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RESEARCH ARTICLE

Leveraging natural history collections to understand the impacts of global change

Testing enemy release of non-native plants across time and space using herbarium specimens in Norway

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Abstract

1. The enemy release hypothesis predicts that invasive plant success is in part due to the absence of natural enemies in the invaded range. However, few studies have assessed how enemy release may vary over time or space.
2. Norway has seen a large increase in non-native plant species over the past few decades. We used historical herbarium records to test whether 10 non-native plant species in Norway have suffered less from natural enemies (foliar herbivores) at different latitudes and over the past 195 years, compared to closely related (congeneric) native species.
3. We analysed over 2200 specimens over 26 species. Chewing herbivory was lower at higher latitudes for both non-native and native species. However, there was no evidence of change over time in overall chewing herbivory for either native or non-native species on average. Chewing herbivory of native and non-native species differed within the genera *Centaurea*, *Epilobium* and *Salix* across latitudes, and in the genera *Acer*, *Barbarea*, *Campanula* and *Epilobium* across time.
4. *Synthesis*: Our results suggest that enemy release is unlikely to facilitate these non-native plants in Norway since herbivory levels are similar between both non-native and native plant species. Herbivory of these non-native plants did not change over time, suggesting that they were quickly recognized as food sources by native herbivores. Lower levels of herbivory at higher latitudes suggest that herbivory is unlikely to limit non-native plants further north and that herbivory is likely to increase at higher latitudes as the climate warms.

KEYWORDS
climate change, herbaria, herbivory, insect, spatio-temporal, species interactions

1 | INTRODUCTION

Invasive species are one of the key components of global change today (IPBES, 2019), affecting ecosystem function world-wide. Impacts to ecosystems include changes in insect diversity and hybridization or competition with native species (Litt et al., 2014; Pyšek et al., 2012) and there is an increasing amount of research aiming to understand the drivers of invasive species success. Enemy release, or the movement of a species outside the range of its natural enemies, is one of the leading hypotheses used to explain invasive plant success. However, the mixed results from tests of this hypothesis in the literature (Fenner & Lee, 2001; Siemann et al., 2006;

Wolfe, 2002) suggest that enemy release is extremely system specific and cannot be applied to all invasive plant scenarios.

When assessing the evidence for enemy release in non-native plants, the phrase 'natural enemies' often refers to insect herbivory. Herbivory can have a great impact on the success of non-native plants (Elton, 1958; Huang et al., 2012; van der Putten et al., 2005), but is influenced by a wide variety of factors which makes comparing herbivory damage between native and non-native plants difficult. However, it has been documented that biotic interactions are spatio-temporally dynamic and various studies exist which investigate links between herbivory and either latitude or time (e.g. Cronin et al., 2015; Harvey et al., 2013; Schemske et al., 2009; Siemann et al., 2006).

The Latitudinal Biotic Interaction Hypothesis predicts that there are fewer biotic interactions, and therefore less herbivory, at higher latitudes (Schemske et al., 2009). Some studies of native species have shown evidence for this (e.g. Schemske et al., 2009) whereas others show little or no difference in herbivory at different latitudes (Adams et al., 2010; Kelly et al., 2008; a meta-analysis of the literature by Moles et al., 2011). Studies between herbivory and latitude for non-native plant studies are equally mixed. Cronin et al. (2015) found no difference in herbivory of non-native species at different latitudes, and a meta-analysis by Xu et al. (2021) found that herbivory of non-native species was consistently lower than native species but that there was no difference between different latitudes. Nunes et al. (2016) found mixed support for the Latitudinal Biotic Interaction Hypothesis, and their results are highly dependent on the study species and tissue type being investigated. However, Kambo and Kotanen (2014) found that herbivory declined sharply at higher latitudes for a non-native plant, resulting in enemy release at the northern limit of its range.

Temperature is a key factor limiting growth and reproduction of plants (Walther et al., 2009) and is strongly linked to latitude; climate warming therefore means that non-native species globally are predicted to move to higher latitudes (Walther et al., 2002), particularly nearer the poles where warming is occurring at a faster rate (Serreze & Barry, 2011). How herbivory varies with latitude is therefore of particular importance in countries situated at relatively high latitudes such as Norway, which is one of several Arctic-bordering countries and is already home to thousands of non-native plants (Norwegian Biodiversity Information Centre, 2020). This large number of non-native plants in Norway is predicted to increase in abundance even further (Bjørnøy et al., 2007) in part because human activity is increasing (Crowl et al., 2008), which is likely to result in a greater extent and volume of plant introductions. Within Norway, an increase in non-native plant numbers and their range shifting to higher latitudes means that there is likely to be an influx of new species to the vulnerable Arctic ecosystem (Alsos et al., 2015). Latitudinal studies are therefore valuable in determining how non-native plants and their enemies will respond at higher latitudes in the future, when higher latitudinal climate will resemble that of current lower latitudes. No studies investigating both latitude and herbivory have yet been carried out in Norway.

How herbivory of non-native plants changes over time is also key in determining the success of non-native plant spread in future. Herbivory of native plant species has increased over the last century (Meineke et al., 2019) but observed trends in non-native plants are so far mixed. It is proposed that low herbivory of non-native plants due to enemy release is followed by an increase in herbivory as herbivores adapt to their non-native hosts (Strong, 1974) or begin to recognize non-native species as a food source (Carpenter & Cappuccino, 2005). If this is the case, non-native herbivory may continue to increase until it is at a comparable level to that of native species. Some studies have observed this trend, and have found that herbivory gradually increases over several centuries until levels resemble herbivory of native species (Hawkes, 2007; Leather, 1986; Siemann et al., 2006; Strong, 1974). Other research, however, has found no relationship between time since introduction of a plant and herbivory levels (Carpenter & Cappuccino, 2005).

To determine how non-native plant herbivory changes over time, some studies substitute space for time and sample plants from their original introduction point (older samples) and at the edge of their introduced ranges (more recent samples) (e.g. Harvey et al., 2013; Siemann et al., 2006). However, it has been suggested that space-for-time substitutions lead to inaccurate patterns (Damgaard, 2019). This can be avoided by using natural history collections such as herbaria. Herbaria can be invaluable tools for tracking variation in plant–herbivore relationships over both time and space. Herbarium specimens and their associated records can span decades and are taken from a wide variety of locations, and can be used to provide information on herbivory at a point in time and space (Meineke et al., 2019). Sampling of multiple records can then be used to capture changes in the occurrence and level of herbivory suffered by plant species. By studying herbivory changes at higher latitudes and over time, we can begin to understand the role that herbivores might play in limiting the spread of non-native plants in these regions, and how temperature change in Norway under climate change, represented by latitude, may impact these interactions. Here, we used digitized herbarium records from the last 100 years in Norway to determine if herbivory differs between native and non-native plants (assessing enemy release), and whether differences between native and non-native plants have changed through time and with latitude.

Specifically, we sought to answer the following questions: (1) do herbivory levels differ between native and non-native species in Norway? (2) Do native and non-native plants both exhibit a decline in herbivory levels with increasing latitude (in line with the Latitudinal Biotic Interaction Hypothesis)? (3) How do herbivory levels of non-native plants change over time (using sample year as a measure of time)?

2 | MATERIALS AND METHODS

2.1 | Area of study

The study focused on two regions in Norway from which to select native and non-native herbarium specimens, originally to compare two latitudinal groups. However, as is mentioned under *Data analysis*, latitude was later treated as a continuous variable. The first region was classed as 'southeast' Norway with a latitude below 62°N and a longitude above 9°E (Figure 1). This area contains the capital city of Oslo and the surrounding region, where a large number of non-native species were first introduced (Norwegian Biodiversity Information Centre 2020), and therefore a large number of herbarium specimens (over 280,000 of vascular plants) have been sampled in this region (GBIF, 2022). The second region was classed as 'central' Norway, with a latitude of between 62 and 66 °N (Figure 1) and was included to increase the latitudinal range of the study in order to address Q2. This area contains the major city of Trondheim where again a large number of herbarium specimens have been collected (over 180,000 of vascular plants [GBIF, 2022; Speed et al., 2018]).

2.2 | Species sampling and selection

A group of 30 non-native plant species were selected with populations in both central and southeast Norway, the majority of which were classed as having a severe impact in Norway according to the Norwegian Biodiversity Information Centre (2020) alien species impact classification. To compare these non-native species with native species, therefore addressing Q1 of our research aims, these species were then matched with at least one congeneric native species, the exception being *Myrrhis odorata* which was matched with a confamilial native species *Anthriscus sylvestris*. From now on, *A. sylvestris* and *M. odorata* will be referred to as congeners, for simplicity. Congeneric species were chosen to allow comparison of native and non-native status while minimizing taxonomic bias, and to avoid the confounding of native status by phylogenetic differences between native and non-native species. Many species did not have sufficient samples for this study due to few older records and were discarded. This left a total of 26 species, 16 native and 10 non-native within 10 congeneric species 'sets' of trees and herbs from a range of Families (Table 1). All included species had sufficient records to allow herbivory rates to be analysed over a 100-year period, with some specimens dating back 200 years, and across a wide latitudinal range.

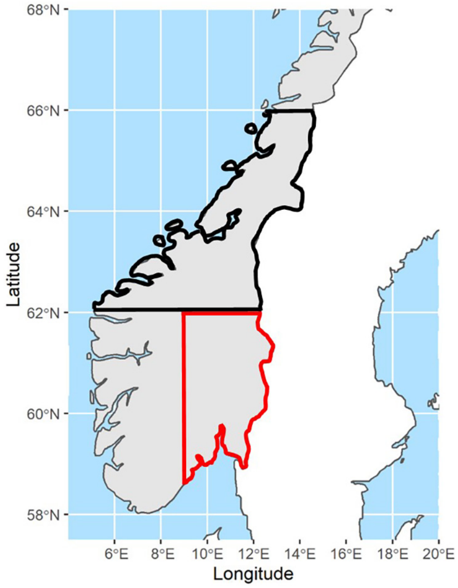

FIGURE 1 Two study regions in Norway. Red border = 'southeast' region. Black border = 'central' region

Occurrence records with accompanying herbarium images were downloaded for each species using the R package RGBIF (Chamberlain et al., 2020). Two sampling methods were used to select (a) recent records (since the year 2000) across different latitudes within Norway to address Q2 and (b) records from the previous 100 years in the 'southeast' of Norway to address Q3. Our sampling design was largely dictated by the availability of specimens for both native and non-native species. Specifically, while there were sufficient numbers of specimens available after the year 2000 in both regions (Figure 1) to assess the relationship between latitude and herbivory, the numbers of specimens available from earlier time periods in the central region were too low to assess sampling year and latitude simultaneously. Doing so would have led to a conflation of latitude and time, making it impossible to separate their effects. We therefore decided to focus sampling across the latitudinal gradient in both regions, constraining the time period to post-2000 (method a), and then sampling across the 100-year period in SE Norway only (method b), where representation of species specimens through time was optimal. For sampling method (a), up to 15 records were taken for each species after the year 2000 from each of the 'central' and 'southeast' regions (Figure 1), unless there were fewer than 15 photos in which case all photos within that category were used for analysis (Figure S1). This resulted in up to 30 photo specimens per species for the latitudinal study. For method (b), southeast records taken after the year 2000 (sampled in method (a)) were combined with samples from the following 20-year categories, again in the 'southeast' region: 1980–2000; 1960–1980; 1940–1960; 1920–1940; before 1920. For each species, up to 15 photo records were randomly sampled within each 20-year category resulting in up to 90 photo specimens per species in the sample year study. The use of 20-year categories provided us with relatively even representation of species throughout the 100-year period. All shortlisted non-native species were first recorded in Norway during the 1800s (Norwegian Biodiversity Information Centre 2020; Table 1). Identifying numbers for all sampled herbarium specimens can be found in File S1. Downloaded specimen images were from the following herbaria: Vascular Plant Herbarium, UiB (University of Bergen, 2022); Norwegian University of Science and Technology vascular plant herbarium TRH (Norwegian University of Science and Technology, 2022); University of Agder vascular plant herbarium KMN (University of Agder, 2022); Vascular Plant Herbarium, University of Oslo UiO (University of Oslo, 2022).

2.3 | Image analysis

To analyse herbivory rate, the image software 'ImageJ' with the plug-in 'Fiji' was used (Schindelin et al., 2012; Schneider et al., 2012). Most herbarium photos in this study were photographed with a ruler

TABLE 1 List of congener sets of native and non-native species used in this study, with year each non-native species was first observed in Norway according to the Norwegian Biodiversity Information Centre (2020) and native range (POWO, 2022)

	Non-native				
Native	**Species**	**First observed**	**Native range**	**Family**	**Growth form**
Acer platanoides	*Acer pseudoplatanus*	1870s	Central and western Europe	Sapindaceae	Tree
Anthriscus sylvestris	*Myrrhis odorata*	1820s	Central and western Europe	Apiaceae	Herb
Barbarea stricta	*Barbarea vulgaris*	1820s	Europe, northern Africa, central Asia	Brassicaceae	Herb
Campanula cervicaria *Campanula latifolia*	*Campanula rapunculoides*	1820s	Europe, central Asia	Campanulaceae	Herb
Centaurea jacea *Centaurea scabiosa*	*Centaurea montana*	1870s	Central & western Europe	Asteraceae	Herb
Epilobium collinum *Epilobium montanum*	*Epilobium ciliatum*	1860s	Northern Europe, North America, southern South America, central Asia	Onagraceae	Herb
Lonicera periclymenum *Lonicera xylosteum*	*Lonicera tatarica*	1880s	Central Asia	Caprifoliaceae	Herb
Populus tremula	*Populus balsamifera*	1870s	North America, eastern Russia	Salicaceae	Tree
Primula veris	*Primula elatior*	1880s	Europe, central Asia	Primulaceae	Herb
Salix caprea *Salix pentandra* *Salix triandra*	*Salix fragilis*	1834	North Caucasus	Salicaceae	Tree

measurement. Using this ruler as a guide, the image was overlaid with a grid, and each grid cell had an area of 625 mm^2 which gave a total of 240 grid cells across each specimen photo. This grid size was chosen as a compromise between a high grid cell resolution, for more accurately estimating proportion of each specimen with herbivory damage, and time constraints. If no ruler was present, the herbarium specimen labels were used to estimate scale. Each grid cell which contained part of a leaf was counted using the Fiji plug-in 'Cell counter', and all leaves in each herbarium photograph were counted regardless of size or position on the plant. Cells which contained each of the following types of leaf damage were then counted: 'Chewing', 'Galling', 'Leaf-mining' and 'Fungal' damage. Although galling, leaf-mining and fungal damage was not part of our analyses, the data are presented here for completeness.

2.4 | Data analysis

All analyses were done in the R environment (R Core Team, 2019). Negative binomial generalized linear mixed models (GLMMs) were built using the R package glmmTMB (Brooks et al., 2017) to assess the proportion of chewing herbivory damage between native and non-native species and in relation to (1) latitude and (2) year of specimen sample. Negative binomial GLMMs were chosen as model convergence was not possible when using other methods of binomial GLMM (e.g. the lme4 package Bates et al., 2015). Latitude and sample year were treated as continuous variables in all analyses due to relatively even spread of data across each delineated region/time period. Chewing was selected for analysis as this damage type was observed most frequently across samples (Figure 2). In each model, native status and either latitude or sample year were considered fixed effects and we included the interaction between native status and latitude/sample year. To account for non-independence between samples in a species and between species in a congeneric set, genus and species were included as nested random effects as we wanted to investigate overall trends between native and non-native species across the whole dataset. We did not include phylogeny in the model structure, as our study was designed to account for phylogenetic relatedness by selecting closely related congeneric species. Herbivory rates observed on records may also vary depending on the time of year which they were collected (Meineke et al., 2021). To account for this, we added day of year as a covariate in both models. Overdispersion was found in both models via investigation of model residuals using the package DHARMa (Hartig, 2016; Figures S2 and S3). To address this, a further observation-level random effect (individual sample ID) was added (Maindonald & Braun, 2007). To determine whether certain genera had a high influence over the effects of latitude/sample year, we re-ran the models, each time without one of the congener sets. We then inspected the change in model effect sizes compared to the original models with all congener sets. Spatial autocorrelation between specimens was assessed using a correlogram from the R package pgirmess (Giraudoux, 2013). Finally, negative binomial GLMMs were used to analyse proportion damage for each individual genus to assess single-species effects of latitude and sample year. For these models, latitude or sample year and their interaction with species were used as fixed effects, with a covariate of sample day of year. Individual sample ID was again used as an observation-level random effect to account for overdispersion.

3 | RESULTS

A total of 2224 herbarium record images were analysed, 1534 native and 690 non-native species records. Of this total, 1875 were sampled from southeast Norway and 349 from central Norway (Table S1). The earliest record was collected in the year 1821, and records ranged from a latitude of 58.59° to 66.18°N.

3.1 | Damage types

Of the four damage types assessed (chewing, mining, galling, fungal infection) chewing damage was observed the most frequently, present in over 75% of all native and non-native samples in all six time periods. The proportion of samples with fungal damage was lowest before 1920 (23.8% of native and 22.0% of non-native species) and highest after 2000 (38.3% of native and 32.0% of non-native species; Figure 2). Mining and galling were found in consistently low proportions of specimens. The proportion of samples with each damage type was similar across native and non-native species.

3.2 | Overall trends of chewing herbivory

3.2.1 | Latitude

There was strong evidence that the proportion of chewing herbivory damage on post-2000 herbarium records was lower at higher latitudes ($p<0.01$; Table 2). However, this effect size was small compared to variation in damage proportions across genera (*SD* = 0.564); at the lowest latitude of 58.59°N the model predicted 0.083 proportion chewing damage for native and 0.095 for non-native species, and at the highest latitude of 66.18°N the model predicted 0.045 proportion chewing damage for native and 0.047 for non-native species (Figure 3). There was no evidence of any difference between chewing herbivory of native and non-native species on average and no evidence of any

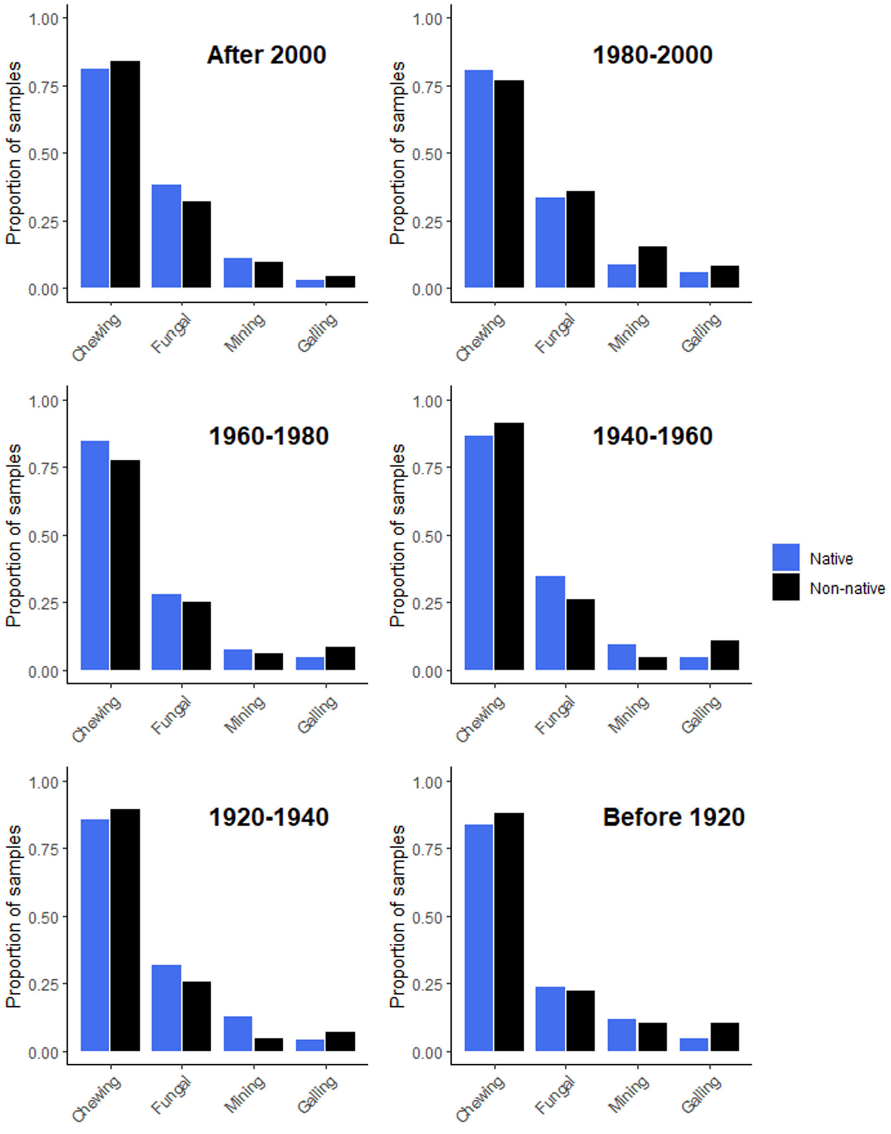

FIGURE 2 Proportion of herbarium samples with each damage type across all native and non-native plant species, split into year categories.

interaction between latitude and native status. There was strong evidence that removal of the genus *Campanula* resulted in a stronger negative relationship between chewing herbivory and latitude whereas the removal of *Anthriscus/Myrrhis* weakened evidence for this negative interaction further. The removal of *Centaurea* increased the difference between native and non-native chewing herbivory levels but evidence for this was weak. The removal of *Salix* had the biggest impact on results, creating a less strong positive relationship between chewing and day of year, and resulting in a stronger negative interaction between latitude and native status, so that latitude had a larger effect on non-native species (Figure S4; Table S2).

3.2.2 | Sample year

There was no evidence of chewing herbivory change with sample year ($p = 0.604$) and there was no evidence of a difference in chewing proportion between native and non-native species on average. There was no evidence of any interaction between sample year and native status (Figure 3; Table 2). The removal of *Barbarea* and *Salix* resulted in a stronger negative relationship between year and chewing herbivory levels and stronger evidence for this relationship, whereas the removal of *Campanula* resulted in this relationship becoming positive, although evidence for this was weak. The removal of *Centaurea* and *Salix* resulted in a greater difference between chewing on native and non-native species, but evidence or this did not differ greatly from the original model. The absence of *Salix* also resulted in a stronger positive relationship between chewing and day of year (Figure S5; Table S3).

3.2.3 | Day of year

In both latitude and year models, there was strong evidence of an increase in herbivory with day of year (latitude: slope = 0.277, $p < 0.001$; year: slope = 0.181; $p < 0.001$; Figure 4).

3.3 | Spatial autocorrelation

There was no significant spatial autocorrelation within the residuals of the negative binomial GLMMs as all Moran's I coefficients were close to 0 (latitude vs. chewing damage model coefficients range from 0.016 to −0.141; sample year vs. chewing damage model coefficients range from 0.029 to −0.045; Figure S6).

3.4 | Genus-specific trends of chewing herbivory

3.4.1 | Latitude

Strong evidence of lower levels of chewing herbivory at higher latitudes were found in *Acer* and *Barbarea*, with weaker evidence of this trend observed in *Anthriscus/Myrrhis*, *Epilobium* and *Lonicera*. Higher levels of herbivory at higher latitudes were found in *Salix*. Differences in chewing proportion between native and non-native species varied greatly among genera, with greater chewing on non-natives in *Centaurea* but greater chewing herbivory on natives for *Epilobium* and *Salix*. Only *Salix* showed evidence of a negative interaction between latitude and native status, whereby latitude, which had a positive effect on chewing damage, had a stronger effect on non-native species (Figure 5; Table S4). Four of the 10 genera showed an increase in herbivory with day of year (Table S4).

3.4.2 | Sample year

There was evidence of herbivory decreasing over time in *Centaurea* only, and there was no evidence of any increase in herbivory over time. Greater herbivory was observed on native species than non-native species for the genus *Anthriscus/Myrrhis*, whereas greater herbivory was observed on non-native species for the genera *Acer*, *Campanula* and *Epilobium*. The only evidence of interactions between sample year and native status was found in *Centaurea*, where sample year had a stronger effect on non-native species (Figure 6; Table S5).

4 | DISCUSSION

In this study, we aimed to determine whether enemy release is occurring on non-native plants by assessing chewing herbivory and its variation through time and space on non-native and native plants in Norway. First, we found little significant difference in chewing herbivory between native and non-native plants within each genus. All species groups were congeneric except for *Anthriscus sylvestris* and *Myrrhis odorata*, which are both in the same family, subfamily, tribe and subtribe (Apiaceae; Apioidea; Scandiceae; Scandicinae [Downie et al., 2000]). A link between phylogenetic relatedness and herbivory has been investigated by several past studies on herbivory levels of native and non-native species. These studies found that herbivory was lower in non-natives that were more distantly related to native species than those more closely related (Harvey et al., 2012; Hill & Kotanen, 2009; Pearse & Hipp, 2009). Pearse and Hipp (2009) concluded that biotic interactions are driven by leaf traits associated with phylogenetic relatedness. If true, this means that similar levels of herbivory between native and non-native congeners might be expected, particularly when concerning chewing herbivores, which may often be generalists (Vidal & Murphy, 2018) and might switch more readily from native to non-native food plants. However, we specifically chose closely related species to ensure that one of the main differences between each grouping was their native status.

Across species chewing herbivory rate was lower at higher latitudes, but we found no difference in the effect of latitude between natives and non-natives. These results contrast with much of the current literature which has frequently found that latitude has no effect on herbivory of non-native plants (Cronin et al., 2015; Moles

TABLE 2 Coefficients for negative binomial GLMMs determining the relationship between latitude/sample year and herbivory damage levels. Bold number indicate significant values ($p = <0.05$)

Latitude	Est.	SE	z	p
Intercept (native)	−2.640	0.212	−12.466	**<0.001**
Latitude	−0.174	0.064	−2.704	**0.007**
Non-native	0.145	0.153	0.949	0.343
Day of year	0.277	0.052	5.294	**<0.001**
Latitude: non-native	−0.031	0.100	−0.305	0.760

Random effects	SD	Variance
Genus	0.564	0.318
Species	0.292	0.085

Sample year	Est.	SE	z	p
Intercept (native)	−2.448	0.224	−10.936	**<0.001**
Sample year	−0.019	0.037	−0.518	0.604
Non-native	0.054	0.142	0.382	0.702
Day of year	0.181	0.032	5.743	**<0.001**
Sample year: non-native	−0.025	0.072	−0.341	0.733

Random effects	SD	Variance
Genus	0.555	0.308
Species	0.302	0.091

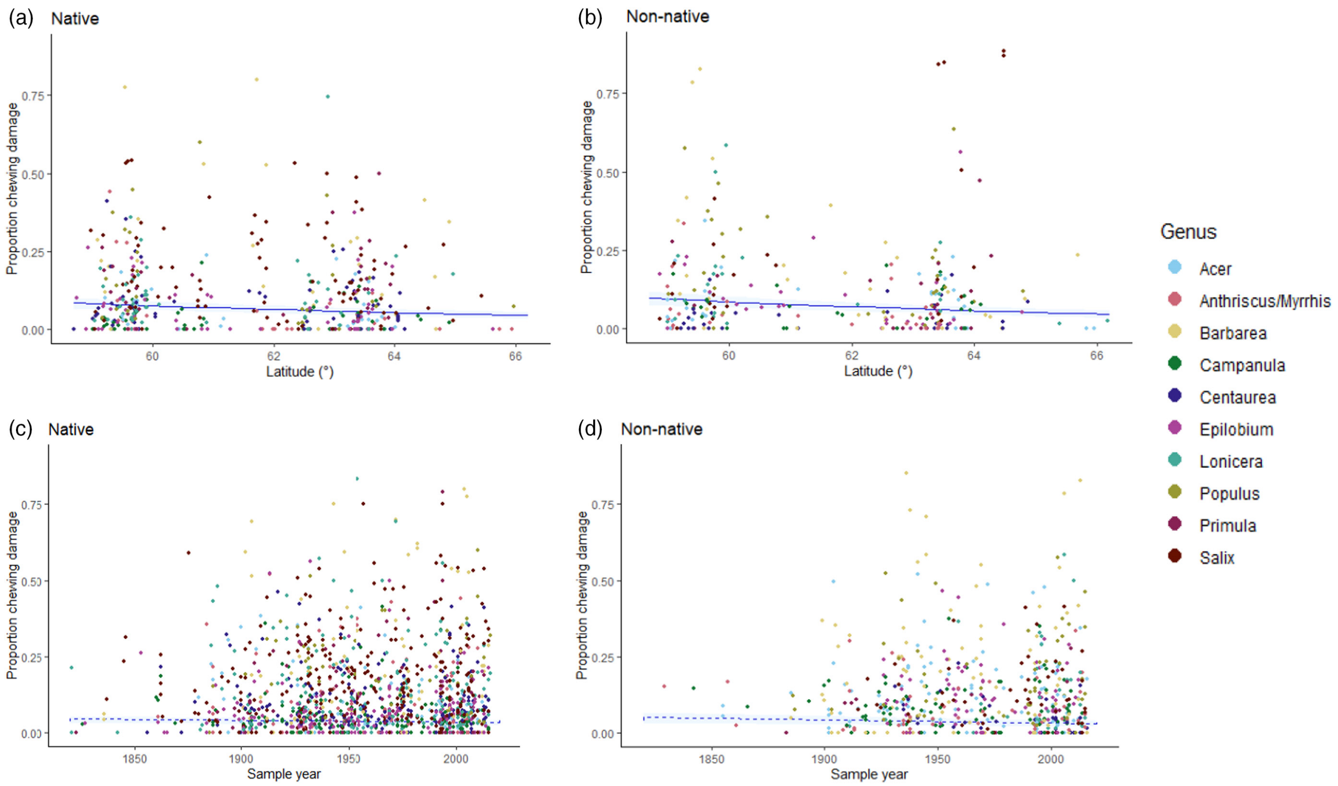

FIGURE 3 Effect of latitude (a, b) and sample year (c, d) on 16 native and 10 non-native plant species within 10 genera based on two negative binomial GLMMs (fitted values ±SE). Dashed lines represent non-significant and solid lines represent significant relationships ($p < 0.05$)

et al., 2011; Xu et al., 2021). It also contrasts with the finding of the meta-analysis by Xu et al. (2021) that herbivory on non-native plant species is often significantly lower than herbivory on native species. It has been posited that non-native species have not existed in their invaded ranges for long enough to develop latitudinal patterns in herbivore damage (Lu et al., 2019). However, in our study, non-native

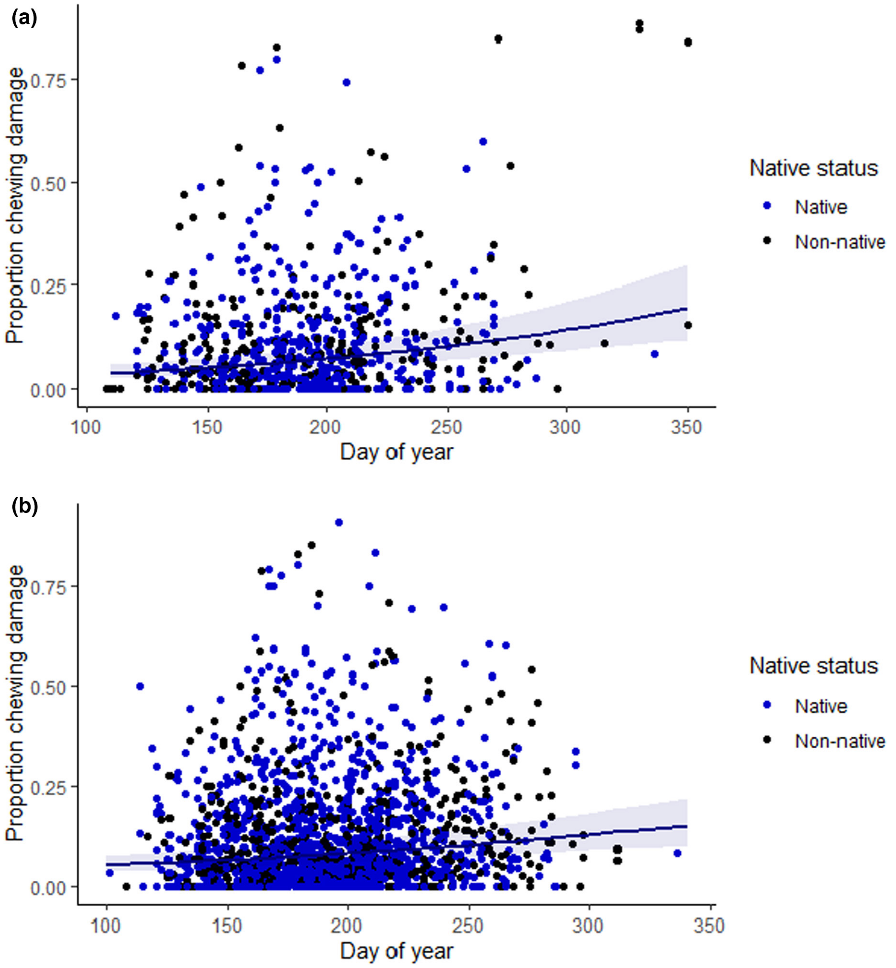

FIGURE 4 Day of year against proportion of chewing damage for specimens used in (a) latitude model (taken from both regions from year 2000) and (b) year model (taken from SE region over the last >100 years). Lines represent negative binomial GLMM fitted values (±SE).

plants appeared to follow the often-documented trend exhibited by native plants (Schemske et al., 2009)—that herbivory rates are lower at higher latitudes. This has implications for herbivory responses under climate change, suggesting that herbivory levels of these species at higher latitudes may increase to resemble the current lower latitude herbivory levels as temperatures rise in the future.

There was no evidence of a relationship between chewing herbivory and sample year across all genera in our system of study, or of any difference in sample year effects between native and non-native species. This corresponds with a study by Carpenter and Cappuccino (2005) who also found no significant change in non-native herbivory over time, although there are other studies which demonstrated an increase in herbivory of non-native plants over time (e.g. Hawkes, 2007; Siemann et al., 2006). One possible explanation for the similar levels of chewing herbivory between native and non-native species over time in our study is that any increase in herbivory levels occurred before our earliest sampling date. Herbivory of non-natives can increase to resemble herbivory levels of native species within several centuries of the species' introduction to its non-native range (Hawkes, 2007; Leather, 1986; Strong, 1974). All of the non-native species in this study were first observed in Norway well before the 1900s, with some as early as 1810–1820 (Norwegian Biodiversity Information Centre 2020; Table 1). There are too few herbarium records before the year 1900 to accurately observe their levels of herbivory when they were first observed in Norway. It is nonetheless possible that chewing herbivory was lower when each species first arrived in Norway and had increased to resemble that of their congeneric native species by the time herbarium specimens existed in sufficient number for this study, despite this time only spanning decades rather than centuries. This could also help to explain why the latitudinal gradients of non-native and native species showed similar trends to each other. Alternatively, due to the closely-related nature of the congeneric groups of native and non-native species, non-native plants may have been recognized as a food source soon after their introduction to Norway.

The absence of expected general differences between native and non-native species in the latitude and sample year relationships may have resulted from variation among congener sets. We determined how influential each genus was in affecting the estimated relationship between chewing herbivory rate and latitude or sample year, and differences between native statuses. Dropping of some genera (*Anthriscus*/*Myrrhis*, *Campanula*) markedly affected the latitude relationship, and in fact removing *Anthriscus*/*Myrrhis* led to a lack of any observed latitudinal trend. When considered alone, *Anthriscus*/*Myrrhis* showed some evidence of a negative relationship between latitude and chewing, whereas no such relationship was apparent for *Centaurea* or *Primula*. Despite these differences among genera, we still encountered an overall negative relationship

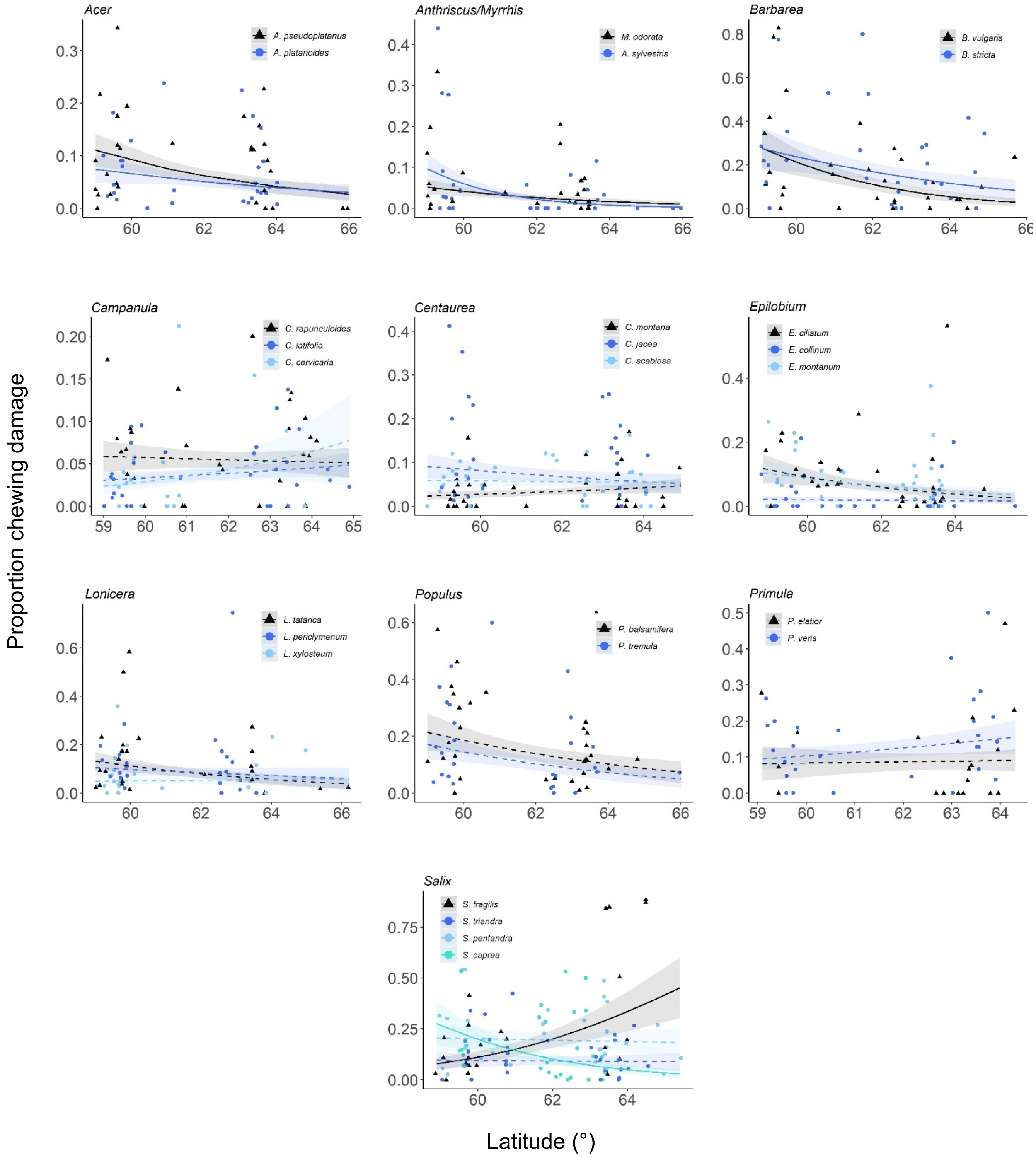

FIGURE 5 Proportion of chewing damage of herbarium samples in each genus across latitudes in Norway. Black triangles and black fitted lines (±SE) represent non-native species, and blue circles and blue fitted lines (±SE) represent native species. Dashed lines represent non-significant relationships and solid lines represent significant relationships ($p < 0.05$). Samples represented here are taken from the years 2000–2021.

between latitude and herbivory in most cases when a genus was removed. There was strong evidence of this negative trend for 3 out of 10 genera and weak evidence for a further 4 genera; we therefore argue that this latitude effect is general and robust. In contrast, removing certain genera (*Barbarea*, *Campanula*, *Salix*) affected the sample year relationship in a weak way, but when considered alone there was only evidence of herbivory change across sample year in one genus (*Centaurea*).

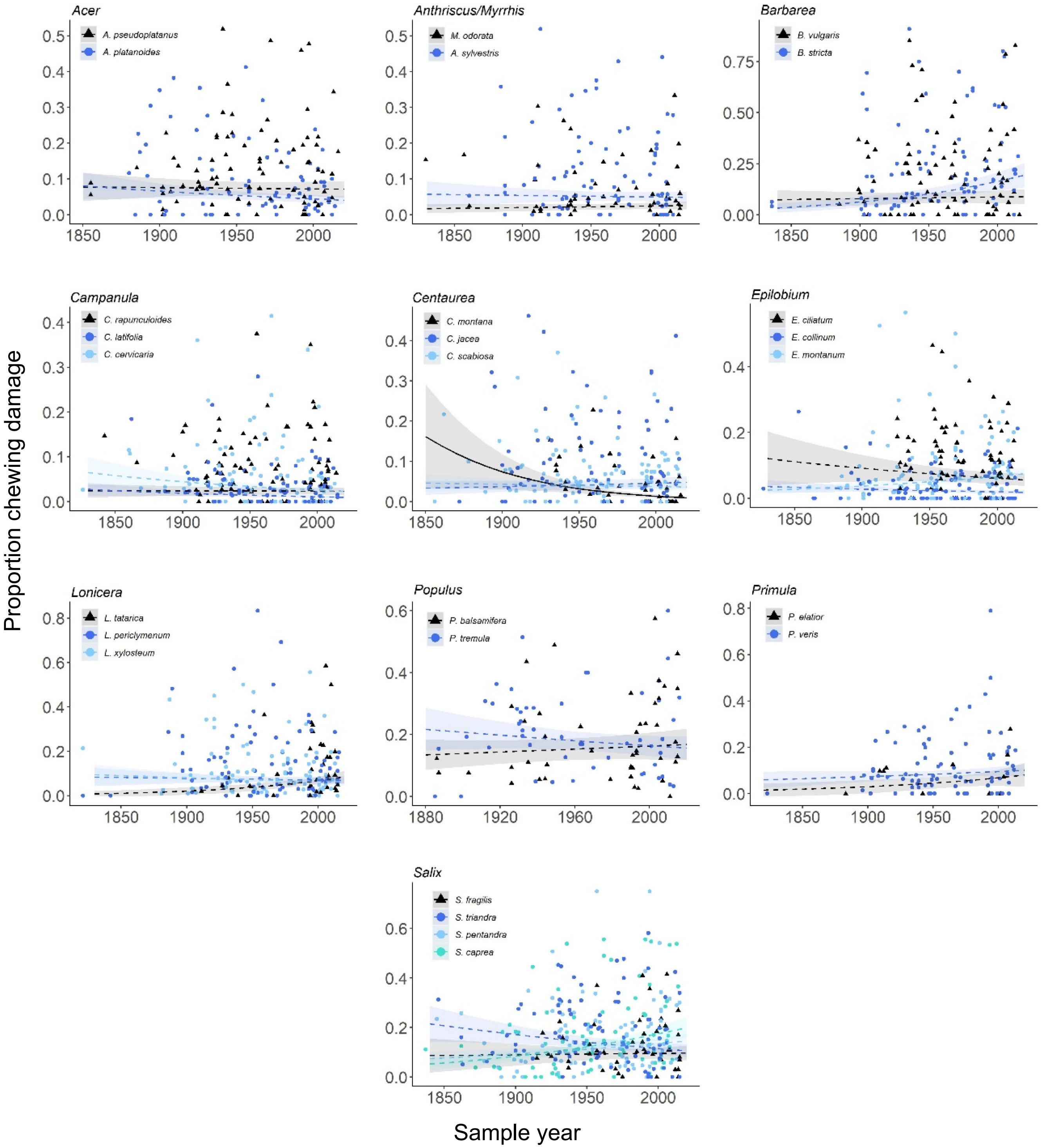

FIGURE 6 Proportion of chewing damage of herbarium samples in each genus. Black triangles and black lines (±SE) represent non-native species, and blue circles and blue lines (±SE) represent native species. Dashed lines represent non-significant trends and solid lines represent significant trends ($p < 0.05$). Samples represented here are taken from the southeast of Norway (latitude <62°, longitude >9°).

The smaller sample sizes per species may have prevented us from detecting evidence for sample year effects. We sampled up to 30 specimens per species for the latitude analysis, and up to 90 for the sample year analysis. This contrasts with Beaulieu et al. (2019) who analysed over 1300 specimens of a single species of non-native plant *Lythrum salicaria* in Canada and observed in detail the gradual increase in chewing herbivory of this species over time. Instead of focusing on one species, we decided to look at a higher number of species but analysed fewer specimens for each, as our interest was primarily in comparing native and non-native species and assessing latitude and time relations across species more generally. To assess the generality of herbivory relationships and differences between native and non-native species, we therefore traded per-species sample sizes off against including more genera and species. This approach increases estimate accuracy more in a multispecies study than increasing the number of observations per species (van Kleunen et al., 2014). Moreover, we found strong evidence of latitude effects on herbivory with smaller sample sizes per species than for sample year (for which no evidence of effects was found). This may reflect that the effects of latitude are stronger and more directional than year and so are easier to detect with lower sample sizes, and/or that inter-year variability in herbivory rates is too high to detect biological meaningful trends. We are also confident that we were not biased in our selection of herbarium specimen images because the individual photo ID numbers were randomly selected without viewing the images a priori (Zvereva & Kozlov, 2019).

We carried out this study using herbarium records, which are an invaluable tool for observing trends over time and across regions. One of the key benefits of herbarium records is that specimens are increasingly digitized which allows specimens to be viewed online. This means that specimens can be analysed either in-situ using a microscope to assess damage (as in Meineke et al., 2019), or analysed digitally using image analysis software as was carried out in this study. Both methods have their benefits. In-situ analysis means that categorization of damage types may be more accurate, and pre- and post-collection damage may be easier to differentiate; digital analysis, however, allows specimens from multiple herbaria to be incorporated into a study without the need to travel between locations.

However, there are certain downsides to using herbaria. The very nature of natural history collections means that there are only a limited number of historical specimens available for ecological studies. For many of our species, we used the maximum number of specimens that exist in our selected locations. This does mean that there may be limited statistical power available to detect subtle trends in herbivory over time due to lower numbers of historical than present-day samples. Despite this, we are confident that stronger, biologically meaningful effects would have been detected as significant, such as that found for the effect of latitude on herbivory. The variances in herbivory per species for the latitude data subset were similar to the variances of the sample year dataset (Table S6) and variance among genera in both latitude and year models was similar (Table 2). Given the similar variances and the larger sample sizes for the sample year dataset (Table S6), if there was an effect of year at least as strong as the effect of latitude, we should have detected it as significant. The fact that we did not indicates that evidence for a latitudinal trend in herbivory is stronger than the evidence for a temporal trend.

Sampling bias by collectors, such as selecting plants with little or no herbivory, is a problem which could significantly impact the results of any study based on herbarium collections. A recent study (Kozlov et al., 2020) found large differences between herbivory levels of ecological samples and herbarium records, with collectors favouring specimens with little or no chewing herbivory damage, but conversely choosing specimens with the presence of other organisms such as leaf miners. These differences varied between species, which suggests that assuming lower levels of herbivory across all herbarium specimens is not valid when using herbarium data (Kozlov et al., 2020). However, a recent re-analysis of the data collected by Kozlov et al. (2020) showed that with sufficient samples (more than 10 data points), herbivory levels of field-observed samples and herbarium specimens are highly correlated, and that there is little difference in sampling bias across species (Meineke et al., 2020). For our study, we therefore assume that if a collection bias exists, it would be consistent for native and non-native species and would therefore not affect the interpretation of our results.

In addition to the above findings, it is possible that collection bias could be more apparent for the more abundant native species, particularly several decades ago when non-native species were less common and collectors sampled specimens regardless of their condition. In our data, all damage types were found in relatively similar proportions across all time periods and between native and non-native species, which indicates that in this case abundance of species does not seem to have influenced the proportion of damage on collected specimens. Moreover, the presence of the significant latitudinal trend corroborates findings from other studies carried out in the field rather than in natural history collections (Kambo & Kotanen, 2014; Nunes et al., 2016). This lends support to the view that, despite any potentially collection bias, herbarium data can reveal ecologically meaningful patterns in herbivory rates.

Another potential issue with using herbarium photos is that some damage can occur after sampling, such as by invertebrate herbivores living within the herbarium. Meineke et al. (2019) accounted for this problem by close observation of damage through microscopes to determine if the damage was done pre- or post-collection. In our study, we used only photographs of the samples. However, if significant post-collection herbivory occurred, we would expect to observe lower herbivory rate in newer than older samples. This was not the case, so we can assume that post-collection herbivory was not present in large quantities and a resulting source of error in our dataset. In addition, Norwegian herbaria are aware of the potential for post-collection damage, and measures have been in place to eradicate insects from collections.

Samples taken at the same time of year are more comparable than those taken at different times, as insect herbivory levels vary depending on ambient temperature (Lemoine et al., 2014) and therefore time of year. We included day of year in the models to account for this, and found across our entire dataset and for several genera individually (four in latitudinal study and four in sample year study) that chewing herbivory was positively related to day of year. In the remaining genera the trend was still positive but evidence was weaker (Tables S2 and S3). This trend is consistent with Meineke et al. (2021) and was expected to be present in our data, as invertebrate herbivory is likely to accumulate throughout the year until senescence of leaves in the winter. The lack of consistent strong positive trends within each individual genus could have been due to the lower numbers of samples in each genus, giving lower statistical power to detect effects.

Finally, we must highlight that this study is system specific, and our aims were not to test the general validity of the enemy release hypothesis per se. Instead, we have explored variation in herbivore damage (as a measure of enemy release) over space and time in phylogenetically related native and invasive plants, and found evidence in support of a latitudinal cline in herbivory which affects native and non-native plants in a similar way. Thus, our study contributes to our understanding of plant–herbivore interactions involving invasive plants in higher-latitude systems.

5 | CONCLUSIONS

Plant introductions and invasions are a major contributor to global changes in ecosystem function and composition. A survey in 2019 revealed that there are almost 2500 non-native species in Norway, over 1000 of which are naturalized and the majority of which are plants. This means that Norway currently contains the highest number of non-native species in Europe outside the United Kingdom (Sandvik et al., 2019, 2020). To predict the long-term effects of these plant introductions on local ecosystems, it is important to determine how these non-native plants may survive in the future. To do this we can investigate how they interact with, and may be controlled by, native enemies over time and across different areas. Our results highlight three key points for our region of study. First, there is little evidence that non-native species will benefit from lower herbivory rates than related native species generally. Second, environmental conditions related to latitude, namely climate, constrain herbivory of non-native and native species in a similar way, with lower herbivory at higher latitudes. Third, herbivory levels have not changed through time in a directional manner for either native or non-native species in general. Our findings have several implications for the future of these non-native plants in Norway. Lower chewing herbivory rates at higher latitudes fit with the Latitudinal Biotic Interactions Hypothesis, and similar herbivory levels of both native and non-native species mean that these plants might be impacted equally by these biotic interactions as they move further north, assuming that there is northward range expansion by herbivores occurring at lower latitudes under climate change. This would mean that enemy release is unlikely to play a major role in the success of non-native plants at higher latitudes in Norway under a warmer climate, at least for non-natives with close native relatives. Enemy release also seems to have been absent in over the period of time considered, indicated by the constant levels of chewing herbivory throughout the last 200 years in the southeast of Norway, suggesting that although herbivory on non-natives occurs, it is unlikely to increase relative to natives and so further limit non-native plants in the future. It remains to be seen if changes in herbivory will become more apparent at both lower and higher latitudes as temperatures increase. However, herbarium records provide a valuable baseline of herbivory levels for native and non-native plants alike, which will allow us to put current and future herbivory in context.

AUTHOR CONTRIBUTIONS

James D. M. Speed, Tommy Prestø, Wayne Dawson and Katy Ivison conceived the ideas and designed methodology; Katy Ivison collected the data; Katy Ivison analysed the data; Katy Ivison and Wayne Dawson led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

There was no conflict of interest in this study.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in this study can be found at: https://figshare.com/articles/dataset/Herbarium_data/21164464 (Ivison et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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