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Master's thesis in Ecology, Behaviour, Evolution and Biosystematics

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## **ABSTRACT**

Herbivory is a key ecosystem process that affects structural diversity of vegetation through direct consumption of the plant tissues and indirectly alters the stability of ecosystems. Invertebrate herbivores outweigh vertebrate herbivores in some ecosystem and outbreaks of invertebrates can seriously damage vegetation and reduce the abundance of dominant plant species over a vast area. The Enemy Release Hypothesis (ERH) and the Biotic Resistance are conflicting hypothesis that address the success or failure of non-native plants in an introduced range. The ERH and the Biotic Resistance do not have to be completely contradictory, a non-native species in an introduced range might release from specialists' herbivores (ERH) but may also encounter new generalist herbivores that it has not been able to deter (Biotic Resistant). The interaction between invertebrate herbivory, with different feeding guilds, as a driver of success of non-native plants in an introduced region is poorly understood. The herbivory prevalence and intensity of herbivory damages using five different feeding guilds of herbivores in a botanical garden in Trondheim, Norway was investigated. Invertebrate herbivory data from 629 individual plant species, of which 110 were native plant species and 519 were non-native species in two seasons (early summer and late summer) were recorded. Herbivory prevalence as well as intensity of herbivory damages among native plant species and non-native plant species were compared in two seasons. The herbivory variation between non-native plants with a greater number of native congeners or confamilial plant species and non-native plants with lesser native congeners or confamilial plant species was also studied in the garden. Native plant species suffered significant higher herbivory prevalence (the proportion of species with damage) than non-native in three herbivory damages (chewing, sap-sucking and unknown damages) while in two damages (leaf mining and galls damage) natives had lesser herbivory prevalence than non-native plants. Intensity of herbivory damage (the proportion of leaves damage) for all herbivore feeding guilds was higher in natives than in non-native plant species. Non-native plant species with higher number of native congeners or native confamilial species suffered higher prevalence of herbivory than those with fewer congeners or confamilial species and congeners pair showed significant variation than confamilial pair in this study. Our study supports the ERH to only a certain extent as a mechanism explaining non-native suffer less herbivory damages than non-native, in fact the herbivory damages vary with different herbivores feeding guilds. This means the ERH probably applies to a limited subset of herbivores.

**Keywords:** Herbivory prevalence, Intensity of herbivory, Congeneric species, Confamilial species.

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## 1. INTRODUCTION

Herbivory is a key ecosystem process that reduces plant biomass and density of plant materials, transfers mass and nutrients to the soil or water column and influences habitat and resource conditions for other organisms (Schowalter, 2022). Herbivory can affect structural diversity of vegetation through direct consumption of the plant tissues across large landscapes (Asner et al. 2009). The direct effects of herbivory on plant performance are in proportion to the amount of plant tissue loss or damage (Schowalter, 2022). Indirectly herbivory alters the stability of ecosystems through effects on the balance of the vegetation types (Van Langevelde et al., 2003). These effects, however, differ within and among ecosystems (Hillebrand et al., 2007). It varies depending upon the type of herbivore and consumption pattern, as well as its intensity and the scale at which it is recorded (Brown and Allen, 1989; cited in Schowalter, 2022). Invertebrate herbivories outweigh vertebrates in some ecosystems (Pimentel and Andow 1984; La Pierre et al., 2015). Outbreaks of invertebrates can seriously damage vegetation and reduce the abundance of dominant plant species over a vast area through direct consumption (Carson & Root 1999; Carson & Root, 2002) and through many indirect effects (Van Ruijven et al., 2005).

The Enemy Release Hypothesis (ERH) states that plant species, on introduction to an exotic region, should experience a decrease in regulation by herbivores and other natural enemies (Keane & Crawley, 2002). The theory implies that natural enemies have greater regulatory influence on native species than non-native species in the introduced range. Some studies fully support the ERH that exotic plant species have fewer pathogen and herbivore communities in their introduced range than in their region of origin (Fenner & Lee 2001; Wolfe 2002; Mitchell & Power 2003; Schierenbeck et al., 1994; Siemann & Rogers 2003; Cincotta et al., 2009) and some do not (Keane & Crawley 2002; Agrawal & Kotanen 2003; Wein et al. 2016; Dawson 2010; Liu & Stiling 2006). It is also equally crucial to recognize that a decrease in natural enemies does not always translate to low proportion of herbivory damage. Biotic resistance, on the other hand, predicts that the native generalist herbivores will suppress exotic plants that have not been adapted to deter these herbivores. ERH and Biotic resistant hypotheses do not have to be completely contradictory (Verhoeven et al. 2009). A non-native species in an introduced range might release from specialists' herbivores (ERH) but may also encounter new generalist herbivores that it is not been able to deter (biotic resistant) (Verhoeven et al. 2009). The net impact of herbivores on non-native plants will be therefore, the net effect of escaping old herbivores and acquiring new one (Verhoeven et al. 2009). However, the interaction between invertebrate herbivories with different feeding guilds, as a driver of success of non-native plants in an introduced region is poorly understood.

Seasonal and temporal patterns in herbivory-plant interaction network are also critical for understanding the mechanisms that drive herbivory (Hernandez-Cumplido, 2016; Karban & Adler, 1996; Filip et al., 1995). Invertebrates show robust response to seasonal changes, frequently more than vertebrates (Wolda, 1988). Seasonality affecting herbivory community is scarce and few had investigated (Seifert et al., 2021). The assembly of herbivorous insect communities temporally varies within a year (Shinohara & Yoshida, 2021). Herbivory in tropical dry forests is typically concentrated in the rainy season, given the seasonal

deciduousness of the forest (Filip et al. 1995). Filip et al. (1995) reported a very marked within season variation in the rates of herbivory i.e., the rate of herbivory during early part of the rainy season was 3.6 times higher than in the late season. Rates of herbivory are generally higher in younger leaves than mature leaves however, some herbivores (for example seed bug, *Nicuesa speciosa*) prefer mature leaves (Ernest, 1989). Differences in chemical and nutritional features between leaves of various ages and plants from different environments are likely to impact herbivore feeding and damage patterns (Ernest, 1989; Sandlin and Willig 1993). Invertebrates like insects has many chances for non-genetic adaptation as feeding and oviposition choices are also based on learned preferences (Renwick, 2001- cited by Verhoeven et al. 2009) and through process of learning rapid host shifts are possible. Thus, enemy release in exotic plant species is likely to change with time.

Phylogenetic relationships, on the other hand, among plant species within a community and its impact on herbivory has received additional interest within past few decades as a promising predictor of local and global herbivory pattern (Dawson et al. 2009; Agrawal et al., 2005; Agrawal & Kotanen, 2003; Cappuccino & Carpenter, 2005). Surprisingly, few studies have assessed herbivory among congeneric or confamilial pairs of non-natives with native plant species and without (Hill & Kotanen, 2009; Harvey et al., 2012; Ødegaard et al. 2005; Nipperess et al. 2012; Dawson et al. 2009). These literature post that most of the invertebrate herbivores tend to feed on closely related host plants rather than a random selection of native plants. As the phylogenetic distance between co-occurring host plant species declines, greater similarities are found between the herbivore communities supported by the plants (Ødegaard et al. 2005; Nipperess et al. 2012). In contrast, there are scattering number of literatures which do not support that phylogenetic relation is a crucial factor in explanation in occurrence of herbivory in non-native plants (Duncan & Willams, 2002; Daehler, 2001; Strauss, 2006). Duncan & Willams (2002) carried out a study in exotic plant species introduced for cultivation into New Zealand and found out that individuals with congeneric native relatives were substantially more likely to naturalize than those without, maybe because they share features with native relative that help them adjust to their new environment. Strauss (2006) also posted similar result that highly invasive grass species in California were less related to native grasses. In 2005, Agrawal et al., examined the effects of various enemies on native and nonnative plant congeners and found that although natives experienced greater levels of damage, variations among enemies and over time could cancel out or negate this effect. According to this study, variation in the net effect of enemies may create opportune times when invasive plants are able to temporarily gain ground in their introduced range (Agrawal et al., 2005). However, the proximate factors that may drive the diverging results between literatures have rarely been explored.

This study deals with the herbivory prevalence (the proportion of species with herbivory) and the intensity of herbivory (the proportion of leaves with herbivory) variations among native and non-native plant species in the Ringve Botanical Garden. The variation is investigated along two variables: seasons (early summer and late summer), and native status (native and non-native plants). This enables to explore whether variation in herbivory among native and non-native plants can explain the how the non-native become invasive. Most previous studies, however, lack the direct comparisons of impacts on native vs. non-native plants, important to

understand potential mechanism of invasion, and have evaluated different hypotheses. Phylogenetic relationships between native and non-native species may therefore offer important insights into similarities and differences in the invertebrate herbivores. This study is also doing a comparison of herbivory prevalence between non-native plant species and native plants within the same genus (native congeneric species) or same family (native confamilial species) of non-natives in Norway. To investigate the relationship, the leaf herbivory of plant species in the garden was recorded. The hypotheses of the thesis are:

1. The herbivory prevalence is higher on native plant species than non-native plant species,
2. The intensity of herbivory is greater on native than non-native plant species,
3. Non-native plant species with higher number of native congeners suffer higher prevalence of herbivory than those with fewer congeners,
4. Non-native plant species with higher number of native confamilial species suffer higher prevalence of herbivory damage than those with fewer confamilial species.

## **2. MATERIALS AND METHODS**

### **2.1. Study area**

The study was conducted in 2021 (June – August) at the Ringve Botanical Garden on the Lade peninsula, ca. 3 km east of Trondheim city center, Norway (Latitude: 63° 25' 49.76" N; Longitude: 10° 23' 42.22" E). Trondheim is a southern-boreal, coastal municipality and climate here is classified as Dfb by the Koppen-Geiger system which is cold and temperate. The annual mean temperature and precipitation are approximately 5 °C and 887 mm (Statistics Norway, 2018). The driest month is April, with 72 mm of rain. The greatest amount of precipitation occurs in September, with an average of 107 mm of rain. July is the warmest month of the year. The temperature in July averages 14.6°C. The lowest average temperature in the year occur in; January, when it is around -4.5° C. Summer starts here at the end of June and ends in September (<https://en.climate-data.org/>).

The Ringve Botanical Garden is spread over 13 hectares with an elevation of approximately 28 m and is a part of the Norwegian University of Science and Technology (NTNU). The garden holds collection of plants for conservation, education, research, and enjoyment. The garden has 6 main displays; The Arboretum ( forest trees and shrubs from the Northern Hemisphere); The Old Perennials (old garden plants collected from Central Norway); The Historic Park ( old farm garden dating back to the mid-1800s); The Systematic Garden (illustrating the lines of evolution of flowering plants); The Renaissance Garden ( a herb garden with a local history dating to 1694); The Primrose Garden ( showing species and cultivars of the genus *Primula*) (Figure 1)( Ringve Botanical Garden). The map of the study area was made with the ArcGIS pro-2.9.1 (Fig.1).

### **2.2 Data collection**

Plant assessment was carried out twice; in June 2021 (early summer) and in August 2021 (late summer). All together 629 different plant species (majority of herbs, shrubs, some trees and

few climbers and creepers) were assessed, which includes 110 native plants and 519 non-native species. Different parameters like growth form, height, area of ground coverage etc., were recorded (Appendix A). Height was measured closest to multiple of 5 cm. Growth forms were tree, shrubs, herbs, climbers, and creepers. The phenological stages were divided it into three groups: vegetative, flowering, and fruiting.

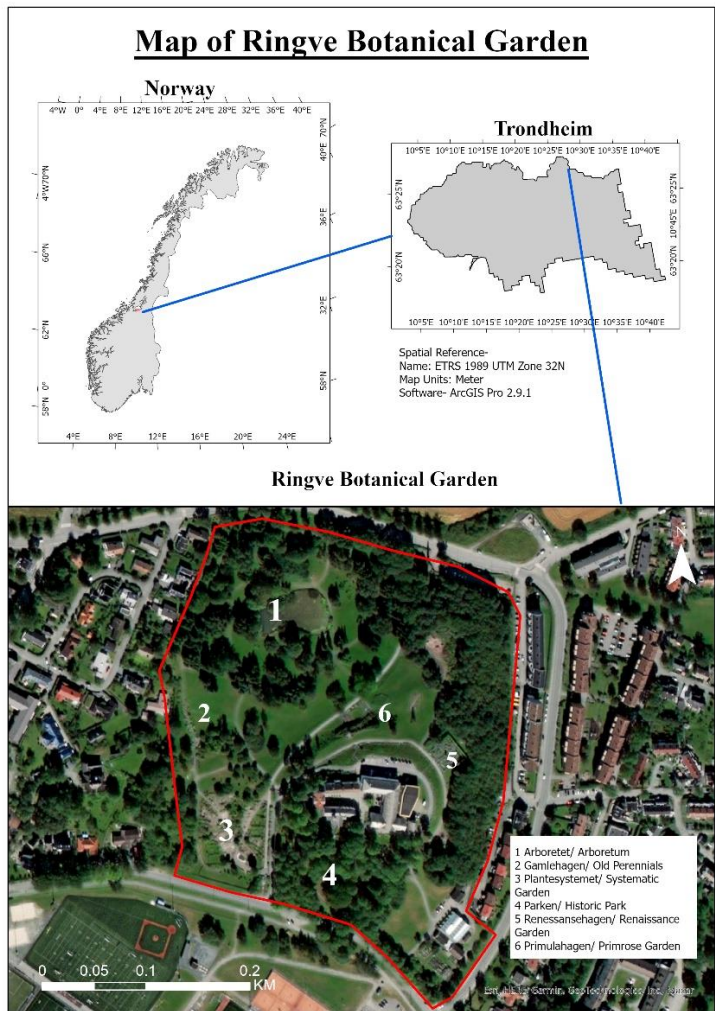


Figure 1. Map of the Ringve Botanical Garden with six main displays (marked 1-6 numbers).

Herbivory prevalence is the proportion of species with herbivory damage. For herbivory prevalence data, we first recorded presence/ absence of herbivory at the whole plant level. Herbivores feeding on plant if observed were noted down. We divided herbivory damages into five groups: chewing damage, leaf-mining damage, sap-sucking damage, galls damage and unknown damage. Different invertebrate herbivores were grouped according to their feeding guilds; chewing damages include chewer that chew foliage, stem, flower (seeds & roots not included in this study); leaf-mining damages include miner and borers that feed between plant surface; gall damages include gall-formers that reside and feed within the plant and induce the production of abnormal growth reaction by plant tissues; sap-sucking damages include sap-suckers that siphon plant fluids (Romoser and Stoffolant ,1998; cited in Schowalter, 2022). Those herbivory damages which we were unable to classify were kept under unknown

damage type. Intensity of herbivory damage is the proportion of the leaves with herbivory within each observation. For measuring the intensity herbivory damages, we selected 10 leaves from a plant. We did not pluck the leaves, instead counted damaged leaves visually out of 10. Most plants have large numbers of branches, stems, or leaves, so selection of 10 leaves were done differently according to growth form:

- Rosettes: we selected 10 fully expanded leaves in one quarter of the rosette randomly for recording leaf damage.
- Herbs: we selected 10 leaves randomly from a single branch.
- Woody, branched plants (shrubs, & trees): two branches were selected at random, and on each of these branches we selected 5 fully expanded leaves nearest to the apical meristem for recording herbivory damage.
- Rhizomatous plants with multiple stems from ground level: haphazardly two stems from plant, and 5 fully expanded leaves on each branch nearest apical meristem were selected for measurement.
- If a plant had few leaves (<10) in total, the plants were excluded from the experiment.

This study does not include root feeding damage as the intensity measurement might need extraction and dissection of the root (Strong et al., 1995) which is not allowed in the garden and short-term study's may be inadequate to assess the impact of root herbivory.

### **2.3 Statistical analysis**

Herbivory prevalence data involve binary response variables like presence (1) or absence (0).  $\chi^2$  tests of proportions for each damage types were also done to test if difference in herbivory and native status was significant or not. The generalized linear mixed-effect models (glm) with family binomial were also fitted in R to assess herbivory prevalence variation with native status (native and non-native) and seasons (early summer and late summer). Native status and seasons were explanatory variables, whereas herbivory was response variables. Likelihood ratio test was performed ( $\chi^2$  values) to assess the significance of interaction between herbivory prevalence with seasons and native status. Intensity of damage was scored 0 to 10. In this case also, we also used the binomial model, but first we changed the values 0-10 to 0-1, as the data will then reflect a binary process.  $\chi^2$  tests of proportions for each damage types for the intensity of herbivory were also done. Likelihood ratio test was also performed ( $\chi^2$  values) to assess the significance of interaction between intensity of herbivory with seasons and native status. The visualization of herbivory prevalence variation between seasons and native status and intensity of herbivory were done with ggplot package in R-studio. The number of native plant species in Norway with the same genus or the same family of non-native plants were also counted to test if there was any relation in herbivory in presence of native relatives. We also used likelihood ratio test ( $\chi^2$  values) to assess the significance of interactions between these factors. All statistical analysis were done with R version 4.1.2 (2021-11-01).

### 3. RESULTS

To examine whether native plant species suffer higher herbivory than non-native plant species, herbivory prevalence and intensity of herbivory was calculated. Overall, herbivory prevalence and intensity of herbivory was higher in native than non-native plant species.

#### 3.1 Herbivory prevalence

Herbivory damages was studied for five damage types: Chewing, Sap-sucking, Leaf-mining, Galls and Unknown. Among these types, herbivory prevalence was higher in natives than in non-natives for chewing, sap-sucking and unknown damages.

Table 1. Proportion test for the seasons and native status on the herbivory prevalence.

Types	Seasons	Native status	Obs.	Damages	Proportion	$\chi^2$	df	p-value
Chewing	Early	Native	110	62	0.555	1.715	1	0.190
		Non-native	519	254	0.489			
	Late	Native	110	72	0.661	0.056	1	0.812
		Non-native	519	331	0.640			
Sap-sucking	Early	Native	110	45	0.400	10.293	1	0.001**
		Non-native	519	131	0.257			
	Late	Native	110	56	0.523	1.963	1	0.161
		Non-native	519	223	0.426			
Leaf-mining	Early	Native	110	1	0.009	6.1E-30	1	1.00
		Non-native	519	7	0.013			
	Late	Native	110	1	0.009	8.7E-30	1	1.00
		Non-native	519	2	0.004			
Galls	Early	Native	110	1	0.009	3.39E-30	1	1.00
		Non-native	519	5	0.010			
	Late	Native	110	6	0.055	8.177	1	0.004**
		Non-native	519	5	0.010			
Unknown	Early	Native	110	3	0.027	0.397	1	0.528
		Non-native	519	7	0.013			
	Late	Native	110	9	0.083	2.927	1	0.087
		Non-native	519	20	0.039			



The prevalence of chewing damage was high in native (0.55) than non-native (0.48) in early summer as well as in late summer (0.66 for native; 0.64 for non-native- see table 1 & figure 1). The difference in herbivory prevalence in chewing damage among native and non-native was not significant in both seasons (early summer,  $\chi^2 = 1.7148$ ,  $df=1$ ,  $p\text{-value} > 0.05$ ; late summer  $\chi^2 = 0.0564$ ,  $df=1$ ,  $p\text{-value} > 0.05$ ; See table 1). If we compare between the seasons, the prevalence of chewing damage was higher in late summer than in early summer for both native (0.55 in early and 0.66 in late summer, table 1 & figure 1) as well as non-native plant species (0.48 in early and 0.64 in late summer). The herbivory prevalence for sap-sucking damage was also higher in native (0.40) than in non-native plants (0.25) in early summer as well as in late summer (0.52 for natives; 0.42 for non-natives). There was significantly higher proportion of species with sap-sucking damage in native species than non-native species in early summer ( $\chi^2 = 10.293$ ,  $df = 1$ ,  $p\text{-value} < 0.01$ , table 1). Also, the prevalence of herbivory of unknown damage as in chewing damage and sap-sucking damage was high in native (0.027) than non-native (0.013) in early summer as well as in late summer (0.083 for native; 0.039 for non-native). But the difference was not significant ( $p\text{-value} > 0.05$ , table 2). The same trend i.e., increased herbivory damage with seasons goes with unknown damages as well for native (0.027 in early and 0.088 in late summer) and non-native plant species (0.013 in early and 0.039 in late summer) (see table 1).

Leaf-mining damage had low herbivory prevalence in native (0.009) than non-native (0.013) in early summer, but trend was not same in late summer (0.009 for native; 0.004 for non-native). But the difference in leaf-mining herbivory prevalence among native and non-native was not significant ( $p\text{-value} > 0.05$ ) in both seasons. The herbivory prevalence for leaf-mining damage was same for native (0.009 in early and late summer) while decreased in non-native plant species (0.013 in early and 0.004 in late summer) through the seasons. Native plants had low prevalence (0.009) of galls damage than non-native plants (0.010) in early summer, however there was significantly higher proportion of species with galls damage (0.055 for native; 0.010 for non-native) in native species than non-native species in late summer ( $\chi^2 = 8.1772$ ,  $df = 1$ ,  $p\text{-value} < 0.01$ ). The prevalence of galls damage increased in late summer for natives (0.055 in early and 0.009 in late summer) but for non-native plant species it was same (0.010 in early and 0.010 in late summer).

Exception cases were seen in case of leaf-mining damage and gall damages in early summer where natives had less herbivory prevalence than non-native ones. Only one native plant (out of 110) showed leaf-mining damage (*Dryas octopetala*, Rosaceae) in early summer while seven (out of 519) non-native plants species had leaf-mining damage in early summer and among these three plants were from Rosaceae family (*Sorbus hostii*, *Prunus pensylvanica*, *Prunus virginiana* (the garden, Appendix B). In late summer, a native species from Rosaceae (*Prunus padus*) showed leaf-mining while two non-native plant species (*Prunus nipponica* (Rosaceae); and *Lonicera caerulea*- (Caprifoliaceae)) had leaf-mining damage (Appendix B). *Myrica gale* (Myricaceae), was the only one native plant which had galls formation in early summer in the garden. Among non-native, five species (*Sorbus hostii*, *Passiflora citrina*, *Amelanchier alnifolia*, *Acer saccharum*, *Rhododendron hirsutum*)

had galls in early summer. In late summer six natives (*Alnus incana*, *Sorbus aucuparia*, *Salix caprea*, *Schoenoplectus lacustris*, *Prunus padus*, *Myrica gale*) and five non-natives (*Acer pseudoplatanus*, *Amelanchier alnifolia*, *Passiflora citrina*, *Acer saccharum*, *Rhododendron praevernium*) developed galls (see Appendix C). Overall, the occurrence of endophytic damages (leaf-mining and galls) was pronounced in Rosaceae family in the garden. Likelihood ratio test result shows that there were no significant interactions between seasons and native status (table 2).

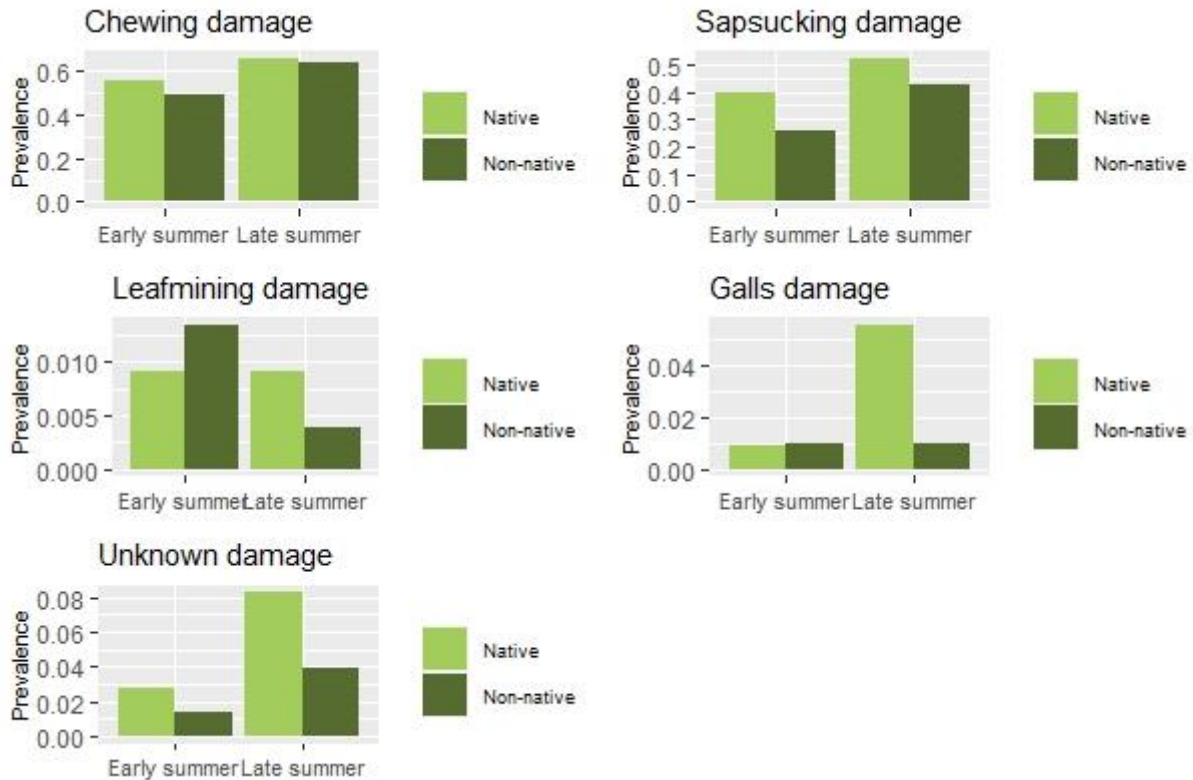


Figure 2. Herbivory prevalence among the native and the non-native plant species in the early and the late summer in the garden.

Table 2. Likelihood ratio test result for herbivory prevalence with native status and seasons.

Prevalence	Coefficients	Native status	Seasons	Native* Seasons
Chewing	Estimate	-0.179	6E-01	0.176
	Std Error	0.152	1E-01	0.306
	Z-value	-1.176	5E+00	0.574
	Pr(>Chi)	0.238	0.00000024***	0.567
Leaf-mining	Estimate	-0.053	-1E+00	-1.262
	Std Error	0.785	7E-01	1.633
	Z-value	-0.068	-1E+00	-0.773
	Pr(>Chi)	0.946	1E-01	0.443
Sap-sucking	Estimate	-0.505	7E-01	0.266

	Std Error	0.151	1E-01	0.304
	Z-value	-3.352	6E+00	0.873
	Pr(>Chi)	0.00086***	0.0000000026***	0.383
	Estimate	-1.223	6E-01	-1.839
	Std Error	0.499	5E-01	1.261
	T-test	-2.453	1E+00	-1.458
Galls	Pr(>Chi)	0.0206*	2E-01	0.110
	Estimate	-0.784	1E+00	-0.081
	Std Error	0.357	4E-01	0.813
	Z-value	-2.193	3E+00	-0.100
Unknown	Pr(>Chi)	0.03819*	0.001446**	0.921

Note (\* for P<0.05, \*\* for P<0.01 and P<0.001)

### 3.2 Herbivory intensity

Herbivory intensity (the proportion of leaves with herbivory within each observation) was higher on native than non-native plant species in both seasons (early and late) in all five types of feeding guilds of herbivores (table 3 & figure 3). The intensity of sap-sucking damage was significantly different from native and non-native plants in early summer as well as late summer (early summer,  $\chi^2 = 39.3$ , df=1, p-value< 0.0001; late summer  $\chi^2 = 57.92$ , df=1, p-value<0.0001-See table 3). Also, intensity of unknown damage was significantly different from native to non-native in both seasons (early summer,  $\chi^2 = 15.824$ , df=1, p-value< 0.0001; late summer  $\chi^2 = 20.847$ , df=1, p-value<0.0001-See table 3).

Table 3. Proportion test for the seasons and native status on the intensity of herbivory.

Intensity of	Season	Native status	Obs.	Damaged	Proportion	$\chi^2$	df	p-value
Chewing	Early	Native	1100	<b>162</b>	<b>0.147</b>	9.1744	1	0.002
		Non-native	5190	<b>592</b>	<b>0.114</b>			
	Late	Native	1100	<b>274</b>	<b>0.249</b>	18.33	1	<b>1.8E-05***</b>
		Non-native	5190	<b>994</b>	<b>0.192</b>			
Sap-sucking	Early	Native	1100	<b>117</b>	<b>0.106</b>	39.3	1	<b>3.6E-10***</b>
		Non-native	5190	<b>285</b>	<b>0.055</b>			
	Late	Native	1100	<b>246</b>	<b>0.224</b>	57.92	1	<b>2.7E-14***</b>
		Non-native	5190	<b>691</b>	<b>0.133</b>			
	Early	Native	1100	<b>10</b>	<b>0.009</b>	1.0E+01	1	<b>0.0015**</b>

Leaf-mining		Non-native	5190	<b>12</b>	<b>0.002</b>			
		Native	1100	<b>3</b>	<b>0.003</b>			
	Late	Non-native	5190	<b>7</b>	<b>0.001</b>	3.9E-01	1	0.531
Galls		Native	1100	<b>0</b>	<b>0.000</b>			
	Early	Non-native	5190	<b>7</b>	<b>0.001</b>	5.2E-01	1	0.470
		Native	1100	<b>5</b>	<b>0.005</b>			
	Late	Non-native	5190	<b>12</b>	<b>0.002</b>	0.953	1	0.329
Unknown		Native	1100	<b>21</b>	<b>0.019</b>			
	Early	Non-native	5190	<b>33</b>	<b>0.006</b>	15.824	1	<b>6.9E-05***</b>
		Native	1100	<b>37</b>	<b>0.034</b>			
	Late	Non-native	5190	<b>70</b>	<b>0.013</b>	20.847	1	<b>4.9E-06***</b>

Note (\* for P<0.05, \*\* for P<0.01 and \*\*\*P<0.001)

There was significant difference in intensity of chewing damage in native and non-native species in late summer ( $\chi^2 = 18.33$ , df=1, p-value<0.0001) but not in early summer. And intensity of leaf-mining also had significant difference between native and non-native plant species only in early summer ( $\chi^2 = 10.1$ , df=1, p-value<0.01). Galls were absent in native in early seasons (0.005, table 3) and in late summer (0.002) the intensity of galls damage was high in native than non-native plant species, but the difference was not significant ( $\chi^2 = 0.953$ , df=1, p-value >0.05). The intensity of herbivory also does not have any significant interactions between seasons and native status (table 4).

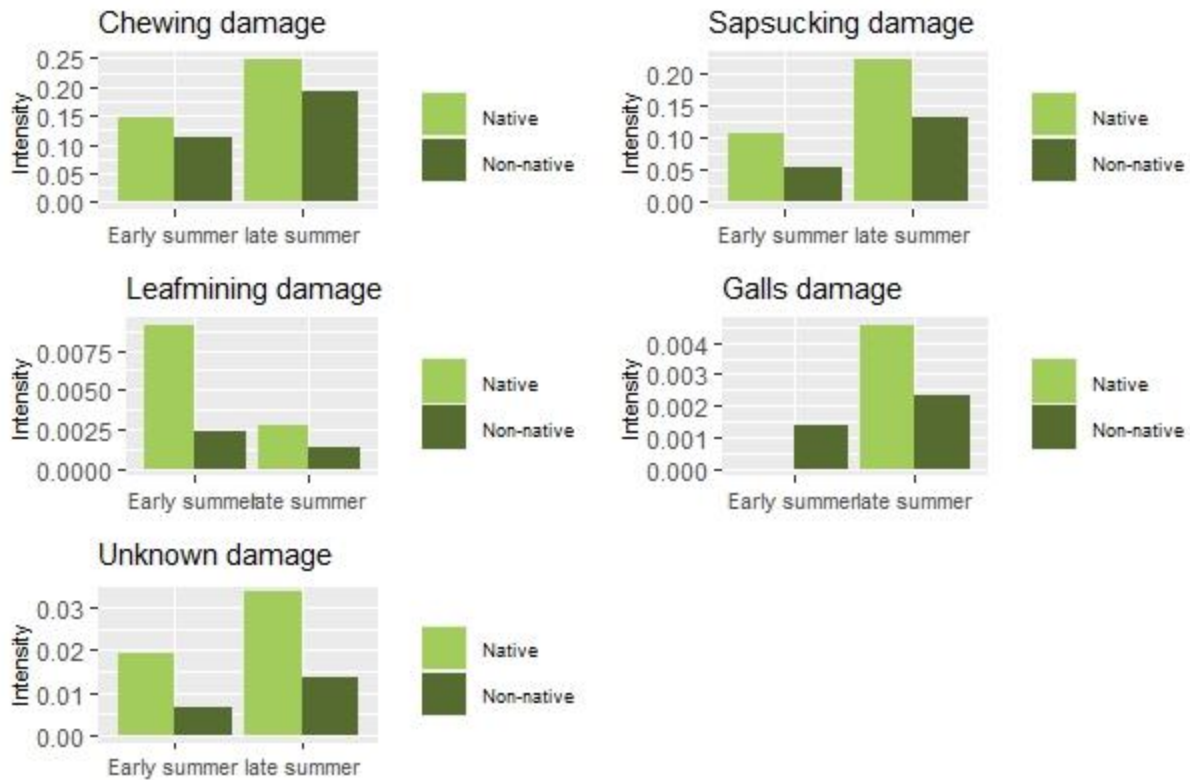


Figure 3. Intensity of herbivory damage (Proportion of leaves with herbivory damage) of the native and the non-native plant species in both seasons.

Table 4. Likelihood ratio test result for intensity of herbivory damages with native status and seasons.

Intensity of	Coefficients	Native status	Seasons	Native* Seasons
Chewing	Estimate	-0.350	0.597	-0.124
	Std Error	0.191	0.159	0.392
	T-test	-1.837	3.755	-0.316
	Pr(>Chi)	0.072	0.00014 ***	0.751
Leaf-mining	Estimate	-1.182	-0.781	0.671
	Std Error	1.141	1.207	2.572
	T-test	-1.036	-0.647	0.261
	Pr(>Chi)	0.329	0.502	0.790
Sap-sucking	Estimate	0.015	0.929	0.015
	Std Error	0.450	0.197	0.450
	T-test	0.032	4.714	0.032
	Pr(>Chi)	0.00296**	0.0000009***	0.974
Galls	Estimate	-0.222	0.899	-15.640
	Std Error	1.591	1.421	2787.2
	T-test	-0.140	0.632	-0.006
	Pr(>Chi)	0.891	0.507	0.529

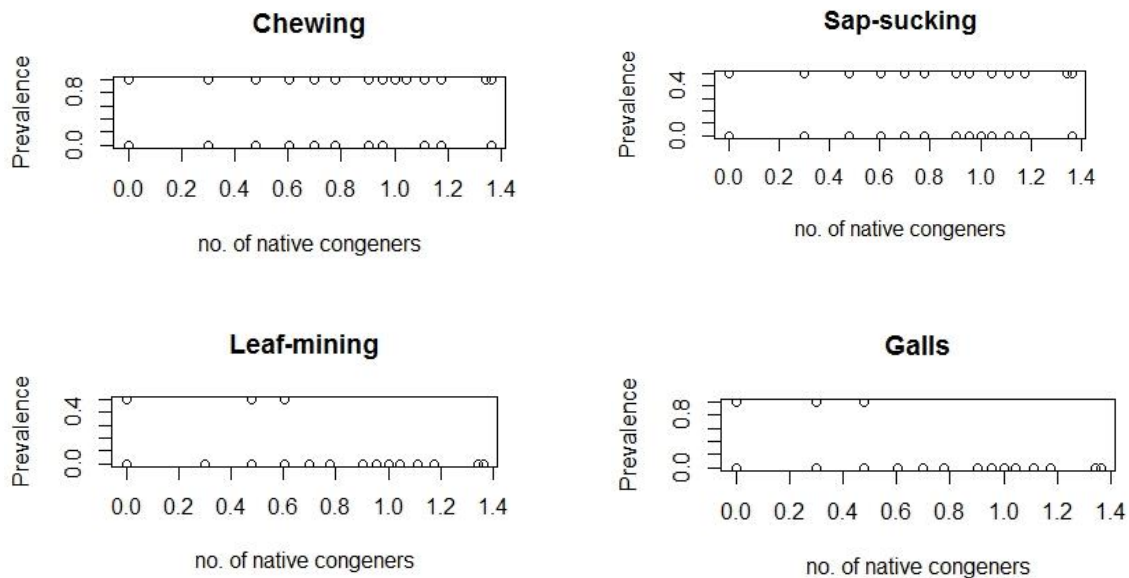
	Estimate	-1.000	0.702	0.178
	Std Error	0.525	0.531	1.102
Unknown	T-test	-1.905	1.322	0.162
damage	Pr(>Chi)	0.073	0.1736	0.872

Note (\* for  $P < 0.05$ , \*\* for  $P < 0.01$  and  $P < 0.001$ )

### 3.3 Herbivory prevalence/ Intensity of herbivory in non-native plants with congeneric/confamilial native plant species in Norway.

The number of native plant species in Norway with the same family (confamilial species) or the same genus (congeneric species) with non-native plant species was counted. The relation was obtained by likelihood ratio test as presented in the tables 5 and 6.

Herbivory prevalence for chewing, sap-sucking, leaf-mining, and galls damage vary significantly with the number of native plant species in the same genus of non-native plant species (Table 5; Fig 4). The proportion of species with chewing damage and leaf-mining increased significantly ( $p$ -value  $< 0.05$ ) with the number of confamilial native species (Table 5; Fig 5). Herbivory prevalence for sap-sucking damage, galls and unknown damages prevalence did not vary significantly with the number of confamilial natives. Congener pairs showed significant variation than confamilial pairs in this study (table 5).



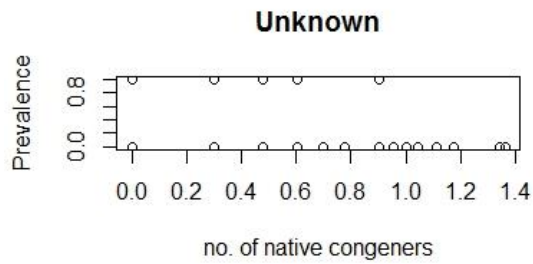


Fig. 4 Relation of herbivory prevalence of different damage types with log (number of native congeneric species +1).

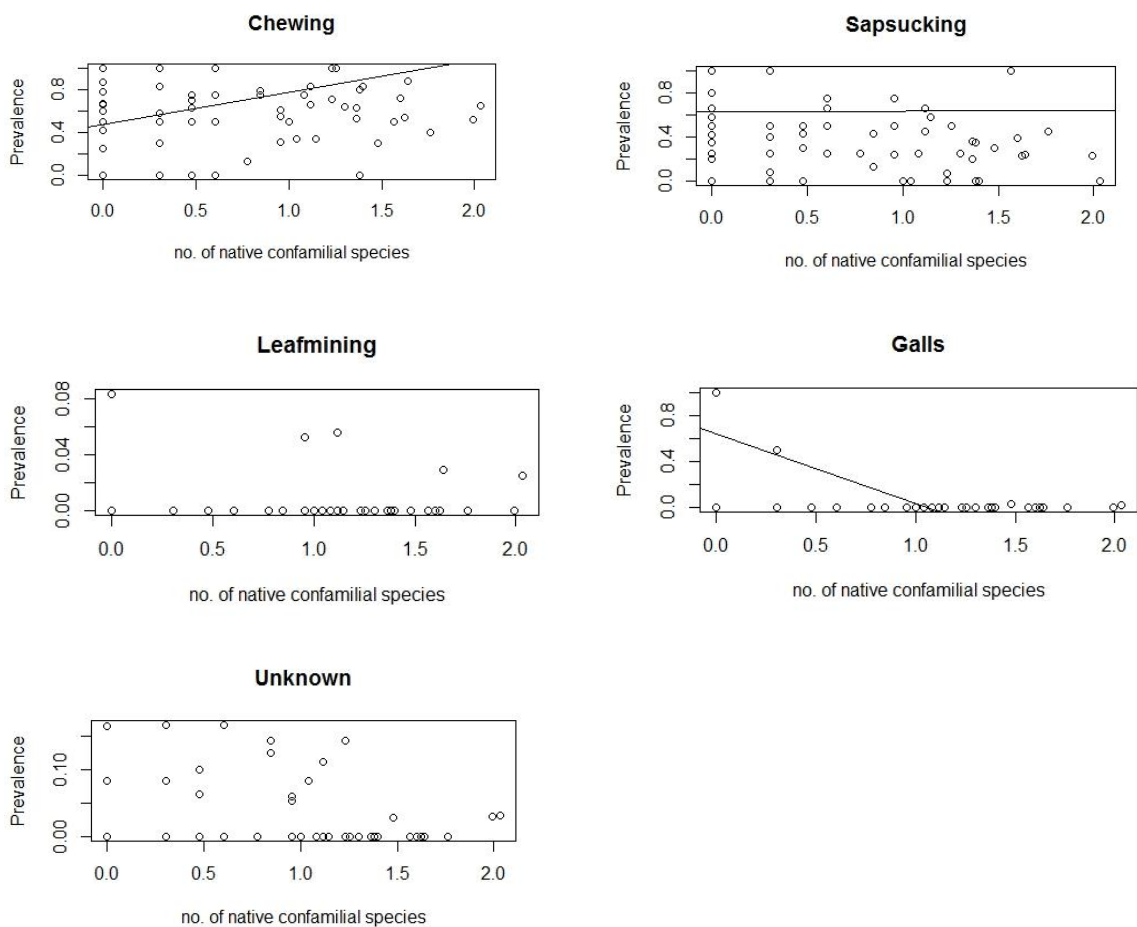


Fig. 5. Relation of herbivory prevalence of different damage types with log (number of native confamilial species +1).

Table 5. Likelihood ratio test result for herbivory prevalence and number of native plants in same genus of non-native plants or same family of non-native plants

Prevalence of	Coefficients	No. of native plants in	
		non-native genus	non-native family

Chewing	Estimate	0.011	0.004
	Std Error	0.003	0.002
	z value	3.126	2.477
	Pr(>Chi)	<b>0.002</b>	<b>0.013</b>
Sap-sucking	Estimate	0.018	0.002
	Std Error	0.003	0.002
	z value	5.432	1.233
	Pr(>Chi)	<b>0.000</b>	0.218
Leaf- mining	Estimate	0.024	0.016
	Std Error	0.011	0
	z value	2.229	2.326
	Pr(>Chi)	<b>0.026</b>	<b>0.020</b>
Galls	Estimate	0.028	0.005
	Std Error	0.011	0.006
	z value	2.419	0.867
	Pr(>Chi)	<b>0.016</b>	0.386
Unknown damage	Estimate	0.005	-0.005
	Std Error	0.010	0.005
	z value	0.479	-0.952
	Pr(>Chi)	0.632	0.341

Note (\* for  $P < 0.05$ , \*\* for  $P < 0.01$  and  $P < 0.001$ )

Intensity of herbivory damage had no significant differences in non-natives with native congeneric species or confamilial species in all herbivory damage types except for sap-sucking (  $p$ -value $<0.001$ ) in congeneric relatives (Table 6, Appendix D, Appendix E).

Table 6. Likelihood ratio test result for intensity of herbivory damage and number of native plants in the same genus of non-native plants or same family of non-native plants.

Intensity of	Coefficients	No. of native plants in	
		non-native genus	non-native family
Chewing	Estimate	0.005	0.002
	Std Error	0.004	0.002
	z value	1.167	1.248
	Pr(>Chi)	0.243	0.212
Sap-sucking	Estimate	0.017	0.003
	Std Error	0.005	0.002
	z value	3.661	1.249
	Pr(>Chi)	<b>0.000</b>	0.212
Leaf-mining	Estimate	0.025	-0.002
	Std Error	0.026	0
	z value	0.982	-0.120
	Pr(>Chi)	0.326	0.905



Galls	Estimate	-0.019	-0.011
	Std Error	0.051	0.021
	z value	-0.384	-0.504
	Pr(>Chi)	0.701	0.614
Unknown damage	Estimate	0.011	-0.013
	Std Error	0.017	0
	z value	0.626	-1.419
	Pr(>Chi)	0.531	0.156

## 4. DISCUSSIONS

### 4.1 Herbivory prevalence

Comparisons between native and non-native plant species, showed that the native plants species had higher herbivory prevalence than non-native plant species in the garden. The hypothesis that the prevalence of herbivory is higher on native plant species than non-native plant species was supported by the herbivory data from the garden. The finding of this study partially supports the Enemy Release Hypothesis, which predicts that non-native plants lack enemies from their native range, hence escaping from their co-evolved herbivores in the new range and are unrecognized by native herbivores. The ERH hypothesis was supported by three out of five herbivores feeding guilds i.e., chewing, sap-sucking, and unknown damages while rest of two (leaf-mining & galls) did not. Less herbivory prevalence in non-native in the new range compared to the native plant species might be due to lack of highly coevolved specialists and broad generalists' natural enemies (Colautti et al., 2004). Few other studies also support the result that non-native plant species suffer less herbivory damage than native overall (Harvey, 2015; Cincotta, 2009; Lieurance, 2015; Agrawal, 2005). Cincotta (2009) did a comparison of foliar insect herbivory of the exotic Norway maple and the native sugar maple and found that non-native had significantly less leaf damage than native one. The Novel Weapon Hypothesis (Callaway & Ridenour, 2004) states that novel phytochemical compounds to which native plants and soil organisms are not adapted, give some non-native plant species an advantage over native in their new range. Hence, low herbivory prevalence in non-native might be also due to novel defensive compounds and novel allelopathic agents that are relatively ineffective against their natural neighbors because of co-evolution but are highly inhibitory in the introduced range (Callaway & Ridenour, 2004).

In contrast to other damages, damages by endophytic herbivores, generally have narrow host preferences, had different cases. In leaf-mining damage low herbivory prevalence was seen in native than non-native plant species while galls were completely absent from native in the early summer. Low prevalence in native might be due to predators and parasitoids present in the garden probably regulating leaf miners. The level of parasitism's is much higher in leaf-mining damage than ectophytic herbivores as it has limited mobility (Djemai & Casaa, 2000). Presence of leaf miner induce premature leaf abscission (Gross & Price, 1988), which might be a probable reason for occurrence of leaf-miner in *Dryas octopetala* (a native plant, Appendix B)

in only early summer but not in late summer. Limited mobility and higher mortality related with abscission of premature leaf by leaf miners also added a benefit for native plants. The prevalence is also dependent on the place of occurrence of the plant species for eg. shaded plants can have more leaf-mining damages than in sun (Bultman & Faeth, 1988).

Most of the new leaves at the Ringve Botanical Garden were produced during early summer (April and May) with no damages at the start of the seasons. Leaves accumulated herbivory damage over the seasons in the garden. The prevalence of herbivory was high during late summer as herbivores are commonly more abundant on mature plants than on younger ones (Kearsley & Whitham, 1989), but it depends upon the feeding guilds of herbivores. Other studies have also shown a similar pattern of increased herbivory over the seasons (Shiojiri and Karban, 2008). A study done by Filip et al. (1995), showed marked differences in the herbivory within seasons in the rate of herbivory, where during early part of rainy season, the main rate was considerably higher than in late season i.e., 3.6 times higher. The reason was explained by nutritional component of foliage which decreased with leaf age. However, Moreira et al. (2016) showed leaf nutrient content had no independent influence on herbivory. Filip et al. (1995) study was conducted in tropical deciduous forest in Mexico and the effect of herbivory might vary with time and space (Agrawal et al., 2003).

Response induced by the attack of early season herbivores can influence the response to subsequent attack and influence the abundance and performance in late season herbivores (Viswanathan et al., 2007). Plants whose neighbors were eaten by herbivores accumulated less damage than plants without damaged neighbors (Karban, 1987; Shiojiri and Karban, 2006). Plants become more resistant when a close neighbor has been attacked which might be due to volatiles released from damaged plants function as chemical communication between plants (Rodriguez-Saona et al., 2003). Plant age influence the signaling process i.e., young plants are more effective emitters of volatile cues as well as more responsive receivers of cues (Shiojiri and Karban, 2006). A reason for low prevalence of herbivory in the early summer can be also related to the fact that most of the plants were young and good emitter of signals due to which neighboring plants might become resistant to herbivory. As plants (most of the herbaceous plants in the garden) became mature in the late season, they became poor emitters and receiver of cues, hence faced more damages.

#### **4.2 Intensity of herbivory**

The proportion of leaves with herbivory damage i.e intensity was also high in native than non-native plant species in both seasons in all studied herbivory types. Herbivory damages in early season was mainly caused by generalists like aphids, slugs, snails, and few specialists like *Lilioceris lilli* (Lilly beetle) whereas in late summer in addition to these other specialists' herbivores were seen like *Pyrrhalta viburni* (Brown beetle), some unidentified caterpillars, and some unidentified larvae. Aphids were the most abundant group of herbivores in the garden. The ability of native herbivores to exploit non-native plants often differs between specialists and generalists (Bezemer et al., 2014). Some studies show generalists herbivores avoid non-native plants species (Cappucinno & Carpenter, 2005) others post that native herbivore prefer non-native plants (Parker and Hay, 2005).

Intensity of herbivory damage was high (out of 10 leaves, all 10 leaves were damaged) for some of the native plant species (*Salix lantana*, *Viburnum opulus*) in the garden. *Salix lantana* had high chewing intensity in both seasons as well as high sap-sucking damage intensity in early summer, but we were unable to observe which herbivore was causing the damage. *Viburnum opulus* also had high intensity of chewing damages, almost all the leaves of plant (only veins left) were chewed by a specialist herbivore brown beetle (*Pyrrhalta viburni*) (Appendix F, photo i). The brown beetle was not seen on any other plants at the garden which means it completely rely on only one plant i.e., *Viburnum opulus* for food at the garden, therefore resulting in overexploitation of the plant. Non-natives that suffered from high intensity of herbivory were from Brassicaceae family, Polygonaceae and few from other families. Brassicaceae, Polygonaceae, and few other families were seen to be commonly feed by generalist herbivores like aphids, snails, slugs of the garden etc. Only a non-native plant (*Acer pseudoplatanus*) had 10 out of 10 leaves galls formation during late summer while other had very few.

### **4.3 Herbivory prevalence/ Intensity of herbivory in non-native plants with congeneric/confamilial native plants in Norway.**

Phylogenetic similarity to native species has been always viewed as a strong factor in explanation in occurrence of herbivory in non-native plants in many studies. It is found that phylogenetic relatedness of non-native plant species to native plant species is a significant predictor of herbivory in this study as well. Non-native plant species with higher number of native congeners or native confamilial species suffered higher prevalence of herbivory than those with fewer congeners or confamilial species in this study. Few other literatures to date have also tested whether the herbivory for non-native with native relatives have positive (Conner et al., 1980; Dawson et al., 2009; Liu & Stiling, 2006) or negative (Cappucino and Carpenter, 2005; Agrawal et al., 2005). Non-natives that are more closely related to natives are more likely to share herbivores, resulting in more damage than phylogenetically isolated species (Odegaard et al. 2005) and the proportion of herbivory damage declines with mean phylogenetic distance to native relatives (Hill & Kotanen, 2009; Harvey et al., 2012).

Non-natives in presence of native congeners or confamilial species is supposed to have more herbivory than non-native without native congeners or confamilial plant species because of higher density of specialized insect herbivores (Root, 1973 cited in Dostal et al., 2013). Alternatively, this means if generalist herbivores are more common in species-rich communities then the difference between non-native with native relatives with non-native without native relative might not be significant. However, the impact of native relatives of non-native-to-non-native plants can vary with other confounding factors like the ecosystem types, habitat characteristics (Dostal et al., 2013), plant traits (Svarcova et al., 2007) etc. Dawson et al., (2009) study, which post that the proportion of leaves damage for species with native congeners was greater than those without result, was carried out in lowland and submontane rain forests of the Eastern Usambara Mountains in northeast Tanzania where rainfall is high throughout the year. In contradictory, Cappuccino and Carpenter (2005) worked in natural areas of Canada and U.S.A. found that herbivore damage to exotic plants was unrelated to the number of native congeners or confamilial native genera. The link of other similar plant traits

to the traits of the native host which may or may not exhibit phylogenetic signal might explain these deviations along with phylogenetic relation. Among congeneric and confamilial pair, the congeners pair showed significant variation in this study which might be due to more similar herbivore assemblages in congeners than confamilial species (Ødegaard et al.2005). Increasing phylogenetic distance from the nearest native relative, total leaf damage and the variety of damage types decreases (Harvey et al., 2012). The observed pattern suggest that congeners have stronger influence on the strength of herbivory than confamilial species and might fall away above the family level.

## **5. LIMITATIONS**

Limitation of this study could be that this study lacks proper identification of herbivores as it is vital in this study. Also, there is no reference data for the herbivores at the garden which states specialists or generalist of the study area. In this study we are only discussing about native/non-native plants and native herbivores, but it not confirmed that the study area lacks non-native herbivores. It would be also concise study if we divide non-native into invasive and non-invasive species and relate it to the herbivory. Studies have found that highly invasive plant suffer less leaf herbivory than non-invasive exotic species (Carpenter & Cappuccino, 2005). The study only considered above ground herbivores; however, the below ground herbivory can have impact on the results. Some abiotic and biotic factors might play key role in herbivory damages variations along with seasons, and native status. For instance, soil porosity, habitat fertility, precipitation, and temperature can have indirect effect on herbivory. Seasonal changes in abiotic condition are also important. Leaf traits, like leaf shape and size as larger leaves could be easily exploited than smaller leaves (Brown et al., 1991).

## **6. CONCLUSIONS**

To the best of my knowledge, this is one of the northern most documentation of the prevalence of invertebrate herbivory on plant species on a regional level including both planted and natural species and includes different herbivore guilds. This study supports the ERH to only a certain extent as a mechanism explaining non-native suffer less herbivory damages than non-native, in fact the herbivory damages vary with different herbivores feeding guilds. This means the ERH probably applies to limited subset of herbivores. The herbivory prevalence and intensity of herbivory would be better if species level identification of the herbivores were done, and this could be a subject of further investigation as well. It was that found that phylogenetic relatedness of non-native plant species to native plant species is a significant predictor of herbivores community and congeneric native relatives were stronger predictor than confamilial native relatives. While the effect of the seasonal variation on prevalence of herbivory on native and non-native plants are already visible within a summer of study year, the conclusions would have been different had this study conducted yearly variations as effects may be influenced by interannual variation in temperature and rainfall patterns, short-term studies may fail to elucidate such effects.

This result of this thesis has implications for management and policy to meet international biodiversity goals such as Aichi biodiversity target 9 (on reducing the impacts of invasive species) and 12 (on preventing extinctions). This study holds conservation implication. The result of this study suggests that non-native plants species may not always get rid of all types of enemies in an introduced area. The baseline of this study, that native plant species support the most of herbivore abundance, followed by non-natives with close native relatives, while non-native plant species that are distantly related to the native species have less or uneven herbivore community, can be used for conservation goals like maintenance of higher tropic levels.

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## APPENDICES

Appendix A. Field survey form for recording of herbivory damages.

Species name	Location	Growth form	Height (cm)	Area (% ground cover)	Phenological stage	Herbivory		Damage type					Intensity of leaf damage (x of 10)				Remark	
						Present/absent	Observed herbivore	Leaf miner	Chewing	Sap sucking	Galls	Unknown	Leaf miner	Chewing	Sap sucking	Galls		Unknown
				0.25, 0.5, 1, >1 m2	V, Fl, Fr													

Appendix B. The intensity of leaf-mining damage in native as well as non-native with leaf mining damage in both seasons.

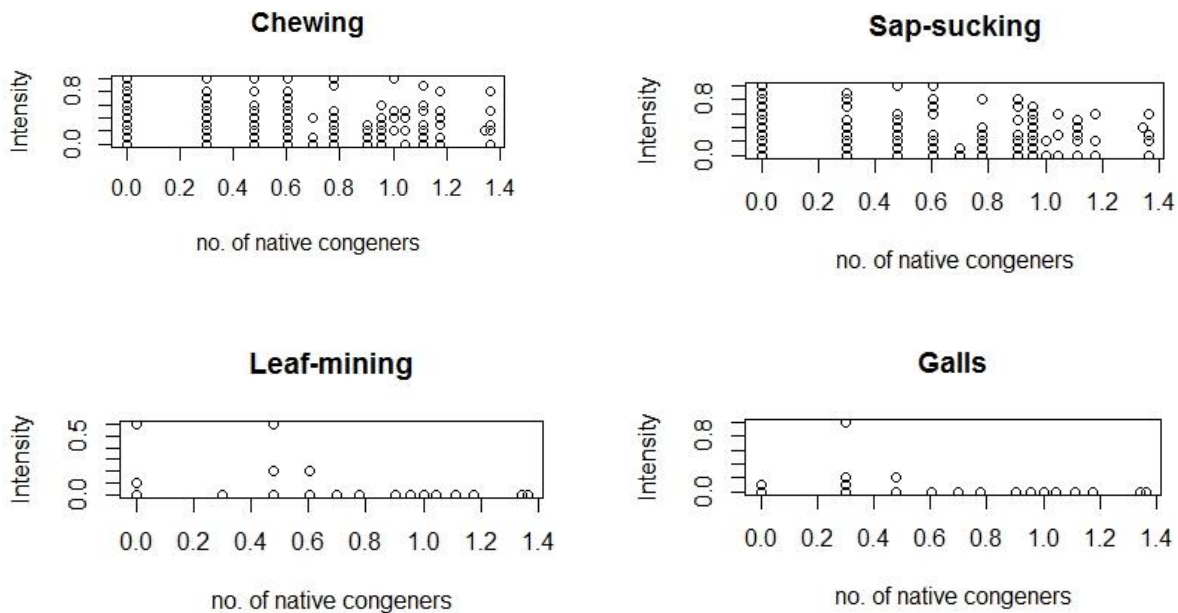
Leaf mining damage							
Name	Family	Native	Place in RBH	Seasons	Growth form	Phen_stage	Intensity
<i>Dryas octopetala</i>	Rosaceae	nat	SYS_Rosa	Early summer	S	V	0
<i>Sorbus hostii</i>	Rosaceae	non-nat	Haugene	Early summer	S	Fr	1
<i>Lunaria rediviva</i>	Brassicaceae	non-nat	SYS_Brassic	Early summer	H	Fr	0
<i>Lonicera caerulea</i>	Caprifoliaceae	non-nat	ARB-B3	Early summer	S	V	2
<i>Epilobium dodonaei</i>	Onagraceae	non-nat	SYS_Myrt	Early summer	H	V	6
<i>Prunus pensylvanica</i>	Rosaceae	non-nat	Haugene	Early summer	S	Fr	0
<i>Prunus virginiana</i>	Rosaceae	non-nat	Haugene	Early summer	T	V	2
<i>Prunus padus</i>	Rosaceae	nat	Haugene	Late summer	T	V	3
<i>Lonicera caerulea</i>	Caprifoliaceae	non-nat	ARB-B3	Late summer	S	V	6
<i>Prunus nipponica</i>	Rosaceae	non-nat	Haugene	Late summer	S	V	0

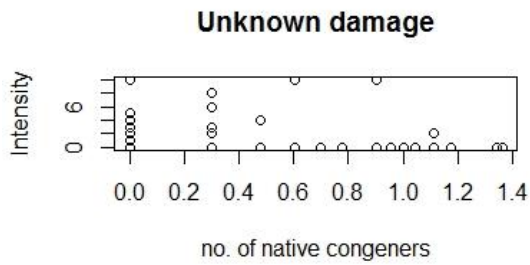
Appendix C. The intensity of galls damage in native as well as non-native with galls damage in both seasons.

Galls damage							
NAME	Family	Native	Place in RBH	Seasons	Form	Phen_stage	intensity

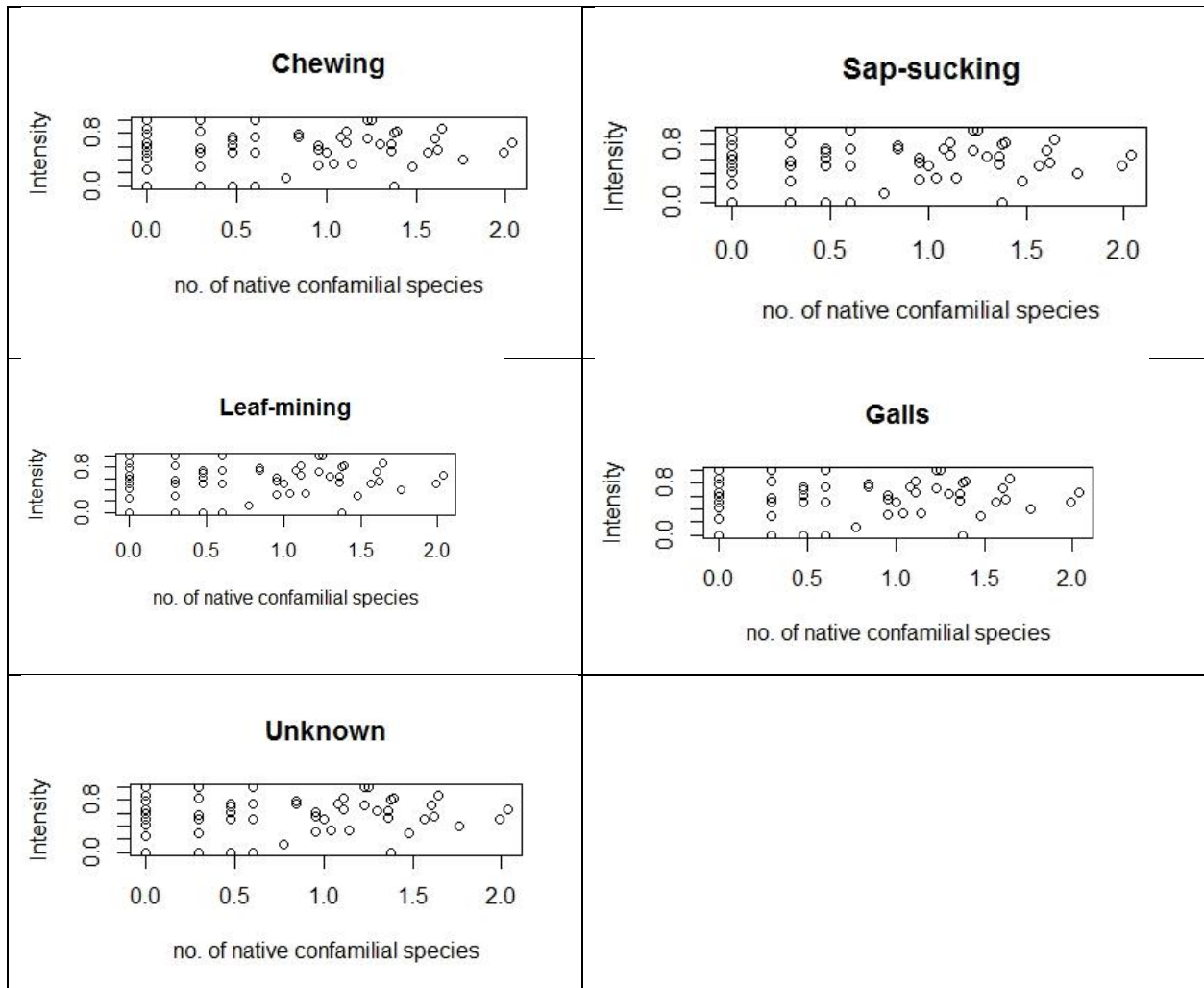
<i>Myrica gale</i>	Myricaceae	nat	SYS_Fagales	Early summer	S	V	0
<i>Sorbus hostii</i>	Rosaceae	non-nat	Haugene	Early summer	S	Fr	1
<i>Passiflora citrina</i>	Passifloraceae	non-nat	SYS_Malp	Early summer	Cl	V	0
<i>Amelanchier alnifolia</i>	Rosaceae	non-nat	ARB-B6	Early summer	S	Fr	1
<i>Acer saccharum</i>	Sapindaceae	non-nat	ARB-B7	Early summer	T	V	1
<i>Rhododendron hirsutum</i>	Ericaceae	non-nat	SYS_Eric	Early summer	S	Fl	0
<i>Alnus incana</i>	Fabaceae	nat	ARB-B2	Late summer	T	Fr	1
<i>Sorbus aucuparia</i>	Rosaceae	nat	ARB-B2	Late summer	S	Fr	0
<i>Salix caprea</i>	Salicaceae	nat	ARB-B4	Late summer	T	Fr	0
<i>Schoenoplectus lacustris</i>	Cyperaceae	nat	ARB-B9	Late summer	H	Fr	0
<i>Prunus padus</i>	Rosaceae	nat	Haugene	Late summer	T	V	0
<i>Myrica gale</i>	Myricaceae	nat	SYS_Fagales	Late summer	S	V	0
<i>Acer pseudoplatanus</i>	Sapindaceae	non-nat	PA	Late summer	T	V	10
<i>Amelanchier alnifolia</i>	Rosaceae	non-nat	ARB-B6	Late summer	S	Fr	0
<i>Passiflora citrina</i>	Passifloraceae	non-nat	SYS_Malp	Late summer	Cl	V	0
<i>Acer saccharum</i>	Sapindaceae	non-nat	ARB-B7	Late summer	T	V	2
<i>Rhododendron praevernium</i>	Ericaceae	non-nat	SYS_Eric	Late summer	S	V	0

Appendix D. Graph plotting intensity of herbivory against number of native plants in the same genus of non-native plant species. (Note: number of native congeners in x-axis is log (number of native congeners +1))





Appendix E. Graph plotting intensity of herbivory of different damages against number of native plants in the same family of non-native plant species. (Note: number of native confamilial species in x-axis is  $\log(\text{number of native confamilial species} + 1)$ )



Appendix F. Photos



a. Common slug of the garden



b. Common snail of the garden



c. Lilly beetle



d. Caterpillar chewing *Salix fargesii*



e. Chewing damage on *Brassica rapa* leaves



f. Galls on leaves of *Acer pseudoplatatanus*



g. Unknown damage on *Saxifraga*



h. Galls on *Alnus incana*



i. Brown beetle on *Vibrunum*

j. Leaf mining damage



