

Ecosystem retrogression leads to increased insect abundance and herbivory across an island chronosequence

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Summary

1. Ecosystem retrogression, the decline-phase of ecosystem development, occurs during the long-term absence of catastrophic disturbance. It usually involves increased nutrient limitation over time, and leads to reductions in primary productivity, decomposition, and nutrient cycling.

2. As a consequence, retrogression can alter the quality and abundance of host plants as food resources, but little is known about how these changes influence herbivore densities and foliage consumption.

3. In this study, we used a 5000-year-old chronosequence of forested islands in northern Sweden on which retrogression occurs in the absence of lightning-induced wildfire. We asked whether retrogression affected the abundance and herbivory of a dominant herbivorous weevil (*Deporaus betulae*) and the quality and productivity of a dominant host-tree, mountain birch (*Betula pubescens*).

4. *Betula pubescens* trees on retrogressed islands were less productive and produced smaller, tougher leaves that were lower in nutrients and higher in secondary metabolites than did those trees on earlier-successional islands.

5. Despite the lower density and what ecologists might perceive as poorer quality of host plants, we observed several-fold higher weevil abundance and damage on retrogressed islands. This suggests that weevils might prefer the poorer quality leaves with higher secondary metabolites that occur on nutrient stressed host trees.

6. Our results show that ecosystem retrogression increases susceptibility of *B. pubescens* trees to attack by herbivorous weevils.

7. Our study provides evidence that ecosystem retrogression and associated shifts in the quantity and quality of available resources can operate as an important driver of abundance of a dominant insect herbivore.

Key-words: arthropods, *Betula pubescens*, chronosequence, *Deporaus betulae*, ecosystem retrogression, herbivory, islands, nutrient limitation

Introduction

Long-term absence of catastrophic disturbances in ecosystems often leads to increased limitation by key nutrients, notably nitrogen (N) and phosphorus (P), over time (Walker & Syers 1976; Walker *et al.* 2001; Vitousek 2004). As a consequence, 'ecosystem retrogression' occurs, typically over millennia, and is characterized by reduced plant primary productivity, standing biomass, and rates of soil processes such as decomposition and nutrient cycling (Walker & Syers 1976; Vitousek 2004; Wardle, Walker & Bardgett 2004; Coomes *et al.* 2005).

Most of our understanding of patterns and processes associated with retrogression comes from studies that substitute space for time and take advantage of natural long-term chronosequences (Crews *et al.* 1995; Walker *et al.* 2001; Wardle *et al.* 2004, 2008). For example, volcanic islands (Vitousek 2004), marine terraces (Coomes *et al.* 2005), and glacial deposits (Richardson *et al.* 2004) create natural gradients that can span several millennia, from young or recently disturbed ecosystems to highly retrogressed, older ecosystems. Young or disturbed systems often are dominated by early-successional, faster-growing plant species that produce high quality litter, promoting decomposer processes and soil nutrient availability to plants (i.e. the 'build-up phase') (Wardle *et al.* 2003).

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Conversely, as ecosystems retrogress, they become characterized by more dominance by less productive plant species that input poor quality litter to the soil (i.e. the 'decline-phase'). Recalcitrant litter can slow decomposition and reduce nutrient availability to plants and higher trophic levels (Coomes *et al.* 2005; Wardle & Zackrisson 2005; Doblas-Miranda *et al.* 2008).

Through its effects on host plants, ecosystem retrogression can have substantial implications for bottom-up control of insect herbivores. Yet, while many studies have focused on insect herbivory during the build-up phase immediately following disturbance (e.g. Brown 1985; Siemann, Haarstad & Tilman 1999; Fagan & Bishop 2000), few studies have focused on insect herbivores during the decline phase (but see Gruner 2007). Retrogression can greatly influence the composition and density of host plants (Vitousek & Farrington 1997; Wardle *et al.* 2003), thereby altering the availability of resources for herbivores. In addition, host-plant biomass production, nutrient concentrations in tissues, and secondary metabolites can be affected by increasing nutrient limitation that occurs during retrogression (Wardle *et al.* 1997; Hättenschwiler, Hagerman & Vitousek 2003; Richardson *et al.* 2004; Vitousek 2004). Changes in all of these factors could potentially influence insect herbivore feeding preference and performance (Root 1973; Feeny 1976; Hunter & Price 1992; Agrawal 2001; Glynn *et al.* 2007). While it is clear that ecosystem retrogression can alter host plants as food resources, little is known about how these changes ramify to affect higher trophic levels.

In this study, we use an island chronosequence for which ecosystem retrogression occurs in the absence of lightning-induced wildfire (Wardle *et al.* 1997, 2003, 2004) to examine herbivory by an herbivorous weevil *Deporaus betulae* on mountain birch *Betula pubescens*, a common tree species on the islands. In addition, we examine variation in host-plant traits across the chronosequence that could serve as mechanistic links between ecosystem retrogression and the abundance of and damage by this herbivore. We predict that the abundance of this common insect herbivore and patterns of herbivory will track host-plant qualitative and density changes that occur during retrogression. Ultimately, our goal is to develop a better understanding of the potential influences of long-term ecosystem development, and notably the decline-phase, on trophic interactions.

Methods

STUDY SYSTEM

We performed this study on a 5000-year-old, post-fire chronosequence in the boreal forest of northern Sweden (65° 55'N to 66° 09'N; 17° 43'E to 17° 55'E). Mean annual precipitation is 750 mm, and the mean temperature is +13 °C in July and -14 °C in January. The study site consists of over 400 islands that occur in an archipelago in Lakes Hornavan and Uddjaure that vary in size from a few square meters to over 80 ha. The islands are all of the same geologic age (all being formed by the most recent glaciation 9000 years ago), and the only major extrinsic factor that varies among them is wildfire frequency

through lightning strike. Larger islands burn more often than smaller ones simply because they have a greater area to be struck by lightning. Fire frequencies have been estimated through scars on trees and from dating of ^{14}C of the most recent charcoal present in humus profiles (Wardle *et al.* 1997, 2003). The forested portions of the islands are not subjected to other major disturbances such as flooding and ice formation, as the level of the lake is always below the level of the lowest forested vegetation. These islands collectively form a retrogressive chronosequence, with retrogression increasing with decreasing island size. Larger, regularly burned islands are dominated by faster growing species, such as *Pinus sylvestris*, *B. pubescens*, *Vaccinium myrtillus*, and *V. vitis-idaea*. Smaller, infrequently burned islands are dominated by slower growing species such as *Picea abies* and *Empetrum hermaphroditum*. Plants on small islands produce low nutrient, high phenolic litter, which further reduces decomposition rates and nutrients release, along with N and P availability (Wardle *et al.* 1997, 2004; Wardle & Zackrisson 2005).

For this study, we used 30 islands chosen so that their areas are distributed log-normally. We divided islands into three size classes with 10 islands per class: large (> 1.0 ha), medium (0.1–1.0 ha) and small (< 0.1 ha), with a mean time since last major fire of 585, 2180 and 3250 years, respectively (Wardle *et al.* 2003). *Betula pubescens* occurred in varying densities on all of the islands, and each island served as an independent replicate ecosystem, as in previous studies (e.g. Wardle *et al.* 2004).

The birch leaf roller, *D. betulae*, is a common leaf weevil throughout Europe and is the dominant insect herbivore of *B. pubescens* on the islands. It feeds primarily on species of *Betula*, although it also is known to attack other plant species throughout its range, such as alder (*Alnus*) and hazel (*Corylus*). In early summer, the adult weevils (3–5 mm in length) emerge for several weeks to feed on *B. pubescens* leaves. The dispersal ability of *D. betulae* has not been well documented. Adult weevils are capable of flight and can move at least among host trees in a local habitat (Riihimäki, Kaitaniemi & Ruohomäki 2003). Likely adults can easily disperse among the islands in our study system. Female weevils roll conspicuous, conical leaf rolls, or 'cigars', in which they oviposit one to four eggs (Fig. 1). Leaf rolls dry out while attached to *B. pubescens* branches and then fall to the forest floor a few weeks later. The larvae chew through the roll and complete their development and overwintering in the soil (Horvath 1988). The autumnal moth *Epirrita autumnata* is another important herbivore on *B. pubescens* in some forests of northern Sweden when it outbreaks (Haukioja 2003), but there was no evidence of its being an important herbivore in our system, or in other nearby forests on the mainland, during the course of this study.

HERBIVORE DENSITY AND DAMAGE

To examine how weevil abundance and damage on *B. pubescens* varied across the island chronosequence, we surveyed each of the 30 islands three times during the 2007 growing season (14–18 June, 10–12 July and 4–15 August). In this system, *B. pubescens* leaves flush in early June and senesce in late August. During each survey period, we randomly selected seven trees per island. We recorded whether the trees were located at the edge (< 5 m from shore) or middle (> 5 m from shore) of each island. We then randomly selected three branches on each tree and counted the total number of weevils and leaf rolls present by scanning each branch. Next, we visually surveyed ten leaves on each branch to estimate the percent leaf area damaged by weevils (0%, 1–5%, 10–20%, 20–30% ... 90–100%), starting with the first full-sized leaf and working down the branch



Fig. 1. The birch leaf roller, *Deporaus betulae*, is the dominant insect herbivore of *Betula pubescens* on islands in lakes Hornavan and Uddjaure. Female weevils (top left photo) roll conspicuous, conical leaf rolls (top right photo) in which they oviposit. Weevil leaf damage is highest on small, retrogressed islands (bottom photo).

surveying every other leaf until 10 leaves were surveyed. Leaf damage by weevils is characterized by obvious scraping of the top of leaves and is easy to distinguish from other (less common) forms of herbivory. During July and August surveys, we also counted the total number of ants and spiders on each branch after surveying weevils and leaf rolls. Ants and spiders are generalist predators, and we considered them potential predators of weevils after observing avoidance behaviour of these predators by adult weevils (G. Crutsinger, personal observation).

BETULA PUBESCENS TRAITS

We examined a suite of *B. pubescens* traits that could potentially vary along the chronosequence and subsequently affect herbivore abundance and damage. To quantify host-plant density, we placed one 15 × 4 m transect on each island. Within that transect, we counted the total number of *B. pubescens* stems and measured the height (m) and stem diameter (cm) of every stem. We used a previously established allometric equation based on stem diameter to estimate above-ground biomass (kg m^{-2}) of trees for each island (Marklund 1988; Wardle *et al.* 2003). In August, we randomly chose two branches on each of 15 trees on each island and measured the largest leaf on each branch, or 30 leaves total per island. Several randomly selected leaves from each branch were then collected, immediately weighed, oven-dried for 48 h at 60 °C, and re-weighed to estimate leaf moisture content. A separate set of leaves was also collected from each branch, air-dried, and then ground for the nutrient, fibre, and secondary chemistry analyses described below. Also in August,

we estimated leaf toughness of 10 randomly selected fresh leaves per island using a force-gauge penetrometer (Type 516, Chatillon Corp., New York, NY) that measures the grams of force needed to penetrate the leaf surface. Two estimates of toughness were taken for each leaf and averaged as a single data point for that leaf.

We measured leaf fibre, cellulose, and lignin content for leaves from each island using the acid detergent fibre-sulphuric acid procedure, which involved sequential treatment of the sample with reagent to destroy various fractions, followed by gravimetric determination of the residues (Rowland & Roberts 1994). We also measured leaf C and N concentration using a Leco furnace (Laboratory Equipment Corporation, St Joseph, MI), and P concentration using the modified semi-micro Kjeldahl method (Geiger *et al.* 1987). Total soluble phenolics, tannins (condensed, hydrolysable and wall-bound), anthocyanins, catechin, chlorogenic acid and kaempferol were also measured for each island. Total soluble phenolics were estimated using the Folin-Ciocalteu assay (Singleton & Rossi 1965); Anthocyanins as described previously by Mancinelli & Schwartz (1984); Condensed and cell wall-bound tannins were determined by the butanol-HCl method following the methodology described by Ossipova *et al.* (2001). Hydrolysable tannins (Gallic and Ellagic acid) were analyzed by HPLC-DAD as described by Salminen *et al.* (1999) using a water column (Symmetry – 0.5 M, 3.9 × 150 mm). Chlorogenic acid, catechin and kaempferol were measured using the same column, following the elution system: A-Acetic acid (1%), B-Methanol (60%): 0–8 min, 15% B; 30 min, 60% B; 35–45 min, 100% B. Retention time and co-injection of the pure standards were used to identify the substances in the extracts.

STATISTICAL ANALYSES

For all analyses, individual islands were used as the unit of replication and we log-transformed variables as necessary to meet assumptions of normality and homogeneity of variance. We used separate repeated-measures one-way Analysis of Variance (ANOVA) to test for the effects of island size (large, medium, and small) on the number of leaf rolls and percent herbivory across the three surveys. Weevil densities were relatively low during all surveys (despite exerting substantial damage to *B. pubescens* leaves), so we examined the effects of island size on the cumulative number (summed across the three surveys) of weevil individuals, as well as weevil loads (no. of weevils per kg of *B. pubescens* biomass, using the tree biomass estimates described above) using separate one-way ANOVAs. As weevil abundance co-varied with leaf damage across islands, we also asked whether leaf damage varied among islands once variation in weevil abundance was factored out. To do this, we plotted leaf damage against log-transformed weevil abundance. We then took the residuals from a quadratic regression, which was the best-fit relationship between leaf damage and weevil abundance. We did this for each survey and used one-way repeated-measures ANOVA to test for the effects of island size on herbivory corrected for weevil abundance across the three surveys. Note that because there were no adult weevils observed on large islands during our surveys (see Results section), leaf damage values for large islands remain unchanged when we corrected for the abundance of weevils. We used separate one-way ANOVAs to examine the effects of island size on spider and ant abundance in August, when their abundances were highest.

On small islands, most trees fell within the 'edge' category (< 5 m from shore) because small islands have higher edge to area ratios than do large islands, so we tested for the influence of island edge effects on weevil herbivory. We first calculated the average herbivory for 'edge' and 'middle' trees for each large- and medium-sized island. We did this during the August survey so that damage could accrue throughout the growing season and we used separate paired *t*-tests to compare herbivore damage on edge and middle trees within large- or medium-sized islands. We surveyed approximately equal numbers of edge- and middle-categorized trees on both the medium and large island size classes. We also estimated degree of isolation for each island. This was done by measuring the area (ha) of land within 500 m of the edge of each island, which included other islands and the mainland. We then calculated an isolation ratio as follows: $[1 - ((\text{landmass area})/(\text{water area} - \text{landmass area}))]$. We examined whether herbivory rates were correlated with this island isolation ratio within each survey period.

We used separate one-way ANOVAs to test for the effects of island size on each of the host-plant traits we measured. To relate herbivore damage to *B. pubescens* traits we first examined covariation among traits. In our study we collected data on randomly selected trees on each island for *B. pubescens* traits, herbivory, and weevil abundance. As individual islands served as our units of replication, we did not necessarily use the same trees for every variable but instead derived an average for each island for each variable. We used principal components analysis (PCA) with a minimum eigenvalue of 2 to reduce the number of traits, with the first four axes of the PCA explaining 59% of the variation in the 25 traits. We then ran the least correlated traits from the PCA within a forward stepwise multiple regression (with $P = 0.10$ used as the threshold for variables to be included or excluded) to examine which traits best explained variation in herbivory among island size classes. In the stepwise regression, we included total above-ground biomass, leaf size, % N, total phenolics, ellagic acid, wall-bound tannins, anthocyanins, leaf toughness, cellulose, and % leaf moisture.

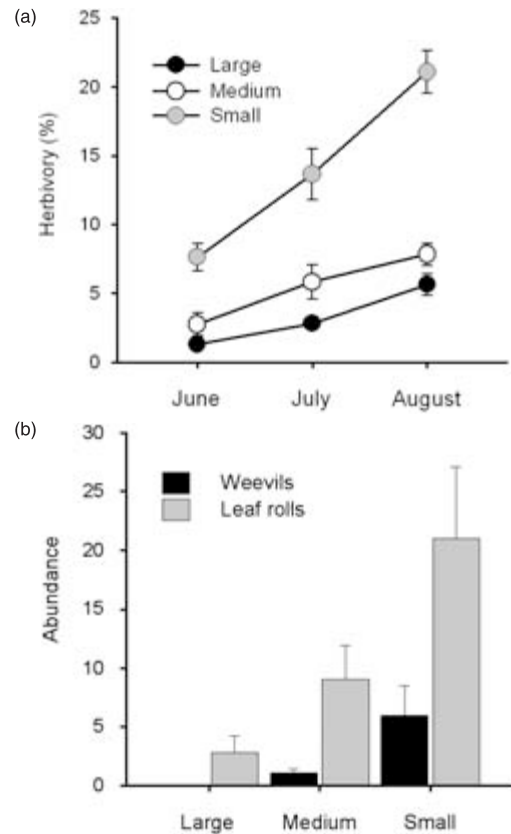


Fig. 2. (a) Mean (\pm SE) leaf area damaged by weevils on *Betula pubescens* throughout the growing season. (b) The effects of island size on mean (\pm SE) abundance of adult weevils per island (black bars; cumulative for the entire season) and leaf rolls (gray bars; only for the August survey when leaf rolls were most abundant). Weevils and leaf rolls were analyzed separately with lower and uppercase letters distinguishing significant differences ($P < 0.05$, Tukey's *post hoc* test) between island size classes.

Table 1. Repeated-measures ANOVA results examining the effects of island size on percent leaf damage by weevils, percent damage corrected for the abundance of weevils, and leaf roll abundance (number per island) throughout the growing season

Variable	Effect	df	F	P
Herbivory (%)	Size	2, 27	54.2	< 0.0001
	Time	2, 26	90.2	< 0.0001
	Size \times time	4, 52	3.7	0.009
Corrected herbivory	Size	2, 27	3.8	0.034
	Time	2, 26	0.0	0.999
	Size \times time	4, 52	0.6	0.653
Number of leaf rolls	Size	2, 27	6.8	0.003
	Time	2, 26	6.1	0.001
	Size \times time	4, 52	1.5	0.206

Results

Weevil herbivory varied significantly among island size classes during every survey period (Fig. 2a, Table 1). Small islands had two times more leaf damage than large islands

Table 2. Separate one-way ANOVA results examining the effects of island size on weevils (number per island), weevil loads (no. of weevils/kg biomass of *Betula pubescens*), arthropod predators (number per island), and measures of host-plant quantity. Included are also the means (\pm SE) for each variable on large, medium, and small islands

Variable	Large	Medium	Small	F*	P
Number of weevils	0 (0)	1.1 (0.34)	6 (2.54)	4.6	0.018
Weevil loads	0 (0)	0.46 (0.28)	4.92 (1.48)	9.6	0.007
Number of spiders	2.50 (0.67)	7.28 (1.64)	23.12 (7.14)	24.2	< 0.0001
Number of ants	15.36 (12.47)	6.06 (3.45)	5.56 (4.68)	2.2	0.109
Tree biomass (kg m ⁻²)	2.73 (0.55)	4.23 (0.56)	1.65 (0.45)	6.0	0.006
Tree density (m ⁻²)	0.32 (0.05)	0.57 (0.10)	0.44 (0.05)	3.1	0.059
Tree height (m)	0.96 (0.16)	1.48 (0.16)	0.80 (0.09)	5.8	0.007

*df for all variables = 2, 27.

Table 3. Separate one-way ANOVA results examining the effects of island size on measures of *Betula pubescens* leaf quality. Included are also the means (\pm SE) for each variable on large, medium, and small islands

Variable	Large	Medium	Small	F*	P
Leaf size (mm)	51.34 (0.75)	49.86 (0.58)	42.84 (0.83)	38.38	< 0.0001
P (%)	0.20 (0.003)	0.20 (0.009)	0.18 (0.009)	1.18	0.327
C (%)	51.63 (0.13)	51.64 (0.11)	51.20 (0.10)	4.76	0.016
N (%)	2.11 (0.06)	2.09 (0.06)	1.89 (0.06)	3.43	0.047
C : N	24.64 (0.71)	24.84 (0.80)	27.28 (1.0)	2.98	0.067
N : P	10.32 (0.22)	10.31 (0.22)	10.11 (0.32)	0.21	0.729
Moisture (%)	0.33 (0.01)	0.33 (0.007)	0.35 (0.007)	2.31	0.118
Toughness (g)	34.19 (2.64)	39.50 (2.52)	48.32 (4.62)	4.38	0.022
Fibre (%)	28.25 (0.35)	29.51 (0.74)	30.44 (0.53)	3.74	0.036
Cellulose (%)	11.74 (0.75)	12.67 (0.41)	14.01 (0.59)	3.58	0.041
Lignin (%)	16.60 (0.64)	16.90 (0.81)	16.45 (0.71)	0.09	0.908

*df = 2, 27 for all variables.

and 1.3 times more damage than medium islands by the end of the growing season. There was a significant interaction between island size and time (Table 1), likely driven by greater differences in weevil herbivory among island size classes later in the season (Fig. 2a). Small islands had approximately five times more weevils and leaf rolls than medium islands and 12.5 times more leaf rolls than large islands (Fig. 2b, Tables 1 and 2). We did not observe any adult weevils on large islands during the study, even though leaf damage by weevils was clearly present. There was still greater leaf damage on small islands than on medium- or large-sized islands, after correcting for higher weevil abundances (Table 1). Weevil loads were c. 10 times higher on small islands than medium islands (Table 1).

Potential predator release did not account for higher *D. betulae* herbivory on small islands. There was no effect of island size on ant abundance, and spiders were actually more abundant on small islands than on larger islands (Table 2). Island edge effects were not an important influence on weevil herbivory: there was no effect of tree proximity to island edge on herbivore damage for either large islands (df = 18, $t_{\text{paired}} = 0.718$, $P = 0.481$) or medium islands (df = 18, $t_{\text{paired}} = 0.795$, $P = 0.436$). Island isolation also did not explain higher *D. betulae* herbivory on small islands. There was no significant correlation between herbivory rates and island isolation during any survey ($P > 0.21$ for all surveys).

Betula pubescens trees were 20% shorter and had 65% lower biomass on small islands than on large- or medium-sized islands, but stem density was lowest on large islands (Table 2). Tree height, density, and biomass were greatest on medium-sized islands, indicating that *B. pubescens* trees are most productive and have the highest abundance on islands that are intermediate in time since disturbance.

Many *B. pubescens* leaf traits varied with island size. Leaves from small islands were c. 20% smaller and c. 30% tougher than those on larger islands, and had a 7% higher fibre and 20% higher cellulose content (Table 3). Lignin content was unaffected by island size. Leaf N concentration was 11% lower and C : N ratio was 8% higher on small islands than on larger islands. There was no effect of island size on leaf moisture content (Table 3). Leaf secondary chemistry also varied with island size. Leaves from smaller islands contained 8% more total phenolics, 7.8 times more ellagic acid, and 2.3 times higher gallic acid than those from large islands. Leaves from medium islands had the highest anthocyanin concentrations, which were c. 15% more than for leaves from small and large islands. There was no effect of island size on condensed tannins, wall-bound tannins, catechin, chlorogenic acid, or kaempferol (Table 4). Multiple regression analysis showed that leaf size, moisture content, cellulose, and total phenolics collectively explained c. 69% of the variation in *D. betulae* herbivory across islands (Fig. 3, Table 5).

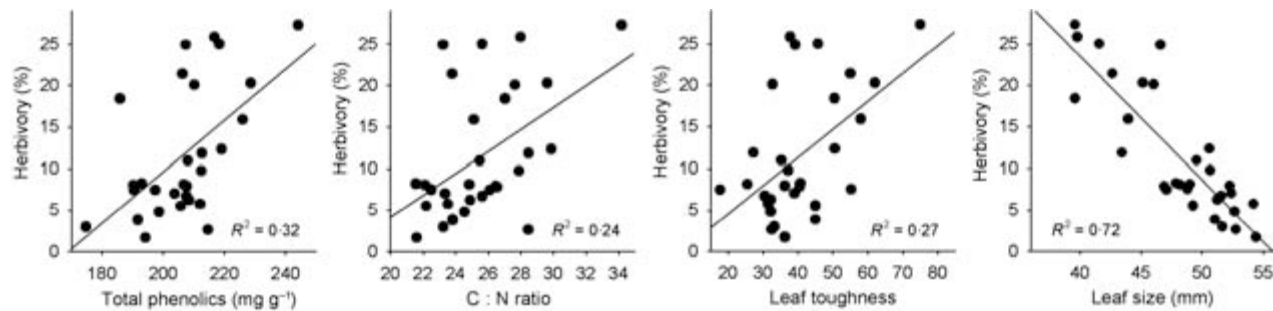


Fig. 3. Percent damage of *B. pubescens* leaves by weevils in relation to leaf traits, during August 2007. Each point represents the average for an island ($P < 0.006$ for all regressions).

Table 4. Separate one-way ANOVA results examining the effects of island size on *Betula pubescens* secondary chemistry (in mg/g leaf material). Included are also the means (\pm SE) for each variable on large, medium, and small islands

Variable	Large	Medium	Small	F^*	P
Total phenolics	203.7 (2.53)	199.0 (4.17)	215.6 (4.92)	4.5	0.019
Wall-bound tannins	8.85 (0.31)	8.68 (0.41)	8.42 (0.41)	0.3	0.732
Anthocyanins	0.21 (0.006)	0.24 (0.008)	0.20 (0.005)	6.2	0.006
Condensed tannins	101.1 (8.58)	115.8 (6.16)	98.02 (8.65)	1.4	0.250
Catechin	1.09 (0.19)	1.17 (0.20)	1.46 (0.21)	0.9	0.339
Chlorogenic acid	10.67 (1.57)	9.66 (1.40)	8.48 (1.41)	0.5	0.576
Kaempferol	121.9 (12.64)	112.2 (7.53)	113.0 (20.17)	0.1	0.871
Gallic acid	0.92 (0.14)	1.91 (0.52)	2.20 (0.47)	4.3	0.023
Ellagic acid	2.97 (1.30)	8.50 (1.79)	23.21 (5.25)	10.0	0.0005

*df = 2, 27 for all variables.

Table 5. Stepwise multiple regression model results using host-plant traits as predictors of *Betula pubescens* leaf damage (% removed) by weevils

Independent variable(s)	Parameter	Partial r^2	Model r^2	F	P
Leaf size (mm) (LS)	-0.15	0.55	0.55	6.4	< 0.0001
LS and moisture (%) (M)	18.11	0.04	0.60	5.6	0.087
LS, M and cellulose (%) (C)	0.25	0.05	0.65	4.7	0.060
LS, M, C and total phenolics (mg g ⁻¹)	0.02	0.03	0.69	3.1	0.089

Discussion

We found that ecosystem retrogression within a fire-driven chronosequence affected both the quantity (productivity and density) and quality (leaf nutrients and secondary chemistry) of host plants available to the dominant herbivore, *D. betulae*. *Betula pubescens* trees on small, retrogressed islands were less productive than those on larger islands, and produced smaller, tougher leaves that contained lower nutrient levels and higher concentrations of secondary metabolites. Despite host plants on small islands being less abundant and what could be perceived as poorer quality, we observed substantially higher weevil abundance and damage on these islands. Other factors such as predator abundance, island edge effects, and island isolation did not appear to affect weevil herbivory. Taken together, these results show that ecosystem retrogression mediates above-ground trophic interactions between a dominant insect herbivore and a dominant tree species in northern Sweden.

Our results differ from those obtained for arboreal arthropods associated with *Metrosideros polymorpha* trees across a long-term retrogressive chronosequence on volcanically derived substrates of different ages on the Hawaiian islands (see Crews *et al.* 1995; Vitousek 2004). In that system, Gruner (2007) found that total herbivore abundance showed a unimodal relationship with substrate age, and declined with ecosystem retrogression. In our study, weevil abundance increased consistently as retrogression proceeded. Though Gruner (2007) found that the abundance of arboreal beetles was highest on the oldest islands, most beetles in that system were not herbivores (Gruner 2004). It's probable that herbivore responses to retrogression are species specific. To our knowledge, no other studies to date have examined above-ground arthropod response to ecosystem retrogression. However, a few have examined the responses of soil invertebrates to ecosystem retrogression, and our results contrast with those. Two previous studies in rainforests in southern New Zealand (Williamson, Wardle & Yeates 2005; Doblus-Miranda *et al.*

2008) both found that litter-associated soil invertebrates generally declined with retrogression, apparently because of reduced litter quality and lower soil nutrient availability. One potential caveat of our study is that we surveyed potential predators of weevils only on the foliage of trees where adults weevils forage. We did not survey for potential predators on the ground or in the soil where weevil larvae overwinter, but recent pitfall trapping studies on these islands show that these predators are either unrelated to island size or are more abundant on smaller islands (M. Jonsson, D. Wardle & G. Yeates, unpublished data).

Nutrient stress that occurred during retrogression resulted in lower *B. pubescens* productivity and density on small islands, which is consistent with previous results from this system (Wardle *et al.* 1997, 2003). Yet, weevil abundance did not track *B. pubescens* productivity, which contrasts with our initial predictions and the results from Gruner's (2007) study of herbivores associated with *M. polymorpha* on the Hawaiian islands. Higher levels of herbivory on small islands relative to medium and large islands could be because of two reasons: (i) there were more weevil individuals on small islands, or (ii) there were more herbivory per weevil on small islands. When we corrected islands for variation in weevil abundance, we still observed higher weevil herbivory on small islands. This result suggests that weevils are both more abundant and eat more per capita on small islands.

We found that leaf secondary metabolites increased and nutrient content decreased with time since disturbance, which is consistent with previous work in this system (Wardle *et al.* 1997, 2004) and other chronosequences (Vitousek, Turner & Kitayama 1995; Richardson *et al.* 2004; Coomes *et al.* 2005). There has been a considerable research on plant defence and insect herbivores associated with *B. pubescens* trees (for a review, see Haukioja 2003), particularly in relation to phenolics and the autumn moth that undergoes outbreaks. This moth species is adapted to high levels of hydrolysable tannins present in *B. pubescens* and metabolises these tannins to sugar and gallic acid to make use of the sugars when the plant is nutrient limited. Haukioja (2003) suggested an adaptive model in which the effects of defensive compounds on insect growth depend strongly on leaf nutrient content. For example, insects may compensate for low amounts of leaf nutrients through compensatory feeding, thereby increasing the intake of secondary compounds. We found high levels of byproducts such as gallic and ellagic acids associated with high weevil herbivory on mountain birch, which is in agreement with the model by Haukioja (2003). However, this does not explain why weevils feed on birches on retrogressed islands when productive trees with more nutritious and less defended leaves occurred in close proximity on adjacent larger islands; weevils seemingly could have colonized those trees.

One reason for the herbivory patterns that we observed across the chronosequence could be that *D. betulae* prefers trees with higher concentrations of secondary metabolites on the small islands. Supporting this explanation, Kuokkanen, Yan & Niemela (2003) found that the leaf weevil *Phyllobius maculicornis* preferred leaves of a closely related birch species,

Betula pendula, that were grown under elevated CO₂ over those grown under ambient CO₂ conditions. Elevated CO₂ leaves were lower in nitrogen and higher in phenolics and condensed tannins than those grown under ambient conditions. Another study on *B. pendula* showed that four species of caterpillars varied from no preference to preferring leaves with higher phenolics in a cafeteria experiment (Hartley & Lawton 1987). Determining the chemical feeding cues that insects use to select particular host plants is challenging. Without extensive cafeteria experiments and physiological studies of *D. betulae* on the islands, we cannot determine the precise chemical mechanisms responsible for weevil herbivory patterns. Late-season tree quality (nutrient and secondary chemistry) could also be reduced by early-season weevil herbivory. More research is needed to tease apart the degree that weevils prefer low quality trees vs. contribute to declines in tree quality. What is clear from our results is that long-term absence of catastrophic disturbance, and subsequent nutrient limitation, has led to increased susceptibility of *B. pubescens* trees to damage by *D. betulae*. The fact that there were more weevils per kilogram of tree biomass on small islands than on medium or large islands also supports the idea that weevils might perform better on host trees on small islands than on host trees on larger islands. Estimating survival and fitness of weevils on the different islands was beyond the scope of the current study, but would reveal whether weevils benefit from increased host susceptibility.

Our results are consistent with theory predicting that abiotic stress, as characterized by decreased *B. pubescens* biomass and leaf quality in this system, increases host-plant susceptibility to insect herbivores (Mattson & Haack 1987; Koricheva, Larsson & Haukioja 1998; Inbar, Doostdar & Mayer 2001). Herbivore responses to ecosystem retrogression are probably species specific, both in terms of host-plant responses to nutrient limitation, and insect preferences for the quality and productivity of hosts. For example, Hawaiian herbivorous arthropods density was positively correlated with productivity and foliar nutrient status of *M. polymorpha* individuals, and fertilization of nutrient-limited trees increased herbivore density and richness (Gruner, Taylor & Forkner 2005). In contrast, N fertilization experiments of nutrient-stressed *B. pubescens* can increase leaf N content and decrease secondary metabolites (Tuomi *et al.* 1984). If weevils prefer nutrient-stressed *B. pubescens* trees on small islands, we would predict that addition of nutrients would reduce weevil density and attack.

In this study, host-plant productivity and leaf quality were reduced across a retrogressive chronosequence, while interactions involving a dominant foliar herbivore were intensified. It is also possible that chronic insect herbivory may further reduce foliar nutrient levels and increase secondary metabolites in leaf litter inputs, thereby slowing decomposition and leading to further nutrient immobilization in retrogressed systems (Findlay *et al.* 1996; Bardgett & Wardle 2003). Our study provides evidence that ecosystem retrogression and associated shifts in the quantity and quality of available resources can operate as an important driver of trophic interactions.

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