

Spatial prediction of caterpillar (*Ormiscodes*) defoliation in Patagonian *Nothofagus* forests

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Abstract In the temperate forests of the southern Andes, southern beech species (*Nothofagus*), the dominant tree species of the region, experience severe defoliation caused by caterpillars of the *Ormiscodes* genus (Lepidoptera: Saturniidae). Despite the recent increase in defoliation frequency in some areas, there is no quantitative information on the spatial extent and dynamics of these outbreaks. This study examines the spatial patterns of *O. amphimone* outbreaks in relation to landscape heterogeneity. We mapped defoliation events caused by *O. amphimone* in northern (ca. 40–41°S) and southern Patagonian (ca. 49°S) *Nothofagus* forests from Landsat imagery and analyzed their spatial associations with vegetation cover type, topography (elevation, slope angle, aspect) and mean annual precipitation using overlay analyses. We used these data and relationships to develop a logistic regression model in order to generate maps of predicted susceptibility to defoliation by *O. amphimone* for each study area. Forests of *N. pumilio* are typically more susceptible to *O. amphimone* outbreaks than lower elevation forests of other *Nothofagus* species (*N. dombeyi* and *N. antarctica*). Stands located at intermediate elevations and on gentle slopes (<15°) are also more susceptible to defoliation

than higher and lower elevation stands located on high angle slopes. Stands in areas with intermediate to high precipitation, relative to the distribution of *Nothofagus* along the precipitation gradient, are more susceptible to *O. amphimone* attack than are drier areas. Our study represents the first mapping and spatial analysis of insect defoliator outbreaks in *Nothofagus* forests in South America.

Keywords Defoliation · Herbivory · Insect outbreak · *Nothofagus pumilio* · South America

Introduction

Southern beech (*Nothofagus*) species are the most widely distributed and abundant trees in southern South America (south of 38°S). An increasing number of defoliation events have been observed over the past three decades in multiple locations (Veblen et al. 1996; Paritsis et al. 2009) suggesting a potential link to climate warming in the region. Defoliations are caused by native *Ormiscodes* (Saturniidae: Hemi-leucinae) moth species during their larval stage. *Ormiscodes amphimone*, one of the most widespread *Ormiscodes* species in southern South America (Lemaire 2002), is a polyphagous saturniid moth known to cause severe defoliation on *N. pumilio* and other *Nothofagus* species (Bauerle et al. 1997; Baldini and Alvarado 2008; Paritsis et al. 2010). Defoliation

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by *O. amphimone* apparently does not generate widespread mortality of mature *Nothofagus* trees, most likely due to the short duration of these outbreaks (i.e., one season) (Carrillo and Cerda 1987; Veblen et al. 1996). Nonetheless, *O. amphimone* defoliation significantly reduces *N. pumilio* radial growth (Paritsis et al. 2009) and has been reported to kill saplings of *Nothofagus* species even under moderate larval densities (Bauerle et al. 1997). In addition, severe defoliation may promote secondary attacks by *Gnathotrupes* bark beetles and other insects (Baldini and Alvarado 2008) and repeated defoliation has been suggested as a predisposing factor for the partial crown dieback observed in multiple *N. pumilio* stands (Veblen et al. 1996).

Despite the increased frequency of *O. amphimone* outbreaks in *Nothofagus* forests in Patagonia, there is no information on the spatial dynamics of these outbreaks. Basic information, such as which *Nothofagus* species are more extensively attacked during outbreaks, is based only on field observations (Baldini and Alvarado 2008; Paritsis et al. 2010). Likewise, there are no quantitative spatial analyses available of potential associations of defoliation events with topographic variables and spatial climate gradients. Given the potential effects of climate warming on *Ormiscodes* outbreaks in the *Nothofagus* forests of Patagonia (Paritsis and Veblen 2011), research is needed on how vegetation heterogeneity and abiotic sources of landscape heterogeneity affect susceptibility of *Nothofagus* stands to *Ormiscodes* attack.

Quantifying spatial relationships between insect outbreaks and potential environmental predictors is an effective approach to identify and understand key mechanisms driving insect outbreak dynamics. These relationships can be effectively addressed by combining descriptive approaches with spatial modeling techniques (e.g., Bigler et al. 2005; Eisenbies et al. 2007). There are two basic approaches for modeling the influence of environmental variables on the spatial dynamics of disturbances such as fire and insect outbreaks. Deductive methods (e.g., process models), which are based on expert opinion and well supported theory, require a priori knowledge of the system to define relationships between predictor and dependent variables (e.g., Cox et al. 2006). Conversely, inductive methods (e.g., logistic regression) use exploratory empirical techniques to identify relationships between predictor and dependent

variables (e.g., Buckland and Elston 1993). An inductive approach is appropriate for studying and modeling systems for which there is little or no prior information available (Dilts et al. 2009), such as *Ormiscodes* outbreaks in *Nothofagus* forests.

In this study, we examined spatial associations of *O. amphimone* outbreaks with vegetation type, topography and mean annual precipitation in two climatically contrasting regions in Patagonia. In addition, we quantified these observed associations using a logistic regression model in order to generate maps of predicted susceptibility to defoliation by *O. amphimone* for each study area.

Methods

Study area

We conducted this study in two climatically contrasting study areas in the Patagonian Andes, one in northern (40–41°S; 71°W) and the other in southern Patagonia (49°S; 72°W) (Fig. 1). In northern Patagonia the study area corresponds with Nahuel Huapi National Park (NHNP), which is delimited by the Andean ridge to the west (Argentina-Chile border) and by the forest-steppe ecotone to the east. This area includes ca. 753,300 ha of which ca. 424,000 ha are covered with *Nothofagus*-dominated vegetation potentially susceptible to defoliation by *O. amphimone*. In southern Patagonia the study area was defined by the north–south edges of the distribution of observed defoliations (1999, 2001, 2003, and 2005 outbreaks) and the west-east boundaries of the geographic range of *N. pumilio* and *N. antarctica* excluding some outlier stands, which occur far to the east. This rectangular area includes the northern portion of Los Glaciares National Park (LGNP) and extends ca. 25 km northeast into provincial forest and privately owned land covering ca. 148,500 ha and containing 25,200 ha of potentially susceptible vegetation.

The southern Andes (40–55°S) experience strong westerly winds that carry moist air and generate abundant orographic precipitation on their western flank and near the Andean divide to the east. Precipitation declines sharply to the east in the rain shadow of the Andes so that there is a strong west-to-east gradient of declining precipitation. From north to

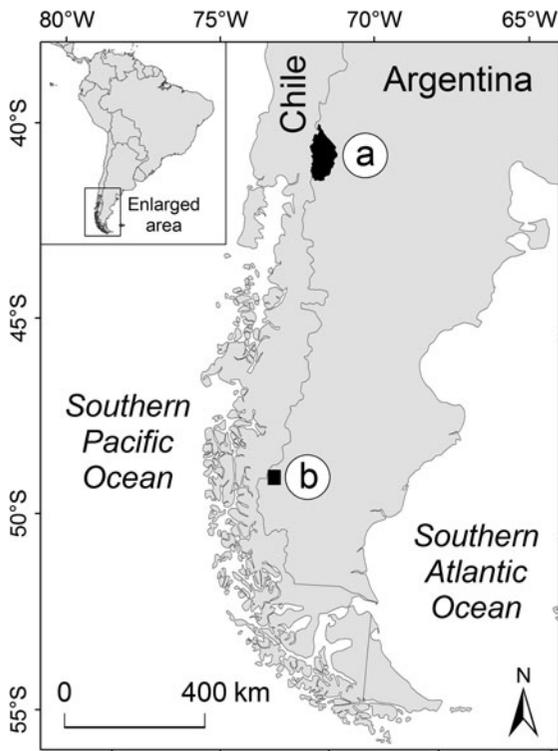


Fig. 1 Location of the study areas. The northern study area (a) corresponds to the Nahuel Huapi National Park, while the southern study area (b) was defined as a *rectangle* based on environmental variables such as vegetation and outbreak extent

south in Patagonia the summer drought associated with the seasonal dominance of the subtropical anticyclone gives way to a relatively even seasonal distribution of abundant precipitation associated with nearly year-round dominance of storm tracks in the westerlies. In northern Patagonia (ca. 40°S), annual precipitation decreases from ca. 3,000 mm, at the Andean divide, to ca. 800 mm in the foothills of the Andes less than 50 km eastwards (Barros et al. 1983), whereas in southern Patagonia (ca. 50°S) annual precipitation declines from ca. 7,000 mm on the Pacific coast to ca. 400 mm in the foothills on the eastern side of the Andes (Aravena and Luckman 2009; National Park Service unpublished). In the northern Patagonia study area, mean annual temperatures are higher and growing seasons longer than in the southern Patagonia study area.

The main tree species susceptible to defoliation by *O. amphimone* in the northern Patagonia study area are *N. pumilio*, which grows from ca. 1,000 to 1,600 m elevation above sea level, *N. dombeyi*

found at lower elevations (ca. 700–1,200 m), and *N. antarctica* at low to intermediate elevations (ca. 700–1,400 m) (Veblen et al. 1996; Lara et al. 1999). In the southern Patagonia study area *O. amphimone* commonly defoliates *N. pumilio* and *N. antarctica*. Another species, *N. betuloides* occurs west of the study area but its susceptibility to defoliation by *Ormiscodes* is unknown. At these high latitudes *N. pumilio* occurs at ca. 400 up to ca. 1,000 m and *N. antarctica* typically occurs from 200 to 500 m elevation.

Environmental variables

Based on previous studies of landscape influences on insect outbreaks occurrence (e.g., Powers et al. 1999; Davidson et al. 2001) and available environmental data for our study areas, we selected vegetation cover, topographic features and precipitation as predictor variables for presence/absence of defoliation (Table 1). Continuous variables (i.e., elevation, slope angle, precipitation, and distance to ridge) were classified to form discrete variables. Vegetation cover for NHNP was obtained from a 1:500,000 digital vegetation map of the Valdivian Ecoregion (Lara et al. 1999) that was slightly improved based on field observations of the *Nothofagus* spp. cover types. To map vegetation for southern Patagonia we used a supervised classification (maximum likelihood) of a Landsat TM image from January 1st 2002 (non-outbreak year in the area) in combination with field observations and the elevation ranges of key tree species. The resulting vegetation map was qualitatively assessed for accuracy using field observations and QuickBird imagery covering ca. 90% of the vegetated area (DigitalGlobe®; 0.7 m spatial resolution). Topographic layers (i.e., elevation, slope angle and aspect) were created from a 90 m resolution Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM; <http://dds.cr.usgs.gov/srtm/>). A mean annual precipitation surface of 1 km resolution for NHNP was obtained from a digitized 1:750,000 (200-mm interval) isohyet map (Barros et al. 1983). Given the narrow range of precipitation in the southern study area and the lack of spatially-explicit data on precipitation, we used the distance to the Andean ridge (manually digitalized from the DEM) as a surrogate for mean annual precipitation in southern Patagonia (areas closer to the

Table 1 Variables used in the overlay analyses and tested in the logistic regression

Vegetation type	Elevation (m)	Slope angle (°)	Aspect	Precipitation ^a (mm)	Ridge ^b (km)
<i>N. pumilio</i>	200–400	0–15	NW to NE	1000–1500	30–24
<i>N. antarctica</i>	400–600	15–30	East	1500–2000	24–18
<i>N. dombeyi</i>	600–800	30–45	SE to SW	2000–2500	18–12
	800–1000	45–60	South	2500–3000	12–6
	1000–1200	>60		3000–3500	0–6
	1200–1400				
	1400–1600				
	1600–1800				

Not all classes of vegetation and elevation are present in both study areas. “Precipitation” indicates the mean annual precipitation and “Ridge” indicates the distance to the Andean ridge (used as a proxy for precipitation)

^a Only for northern Patagonia

^b Only for southern Patagonia

ridge indicate higher precipitation regimes). Resolution of the distance to the ridge surface was 1 km.

Defoliation mapping

We acquired all MSS, TM, and ETM⁺ images available for our study areas from the USGS Global Visualization Viewer (<http://glovis.usgs.gov/>) and the Argentinean National Park Service Administration covering our study areas in northern (2 image frames) and southern (1 image frame) Patagonia. Because defoliation events of *Ormiscodes* are only noticeable in Landsat imagery for a short time window, typically from late January to March (i.e., summer), we only selected images collected during these months. Thirty-two scenes were selected for northern Patagonia (1976, 1985–1987, 1990, and 2000–2010) and fifteen scenes for southern Patagonia (1976, 1986, and 1998–2010). Because of the marked difference in wavelength reflectance and absorbance between defoliated and non-defoliated *Nothofagus* forest in the Landsat images, defoliated patches are clearly evident in false-color composite images using spectral bands 3 (red), 4 (near infrared), and 5 (mid-infrared) in the blue, green and red channels, respectively (Paritsis et al. 2009). These spectral bands are highly informative for vegetation studies, and have been widely used for detecting forest defoliation (Leckie et al. 1988; Hurley et al. 2004). Each of the available false color-images was visually examined looking for multiple large defoliated patches (i.e., >50 pixels each; pixel size 30 × 30 m; 4.5 ha) indicating

regional defoliation. When regional defoliation was evident we first extracted all the areas of susceptible vegetation (i.e., *Nothofagus*) from the image by using the vegetation maps described in the previous section as a mask. To determine the wavelength associated with defoliated and non-defoliated vegetation we randomly selected ca. 20 polygons (ca. 50–4,000 pixels each; 4.5–360 ha) within defoliated and non-defoliated forest. We then applied a maximum likelihood classification on the image using bands 3, 4, and 5, to classify defoliated and non-defoliated *Nothofagus* forest. Finally, the resulting class of defoliated forest was exported into a GIS as a polygon layer. To date, all field and remote sensing observations of defoliations by *Ormiscodes* indicate recovery of all or most of the tree foliar cover within 1 year of the defoliation event. Consequently, visual comparison of defoliated areas with images from the year before and the year after a suspected event allowed us to distinguish *Ormiscodes* defoliation events from other disturbances such as fire, avalanches, and tree mortality caused by other factors, which leave longer-lasting signals in the imagery.

To assess accuracy of the resulting defoliation maps we used two independent ground verification procedures. First, forest stands from which tree-ring reconstructions of outbreaks were previously developed were used as ground control points, 23 in northern and 19 in southern Patagonia (Paritsis and Veblen 2011). Second, defoliation maps were qualitatively tested for accuracy by comparing them with ground observations (when observers were in the

defoliated area at the time of the outbreak), landscape photographs taken by T.T. Veblen in 1986 and 1999, and/or produced reports to Argentine National Parks (Queiro 2003). Defoliation events typically begin in late spring (i.e., November–December) but are not distinguishable on Landsat imagery until mid to late summer (i.e., late January to March). Thus, we defined outbreak years as the calendar year in which defoliation is visible in the Landsat image, which is the calendar year subsequent to the year in which the outbreak started. All image processing was conducted in ENVI 4.7 image analysis software (ITT 2007).

Spatial overlay analyses

We conducted spatial overlay analyses to describe relationships between the area of outbreak occurrence and available area of the selected environmental variables (Table 1). Available area of a selected environmental variable refers to the proportion of the study area characterized by *Nothofagus* vegetation, which represents all the vegetation susceptible to defoliation. Overlay analysis calculates the total area within each class of one variable that occurs in each class of a second variable. Hence, if a given variable does not influence the susceptibility of vegetation to *O. amphimone* defoliation, then the amount of defoliated area in each variable class (e.g., vegetation type, elevation class) will be proportional to the amount of defoliated area in the entire area covered by the host species. Overlay analysis has been widely used to describe spatial relationships between environmental variables and forest disturbances (Powers et al. 1999; Bigler et al. 2005; Mermoz et al. 2005). We conducted overlay analyses between all the areas that are susceptible to defoliation (i.e., *Nothofagus* spp.) and the areas that were actually defoliated. We compared expected (i.e., percentage of each variable's class susceptible to defoliation) versus observed (i.e., percentage of each variable's class that was defoliated) percentages graphically. Spatial analyses were conducted in ArcGIS 9.3 (ESRI 2008).

In northern Patagonia, overlay results are based on a census of the entire area during a single regional outbreak event (1986). In southern Patagonia observed percentages of area defoliated per class are based on the sum of four outbreak events that occurred in different years (1999, 2001, 2003, and 2005), which were treated as a single defoliated area. Because the

data are not samples but rather are measures of total areas affected, no inferential statistics were necessary to assess statistical significance of the differences between percent area defoliated and percent area available within each class of the environmental variables. Nevertheless, because of possible measurement error we only emphasize large differences (>10%) between proportion of defoliated area and area available, to avoid spurious interpretations.

Logistic regression

Potential predictor variables of presence/absence of defoliation included extent of vegetation types, topographic variables, and precipitation (derived from point samples or pixel frequency, described below) (Table 1). To quantitatively determine the influences of each environmental variable on outbreak occurrence (i.e., presence or absence of the 1986 outbreak in northern Patagonia and of any of the four outbreaks in southern Patagonia) we applied binary logistic regression. Logistic regression is a generalized linear model that uses a logit link function to define the relationship between a binary dependent variable and its predictor variables (Hosmer and Lemeshow 2000; Menard 2002). Despite the development of new statistical techniques to classify binary variables, logistic regression remains a commonly used method due to its usefulness and relative simplicity (Friedman 2006). Binary logistic regression has been widely used to understand the relationships between environmental variables and the spatial distribution of ecological phenomena such as wildfire and insect outbreaks (Sherriff and Veblen 2007; Lippitt et al. 2008; Negrón et al. 2009).

We randomly selected stratified point samples, using defoliation presence/absence class, within the areas dominated by vegetation susceptible to defoliation. Sample points were at least 1,000 m apart to reduce spatial autocorrelation (Moran's $I < 0.5$). Each point had associated values of vegetation (pixel frequency of vegetation types in a 5-pixel radius; i.e., 150 m), point elevation (m), aspect (pixel frequency of aspect classes in a 6-pixel radius; i.e., 180 m), point slope (°), and point mean annual precipitation (mm) or point distance to the ridge (km). In northern Patagonia 100 defoliated and 200 non-defoliated points were selected, and in southern Patagonia 40 defoliated and 70 non-defoliated points were selected

for model development (training datasets). This selection represents ca. 75% of the available defoliated points and 5 or 30% of the available non-defoliated points in northern and southern Patagonia, respectively. We selected a smaller percentage of available non-defoliated sample points relative to the percentage of selected defoliated points to reduce any problems associated with having a low prevalence of defoliated samples in the dataset (McPherson et al. 2004).

High levels of collinearity among independent variables (i.e., $R > 0.8$) may result in misleading regression coefficients (Lesaffre and Marx 1993; Menard 2002); thus, we verified that none of the variables used for the logistic regression were highly correlated among each other ($R < 0.7$; $P < 0.05$; Spearman correlation). We developed one logistic model for each study area applying a backward stepwise procedure for variable removal to select the simplest model that best explains defoliation variability. The removal of a variable from the model was based on the significance of the change in the log-likelihood (Menard 2002).

Based on the logistic regression models, we generated a map of probabilities for *O. amphimone* outbreak occurrence for each study area. To create these probability maps we converted the sample points into minimum map units of 1 km². We tested a range of probability threshold values (from 0.4 to 0.6) to delineate defoliated/non-defoliated areas. Probability threshold values can be selected to reduce omission and commission errors, which improves the agreement between predicted and observed values in a test dataset (Guisan and Zimmermann 2000).

Model evaluation

Model evaluation was performed using both the training dataset and the test dataset, which consisted in all sample points not used to generate the model. Classification accuracy of the models was assessed using confusion matrixes of correctly (true positives and true negatives) and incorrectly (false positives and false negatives) classified sampled points on the training and the test datasets separately. We calculated the sensitivity, specificity, and correct classification rate (CCR) of each model (Fielding and Bell 1997). Sensitivity measures the proportion of actual positives that are correctly classified as such, whereas

specificity measures the proportion of negatives that are correctly classified. The CCR is an intuitive measure of discrimination that indicates the percentage of samples that were correctly classified by the model overall (McGarigal et al. 2002). However, sensitivity and specificity may be more adequate to evaluate model accuracy when the dependent variable is rare as is the case with defoliation in the study areas (Fielding and Bell 1997).

Results

Defoliation mapping

In northern Patagonia we detected and mapped one regional defoliation (1986) that affected ca. 11,600 ha. Images from 1976, 1985, 1987, 1990, and 2000–2010 years did not reveal any other major defoliation events (>50 ha), which is also consistent with National Park rangers' field observations and reports. In contrast, in southern Patagonia four regional defoliations (973 ha in 1999, 1,202 ha in 2001, 2,052 ha in 2003, and 976 ha in 2005) affecting a total of ca. 4,370 ha were detected and mapped from the imagery. Only a small percentage (16%) of the defoliated area in southern Patagonia was affected by more than one outbreak. Based on comparing mapped defoliations versus the location of the stands used for the tree-ring outbreak reconstructions in northern Patagonia, there was an omission error of 12% (i.e., tree-ring reconstructions detected defoliations in stands that did not show as defoliated in the map) and a commission error of 28% (i.e., mapped defoliated areas that were not detected in the tree-ring record). In southern Patagonia the omission error was 6% and the commission error was 18%. For the purposes of this study, omission errors are more relevant than commission errors because of the uncertainty that low severity defoliations would be detected in a tree-ring record (Paritsis et al. 2009). Both, omission and commission errors were caused by mismatches between the stand location and the mapped defoliation boundary by an average of 49 m. This implies that location errors and errors in defoliation detection would not significantly bias the assessment of predictor environmental variables. Qualitative testing of mapping accuracy showed satisfactory matches between defoliation maps and

the spatial extent of defoliation in ground observations and 1986 and 1999 photos from Veblen, and reports from National Park rangers.

Spatial overlay analyses

In northern Patagonia, areas of *N. pumilio* were more extensively defoliated than expected whereas areas of *N. dombeyi* and *N. antarctica* were less extensively defoliated than expected (Fig. 2a). *Nothofagus* stands at mid elevations (1,200–1,400 m) and on low angle slopes (0–15°) were more extensively defoliated than expected (Fig. 2b, c). Differences between observed and expected classes of aspect in defoliated areas were not substantial (Fig. 2d). Areas with intermediate annual precipitation (2,000–2,500 mm), relative to the distribution and cover of *Nothofagus* species in northern Patagonia, (Fig. 2e). In southern Patagonia neither of the two vegetation cover types (i.e., *N. pumilio* and *N. antarctica*) showed appreciably higher percentages of areas defoliated than expected (Fig. 2f). Vegetation at low- to mid-elevations (400–800 m) and on low angle slopes (0–15°) was defoliated to a greater extent than expected (Fig. 2g, h) but there were no clear differences in classes of aspect in southern Patagonia (Fig. 2i). *Nothofagus* stands at intermediate distances to the Andean ridge, implying intermediate precipitation levels, were more extensively defoliated than expected (Fig. 2j).

Probability of outbreak occurrence

Significant predictor variables selected for the logistic regression model in northern Patagonia were pixel frequency of all three *Nothofagus* species, mean annual precipitation, and slope angle (Table 2). Using a probability threshold of 0.4 (to define high susceptibility), the logistic regression model predicts that ca. 32% of the *Nothofagus* vegetation in the northern study area is highly susceptible to be defoliated by *O. amphimone* (Fig. 3a). Areas of high defoliation probability tend to have high frequency values of *N. pumilio* cover, mid- to high-annual precipitation, and low angle slopes. In southern Patagonia elevation and distance to the Andean ridge were the only significant predictor variables of presence of defoliation (Table 2). In this study area, the logistic regression model predicts that ca. 35% of the *Nothofagus* vegetation is highly susceptible to defoliation

(threshold = 0.4) (Fig. 3b). Areas of high outbreak probability tend to be at intermediate to close distances to the Andean ridge and at mid- to low-elevations.

Model accuracy is relatively high in northern Patagonia as indicated by its sensitivity, specificity, and CCR (Table 3). Conversely, the accuracy of the model for southern Patagonia is low when evaluated with the test dataset, especially regarding its poor specificity, which indicates high commission errors (Table 3). In both study areas models perform better in predicting defoliation presence than absence (i.e., higher sensitivity than specificity) (Table 3).

Discussion

In this work, we present the first mapping and spatial analysis of *Ormiscodes* outbreaks (and of any defoliator insect) in *Nothofagus* forests in South America. We show evidence that defoliation caused by *O. amphimone* is differentially distributed with respect to vegetation, elevation, slope angle, and precipitation regime. In addition, we developed spatially-explicit models, which predict (with variable success) areas more susceptible to be defoliated during *O. amphimone* outbreaks. While these analyses are primarily descriptive, the spatial associations documented in this study provide a basis for exploring underlying mechanisms through experimental studies that may explain the observed patterns.

Defoliation mapping

Defoliation maps are the basis for exploring spatial associations of *O. amphimone* outbreaks with environmental variables and also create opportunities for future research assessing the effects of defoliation on stand conditions during the years after the outbreak event. The relatively high occurrence of commission errors in the defoliation mapping are likely explained by the conservative nature of the tree-ring protocol used to detect outbreaks; this protocol fails to recognize defoliation events in stands affected only by low-severity defoliation (Paritsis et al. 2009). In addition, because errors occurred close to the edge of the mapped defoliated patches, trees in these locations were probably defoliated late in the season (because defoliated patches expand outward over the

Fig. 2 Percentages of defoliated area (observed versus available area (expected) of vegetation cover types (a), topographic (b–d), and precipitation (e) classes in the study area in northern Patagonia based on the 1986 outbreak; and percentages of defoliated area versus available area of vegetation cover types (f), topographic (g–i) and distance to ridge (j) (used as a surrogate for precipitation) classes in the study area in southern Patagonia based on four outbreak events (1999, 2001, 2003, and 2005). Vegetation cover types are: *Nothofagus antarctica* (N.a.), *N. dombeyi* (N.d.), and *N. pumilio* (N.p.). Only differences between observed and expected greater than 10% are labeled

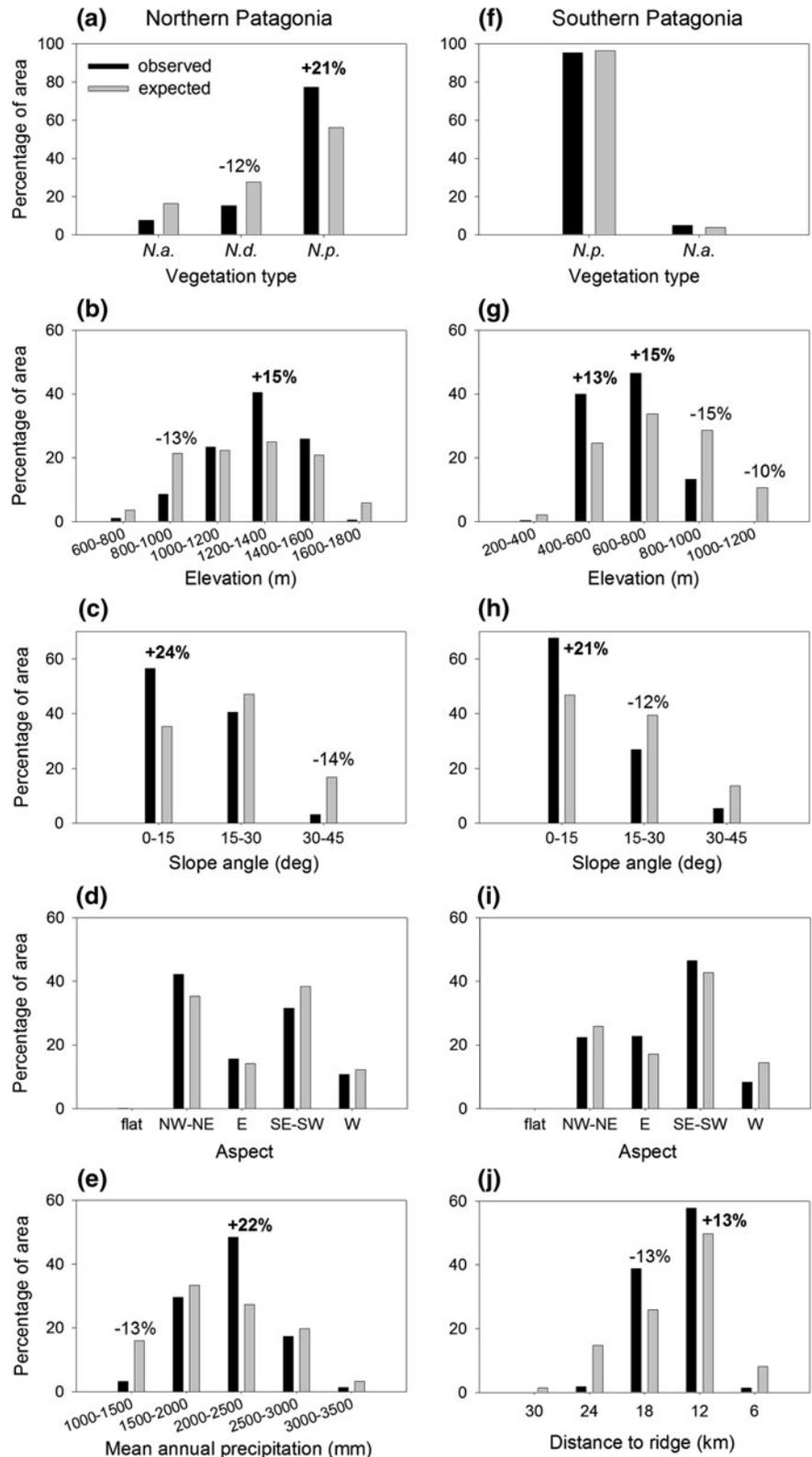


Table 2 Model terms used in the selected logistic regression model in both study areas and their associated statistics

Study area	Model terms	Odds ratio	SE	P
Northern	Frequency <i>N. pumilio</i>	1.187	0.073	0.019
	Frequency <i>N. dombeyi</i>	1.16	0.073	0.042
	Frequency <i>N. antarctica</i>	1.16	0.073	0.042
	Precipitation	1.001	<0.001	0.007
	Slope angle	0.901	0.018	<0.001
	Constant	<0.001	5.892	0.018
Southern	Elevation	0.995	0.002	0.004
	Distance to ridge	0.659	0.102	<0.001
	Constant	0.003	2.028	<0.001

The odds ratios are the exponentiation of the coefficients for the model terms

season) and therefore the impact on radial growth was less noticeable when compared to trees defoliated earlier in the season. Finally, the positional accuracy of the Global Positioning System (GPS) device (5–20 m) and the collection of tree-ring samples within a 40 m radius of the georeferenced point

(Paritsis and Veblen 2011) both potentially contributed to commission error. Hence, the relatively high occurrence of commission errors seems less related to the delineation of defoliation areas but rather stems from the method used to conduct the ground verification. Nevertheless, given the lack of clear permanent changes in the vegetation after defoliation, the use of the tree-ring record is a useful approach for assessing the accuracy of the defoliation mapping when no spatially-explicit historical records are available, as is the case in the current study.

Spatial overlay analyses

Overlay analyses of vegetation types indicate that in northern Patagonia *N. pumilio* is the preferred host of *O. amphimone*, which is consistent with field observations indicating *N. pumilio* is the most common host species (Baldini and Alvarado 2008; Paritsis et al. 2010). However, in southern Patagonia the preference of *O. amphimone* for *N. pumilio* over *N. antarctica* is not clear. The lack of a clear difference regarding defoliated vegetation in the southern study area could be related to a potential

Fig 3 Map of probability of *O. amphimone* outbreak occurrence in the northern (a) and southern (b) study areas, and actual defoliation (inset maps). Notice that the northern study area coincides with the Nahuel Huapi National Park boundaries

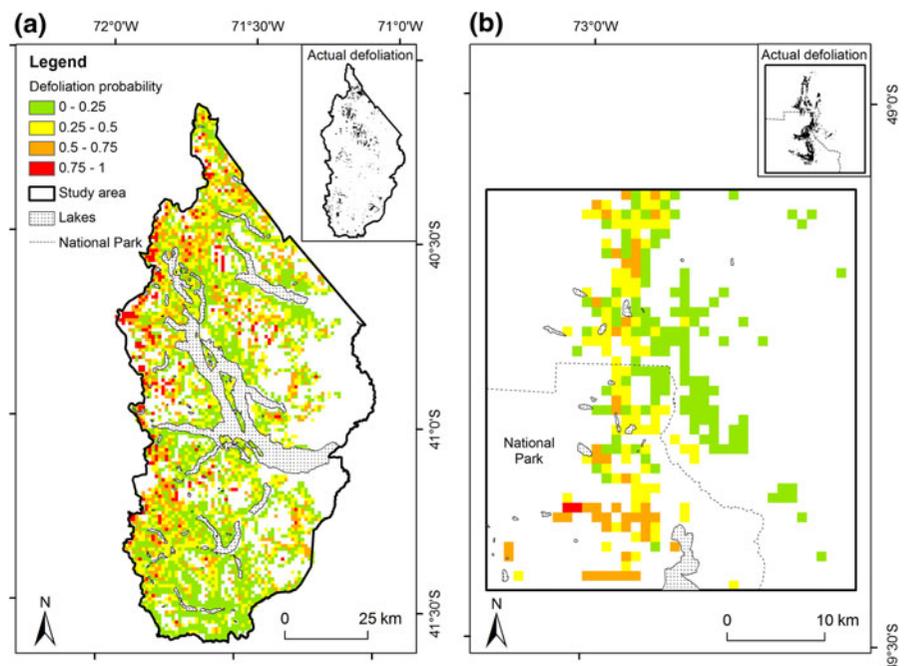


Table 3 Accuracy indicators (in percentage) derived from the training and test datasets of correctly and incorrectly classified defoliation class predictions using a probability threshold of 0.4

Study area	Training dataset				Test dataset			
	Sen	Spe	CCR	<i>n</i>	Sen	Spe	CCR	<i>n</i>
Northern	81.0	71.0	74.3	100, 200	78.8	65.6	65.7	33, 3900
Southern	75.0	70.0	71.8	40, 70	58.3	42.9	44.0	12, 153

Sample size (*n*) indicates the number of defoliated followed by the non-defoliated sample points within each dataset

Note: sensitivity (*Sen*) = TP/(TP + FN); specificity (*Spe*) = TN/(TN + FP); correct classification rate (CCR) = (TP + TN)/N. Where *TP* true positives, *TN* true negatives, *FP* false positives, *FN* false negatives

neighborhood effect in which *O. amphimone* larvae spread from *N. pumilio* to the few adjacent *N. antarctica* stands. An alternative explanation for this pattern is that the same abiotic factors that favor outbreaks in *N. pumilio* are similar in adjacent *N. antarctica* stands. Similar neighborhood effects interpreted to be explained by proximity to large quantities of the host tree species have been reported for insect outbreaks in the northern hemisphere (e.g., White and Whitham 2000; Bebi et al. 2003).

Overlay analyses yielded relatively similar associations of outbreaks to abiotic variables for northern and southern Patagonia. In both study areas, greater area than expected was defoliated at low- to mid-elevations (relative to the altitudinal range of *Nothofagus*, especially of *N. pumilio*), low angle slopes, and intermediate precipitation regimes. These conditions, together with the visual inspection of the location of the areas defoliated (Paritsis 2009) indicate that the most extensively defoliated areas were situated in mid-elevation and mesic valley bottoms. In these mesic environments with relatively poor drainage, *N. pumilio* foliage typically has higher water content and lower leaf toughness than in xeric sites (Mazía et al. 2004; Paritsis et al. 2010). Greater defoliation in mesic valley bottoms is consistent with experimental results, where *N. pumilio* foliage from mesic conditions enhanced *O. amphimone* performance (Paritsis and Veblen 2010). Similarly, in North America, higher susceptibility to spruce budworm (*Choristoneura fumiferana*) defoliation is spatially associated with mesic valley bottoms and interpreted to be a consequence of more productive spruce (*Picea* spp.) stands (Magnussen et al. 2004).

The greater occurrence of defoliated forest at low- to mid-elevations, relative to the altitudinal range of *N. pumilio*, suggests that there is a positive effect of

higher temperature on *O. amphimone* defoliation. It is likely that the lower temperatures at high elevation *N. pumilio* forests are detrimental for *O. amphimone* performance and consequently reduce defoliation occurrence. Consistent with this observation is the evidence from experimental results for northern Patagonia, which show reduced *O. amphimone* performance and consumption rate at low temperatures (Paritsis and Veblen 2010). Furthermore, other elevation-dependent variables, such as soil moisture might also directly or indirectly play an important role. For instance, in *N. pumilio* stands near the southern Patagonian study area, summer soil moisture (i.e., when larvae feed) decreases with increasing elevation (Hertel et al. 2008). This moisture gradient may directly affect foliage quality and consequently influence defoliation patterns (Paritsis and Veblen 2010) along the altitudinal gradient. Although multiple studies have documented spatial associations between elevation and insect outbreaks in the northern hemisphere, specific responses of insect attack in relation to elevation are diverse (Bebi et al. 2003; Magnussen et al. 2004; Kharuk et al. 2009).

Prediction of probability of outbreak occurrence

While vegetation type plays a key role as a predictor variable for defoliation in the logistic regression model developed in northern Patagonia, vegetation is not a significant predictor variable in southern Patagonia. Most likely, this difference is due to the high homogeneity in the composition of susceptible vegetation in southern Patagonia (i.e., ca. 95% of the cover is *N. pumilio*) compared with the relatively diverse *Nothofagus* vegetation in northern Patagonia. Hence, the importance of vegetation type in the spatial dynamics of *O. amphimone* outbreaks should

not be regarded as unimportant in southern Patagonia. Precipitation regime (expressed as distance to the ridge in southern Patagonia) is a significant predictor variable in the models for both study areas, suggesting that spatial variation in mean annual precipitation has a key role for defoliation occurrence. In accordance with these results, precipitation variability across space also was found to be a significant predictor variable for the frequency of spruce budworm (*Choristoneura fumiferana*) defoliation in Ontario, Canada (Candau and Fleming 2005). However, in the Candau and Fleming (2005) study, higher defoliation frequencies were associated with areas of low precipitation in June (i.e., summer).

The high accuracy of the logistic regression model in predicting defoliation in northern Patagonia contrasts with the relatively poor accuracy of the model for southern Patagonia. Although multiple factors may explain this low accuracy, a likely cause is related to the comparatively small size of the southern study area, which exhibits less range of variability in the predictor variables (especially in vegetation which proved to be a key predictor in northern Patagonia). In contrast, the larger size study area in northern Patagonia provides a greater range for predictor variables, which improved the predictive power of the model. Potentially, the logistic regression model for southern Patagonia may be improved by incorporating future *O. amphimone* outbreaks that occur over larger areas. Given that the logistic regression models for both study areas are based on small numbers of outbreak events (i.e., one and four outbreak events in northern and southern Patagonia, respectively) their predictive power is temporally limited. Nevertheless, the outbreak events used to build the models represent the most extensive defoliation events recorded in the study areas over the past ca. 30 years. In addition, the relatively similar results found in both study areas reinforce the validity of the associations between *O. amphimone* defoliations and the analyzed environmental variables documented here.

Defoliation extent and significance of *Ormiscodes* outbreaks on *Nothofagus*

Although defoliation events by *Ormiscodes* undoubtedly have important but short-lived influences on population dynamics across trophic levels, these

events have not been considered to be key disturbances in Patagonian *Nothofagus* forests because they apparently do not result in adult tree mortality (Veblen et al. 1996). The lack of tree mortality associated with defoliation events contrasts with the effects of natural and anthropogenic fire that kill trees over large areas of *Nothofagus* forest in Patagonia (Veblen et al. 2008). For instance, a spatially-explicit study in NHNP detected 8,468 ha affected by fire over the 1985–1999 period (Mermoz et al. 2005). In our study, we detected 11,600 ha defoliated over a single season for nearly the same study area. Hence, although the impacts of *Ormiscodes* outbreaks on tree mortality and regeneration processes are small, the extent of defoliated areas appears to be greater than those affected by fire, at least in some regions. Though unstudied, the impact of defoliation events on annual ecosystem productivity and population dynamics of predators and folivores is likely to have an important ecological role in these forests. Consequently, predicted future increases in the frequency of defoliation events (Paritsis and Veblen 2011) as a consequence of recent trends towards warming and drought conditions over large regions in Patagonia may have far-reaching effects on the structure and function of these ecosystems.

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