over time since introduction or has not affected these species' ability to naturalise. Other means of limiting these species may therefore be necessary to prevent their spread and the subsequent potential negative impact that they may have on their invaded ecosystems. By carrying out surveys like those in this study, we can determine which species are not likely to be controlled by native herbivores in their non-native ranges, which can aid in focusing management efforts on species that can be controlled by natural enemies.

4.3 | Methodology

This is the first study to carry out herbivory surveys on such a large spatial scale within botanical gardens. As well as finding that naturalised non-native species do not show lower levels of herbivory, we have provided herbivory information for a large number of species which may be used in conjunction with future research into herbivory suffered by native and non-native species. Botanical gardens are an invaluable tool for investigating biological processes across multiple species and locations, and we hope that our study will stimulate more research into the interactions between plants and their environments using botanical gardens.

The data for this study were collected at different times; one dataset was collected in 2007–2009, and the second dataset in 2021. One caveat then is that herbivory levels may differ from year to year, or even exhibit overall trends through time. Meineke et al. (2019) found in herbarium specimens that herbivory has been increasing in the northeastern US over the past decades. However, we observed qualitatively the same differences in herbivory between native and non-native plants, and differences between naturalised and non-naturalised plants when focusing on the 2007–2009 data subset. This confirms that neither changes in herbivory over time nor methodological changes affected the herbivore release observed across gardens. Similarly, focusing our analyses on non-European non-natives also resulted in no marked change in the herbivory difference between native and non-natives plants, or non-naturalised and native plants. Our findings are therefore robust and do not depend on whether non-native plants of European origin were included or not.

5 | Conclusions

Our results suggest that the roles of herbivores in plant invasions may differ depending on the stage of the invasion process non-native plants are in, while non-naturalised non-native plants may not be greatly impacted by herbivory in their invaded ranges. This herbivory release may be beneficial prior to becoming naturalised, but may only be transient. Alternatively, non-naturalised plants may suffer less herbivory than natives, but this release plays no role in subsequent success: other factors may prevent their naturalisation despite lower herbivory. Further research into the drivers of enemy release is needed to understand how herbivory intensity and frequency, and its effects on non-native species, change over time. Prioritising management of emerging invasive plants could then benefit from an understanding of which species are least likely to accumulate herbivore enemies over time and will therefore continue to benefit from enemy release.

Author Contributions

M.K., K.I., V.V., J.D.M.S., and W.D. conceived the ideas and designed the methodology; K.I., V.V., S.P., S.B., D.E., Q.G., Z.J., J.M.J., J.J., A.K., J.K., T.K., T.L., D.M., J.R. and K.T. collected the data; K.I. analysed the data; K.I. and W.D. led the writing of the manuscript; all authors revised the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used in this study are available on Figshare at https://doi.org/10.6084/m9.figshare.c.7393852.v5.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.