

Droughts drive outbreak dynamics of an invasive forest insect on an exotic host



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ARTICLE INFO

Keywords:

Spatio-temporal dynamics
Forest pest
Spatial synchrony
Invasive species
Global change

ABSTRACT

Insect outbreaks are among the most important biotic disturbances in forest ecosystems and can exert immense economic and ecological impacts. Understanding the spatio-temporal patterns of eruptive insects can provide insights into the mechanisms driving their dynamics and help predict future responses under climate change. The aims of this study were to analyze the spatio-temporal patterns of outbreaks of the woodwasp *Sirex noctilio* –a major invasive pest of pines– in an invaded region of South America, to assess the relative importance of density-dependent and density-independent mechanisms on population dynamics, and to identify the primary factors that influence the magnitude of outbreaks. We used tree ring and insect sampling data of more than 1000 trees to reconstruct *S. noctilio* outbreaks in 29 pine stands across Patagonia-Argentina over a 16-year period. We found marked spatial synchrony in *S. noctilio* outbreaks at a regional scale. Rates of tree mortality from *S. noctilio* were influenced by both density-dependent and density-independent factors. The occurrence of *S. noctilio* outbreaks are triggered by an abrupt increase in drought, which likely increases the availability of susceptible host trees. The damage caused by the outbreaks is determined by stand level variables, closely related with tree stress. Rates of tree mortality decreased over time due to negative density-dependence in *S. noctilio* populations, likely due to the loss of suitable resources over time. Depicting mechanisms of large-scale tree mortality in ecosystems provides insights to the drivers of forest outbreaks and other factors such as responses to a changing climate.

1. Introduction

Outbreaks of forest insects can cause significant area-wide disturbance, with dramatic ecological and economic effects on forest ecosystems (Gregoire et al., 2015; Schowalter, 2012). Tree mortality caused by outbreaks of insect herbivores has been shown to be one of the major agents of natural disturbance in forests around the globe (Dale et al., 2001; van Lierop et al., 2015). Furthermore, in the context of global changes, increasing trade and human movement has remarkably accelerated the rate of introductions of forest pests (Brockerhoff and Liebhold, 2017), while climate change has been found to have profound effects on some forest insect population dynamics (Bentz et al., 2010). Understanding the spatio-temporal patterns of eruptive populations of insects can provide valuable insights into the mechanisms driving their dynamics and may help predict future responses in the context of global change (Ayres and Lombardero, 2000; Marini et al., 2017).

As both insect invasion and tree mortality rates increase globally (Brockerhoff and Liebhold, 2017), the search for generalities in forecasting invasions speeds, outbreak magnitudes, and/or spatial extents of potential biome level changes would benefit from several pieces of information. First, in the context of current trends in climate change, there is particular urgency to determine if, when, or how extreme climatic events promote eruptions of forest insect populations. Since herbivorous insect are poikilotherms, weather may affect their population dynamics directly by affecting the physiology of individual insects. Temperature, for instance, influences almost all aspects of insect basic population processes such as development rate, seasonality, voltinism, reproduction, and dispersal (Bale et al., 2002; Battisti et al., 2005; Sambaraju et al., 2012; Tobin et al., 2008). Indirectly, temperature may also affect interactions of the target species with their hosts and natural enemies (Bentz et al., 2010; Marini et al., 2012). Precipitation, on the other hand, primarily influences forest insect populations by affecting host-tree vigor (Haavik et al., 2015; Jactel et al.,

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<https://doi.org/10.1016/j.foreco.2018.11.044>

Received 7 September 2018; Received in revised form 16 November 2018; Accepted 23 November 2018

Available online 08 December 2018

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2012). Consequently, changes in temperature and an increase in frequency of droughts have been proposed to be important triggers of insect outbreaks (Jönsson et al., 2009; Raffa et al., 2008).

Second, we require information across feeding guilds. Several studies have explored the drivers of the outbreak dynamics of different forest insects, particularly focusing on the relationship between outbreaks and extreme climatic events (Bentz et al., 2010; Klapwijk et al., 2013; Marini et al., 2017; Williams and Liebhold, 2002). Many of these studies have concentrated on feeding guilds such as defoliators, sap-feeders, and bark-boring insects, however. There is a lack of larger space-time information on wood-boring insect outbreaks, likely because of difficulties in obtaining quality data.

Finally, we require knowledge of insect behavior in novel environments, especially when introduced to potential hosts devoid of historic co-evolutionary associations (Bertheau et al., 2010; Rosenberger et al., 2018). The emerald ash borer, for example is relatively benign in its native Asian range, but threatens to functionally extirpate the North American *Fraxinus* genus in the coming decades (Herms and McCullough, 2014). Similarly, aggressive tree-killing bark beetles in the genus *Dendroctonus* such as mountain pine beetle, *D. ponderosae*, and southern pine beetle, *D. frontalis*, have recently expanded beyond their historic range and threaten range expansion to naïve *Pinus* spp. (Lesk et al., 2017; Rosenberger et al., 2017). There exists few studied continental examples of invasive tree-killing insects where the host is similarly exotic, for example *Ips grandicollis* which is a North American bark beetle species that invaded pine plantations in Australia (Yousuf et al., 2014).

Sirex noctilio F. (Hymenoptera: Siricidae) is a woodwasp native to Eurasia that has successfully invaded most of the regions of the world where pines have been planted, such as Australasia, South America, South Africa, and North America (Lantschner et al., 2014; Slippers et al., 2015). In association with a symbiotic fungus, *Amylostereum areolatum* (Fr.) Boidin (Russulales: Stereaceae) and a phytotoxic venom, *S. noctilio* is capable of killing mature host trees in its invaded range (Madden, 1988; Slippers et al., 2015). This woodwasp is considered one of the most damaging pests of softwood plantations in the Southern Hemisphere. In the last decade, and especially since *S. noctilio* arrived to North America, it has attracted much attention, given the potential risk to native pine forests there and competition with native woodwasp species (Hoebeker et al., 2005). In most of the invaded areas in which pines are cultivated, *S. noctilio* displays a pulse-like eruptive population behavior, causing significant tree mortality (Lantschner and Corley, 2015; Madden, 1988; Slippers et al., 2015). Eruptive dynamics are characterized by lengthy periods during which populations remain at relatively low densities, but may rapidly increase to outbreak levels in an unpredictable fashion (Berryman, 1987). Although many aspects of the biology and control of *S. noctilio* have been intensively studied in the last decades, the spatial and temporal patterning of its outbreaks within invaded ranges remain poorly understood (Slippers et al., 2015).

Analyzing an outbreak in Australia, Madden (1988) proposed a mechanism to explain *Sirex noctilio* population eruptions based on density independent factors: outbreaks are triggered by short and intense above average rains interrupting dry summers. He posited that drought causes tree stress and enhances their attractiveness to female wasps: when short rains interrupt the drought, tree growth is re-initiated, thus improving woodwasp development rates (Madden, 1988). In contrast, Corley et al. (2007) and Aparicio et al. (2013) noted that as woodwasp populations grow, spatial aggregation of attacks becomes stronger, suggesting that aggregation – through a density-dependent process – may be a key factor for the onset of outbreaks, independent of environmental factors. Testing such hypotheses and elucidating the regulating mechanism of population dynamics, however, requires long-term data well-replicated over space and time (Bjørnstad et al., 1999).

In this study, we examined 1015 trees annually across 29 sites for 16 years across a 500 km × 50 km area in the region of Patagonia,

Argentina, southern South America where *S. noctilio* outbreaks occur within pine plantations. We used these data to (a) describe the spatio-temporal pattern of outbreaks of *S. noctilio* at a regional scale in NW Patagonia, (b) explore the importance of density-dependent and independent factors as potential mechanisms behind woodwasp population dynamics; and (c) identify the main variables that determine the magnitude of outbreaks of *S. noctilio* populations. By investigating the spatio-temporal population dynamics of a wood-boring species on a non-native host and in the invaded range, we will contribute to knowledge of the key drivers of forest insect outbreaks. In addition, we expect our findings may help improve the strategies deployed for management of the most damaging pest of cultivated pines in the Southern Hemisphere.

2. Materials and methods

2.1. Study area and system characteristics

The study was carried out in NW Patagonia, Argentina, east of the Andes range, along an area of about 500 × 50 km (extending from 70.96° to 71.56° W, and 39.3° to 43.55°S), where most of the pine plantations are established (Fig. 1). The climate of this area is temperate, dominated by a marked west-to-east decrease in precipitation. Mean annual rainfall within the study area ranges from 600 mm/year in the eastern part to 1200 mm/year in the western part. Rainfall is concentrated in the autumn and winter, leading to dry summers with about 200–400 mm precipitation during October to April (Bianchi et al., 2016).

Approximately 100,000 ha of pines are cultivated in the study area, mainly for wood-producing purposes, and consist primarily of three North American species: *Pinus ponderosa* Dougl. Ex. Laws, *Pinus contorta* Dougl. ex. Loud., and *Pinus radiata* D. Don (Dirección de Producción Forestal, 2014). The growing season of pines in the study area begins approximately in September/October and ends in April of the following year.

Sirex noctilio was first detected in Patagonia in 1993, in the center part of the study area (71.15°W, 41.08°S), and it started spreading north and south at a rate of approximately 17 km/year. In 2004 it occurred across the entire study area, causing tree mortality at low levels (Lantschner et al., 2014). The woodwasp spends most of its life cycle as a larva within the sapwood of its hosts. In the study area, it develops in 1–3 years, although the majority (75%) of emergence occurs after 1 year. After development adults emerge, mate and attack new trees. Flight season in Patagonia begins by late December, when summer starts, and can last until May. Peak adult emergence, is usually observed in January, the hottest month of the year, and a smaller peak can be also seen in March (Corley et al., 2018). Biological control programs in the study area utilize the periodic inoculation of the entomophagous nematode *Beddingia siricidicola* Bedding (Tylenchida: Neotylenchidae). In addition, two species of parasitoid wasps native to the Northern Hemisphere have been introduced and are established in the study area, the hymenopteran species *Ibalia leucospoides* (Hochenwarth) and *Megarhyssa nortoni* (Cresson) (Corley et al., 2018).

2.2. Outbreaks sampling

We selected 29 sites distributed along the study area with pine plantations where *S. noctilio* outbreaks occurred (Fig. 1). To select the sites, we drove through all the pine plantations of the study area and selected stands with outbreaks of *S. noctilio* based on observation of external symptoms (discolouration of foliage and/or dead trees). Each site corresponded to a different outbreak. We defined outbreaks as stands with between 5 and 20 ha in size and with more than 5% of trees visibly attacked by *S. noctilio* (Lantschner and Corley, 2015; Villalba and Corley, 2012). Based on samplings of the woodwasp from the edge of pine plantations up to a distance of 4 km, it was found that 98.7% of

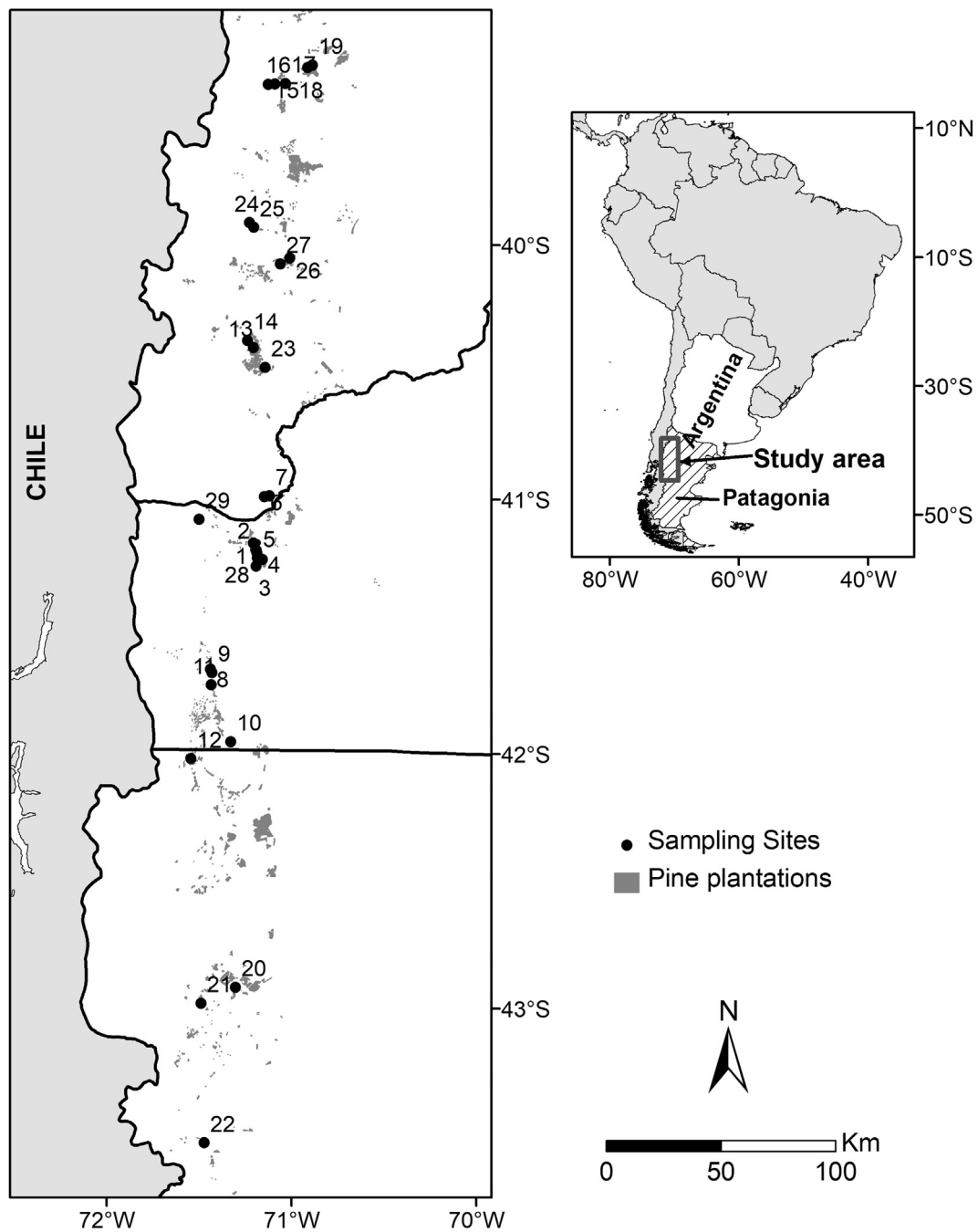


Fig. 1. Location of the study area in Patagonia, Argentina, showing sampling sites of *S. noctilio* outbreaks and distribution of pine plantations (Dirección de Producción Forestal, 2014).

the captures occurred up to 1.6 km away from the plantation (Villacide, 2015). Consequently, sampling sites were separated by a minimum of 2 km from one another to ensure spatial independence among *S. noctilio* populations. The most common planted pine species among the selected sites was *P. contorta* (85% of the sample trees), as this species is by far the most preferred tree by *S. noctilio* in the study area (Lantschner and Corley, 2015), followed by *P. ponderosa* and *P. radiata* (10% and 5% of the sampled trees respectively). The sampled plantations were established between 1973 and 1990. Tree density was relatively high, ranging from about 1000 to 2500 trees/ha. Most of these stands were pruned (79%), but only a few (21%) were thinned (see Table A1 for more detail on site characteristics).

At each sampling site, we randomly established four square plots of 50 trees each (i.e., 200 trees per site) to spatially distribute sampling

along the outbreak, and at each plot we recorded the number of trees attacked by *S. noctilio* (i.e., trees with emergence holes or resin droplets). In Patagonia, *S. noctilio* is the only insect species known to kill live, vigorous pines, and is the only insect that causes characteristic resin droplets and perfectly rounded emergency holes in pines, causing extensive tree mortality (Corley et al., 2007). We randomly selected 30 dead trees (killed by *S. noctilio*) within the four plots and collected two increment cores from each using 5.15-mm (core diameter) increment borers (Haglof, Sweden). We also sampled five live vigorous trees to include the pith in order to date the stand age. In total, 2030 increment cores were collected (35 trees × 2 cores per tree × 29 sites). Increment cores were collected at the base of the tree (ca. 0.3 m high) from two different aspects of each sampled tree (east and south). In a few cases, cross sections of the main stem rather than increment cores were

collected from felled or downed trees. Samplings were conducted during 2015 austral summer.

Core and cross section samples were dried. Cores were glued onto wooden mounts and progressively sanded with 100, 200, and 400 grit sand paper to clearly distinguish growth rings. Ring widths from each increment core were measured using a scanner and analyzed using WinDendroTM software (Regent Instruments Inc., Quebec, Canada).

2.3. Cross-dating samples

Skeleton plots, which graphically represent the width of each annual growth ring relative to the average width of the three tree rings on either side, were generated from ring width measurements for each increment core. Increment cores from live pine trees were inspected first and dates were assigned to each growth ring. Increment cores from dead trees were then visually cross-dated to cores of live trees from the same site, matching marker years (i.e., narrow rings caused by adverse growing conditions) to determine the precise year of formation of each growth ring (Stokes and Smiley, 1968). Death of trees successfully attacked by *S. noctilio* occurs 2 weeks to 8 months after attack (Madden, 1988); consequently, we assumed that the year of death of each tree (last growth ring) was the same as the year of attack. Calendar dates were assigned to rings according to the Southern Hemisphere tree-ring dating convention that assigns an annual ring to the calendar year in which the annual ring formation begins (Schulman, 1956).

2.4. Site variables

To characterize each site, we estimated tree density (trees/ha), using the nearest-neighbor method (Cottam et al., 1953), measuring the distance to four nearest neighbors of five different trees randomly selected at each site, and recorded DBH of each of these trees ($n = 20$). We calculated the basal area based on tree density and mean DBH. We also recorded the latitude and longitude of each site. We used 30-m resolution digital elevation models of the study area (ASTER-GDEM-Validation-Team, 2009) to estimate the topographic variables (altitude, slope angle). Plantation landscapes around each site were described using a circular area of radius = 1 km, estimating the proportion of pine plantation inside this circle, based on a 1:500,000 resolution maps of plantation forests in the study area (Dirección de Producción Forestal, 2014). This size of buffer has been previously shown to be important to evaluate *S. noctilio* perception of landscape features by *S. noctilio* (Lantschner and Corley, 2015). Based on dendrochronology, we calculated the age of the plantation during the outbreak as the year of the outbreak maximum peak (year with the highest mortality rate; see Table A1 for detailed description of the variables).

Mean annual temperature and annual precipitation values for each site were obtained from a 10 arc-second resolution grids from WorldClim (Hijmans et al., 2005). Monthly 0.5° resolution time series data of the self-calibrating Palmer Drought Severity Index (scPDSI) (Palmer, 1965) for the period 1998–2013 were obtained for each site from the CRU global dataset (van der Schrier et al., 2013). The Palmer Drought Severity Index takes into account precipitation, evapotranspiration, and soil moisture conditions, all of which are determinants of hydrologic droughts. We estimated a mean value of scPDSI for each year (1998–2013) in each sampled site. The index uses 0 as normal, positive numbers reflects wet years, while drought is shown in terms of negative numbers, – e.g., –2 is moderate drought, –3 is severe drought. In northern Patagonia about 60% of the precipitation falls during May through August (southern hemisphere autumn–winter), while the growing season (spring – summer) is dry. To incorporate the effect of the rainy season on tree growth, we averaged the scPDSI monthly values of the growing season plus the values of the months of the previous rainy season (i.e.: for the year 2006, we used monthly scPDSI values from May 2006 to April 2007), and assigned each averaged value to the calendar year in which the annual tree increment

growth began (see Fig. A1A for detail on the temporal series of the scPDSI among the sampled sites). We refer to these values simply as PDSI values hereafter.

2.5. Data analysis

2.5.1. Spatial synchrony

To assess if *S. noctilio* population dynamics are spatially synchronized at different scales, we used a nonparametric cross-correlation function (*sncf*) in the NCF library (Bjørnstad, 2012) of R 3.3.3 (R-Core-Team, 2017). This output describes how spatial correlation among time series varies with distance separating the sampling locations, and how spatial correlation at shorter distances compares to the regional synchrony across the study area (Bjørnstad, 2012). For this analysis we used the number of attacked trees per year at each of the 29 sampled locations.

2.5.2. Spatio-temporal population dynamics

We used the number of trees killed by *S. noctilio* each year as a proxy for insect abundance, and we examined discrete time models of the change in tree mortality rate, R , defined as $\ln(N_t/N_{t-1})$, where N_t is the number of trees killed by *S. noctilio* during the year t . *Sirex noctilio* did not arrive in all areas of Patagonia simultaneously, so we removed years prior to arrival in each site to avoid analytical bias from years in which the insect was not present, based on the first detection of the species at each location (Lantschner et al., 2014). We further removed instances where R was zero, infinite, or undefined; leaving 176 observations across 29 sites in the data set.

We regressed R on several independent variables such as N_{t-1} (i.e., a term for density dependence) and various measures of drought (i.e., terms for density-independence, defined in Table 1). We approached model building in two stages. First, we fit each candidate individual variable individually and used information criteria and inferential tests of slope coefficients to select the model most parsimonious with the data. The variable that best explained changing rates in tree mortality caused by *S. noctilio* was the number of *S. noctilio* in a site the previous year (see Results). Then, in a second round of model selection, that variable was retained with all drought variables fit iteratively, one at a time. AIC values and inferential tests of model coefficients were again utilized to identify which drought variable (if any) best explained additional variation in tree mortality beyond that explained by the N_{t-1} term. No further combinations of additional variables improved the models, so are not reported.

All models used a mixed-effects regression framework with a random intercept for site using the lme4 package in R (Bates et al., 2015). The N_{t-1} variable was transformed $\ln(x)$ to fulfill model assumptions of normality and homoscedasticity of errors, which were checked by visual inspection of residual plots. All analyses were conducted in R v3.3.3 (R-Core-Team, 2017).

Table 1

Variables defined for examining effects of *S. noctilio* and drought regimes on changes in interannual rate of tree mortality due to *S. noctilio* at 29 sites in Patagonia, Argentina, 1998–2013.

Variable	Definition
N_{t-1}	Number of trees killed in previous year by <i>S. noctilio</i>
PDSI	Palmer Drought Severity Index in current year
$PDSI_{t-1}$	Palmer Drought Severity Index in previous year
$\Delta PDSI$ (one year)	Change in PDSI from year to year
$\Delta PDSI$ (two years)	Change in PDSI from two years ago to current year
PDSI	Absolute value of PDSI each year
$(1_{dry} 0_{wet}) * PDSI_t$	Only “dry” values of PDSI in current year; zero otherwise
$(0_{dry} 1_{wet}) * PDSI_t$	Only “wet” values of PDSI in current year; zero otherwise
$(1_{dry} 0_{wet}) * PDSI_{t-1}$	Only “dry” values of PDSI last year; zero otherwise
$(0_{dry} 1_{wet}) * PDSI_{t-1}$	Only “wet” values of PDSI last year; zero otherwise

2.5.3. Outbreak magnitude

We explored the primary environmental variables that determine the magnitude of outbreaks of *S. noctilio* populations (% of attacked trees at each stand) in NW Patagonia. We considered a set of nine variables as potential predictors of variation in the total percentage of attacked trees by *S. noctilio* during outbreaks. We chose these variables based on an *a priori* assessments of their biological relevancies to *S. noctilio* population dynamics, effects on woodwasp performance, and effects on tree susceptibility to attacks (Lantschner and Corley, 2015; Villacide and Corley, 2012). Variables examined included measures of plantation management and design (tree density, dbh, basal area, plantation age during outbreak, proportion of land covered by pines plantations in a 1 km radius neighborhood), climate (mean annual temperature, and annual precipitation), and topography (altitude, slope) for each site. We used multiple linear regressions to assess how cumulative tree mortality relates to the selected environmental variables. To avoid multicollinearity, we performed Spearman correlations between pairs of predictor variables, setting a limit of $\rho < 0.55$ for keeping two correlated variables. We used cumulative % of killed trees during the period 1998–2013 in each site as the dependent variable, and included environmental variables as independent variables. Eight regression models were obtained using the backward elimination method, starting with a model that included all variables. Models were then compared using Akaike's Information Criterion for small sample sizes (AICc). Each site was considered as an independent replicate ($n = 29$). Linearity between the independent and dependent variables was visually evaluated from a matrix of scatter plots and plots of residuals against the predicted values, and normality of the residuals was evaluated using the Kolmogorov–Smirnov test.

3. Results

Tree-killing activity of *S. noctilio* frequently erupted rather rapidly from one year to the next, but then would begin to decline over the course of the next five years (Fig. 2). Along the period of this study, 1998–2014, most outbreak peaks occurred between 2007 (48% of the sites) and 2008 (24% of the sites, Fig. 2). In addition, the percentage of attacked trees in different sites varied widely, with values ranging from 12 to 75% of the stand (Table A.1).

We found a high level of spatial synchrony in *S. noctilio* mortality across distances up to 300 km (Fig. 3). The overall regional synchrony within the study area was 0.58 (95% CI = 0.49, 0.69), indicating that across the entire study area, populations were, on average, positively correlated and would rise or fall in tandem with one another (Fig. 3). Spatial synchrony declined with increasing distance, but even populations separated by long distances up to 300 km (which represents about ½ the maximum distance between sites) across the study area were still positively correlated with one another (i.e., correlation > 0; Fig. 3).

Two variables explain variation in interannual tree mortality rates caused by *S. noctilio*: the number of *S. noctilio*-killed trees in a stand in the previous year (i.e., negative density-dependence), and a change in PDSI from the previous to the current year. The effects of these two variables were similar both when considered individually and collectively in a joint model. First, when each variable in Table 2 was examined on their own, the best explanation of tree mortality rates was the number of *S. noctilio*-killed trees in the previous year, as evidenced by the lowest AIC value (model 1, Table 2A). The negative slope estimate indicates negative density dependence; that is, immediately after a population spike, the tree mortality rate may still be positive but begins to decrease (Fig. 4A).

Second, when we included individual drought variables in a model along with the density-dependent term for *S. noctilio* abundance, we found that the most parsimonious model indicated that a negative change in PDSI was also significantly associated with tree mortality (model 13 in Table 2B). That is, a rapid onset of a drought period (i.e., a sharp negative change in PDSI values between successive years)

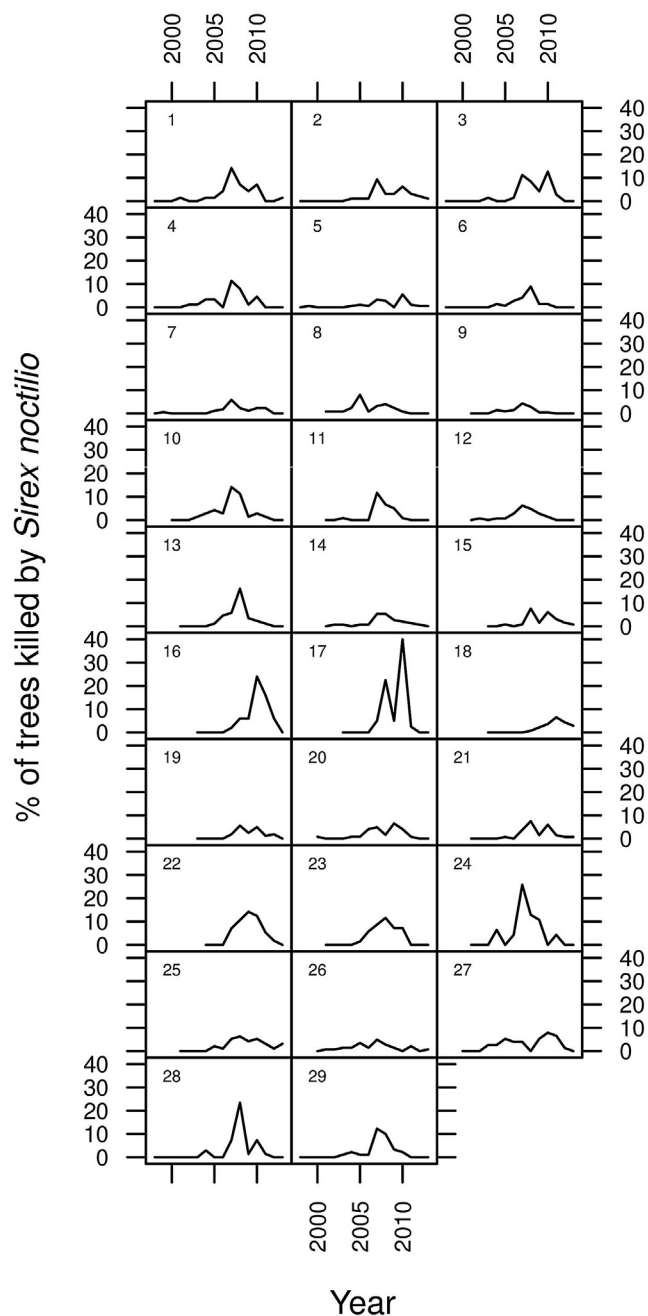


Fig. 2. Temporal fluctuations in percentage of trees killed by *S. noctilio* over the period of the study in the 29 sampled sites in Patagonia, Argentina (see Fig. 1 for spatial reference of sites). Note that calendar year was assigned according to the Southern Hemisphere tree-ring dating convention that assigns an annual ring to the calendar year in which the annual ring formation begins (i.e. the year 2007 represents the tree growing season from about October 2007 to May 2008).

appears to increase tree mortality rate (See Fig. A1B for more detail on temporal series of the change in scPDSI from previous year). These relationships can be described with the following equation:

$$R = 0.543 - 0.524 \ln(N_{t-1}) - 0.150 \Delta PDSI \quad (1)$$

The negative correlation between change in PDSI and tree mortality rate is consistent in both the multiple regression model (negative coefficient in Eqn. (1), Table 2b) and the variable when examined individually (Fig. 4B).

We constructed 8 multiple linear regression models to assess which environmental variables determine the magnitude of *S. noctilio*

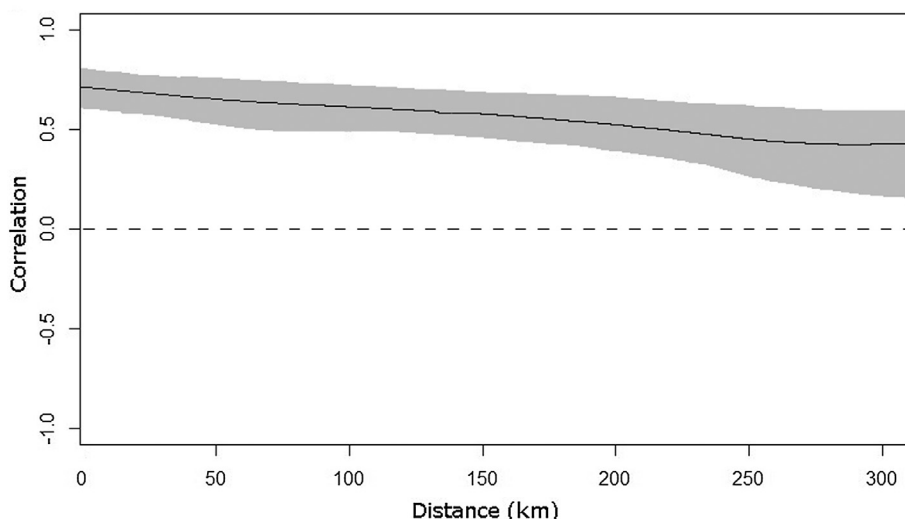


Fig. 3. Nonparametric cross-correlation function (SNCF, black line) and 95% pointwise confidence (grey area) of % of *S. noctilio* attack in Patagonia, Argentina. Regional synchrony level with 95% confidence interval (based on 500 iterations) is 0.58 (0.49, 0.69).

outbreaks. The model with the lowest AIC score contained two variables: stand basal area (BA) and plantation age during the outbreak peak (PA), both positively related with *S. noctilio* outbreak magnitude individually, and together described 30% of the variation in mortality rate (Table A.2). We obtained the following regression equation,

$$\% \text{ Attacked trees} = -19.9 + 0.34 * \text{BA} + 1.35 * \text{PA} \quad \text{Table A.3} \quad (2)$$

4. Discussion

Our results that *S. noctilio* outbreaks in Patagonia are highly synchronized over distances greater than the wasps mean dispersal capability (17.4 km under laboratory conditions, Corley et al., 2018; Fig. 3), supports the hypothesis that an exogenous forcing mechanism synchronizes outbreak patterns across a regional scale via a Moran effect (Hudson and Cattadori, 1999). In population dynamics in general,

two main synchronizing mechanisms have been described: (a) synchronous stochastic effects –typically meteorological– that affects population growth in a density-independent fashion; and (b) dispersal among populations of the focal species or its natural enemies, which are influenced mainly by density-dependent effects (Bjørnstad et al., 1999; Liebhold et al., 2004). Identifying the synchronizing processes present in a specific population is often difficult as both synchronizing mechanisms may produce similar spatio-temporal signatures (Liebhold et al., 2004). However, synchrony over longer distances than the wasps’ dispersal capability (Bruzzone et al., 2009) is likely to be due to regional environmental perturbations (Ranta et al., 1995; Liebhold et al., 2004).

Indeed, outbreaks of *S. noctilio* appear to be triggered by an abrupt decrease in precipitation, consistent with the “intermittent drought hypothesis” (Madden, 1988) positing that rapid changes in the physiological status of host trees are the main triggers of *S. noctilio*

Table 2

Summaries of mixed models results explaining interannual changes in tree mortality rates by *S. noctilio*, *R*, as a function of various combinations of density dependent (i.e., *S. noctilio*) and density-independent (i.e., precipitation) variables. Part A lists single variable models, while Part B reflects models with a term for *S. noctilio* density in the previous year as well as the listed variable. Estimates for intercepts are not shown. Bold type indicates best models.

Model	Regression variables	MLE	SE	t-value ^a	P-value	Effect of variable on tree mortality rate, <i>R</i>	AIC
<i>A. Single variable models; R = β₀ + ...</i>							
0	Intercept						519.2
1	ln(<i>N</i> _{<i>t</i>-1})	-0.622	(0.068)	-9.03	< 0.0001	↓ with more insects in previous year	461.12
2	PDSI _{<i>t</i>}	-0.072	(0.052)	-1.40	0.16	No signal	523.36
3	PDSI _{<i>t</i>-1}	+0.280	(0.051)	5.54	< 0.0001	↓ with previous year drought	496.90
4	ΔPDSI (one year)	-0.218	(0.039)	-5.54	< 0.0001	↑ with sharp annual decrease in PDSI	497.42
5	ΔPDSI (two years)	-0.081	(0.034)	-2.36	0.0194	↑ with sharp two-year decrease in PDSI	520.61
6	PDSI	-0.163	(0.084)	-1.95	0.05	No signal	520.58
7	(1 _{dry} 0 _{wet}) * PDSI _{<i>t</i>}	-0.001	(0.069)	-0.14	0.88	No signal	524.72
8	(0 _{dry} 1 _{wet}) * PDSI _{<i>t</i>}	-0.548	(0.014)	-3.83	0.0002	↓↔ with wet current year	509.10
9	(1 _{dry} 0 _{wet}) * PDSI _{<i>t</i>-1}	+0.390	(0.068)	5.72	< 0.00001	↓ with drought in previous year	494.58
10	(0 _{dry} 1 _{wet}) * PDSI _{<i>t</i>-1}	+0.473	(0.141)	3.36	0.0010	↑ with wet previous year	512.30
<i>B. Two variable models; R = β₀ + ln(<i>N</i>_{<i>t</i>-1}) + ...</i>							
11	PDSI _{<i>t</i>}	-0.112	(0.043)	-2.82	0.0054	↑ with current year drought	459.89
12	PDSI _{<i>t</i>-1}	+0.129	(0.050)	2.58	0.0110	↓ with previous year drought	460.81
13	ΔPDSI (one year)	-0.150	(0.035)	-4.28	< 0.0001	↑ with sharp annual decrease in PDSI	450.59
14	ΔPDSI (two years)	-0.082	(0.028)	-2.92	0.0041	↑ with sharp two-year decrease in PDSI	460.14
15	PDSI	-0.037	(0.075)	-0.50	0.62	No signal	466.24
16	(1 _{dry} 0 _{wet}) * PDSI _{<i>t</i>}	0.123	(0.058)	-2.11	0.0369	↑ with current year drought	462.68
17	(0 _{dry} 1 _{wet}) * PDSI _{<i>t</i>}	-0.433	(0.120)	-3.61	< 0.0001	↓ with wet current year	452.91
18	(1 _{dry} 0 _{wet}) * PDSI _{<i>t</i>-1}	+0.178	(0.069)	2.59	0.0105	↓ with drought in previous year	460.09
19	(0 _{dry} 1 _{wet}) * PDSI _{<i>t</i>-1}	+0.207	(0.125)	1.65	0.10	No signal	462.78

^a 146 and 145 degrees of freedom for parts A and B, respectively.

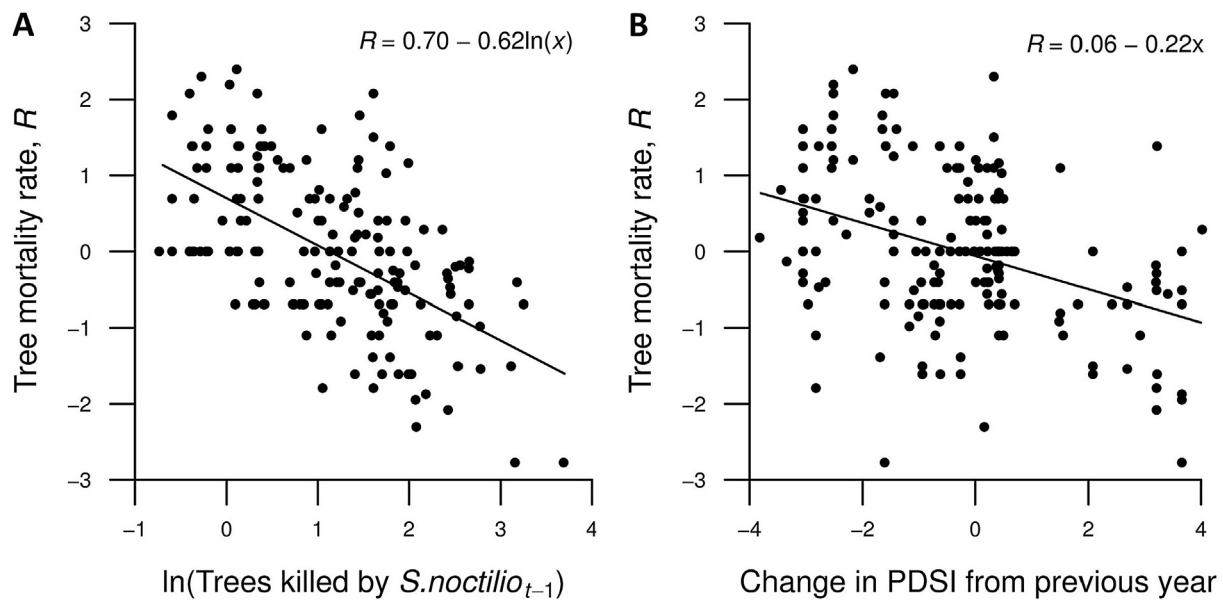


Fig. 4. Regression plots of tree mortality rate by *S. noctilio*, R , vs. (A) natural logarithm of trees killed by *S. noctilio* the year before, and (B) change in self-calibrating Palmer Drought Severity Index (scPDSI) from previous year. Note that drought is indicated by negative values of PDSI index.

outbreaks. Hydric stress affects virtually every plant process including aspects of water, temperature, and nutrient stress (Mattson and Haack, 1987). We believe that an increase in the availability of susceptible stressed host trees due to drought combined with other stress factors, such as overstocked stands, leads to an increase in woodwasp fitness, enabling the population to escape regulation by resources and/or natural enemies, and reach very high densities. The suitability of conditions for attack and development of woodwasp larvae in trees appears to be best when there is variability in drought stress suffered by its hosts, rather than by the absolute magnitude of the drought. Madden (1988) suggested that stress due to a rapid change in the physiological status of the host tree, reduces trees resinosis and polyphenol formation, favoring multiple drilling attacks by woodwasps, and increasing the number of eggs laid and their survival (Martinson et al., 2018). Additionally, the rupture of xylem vessels experiencing high water tension by drilling, with subsequent invasion of air, favors optimal conditions for growth of the woodwasps symbiont, *A. areolatum*, on which *S. noctilio* larvae depend on for successful development (Madden, 1988).

According to the latest report of the Intergovernmental Panel on Climate Change (IPCC, 2014), droughts, as well as other extreme events, could become more frequent and severe around the world. In this context, a major challenge for ecological research is to predict the roles that these extreme events will play in causing massive insect disturbances. Numerous studies have analyzed the effects of drought on forest insect outbreaks with the aim of predicting the direction, magnitude and sources of variation in their responses to drought. Recently, Kolb et al. (2016) found that for the US there is little evidence for a role of drought in outbreaks of bark beetles; defoliators do not show consistent responses to drought, and the response of sap-feeders to drought appears non-linear, with the greatest performance and impacts at intermediate drought intensities or when drought is alleviated by wetter periods. In Europe, Jactel et al. (2012) found that primary damaging agents living inside wood caused low damage to the water-stressed trees, whereas those living on foliage caused more, in all cases irrespective of stress severity. Rouault et al. (2006) found that the performance of foliage feeding insects increased with moderate or intermittent water stress, while bark-beetles were positively influenced by prolonged water stress and the decline of host resistance, although inference was limited by a lack of long term data. These reviews show

that consistent generalizations are lacking on the outcome of interactions between forest insects and water-stressed plants (Jactel et al., 2012; Kolb et al., 2016; Rouault et al., 2006). Our results contribute new information about the role of drought in triggering of population eruptions of wood-boring insects, a less-studied feeding guild (Stephen et al., 2001). Increases in the frequency and severity of drought stress associated with climate change could strongly alter population dynamics of *S. noctilio*, increasing its damage.

Although our results highlight the importance of the effect of abrupt increase in drought levels in triggering and synchronizing *S. noctilio* outbreaks, this does not indicate that dispersal plays no role in promoting outbreak expansion. In fact, at smaller spatial scales (i.e., landscape and stand scales), it has been suggested that dispersal may play a significant role in the spread of population outbreaks (Aparicio et al., 2013; Lantschner and Corley, 2015). Drought and dispersal may interact such that abrupt increases in drought conditions trigger population increases at epicenters where highly susceptible trees are concentrated; dispersal from these epicenters may lead to area-wide epidemic conditions (Corley et al., 2007; Lantschner and Corley, 2015; Royama, 1992).

The strong negative density-dependence found in *S. noctilio* populations may help explain the population decline that rapidly follows outbreaks. Several density-related ecological mechanisms may contribute to the collapse of *S. noctilio* outbreaks, including widespread depletion of susceptible tree resources (Berryman, 1987). During *S. noctilio* outbreaks high density population levels result in high rates of tree attacks resulting in massive tree mortality. This mortality may cause the depletion of the supply of susceptible trees and a simultaneous increase in the proportion of more resistant trees. This situation may increase the number of unsuccessful wasp attacks and decrease survival of the wasp larvae within the trees. In addition, high density populations may also decline through the action of natural enemies (Berryman, 1987). The introduced biological control agents of *S. noctilio* – the parasitoid wasps *Ibalia leucospoides* (Hockenwarth) (Hymenoptera: Ibalidae) and *Megharyssa nortoni* (2Cresson) (Hymenoptera: Ichneumonidae), and the entomophagous nematode *Beddingia siricidicola* – may increase during woodwasp population eruptions, resulting in increased woodwasp mortality and contribute to population decline (Taylor, 1978). However, there is no clear evidence of the role of these agents in preventing the occurrence of outbreaks or regulating

woodwasp population growth during outbreaks in Patagonia (Corley et al., 2014; Villacide and Corley, 2012). More precise information on natural enemies' parasitism levels during *S. noctilio* outbreaks is needed to specifically evaluate the role of biological control agents in regulating woodwasp populations.

The significance of basal area and plantation age in determining the magnitude of *S. noctilio* outbreaks further supports the theory that host stress is a critical factor inducing attack susceptibility and that resource availability plays a key role in regulating population sizes (Økland and Berryman, 2004). Overstocked mature stands strongly influence tree stress, and consequently, these stands have a greater proportion of suppressed trees that are more susceptible to *S. noctilio* attack (Madden, 1988). In this system, while extreme climatic events appear to trigger population outbreaks, the degree to which available trees are attacked and killed is determined by other factors such as the silvicultural management history of individual stands (Lantschner and Corley, 2015). Interestingly, mean annual temperature and precipitation were not significantly associated with the total number of attacked trees, suggesting that drier and warmer sites may not be more susceptible to attack by *S. noctilio* than wetter or colder ones. Thus, the influence of climate in driving the outbreak dynamics appears to be only related with abrupt temporal changes the hydric stress, but not with the spatial variation of these variables. As such, efforts to prevent and manage outbreaks may be effectively be focused on reducing the availability of susceptible host trees through silvicultural management (i.e. "on time" thinning). Such efforts might be prioritized at a regional scale during years with a marked and rapid increases in drought severity, which are likely to become more frequent under climate change scenarios. Alternative proposed control measures, such as breeding programs to select varieties of *Pinus* spp. resistant to *S. noctilio* attack and survival may also be an effective approach to reducing impacts (Slippers et al., 2015).

Further research is needed to more deeply understand the ecological mechanisms underlying the spatio-temporal patterns of *S. noctilio* populations described here. Particularly, it is necessary to improve our understanding of how temperature and hydric stress affect the mechanisms of host resistance to the attacks by *S. noctilio* females, as well as the growth of its fungal symbiont. Additionally, it remains unknown why *S. noctilio* populations attack only suppressed or weakened trees and persist at endemic levels in its native range in Eurasia, despite expressing eruptive and widely damaging behavior in the Southern Hemisphere. This question is particularly relevant in the context of the recent invasion of *S. noctilio* in North America, where pine forests and some of its natural enemies are native. In this context, further efforts should be made to predict if *S. noctilio* will behave as an invasive species in a novel habitat, provoking massive forest mortality, as in the Southern Hemisphere, or will it remain as a secondary pest with low damage, as in its native range.

5. Conclusions

Sirex noctilio outbreaks are highly synchronized at regional scales, and appear to be triggered by density-independent factors, particularly an abrupt increase in the drought severity, which likely increase the availability of susceptible host trees. At this scale, dispersal as a synchronizing agent is likely less important than environmental stochasticity, but may have a significant effect in expanding outbreaks at local scales. The collapse of the outbreak appears to be determined by negative density dependence in *S. noctilio* populations, probably induced through resource depletion. To our knowledge, this is the first study to describe the large scale spatio-temporal dynamics of woodboring insect populations, and to analyze density dependent vs. density independent mechanisms in regulating its outbreak dynamics of this insect. These results may provide valuable information for understanding the mechanisms driving the dynamics of forest insects, and may help predict future responses under climate change.

Acknowledgements

The assistance in the fieldwork by A. Mayoral is grateful acknowledged. We thank J. Villacide, M. Weigandt, and S. Varela for their support in in methodological tools. A. Liebhold provided many useful ideas and comments throughout the development of the study.

Funding

This work was partially supported by grants: PICT2014-419 and PICT2013-0557, Agencia Nacional para la Promoción Científica y Tecnológica (Argentina), and the University of Minnesota College of Food, Agriculture and Natural Resource Sciences (USA). We also acknowledge support from US Forest Service International Programs.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.044>.

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