

## Leaf damage by herbivores and pathogens on New Zealand islands that differ in seabird densities

Christa P. H. Mulder<sup>1\*</sup>, David A. Wardle<sup>2</sup>, Melody S. Durrett<sup>1</sup> and Peter J. Bellingham<sup>3</sup>

<sup>1</sup>Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

<sup>2</sup>Department of Forest Vegetation Ecology, Faculty of Forestry, Swedish University of Agricultural Sciences, S 901 83 Umeå, Sweden

<sup>3</sup>Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

\*Corresponding author (Email: [cpmulder@alaska.edu](mailto:cpmulder@alaska.edu))

Published online: 26 March 2015

**Abstract:** Seabirds impose a high-nutrient, high-disturbance regime on the islands on which they nest, resulting in higher nutrient cycling rates, plant nutrient uptake and leaf nutrient content. On islands off the coast of New Zealand, seabird-dominated islands support greater densities of soil- and litter-dwelling consumer biota. We predicted that islands with high seabird densities would have higher levels of leaf damage as a result of higher densities of foliar consumers (herbivores and pathogens). Damage levels on leaves of six common tree species were compared between 9 islands with active seabird colonies and 10 islands with low seabird densities resulting from invasion by predatory rats. There were no consistent differences in leaf damage by chewing, mining, or phloem-feeding herbivores across plant species; pathogen damage was lower on islands with high seabird densities than on those with low densities, but this was driven by only two of the plant species. Instead, plant species differed in which of several possible damage types responded to seabird presence, and in which plant leaf traits responded to seabird-related environmental changes. Across plant species, those with more resource-acquisitive leaf traits such as high percent nitrogen and low structural investment experienced higher levels of chewing damage (which accounted for 66–100% of all damage), but not other damage types. We conclude that the fertilisation and disturbance regimes imposed by seabirds do not lead to consistent changes in consumer damage to plants, because of variable responses by both individual plant species and different consumer groups.

**Keywords:** leaf economic spectrum; rat invasion; trophic cascades

### Introduction

The productivity of terrestrial plants is frequently limited by nutrients, particularly nitrogen (N) and phosphorus (P) (Epstein 1972; Vitousek & Howarth 1991). This often also results in nutrient limitation for herbivores, and numerous studies have found positive relationships between foliar N or P concentrations and herbivore fitness or foliar damage, both within and across plant species (e.g. Feeny 1970; Mattson 1980; Scriber & Slansky 1981; Molinari & Knight 2010). Plants on islands on which seabirds breed are likely to be released from N and P limitation, because the seabirds deposit labile N and P of marine origin, primarily in the form of guano, thereby increasing nutrient availability to plants (see reviews in Mulder et al. 2011; Smith et al. 2011). Seabirds impose a high-nutrient, high-disturbance regime that selects for fast-growing plant species with high light and nutrient demands, leading to the dominance of these (Ellis et al. 2011). Further, increased densities or biomasses on islands with higher seabird densities have been found for a range of groups of above- and below-ground consumer organisms, including invertebrate scavengers and detritivores, insects, nematodes, spiders, and reptiles (Polis & Hurd 1996; Markwell & Daugherty 2002; Fukami et al. 2006; Towns et al. 2009; Kolb et al. 2010). However, whether impacts of this seabird-imposed fertilisation and disturbance regime extend to consumer damage on plants has not been examined.

Islands off the east coast of northern New Zealand provide an excellent system in which to study impacts of seabirds on community structure and ecosystem function. Although all of these islands were once home to high densities of burrowing seabirds (Procellariiformes), many have been invaded by non-native rats (*Rattus rattus* or *R. norvegicus*), resulting in a mean reduction in seabird density of  $\approx 95\%$  (Fukami et al. 2006). Previous studies in this system have shown that islands with high and low densities of seabirds differ in plant community structure (Wardle et al. 2007; Grant-Hoffman et al. 2010), and in below-ground properties such as soil fertility (i.e. plant-available N and P), microbial activity, litter decomposability, and litter- and soil-inhabiting biota (Fukami et al. 2006; Mulder et al. 2009; Towns et al. 2009; Wardle et al. 2009). Islands on which large seabird colonies are retained (hereafter 'seabird islands') also have higher N cycling rates, higher foliar N content and lower C:N ratios than those on which seabird populations have been greatly reduced or eradicated (hereafter 'non-seabird islands') (Wardle et al. 2009). Despite this, above-ground biomass and canopy density of shrubs and trees are actually reduced on seabird islands (Wardle et al. 2007; Mulder et al. 2009). While chronic disturbance of soils by burrowing and trampling by seabirds may reduce plant growth, another factor that may contribute is increased leaf consumption and damage by herbivores and pathogens on these islands. We would expect higher rates of plant consumption within a host species if plants have higher

nutrient content and/or lower concentrations of secondary compounds when released from nutrient limitation. We would also expect higher relative abundances of plant species on the 'acquisitive' end of the leaf economic spectrum; such species tend to have high foliar N concentrations, low leaf mass per area (LMA), low investment in structural components (e.g. lignin), low concentrations of secondary compounds, and high leaf turnover rates relative to resource-conservative species (e.g. Díaz et al. 2004; Wright et al. 2004), and higher rates of consumption by herbivores (e.g. Coley 1983; Herms & Mattson 1992; Pérez-Harguindeguy 2003; Endara & Coley 2011).

In this study we examined damage caused by foliar herbivores and pathogens (collectively referred to as 'consumers') on islands with high versus low numbers of seabirds, and explored whether variation in foliar traits can explain variation in leaf damage. We focused on six common woody plant species, and tested the following predictions: (1) Across species, plants with traits maximising resource acquisition will sustain higher levels of consumer damage than those with traits favouring resource conservation; (2) Within species, plants on seabird islands will have higher levels of consumer damage to their leaves than those on islands with few seabirds; and (3) Within species, greater consumer damage on leaves on seabird islands can be explained by changes in leaf foliar traits that are driven by seabird density. In combination, our results will indicate whether the bottom-up effects of seabird nutrient inputs that drive greater densities of consumer biota below ground also drive higher foliar consumption rates above ground.

## Methods

### Islands

Nineteen islands located off the warm temperate north-east coast of the North Island of New Zealand (Appendix 1) were selected based on seabird density, size (similar size ranges for islands with and without seabirds), and the presence of well-developed multi-species secondary forest. Nine of the islands support seabird colonies ('seabird islands'; Appendix 1); the most abundant species are *Pelecanoides urinatrix* (common diving-petrel), *Puffinus bulleri* (Buller's shearwater), *Pterodroma macroptera gouldi* (grey-faced petrel), and *Pelagodroma marina* (white-faced storm petrel) (all Procellariiformes). On the other 10 islands ('non-seabird islands'; Appendix 1), seabird numbers have been greatly

reduced by rats (*R. rattus* or *R. norvegicus*) that invaded between 150 and 50 years ago (Fukami et al. 2006). Rats had been eradicated from some of these islands before our study began but seabird colonies were still at low densities, hence they were classified as 'non-seabird islands' (Fukami et al. 2006). There were no significant differences in mean latitude, longitude, island size, or distance to the mainland between uninvaded and invaded islands (Fukami et al. 2006).

Most information available for both groups of islands comes from two 10 × 10 m plots located in the most mature secondary forests that could be found on each island (Fukami et al. 2006). On seabird islands these plots were located on colonies in which these birds nest underground. We obtained an index of seabird density by counting burrow entrances in the 100-m<sup>2</sup> area. Seabird densities on the seabird islands ranged from 3.5 to 101 active burrows per 100 m<sup>2</sup> (mean = 36.5), while seabird densities on non-seabird islands ranged from 0 to 8 burrows per 100 m<sup>2</sup> (mean = 1.5) (Appendix 1). While this classification results in a small amount of overlap in seabird densities between the two seabird status categories, it allows for comparison with other papers on this system, and we also explicitly evaluate relationships with seabird density.

### Focal plant species

Six common species of broadleaved evergreen woody plants were selected, all of which occurred in the forest on at least half of the islands: *Piper excelsum* s.l. (Piperaceae), *Melicytus ramiflorus* (Violaceae), *Melicope ternata* (Rutaceae), *Coprosma macrocarpa* subsp. *minor* (Rubiaceae), *Planchonella costata* (Sapotaceae) and *Corynocarpus laevigatus* (Corynocarpaceae; hereafter all species are referred to by genus). These species differ in their location along the leaf economic spectrum, as indicated by LMA, leaf turnover rates, and foliar concentrations of N, P, fibre, and lignin (Table 1).

### Insect herbivore damage estimates and leaf characteristics

Damage data were obtained between 10 February and 17 April 2004. For each species up to 10 plants per island were selected (Appendix A; total number of plants = 651). Plants came from within or near the 10 × 10 m plots, with additional randomly selected plants located up to 20 m away if needed. From each plant the outermost three leaves (leaflets for *Melicope*) on each of three branches at a height of 1–2.5 m were selected (i.e. nine leaves or leaflets total). For each leaf, we visually estimated the proportion of its area affected by each type

**Table 1.** Leaf trait values of the six focal plant species. Values are means based on plants from non-seabird islands. Leaf retention data are expressed as percent of leaves retained over 1 year (Mulder et al. 2009). 'LEI' is the leaf economic index, the value of the first axis of a principal component analysis on the leaf variables; low and high values indicate maximisation of resource-acquisitive and resource-conservative properties respectively. Species are presented in order of increasing LEI.

Species	%N	%P	LMA (g m <sup>-2</sup> )	% Leaf retention	% Fibre	% Lignin	LEI
<i>Piper excelsum</i> G.Forst.	3.16	0.37	42	3	26.9	8.6	-2.53
<i>Melicytus ramiflorus</i> J.R.Forst. & G.Forst.	2.66	0.37	52	3	34.6	8.4	-1.21
<i>Melicope ternata</i> J.R.Forst. & G.Forst.	2.26	0.25	58	7	29.2	7.6	-1.08
<i>Coprosma macrocarpa</i> Cheeseman	1.45	0.19	70	2	31.6	9.9	0.11
<i>Corynocarpus laevigatus</i> J.R.Forst. & G.Forst.	2.46	0.19	85	25	38.2	12.5	2.19
<i>Planchonella costata</i> (Endl.) Pierre	2.77	0.17	79	28	36.4	19.7	2.52

of damage that could be distinguished. For all plant species except *Piper* we classified damage types by feeding guild into that caused by ‘chewers’ (all forms of herbivory caused by the chewing mouthparts of caterpillars and beetles, e.g. holes, rasps, edge bites); ‘phloem-feeders’ (caused by insects such as aphids and psyllids, and usually evidenced by small holes and a discoloured area surrounding them); and ‘miners’ (evidenced by mine traces left by larvae). If leaf area had been removed, e.g. by chewers, damage was expressed relative to the estimated leaf area originally present.

Since in most cases the herbivore species responsible for the damage was not seen, we primarily described types of damage (e.g. holes on the edges of the leaf versus near the midrib, rasping, mining). However, the same organism may sometimes have been responsible for multiple types of damage, or multiple species may have caused damage of similar appearance. Leaves of *Piper* had only one type of damage (chewing by larvae, primarily *Cleoria scriptaria*, Geometridae; Beever 1987; Hodge et al. 2000). Since *Piper* leaves have a very consistent ‘heart’ shape we established an allometric equation describing the undamaged leaf area on the basis of length and maximum width (area in cm<sup>2</sup> = 0.644 × (length in cm × width in cm) + 12.02, R<sup>2</sup> = 0.96, N = 40; leaves ranged from 4.7 to 12.0 cm in length and 5.3 to 15.6 cm in width). We then predicted undamaged leaf area, measured actual leaf area, and calculated leaf area lost to herbivory as the difference between the two. We recorded damage that could be ascribed to ‘pathogens’ (indicated by appearance of hyphae or asci) on all plant species. Since leaf area or LMA may differ between invaded and uninvaded islands, we also calculated the biomass affected by damage (= % of area damaged × LMA) for all species; however, these results were qualitatively almost identical to area-based results, so we report areal results only.

Our estimates of leaf damage do not take into account the potential loss of entire leaves during or after herbivory. However, there were no differences in leaf turnover rates between invaded and uninvaded islands (Mulder et al. 2009), and the species with the highest turnover rate (*Piper*) exhibits no change in rate of leaf loss when protected from herbivores (Hodge et al. 2000). Therefore, loss of entire leaves is unlikely to bias estimates of consumer damage with respect to the presence of seabirds.

We used data on leaf chemistry and morphology measured on each of the six plant species on each island presented in previous studies (Mulder et al. 2009; Wardle et al. 2009). Briefly, we obtained fresh leaf area, dry mass, and LMA on all leaves, and concentrations of N, P, condensed tannins (vanillin method; Broadhurst et al. 1978), and total phenolics (Price & Butler 1977) on foliage from three individuals per species per island (Mulder et al. 2009). Thirty fully expanded leaves from at least five individual plants per species were collected and bulked for determination of concentrations of lignin, cellulose, and fibre (Wardle et al. 2009).

### Data analysis

Analyses were performed using SAS (version 9.2, SAS Institute). In evaluating impacts of seabird density, islands rather than individual plants were the experimental units; we used means of all leaves for each species–island combination. Where appropriate, data were log<sub>10</sub>-transformed to meet model assumptions. Means in text are means ± SEM.

Principal components analysis (PCA) was used to generate a ‘leaf economic index’ (LEI) to indicate the relative location of each of the six plant species along the ‘leaf economic spectrum’

(sensu Wright et al. 2004). We ran PCA on LMA, leaf retention (% leaves remaining on the plant after 1 year), and foliar %N, %P, % lignin and % fibre, using values from non-seabird islands (Table 1). Values for the first PC axis provided the LEI values. This axis explained 68% of variation; LMA, leaf longevity, fibre and lignin loaded positively, and leaf %N and %P loaded negatively. To test whether interspecific variation in leaf damage could be explained by the LEI we regressed means for the damage variables (chewing, phloem-feeding, mining, pathogen, and total % damage) against LEI.

We used a split-plot ANOVA to test whether there were overall effects of seabird status on damage by consumers across the six plant species. Islands were included as the whole-plot level, seabird status as the whole-plot treatment, and plant species identity as the subplot treatments. Blocks were generated by matching pairs of islands (one seabird, one non-seabird) by latitude and size (see last column in Appendix 1; because we had an odd number of islands, in one case we used a triplet). Response variables were chewing, phloem-feeding, mining, pathogen, and total percent damage. For individual plant species we tested for differences between seabird and non-seabird islands by running separate one-way ANOVAs with each island as the experimental unit. We then performed linear regressions between each response variable and nesting seabird density (using the log<sub>10</sub>-transformed number of burrow entrances per plot) across the 19 islands.

Leaf characteristics that best explained consumer damage were identified using an information theoretic (Akaike’s Information Criteria, AIC) approach (Akaike 1973). Candidate variables for island-level comparisons included foliar characteristics that were likely to impact herbivores and be affected by seabird density: LMA, foliar %N, condensed tannins, total phenolics, lignin, fibre, cellulose, and canopy density. Because for most species data for lignin, fibre and cellulose were available for a smaller number of islands than the other leaf variables (see sample sizes in caption to Table 3) and their inclusion therefore reduced our power to detect relationships, we reran models without those variables where they were not retained in the best models. We selected among competing models using AIC adjusted for small sample size (AICc; Burnham & Anderson 1998) and evaluated the relative importance of each variable by summing Akaike model weights across all models that included that variable (Burnham & Anderson 1998; Arnold 2010). Variables with high model weights (>0.55) were always included in the ‘best’ model (lowest AICc score), but some variables in top models had low model weights (<0.5), and were considered not well supported.

To determine whether seabirds affected leaf trait values we ran separate one-way ANOVAs for each species, with each island as the experimental unit and seabird status as the explanatory variable. We also performed linear regressions between each response variable and nesting seabird density (using the log<sub>10</sub>-transformed number of burrow entrances per plot) across the 19 islands.

We wanted to evaluate whether the observed differences in leaf damage on islands with different seabird densities could be explained by shifts in leaf trait values induced by seabirds. Because our sample size (N = 19 islands) was insufficient for structural equation modelling, we visually combined the results of the three sets of relationships (i.e. seabirds on leaf trait values, leaf trait values on damage levels, and seabirds on damage levels). Although this did not allow us to formally test the importance of indirect effects of seabirds on damage levels via leaf trait values, when connections between all three sets of variables are absent then such indirect effects are unlikely.



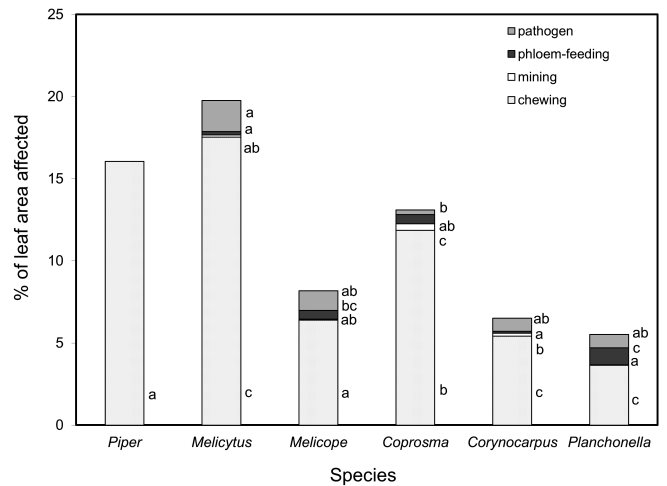
Results

**Overall damage levels and differences between plant species**

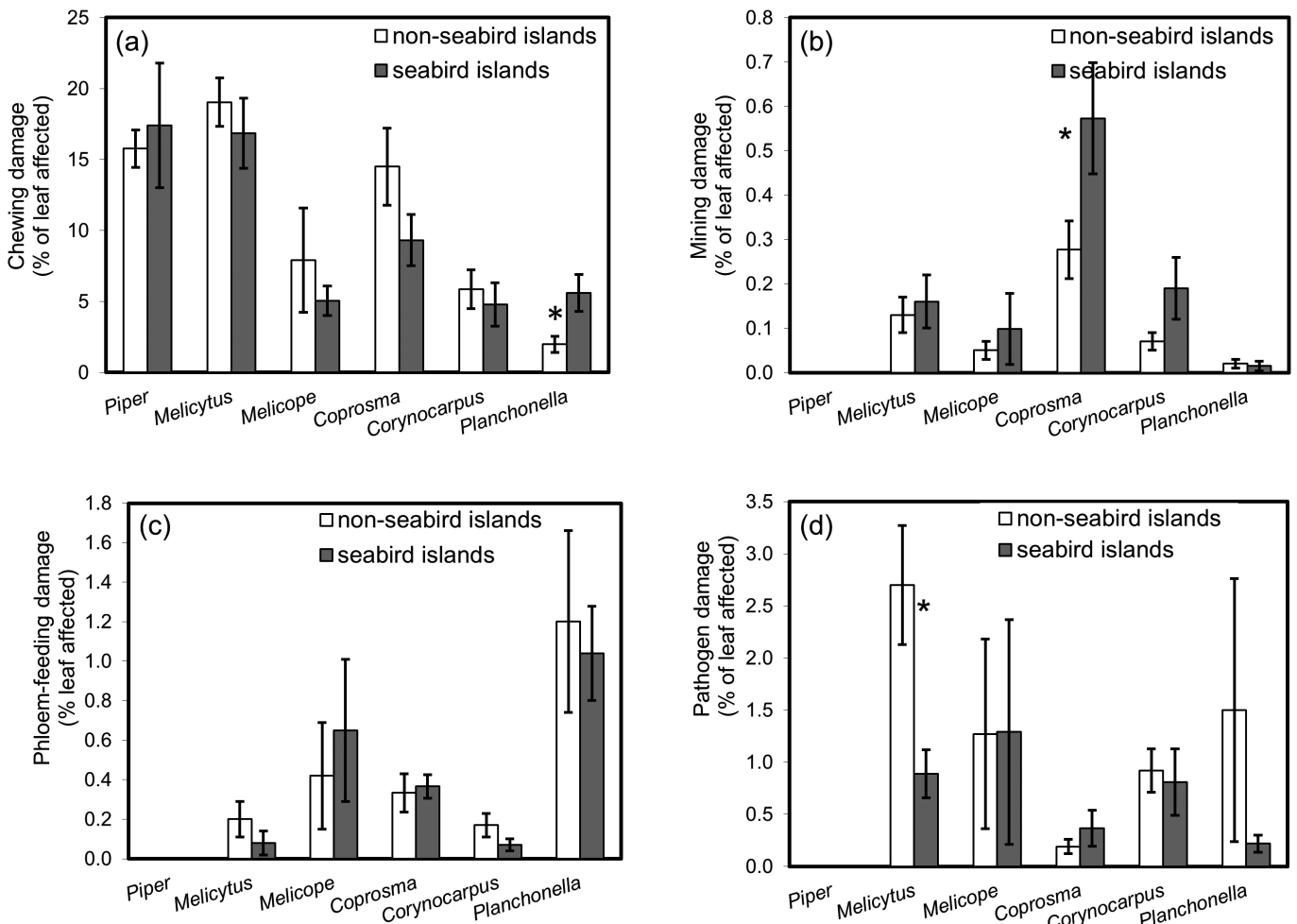
Mean total damage levels to leaves across all plant species on all islands ranged from 5.8% to 20.3%, with most of the damage on all plant species attributable to chewing insects (66–100% of damage percent; Fig. 1). Plant species differed in their mean damage levels for all damage variables (Fig. 1). Only chewing damage was related to species' LEI scores ( $R^2 = 0.61$ ,  $t_4 = -2.51$ ,  $P = 0.07$ ); the other damage types showed no relationships ( $R^2 < 0.01$  for pathogen and mining damage;  $R^2 = 0.32$  for phloem-feeding damage;  $P > 0.2$  for all).

**Damage levels on seabird vs non-seabird islands**

There were no consistent differences in damage levels between seabird and non-seabird islands (Fig. 2). Split-plot analyses including all six host species revealed no significant differences in chewing damage (Fig. 2a;  $F_{1,8} = 0.83$ ,  $P = 0.39$ ), mining damage (Fig. 2b;  $F_{1,8} = 1.50$ ,  $P = 0.26$ ), or phloem-feeding damage (Fig. 2c;  $F_{1,8} = 1.10$ ,  $P = 0.33$ ). However, leaves had significantly lower pathogen damage on seabird islands (Fig. 2d;  $F_{1,8} = 9.74$ ,  $P = 0.014$ ), which was driven by *Melicytus* and *Planchonella* (Fig. 2d).



**Figure 1.** Levels of damage inflicted by chewing, mining and phloem-feeding insects and by pathogens for the six focal plant species (see Table 1), averaged across all islands. Species are in order of leaf economic index (LEI) from resource-acquisitive (left) to resource-conservative (right). Different letters indicate significant differences (Tukey HSD,  $P < 0.05$ ) between plant species for each of the damage types.



**Figure 2.** Differences between seabird islands and non-seabird islands for each plant species. (a) chewing damage, (b) mining damage, (c) phloem-feeding damage and (d) pathogen damage. Within each panel, species are in order of leaf economic index (LEI) from resource-acquisitive (left) to resource-conservative (right). Error bars are standard errors of the mean. Significant differences ( $P < 0.05$ ) between invaded and uninvaded islands are indicated by \*.

When damage levels were examined for individual plant species there were only three significant differences (out of 21 comparisons) between seabird and non-seabird islands (slightly more than the one expected by chance at  $\alpha = 0.05$ ). Chewing damage on *Planchonella* was approximately three times greater on seabird than non-seabird islands ( $F_{1,11} = 5.67, P = 0.036$ ; Fig. 2a); mining damage for *Coprosma* was around twice as high on seabird islands (Fig. 2b;  $F_{1,15} = 5.23, P = 0.037$ ); and pathogen damage for *Melicytus* was around three times as high on non-seabird islands (Fig. 2b; ( $F_{1,15} = 6.42, P = 0.023$ ). These relationships were confirmed using regressions across the 19 islands with burrow density as the independent variable (chewing damage on *Planchonella*: positive,  $R^2 = 0.38, P = 0.025$ ; mining damage on *Coprosma*: positive,  $R^2 = 0.25, P = 0.040$ ; pathogen damage on *Melicytus*: negative,  $R^2 = 0.32, P = 0.018$ ), as was one additional relationship (*Corynocarpus*: positive relationship for mining damage,  $R^2 = 0.40, P = 0.050$ ). For *Coprosma* two additional relationships suggested trends: a negative relationship with chewing damage,  $R^2 = 0.18, P = 0.086$ , and a positive relationship with phloem-feeding damage,  $R^2 = 0.23, P = 0.054$ . Overall, most damage types on most species did not differ according to island status or seabird burrow density.

**Explaining damage levels using leaf characteristics**

The extent to which leaf characteristics could explain damage levels across islands was highly variable by species and damage type (Table 2). As expected, relationships between damage levels and phenolics were negative, while those with %N and LMA were generally positive (except on one occasion for *Corynocarpus*). Unexpectedly, relationships with tannins were

positive, as were those for cellulose (again with an exception for *Corynocarpus*). Relationships with canopy density were not consistent, while fibre and lignin were never included in the best models. Generally, variables that explained damage were most easily identified for mining and phloem-feeding damage (for which there were usually one or two best models) and most difficult to identify for pathogen damage. Although there were significant effects of seabird status or seabird density in at least one plant species for almost all variables (Table 3), only foliar N and LMA showed consistent responses for >2 plant species.

To evaluate whether differences in damage levels under high densities of seabirds (Fig. 2 and second paragraph of the Results) could potentially be mediated by shifts in leaf trait values, we visually combined the results for shifts in leaf trait values due to seabird status or density (Table 3) with those exploring relationships between leaf trait values and damage levels (Table 2). Some of the observed differences in damage levels between seabird and non-seabird islands could be explained by shifts in leaf trait values for *Coprosma* and *Corynocarpus* (Fig. 3d,e), but not for *Melicytus* or *Planchonella* (Fig. 3b,f). For the two species for which there were no observed differences in damage levels (*Piper* and *Melicope*), there was no evidence for shifts in leaf traits that could result in opposing impacts on damage levels (Fig. 3a,c).

**Discussion**

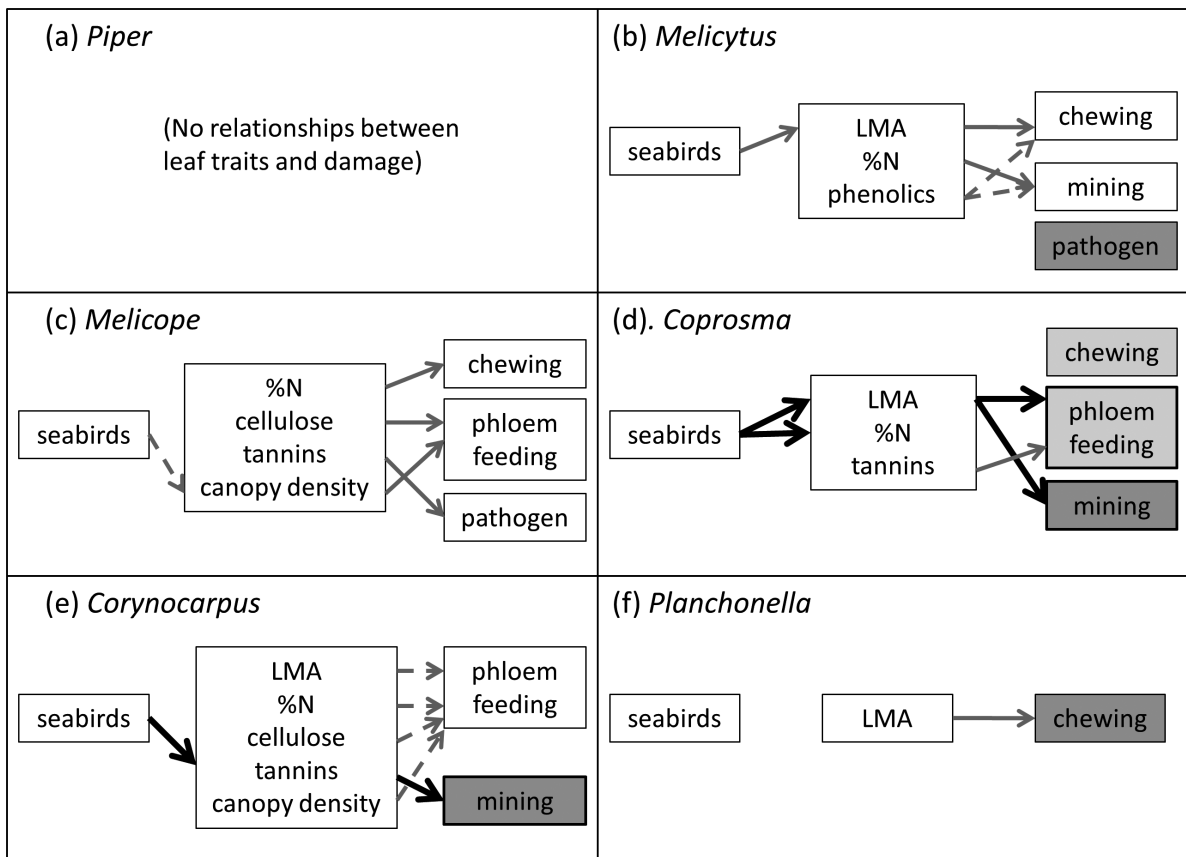
We expected that increases in nutrient availability driven by large seabird populations would indirectly affect leaf

**Table 2.** Results of AIC models aimed at identifying combinations of leaf variables that best explain damage at the whole-island level. LMA refers to leaf mass per area ( $\text{g m}^{-2}$ ); CD is canopy density (% of sky obscured); all other leaf traits are measured as percentages. Only variables from models with AICc scores within 2.0 of the best (lowest AICc) model are included. A ‘+’ indicates a positive relationship, a ‘-’ a negative relationship; for variables with strong support (model weight > 0.55) weights are in parentheses. Where inclusion of lignin, fibre, or cellulose was not supported (indicated with ‘NI’), the analysis was rerun without these variables.

Damage type	Species	No. of models	N	R <sup>2</sup>	LMA	Nitrogen	Phenolics	Tannins	Cellulose	Fibre	Lignin	CD
Chewing	<i>Piper</i>	5	13	0.25	-	-	-	-	NI	NI	NI	
	<i>Melicytus</i>	1	17	0.42	+(0.71)				NI	NI	NI	
	<i>Melicope</i>	1	10	0.58		+(0.94)	-(0.84)		NI	NI	NI	
	<i>Coprosma</i>	6	17	0.12		-	+	-	NI	NI	NI	-
	<i>Corynocarpus</i>	3	10	0.57	-	-	+	+	NI	NI	NI	
	<i>Planchonella</i>	6	13	0.29	+(0.58)	+	-		NI	NI	NI	+
Mining	<i>Melicytus</i>	1	17	0.45		+(0.84)	-(0.78)		NI	NI	NI	+
	<i>Melicope</i>	5	12	<0.10	-	-		-	NI	NI	NI	+
	<i>Coprosma</i>	2	17	0.14	+(0.58)				NI	NI	NI	-
	<i>Corynocarpus</i>	1	10	0.53				+(0.77)	NI	NI	NI	
	<i>Planchonella</i>	1	10	0.77					+(0.64)			-(0.88)
Phloem-feeding	<i>Melicytus</i>	5	17	0.04					NI	NI	NI	
	<i>Melicope</i>	1	7	0.83					+(0.57)			+(0.67)
	<i>Coprosma</i>	2	17	0.46		+(0.76)		+(0.81)	NI	NI	NI	
	<i>Corynocarpus</i>	1	9	0.98	-(0.96)	-(0.97)			-(0.94)			+(0.96)
	<i>Planchonella</i>	1	10	0.34					+(0.60)			
Pathogen	<i>Melicytus</i>	5	17	0.05	+	+	-	-	NI	NI	NI	-
	<i>Melicope</i>	2	12	0.29	-			+(0.64)	NI	NI	NI	
	<i>Coprosma</i>	3	14	0.49	+	+	-	-	NI	NI	NI	-
	<i>Corynocarpus</i>	7	17	0.09	+	+	-	-	NI	NI	NI	-
	<i>Planchonella</i>	5	13	<0.02	-	-	-	+	NI	NI	NI	+

**Table 3.** Leaf traits of plants on non-seabird and seabird islands. Values are mean ± SEM with islands as replicates. ‘LMA’ refers to leaf mass per area. Asterisks refer to significant differences in means between non-seabird and seabird islands (\**P* < 0.05, \*\**P* < 0.01). A § indicates a significant relationship between the variable and seabird burrow density (§ *P* < 0.05, §§*P* < 0.01, §§§*P* < 0.001). Number of islands for most variables (with *N* for fibre, cellulose and lignin in parentheses): *Piper* = 14(16); *Melicytus* = 17(16); *Melicope* = 12(8); *Coprosma* = 17(17); *Planchonella* = 13(11), *Corynocarpus* = 9(9).

Species	Seabird island	LMA (g m <sup>-2</sup> )	Nitrogen (%)	Fibre (%)	Cellulose (%)	Lignin (%)	Tannins (%)	Phenolics (%)
<i>Piper</i>	No	41 ± 3	3.05 ± 0.10*	27.04 ± 1.1	16.53 ± 0.7§§	8.68 ± 0.7	0.13 ± 0.01	2.73 ± 0.17§
	Yes	44 ± 3	3.42 ± 0.14	27.51 ± 1.0	15.04 ± 1.0	10.81 ± 0.6	0.12 ± 0.01	3.05 ± 0.48
<i>Melicytus</i>	No	52 ± 2§	2.51 ± 0.14	34.62 ± 1.0	24.47 ± 0.8	8.49 ± 0.4	0.17 ± 0.02	0.70 ± 0.05
	Yes	53 ± 7	2.87 ± 0.11	33.83 ± 1.3	25.00 ± 1.5	8.29 ± 0.4	0.19 ± 0.02	0.82 ± 0.08
<i>Melicope</i>	No	48 ± 6*	2.26 ± 0.16	29.23 ± 2.3	19.03 ± 2.0	7.57 ± 0.4	0.14 ± 0.06	1.88 ± 0.22*
	Yes	69 ± 4	2.24 ± 0.10	29.62 ± 1.7	20.44 ± 1.2	7.10 ± 1.0	0.12 ± 0.02	2.52 ± 0.16
<i>Coprosma</i>	No	62 ± 4*	1.45 ± 0.04**§	31.53 ± 1.1	21.47 ± 0.6	10.28 ± 2.0**	0.11 ± 0.01	0.44 ± 0.06
	Yes	82 ± 9	1.64 ± 0.03	33.18 ± 1.2	20.51 ± 0.9	13.34 ± 0.7	0.12 ± 0.01	0.49 ± 0.08
<i>Corynocarpus</i>	No	81 ± 03	2.04 ± 0.14	38.23 ± 1.8	25.06 ± 1.0	12.46 ± 0.6	0.10 ± 0.01§§§	0.84 ± 0.05
	Yes	91 ± 07	2.31 ± 0.22	39.44 ± 2.6	24.80 ± 1.7	14.68 ± 1.6	0.12 ± 0.02	0.92 ± 0.16
<i>Planchonella</i>	No	75 ± 3	2.46 ± 0.07**	36.38 ± 2.8	16.45 ± 0.5	19.68 ± 2.6	0.12 ± 0.02	0.73 ± 0.09
	Yes	82 ± 8	3.03 ± 0.15	36.61 ± 1.7	17.96 ± 1.1	18.03 ± 1.0	0.10 ± 0	0.71 ± 0.06



**Figure 3.** Potential linkages between foliar responses to seabirds and damage responses by foliar consumers via changes in leaf traits for each of the six plant species (see Table 1). These diagrams are visualisations of the relationships identified in Tables 2 and 3 and in Fig. 2, and are intended to depict whether impacts of seabirds on leaf trait values could explain shifts in the levels of damage caused by foliar consumers (or, in the case of multiple and opposing effects, lack of shifts in damage levels). For simplicity only leaf traits that affect at least one damage type (middle box of each panel) and only damage types that are explained by leaf trait values or seabirds are shown. LMA refers to leaf mass per area. Arrows between the left and middle boxes indicate impacts of seabird presence or density on leaf traits (from Table 3); arrows between the middle and right boxes indicate correlations between leaf traits and damage levels (from Table 2). Solid arrows indicate positive relationships, dashed arrows indicate negative ones. Damage types with dark grey shading show significant differences between seabird and non-seabird islands or significant responses to increased seabird density (*P* < 0.05), whereas those with light grey shading show marginally significant relationships (0.05 < *P* < 0.10) (from Fig. 2 and second paragraph of the Results). Bold arrows leading to boxes with heavy margins indicate pathways through which impacts of seabirds on leaf traits could explain observed changes in damage levels.

consumers, resulting in increased leaf damage on seabird islands. This prediction was not supported: there was no consistent difference between seabird and non-seabird islands in herbivore damage (chewing, mining or phloem-feeding), and pathogen damage was higher on non-seabird islands than seabird islands across all species. In fact, there were only three significant differences for any plant–damage–type combination between seabird islands and non-seabird islands across 21 comparisons (and one additional effect of seabird density); while higher than expected by chance at  $\alpha = 0.05$ , these results provide little support for the notion that damage by herbivores or pathogens is consistently affected by seabird colonies.

The reason for the lack of consistent response of damage levels to seabird status becomes apparent when the effects of seabirds on leaf traits are evaluated (Table 3). We had expected that shifts in seabird density would lead to consistent shifts in leaf traits that in turn would drive consistent shifts in consumer damage levels, but neither prediction was supported (Fig. 3). While all but one leaf trait responded to seabird presence or density in at least one host species (11 significant relationships, many more than the two expected by chance at  $\alpha = 0.05$ ), the manner in which they did was highly individualistic: only %N and LMA increased consistently (three of six species; Table 3). Leaf traits that explained damage levels also varied across plant species and across damage types (Table 2; Fig. 3, connections between middle and right-hand boxes). While some shifts in consumer damage on seabird islands could be explained by changes in mean leaf trait values (Fig. 3, black arrows), in other cases they could not (e.g. chewing data on *Planchonella*). In sum, the lack of consistent seabird effects was due to species-specific responses of plant chemistry or morphology to seabird density (and associated impacts), and the effects that were found could not always be explained by the foliar characteristics we measured.

### Responses of consumer groups

Species-specific responses by both plants and herbivores to changes in resource availability are consistent with previous work. Numerous studies have found increasing invertebrate herbivore damage, survivorship, growth, and reproduction (both within and across species) as foliar N concentrations increase (e.g. Mattson 1980; Scriber & Slansky 1981; Donaldson & Lindroth 2007; Molinari & Knight 2010), in line with the three positive relationships we found between %N and damage by herbivores. However, plants in high-nutrient environments may increase allocation to N-based defence compounds such as alkaloids or cyanogenic compounds (Bryant et al. 1983; Herms & Mattson 1992). Such compounds could account for the negative correlation between %N and damage by phloem-feeders on *Corynocarpus*, in which  $\beta$ -nitropropanoic acid is a defence chemical in its fruit and nectar; its occurrence in leaves is unknown (Connor 1977). Herbivores can also engage in compensatory feeding when leaf quality is low (review in Haukioja 2003), which could help explain why most plant–consumer combinations showed no relationship. Leaf N content may also be related to other plant or plant community traits that can in turn promote attack by herbivores or pathogens. For example, a spatially explicit study evaluating relationships between soil and plant traits on islands with different seabird densities found that tree basal area was a better predictor of leaf %N in *Melicactus ramiflorus* than was soil ammonium, soil nitrate, or burrow density (Durrett 2014). Tree densities are lower on seabird islands than non-seabird islands (Wardle et al. 2007); such trees could be

less susceptible to herbivores or pathogens because they are healthier or because they are spaced further apart, countering any positive effects of increased %N.

It is unclear why pathogen damage across species was lower on seabird islands. Seabirds reduce canopy densities (Mulder et al. 2009), which in turn could reduce humidity in the understorey and this could result in conditions unsuitable for leaf pathogens (e.g. Tapke 1931; Loria et al. 1982; López-Bravo et al. 2012). We therefore expected either canopy density or LMA (which is affected by light levels) to explain pathogen damage levels, but neither did. Lower canopy densities on seabird islands could also result in greater evapotranspiration in the understorey (e.g. Hawthorne et al. 2013) so we expected that this could result in lower rates of damage caused by phloem-feeders (which are sensitive to leaf turgor; Jones & Coleman 1991; Huberty & Denno 2004). There was some evidence this was the case because damage by phloem-feeders was positively related to canopy density (for *Melicope* and *Corynocarpus*) and negatively to LMA (for *Corynocarpus*); moreover damage levels to both of these species on seabird islands were less than half that on non-seabird islands (Fig. 2c), although neither difference was statistically significant. Island-scale measurements of canopy density or LMA are rather crude indicators of plant water potential or humidity at the leaf surface, and more direct measures might link the impacts that seabirds have on plant water status and subcanopy humidity to damage by these consumers.

Our expectation that that herbivore damage would be negatively correlated with leaf structural components and concentrations of secondary compounds for most species was not supported. Neither lignin nor fibre consistently predicted herbivore damage, and relationships with cellulose content and tannin concentrations were primarily positive; only concentrations of phenolics showed the expected negative correlation, and only for 2 out of 21 comparisons (only one more than expected under  $\alpha = 0.05$ ). Furthermore, there were no consistent differences across plant species between seabird and non-seabird islands for any of these variables. Many plant species show induced responses to herbivore damage that result in greater concentrations of secondary compounds such as tannins, particularly in fast-growing species (see review in Karban & Baldwin (1997) and meta-analysis in Nykänen & Koricheva (2004)); this could account for the observed positive relationships with damage in some species, as could the ability of some herbivores to metabolise tannins (Haukioja 2003). We measured condensed tannins, which are traditionally thought to reduce herbivore activity through protein precipitation capacity, but recent studies suggest that tannin oxidation may play a major role, particularly for arthropods (Appel 1993; see review in Salminen & Karonen 2011). Condensed tannins show lower oxidation activity than another tannin group, the ellagitannins (Barbehenn et al. 2006; Salminen & Karonen 2011), and may therefore be less important in reducing leaf consumption by arthropods. Our measure of total phenolics did include the ellagitannins, and this may explain the two negative correlations between total phenolics and damage levels in the absence of correlations with condensed tannins, as well as the unexpectedly low total damage levels in *Melicope*, the species with the highest concentrations of phenolics.

Our failure to find consistent impacts of seabird density on leaf damage may be driven by factors other than leaf quality. For example, increased top-down regulation exerted by predators of herbivores may have prevented increased herbivore density and leaf damage even when foliar quality was improved (e.g.



Hairston et al. 1960; Marquis & Whelan 1994; Schwenk et al. 2010). Although we cannot rule this out, it does not explain the differences we did see. There may also have been direct impacts of predation by rats on larger invertebrate herbivores on the non-seabird islands (Townes et al. 2009; St. Clair 2011). This is unlikely; damage by chewing insects, the guild with the largest body size, tended to be higher on rat-invaded islands, and damage levels on islands with a history of rat invasion but on which they were controlled at the time of data collection (Appendix 1) were not higher than on islands with rats present (data not shown).

In contrast to the results across species, interspecific comparisons of damage levels among the six species were consistent with expectations (Prediction 1) for one damage type – chewing damage (the predominant type of damage) decreased as plants showed more resource-conservative traits – but other damage types showed no pattern. Caution should be taken in applying these results to a wider range of species. Most forests on these islands are in relatively early stages of succession after fires and other disturbances (Atkinson 2004), and this pattern may not hold over a wider range of species or communities characteristic of later successional stages. Moreover, leaf traits may be driven by factors other than resource availability; for example, taller species such as *Planchonella* and *Corynocarpus* may suffer more than subcanopy species from salt and wind exposure on small islands, and thus require greater investment in thick cuticles and structural components (Alpha et al. 1996).

## Conclusions

Our study demonstrates that large shifts in seabird density on New Zealand islands do not have consistent impacts on the level of leaf damage inflicted by herbivores and pathogens. This result is in sharp contrast to most other above- and below-ground processes evaluated on this set of islands, which differ greatly between those with and without high densities of seabirds (e.g. Fukami et al. 2006; Wardle et al. 2007, 2009; Towns et al. 2009). Furthermore, we also demonstrated that while all plant species exhibited changes due to seabirds in leaf chemical or morphological traits known to be important for driving herbivores and pathogens, these were not consistent across plant species. Such species-specific responses to the fertilisation and disturbance regime imposed by seabirds may explain why we did not observe the types of positive impacts on above-ground consumer activity that we see for consumer densities below ground in this system (e.g. Fukami et al. 2006; Towns et al. 2009).

## Acknowledgements

For permission to work on the islands they own or for which they are kaitiaki (guardians), we thank the following iwi: Ngāti Hako, Ngāti Hei, Ngāti Manuhiri, Ngāti Paoa, Ngāti Puu, Ngāti Rehua, and Ngātiwai, as well as the Ruamāhua (Aldermen) Islands Trust, the Ngāmotuaroha Trust, John McCallum, Oho Nicolls, Bryce Rope, and the Neureuter family. The Department of Conservation and Rau Kirikiri facilitated visits to the islands. We thank Dave Towns, Karen Boot, Aaron Hoffman, Holly Jones, and Dan Uliassi for their assistance in the field and lab. We thank Dave Towns, Sarah Richardson, K. C. Burns, Chris Lusk, and an anonymous reviewer for helpful comments on the manuscript. This

study was supported by the US National Science Foundation (DEB-0317196), the New Zealand Ministry of Science and Innovation (Te Hiringa Tangata ki te Tai Timu ki te Tai Pari programme Bicultural restoration of coastal forest ecosystems – C09X0908), Landcare Research's Capability Fund, and the New Zealand Department of Conservation.

## References

- Akaike H 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csáki F eds 2nd International Symposium on Information Theory. Budapest, Hungary, Akadémiai Kiadó. Pp. 267–281.
- Alpha CG, Drake DR, Goldstein G 1996. Morphological and physiological responses of *Scaevola sericea* (Goodeniaceae) seedlings to salt spray and substrate salinity. *American Journal of Botany* 83: 86–92.
- Appel HM 1993. Phenolics in ecological interactions: the importance of oxidation. *Journal of Chemical Ecology* 19: 1521–1552.
- Arnold TW 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Atkinson IAE 2004. Successional processes induced by fires on the northern offshore islands of New Zealand. *New Zealand Journal of Ecology* 28: 181–193.
- Barbehenn RV, Jones CP, Hagerman AE, Karonen M, Salminen J-P 2006. Ellagitannins have greater oxidative activities than condensed tannins and galloylglucoses at high pH: potential impact on caterpillars. *Journal of Chemical Ecology* 32: 2235–2251.
- Beever RE 1987. The holes in the leaves of the kawakawa (*Macropiper excelsum*). *Auckland Botanical Society Newsletter* 42: 9–11.
- Broadhurst RB, Jones WT 1978. Analysis of condensed tannins using acidified vanillin. *Journal of the Science of Food and Agriculture* 29: 788–794.
- Bryant JP, Chapin III FS, Klein DR 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357–368.
- Burnham KP, Anderson DR 1998. Model selection and inference: a practical information-theoretic approach. New York, Springer. 353 p.
- Coley PD 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209–232.
- Connor HE 1977. Poisonous plants of New Zealand. 2nd rev. edn. DSIR Bulletin 99. Wellington, Government Printer. 247 p.
- Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Monsterrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, and 36 others 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15: 295–304.
- Donaldson JR, Lindroth RL 2007. Genetics, environment, and their interaction determine efficacy of chemical defense in trembling aspen. *Ecology* 88: 729–739.
- Durrett MS 2014. Spatial variability in plant and soil properties on New Zealand seabird islands, and the effects of introduced rats. PhD thesis, University of Alaska Fairbanks, Fairbanks, Alaska, USA.
- Ellis JC, Bellingham PJ, Cameron EK, Croll DA, Kolb GS, Kueffer C, Mittelhauser GH, Schmidt S, Vidal E, Wait



- DA 2011. Effects of seabirds on plant communities. In Mulder CPH, Anderson WB, Towns DR, Bellingham PJ eds Seabird islands: ecology, invasion, and restoration. New York, Oxford University Press. Pp. 177–211.
- Endara M-J, Coley PD 2011. The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology* 25: 389–398.
- Epstein E 1972. Mineral nutrition of plants: principles and perspectives. New York, Wiley. 412 p.
- Feeny P 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565–581.
- Fukami T, Wardle DA, Bellingham PJ, Mulder CPH, Towns DR, Yeates GW, Bonner KI, Durrett MS, Grant-Hoffman MN, Williamson WM 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* 9: 1299–1307.
- Grant-Hoffman MN, Mulder CP, Bellingham PJ 2010. Invasive rats alter woody seedling composition on seabird-dominated islands in New Zealand. *Oecologia* 163: 449–460.
- Hairton NG, Smith FE, Slobodkin LB 1960. Community structure, population control, and competition. *The American Naturalist* 94: 421–425.
- Haukioja E 2003. Putting the insect into the insect-birch interaction. *Oecologia* 136: 161–168.
- Hawthorne SND, Lane PNJ, Bren LJ, Sims NC 2013. The long term effects of thinning treatments on vegetation structure and water yield. *Forest Ecology and Management* 310: 983–993.
- Herms DA, Mattson WJ 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67: 283–335.
- Hodge S, Keesing VF, Wratten SD 2000. Leaf damage does not affect leaf loss or chlorophyll content in the New Zealand pepper tree, kawakawa (*Macropiper excelsum*). *New Zealand Journal of Ecology* 24: 87–89.
- Huberty AF, Denno RF 2004. Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology* 85: 1383–1398.
- Jones CG, Coleman JS 1991. Plant stress and insect herbivory: toward an integrated perspective. In Mooney HA, Winner WE, Pell EJ eds Response of plants to multiple stresses. San Diego, CA, USA, Academic Press. Pp. 249–280.
- Karban R, Baldwin IT 1997. Induced responses to herbivory. Chicago, IL, USA, University of Chicago Press. 330 p.
- Kolb GS, Jerling L, Hambäck PA 2010. The impact of cormorants on plant–arthropod food webs on their nesting islands. *Ecosystems* 13: 353–366.
- López-Bravo DF, Virginio-Filho E de M, Avelino J 2012. Shade is conducive to coffee rust as compared to full sun exposure under standardized fruit load conditions. *Crop Protection* 38: 21–29.
- Loria R, Wiese MV, Jones AL 1982. Effects of free moisture, head development and embryo accessibility on infection of wheat by *Ustilago tritici*. *Phytopathology* 72: 1270–1272.
- Markwell TJ, Daugherty CH 2002. Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. *Ecoscience* 9: 293–299.
- Marquis RJ, Whelan CJ 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75: 2007–2014.
- Mattson WJ 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11: 119–161.
- Molinari N, Knight C 2010. Correlated evolution of defensive and nutritional traits in native and non-native plants. *Botanical Journal of the Linnean Society* 163: 1–13.
- Mulder CPH, Grant-Hoffman MN, Towns DR, Bellingham PJ, Wardle DA, Durrett MS, Fukami T, Bonner KI 2009. Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biological Invasions* 11: 1671–1688.
- Mulder CPH, Jones H, Kameda K, Palmborg C, Schmidt S, Ellis JC, Orrock JL, Wait DA, Wardle DA, Yang L, Young H, Croll DA, Vidal E 2011. Impacts of seabirds on plant and soil properties. In: Mulder CPH, Anderson WB, Towns DR, Bellingham PJ eds. Seabird islands: ecology, invasion, and restoration. New York, Oxford University Press. Pp. 135–176.
- Nykanen H, Koricheva J 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos* 104: 247–268.
- Pérez-Harguindeguy N, Díaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* 28: 642–650.
- Polis GA, Hurd SD 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* 147: 396–423.
- Price ML, Butler LG 1977. Rapid visual estimation of and spectrophotometric determination of tannin content of sorghum grain. *Journal of Agricultural and Food Chemistry* 25: 1268–1273.
- Salminen J-P, Karonen M 2011. Chemical ecology of tannins and other phenolics: we need a change in approach. *Functional Ecology* 25: 325–338.
- Schwenk WS, Strong AM, Sillett TS 2010. Effects of bird predation on arthropod abundance and tree growth across an elevational gradient. *Journal of Avian Biology* 41: 367–377.
- Scriber JM, Slansky F Jr 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26: 183–211.
- Smith JL, Mulder CPH, Ellis JC 2011. Seabirds as ecosystem engineers: nutrient inputs and physical disturbance. In: Mulder CPH, Anderson WB, Towns DR, Bellingham PJ eds. Seabird islands: ecology, invasion, and restoration. New York, Oxford University Press. Pp. 27–55.
- St Clair JJH 2011. The impacts of invasive rodents on island invertebrates. *Biological Conservation* 144: 68–81.
- Tapke VF 1931. Influence of humidity on floral infection of wheat and barley by loose smut. *Journal of Agricultural Research* 43: 503–516.
- Towns DR, Wardle DA, Mulder CPH, Yeates GW, Fitzgerald BM, Parrish GR, Bellingham PJ, Bonner KI 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. *Oikos* 118: 420–430.
- Vitousek PM, Howarth RW 1991. Nitrogen limination on land and in the sea: How can it occur? *Biogeochemistry* 13: 87–115.
- Wardle DA, Bellingham PJ, Fukami T, Mulder CPH 2007. Promotion of ecosystem carbon sequestration by invasive predators. *Biology Letters* 3: 479–482.
- Wardle DA, Bellingham PJ, Bonner KI, Mulder CPH 2009. Indirect effects of invasive predators on litter

decomposition and nutrient resorption on seabird-dominated islands. *Ecology* 90: 452–464.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, and 23 others 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Editorial Board member: Chris Lusk

Received 5 June 2014; accepted 26 October 2014

**Appendix 1.** Location and characteristics of islands used in this study and sampling scheme for the six focal species. Seabird density is the mean number of burrow entrances for two 100-m<sup>2</sup> plots per island. An asterisk indicates that rats on this island have been eradicated or controlled in recent years. Numbers for plant species indicate individuals sampled on that island. Species abbreviations: COPMAC = *Coprosma macrocarpa*; CORLAE = *Corynocarpus laevigatus*; PIPEXC = *Piper excelsum*; MELRAM = *Melicactus ramiflorus*; MELTER = *Melicope ternata* and PLACOS = *Planchonella costata*. Block refers to block identity for the split-plot analyses.

Island	Seabird density	Lat. (°S)	Long. (°E)	Area (ha)	COPMAC	CORLAE	PIPEXC	MELRAM	MELTER	PLACOS	Block
<i>Seabird islands</i> [uninvaded by <i>Rattus</i> spp.]											
Green	101	36.64	175.85	2.5	0	0	6	4	0	2	6
Middle	85	36.60	175.84	13.5	0	6	4	10	5	1	7
Archway	38	35.49	174.74	6.3	0	0	0	0	10	10	4
Tawhiti Rahi	32.5	35.45	174.71	158.2	9	10	0	10	10	10	1
Ruamāhuanui	22.5	36.95	176.09	32.4	0	0	10	10	6	10	8
Aorangi	18	35.48	174.72	107.1	9	10	0	10	10	0	3
Ruamāhuaiti	15	36.97	176.06	25.5	10	0	10	10	0	0	9
Aorangaia	13	35.48	174.41	5.6	5	9	0	0	10	5	2
Ohinauiti	3.5	36.71	175.88	5.9	10	0	10	10	7	10	5
<i>Non-seabird islands</i> [invaded by <i>Rattus rattus</i> or <i>R. norvegicus</i> ]											
Otata*	8	36.41	174.58	15.0	10	0	10	10	0	0	4
Motuhoropapa*	0	36.41	174.57	8.6	0	0	10	10	10	0	2
Motutapere*	0	36.78	175.40	45.6	10	10	10	10	5	6	9
Motueka	5	36.82	175.80	6.2	10	3	10	10	10	10	5
Aiguilles	1	36.03	175.39	74.7	9	10	0	10	0	9	1
Hauturu	0.5	37.21	175.89	10.3	10	0	10	10	0	0	9
Goat	0.33	36.26	174.80	13.4	10	0	7	10	0	0	3
Motukaramarama	0	36.68	175.37	10.1	0	1	10	10	0	5	7
Motuoruhi	0	36.73	175.40	58.0	10	0	10	10	5	4	8
Pakihi	0	36.54	175.10	110	10	3	10	10	1	6	6
Total no. of plants					122	62	127	164	88	88	
Total no. of islands					13	9	14	17	12	13	