

Spatial dynamics of a *Sirex noctilio* woodwasp population within a pine plantation in Patagonia, Argentina

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Abstract

The woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae) is probably the most important pest of pine tree plantations of the southern hemisphere. We studied the spatial arrangement of an endemic population of the woodwasp *S. noctilio* within pine plantations located in northwest Patagonia, Argentina, during three successive years since colonization. By censusing healthy and attacked trees, which provided data on current and past yearly woodwasp attacks, we studied: (i) the spatial pattern of attacked trees during the endemic phase of a woodwasp population, and (ii) the changes in the spatial arrangement through time and with an increasing (i.e., no intervention) pest population. Among a total of 53 649 counted trees, attack rates were low during the study period (accumulated attack below 0.5%). Results of spatial statistical analysis showed that woodwasp attack is highly clumped, and that spatial aggregation increases with time, even with increasing numbers of attacked trees. The observed spatial arrangement, a consequence of a demographic process, can have important implications for the management of woodwasp populations and contributes to our understanding of the nature of outbreak population behaviour in this pestiferous forest insect.

Introduction

The woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae) is a phytophagous insect that naturally infests conifers in Eurasia and North Africa. In the last century, *S. noctilio* has invaded several other regions of the world such as Australasia (Madden, 1988), South America (Iede et al., 1988), and South Africa (Tribe, 1995), where it has become a major pest of softwood afforestation (Madden, 1988).

Sirex noctilio is a waistless, solitary woodwasp with a univoltine life cycle. Females lay eggs by drilling holes through the bark of adult trees. Attraction to potential hosts is mediated by monoterpenes (α - and β -pinene) liberated by the trees as a consequence of physiological stress (Madden, 1988). *Sirex noctilio* does not feed as an adult and lacks conspecific attraction pheromones (Ipinza Carmona & Molina, 1991). Characteristic of the species is the occurrence of severely damaging, pulse-like eruptive population outbreaks (Berryman, 1987; Madden, 1988).

Outbreak dynamics in forest insects has attracted considerable attention from ecological researchers (Capuccino et al., 1995). Knowledge on outbreak dynamics of insects that are significant forest pests can be especially important for prediction models and management strategies. In probably the only attempt to date to understand *S. noctilio* outbreaks, Madden (1988) proposed the 'intermediate drought' hypothesis, which emphasized density-independent factors: intermediate drought levels occurring during woodwasp emergence increase tree susceptibility to woodwasp attacks. According to this hypothesis, drought causes tree stress and hence their attractiveness to female wasps; when short rains interrupt the drought period, tree growth is reinitiated, which subsequently improves woodwasp development rates.

As all wood-boring insects, *S. noctilio* larvae rely for their development on the prior alteration of wood, carried out by species-specific symbiont organisms. *Sirex noctilio* females carry mycangial sacs spores of the basidiomycetous fungus *Amylostereum aerolatum*, which are inoculated into trees during oviposition, together with phytotoxic

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mucus that is responsible for increased tree sagging (Coutts, 1969; Coutts & Dolezal, 1969).

Knowledge on the spatial aggregation of forest insects is also important because of its association with insect population dynamics. Aggregation on host plants or plant patches has been frequently noted in several outbreaking forest insects. In many cases, strong aggregation has explained increased insect performance either by increasing the chances of escaping natural enemies or by collectively dealing with plant chemical defences (Rhoades, 1985). Bark beetles, for example, rely on the active aggregation of attacks to reach densities that can overwhelm the resin defences of their coniferous hosts (Berryman, 1986).

Despite an array of studies on *S. noctilio* ecology, distribution, physiology, and population control methods (e.g., Coutts, 1969; Madden, 1974, 1988; Spradbery & Kirk, 1978; Haugen, 1990; Carnegie et al., 2006), there are no quantitative reports on the spatial arrangement of woodwasp infestations during the initial phases of colonization (Neumann & Minko, 1981) and how this pattern changes with time and increasing populations. The spatial ecology of *S. noctilio*, however, appears as a central aspect in our understanding of local outbreak dynamics. Knowing how attacks are distributed within a plantation could improve control methods and population management.

Sanitary thinning of forests and the introduction of biological control agents such as the parasitic nematode *Beddingia* (= *Deladenus*) *siricidicola*, both well-known methods to minimize the damage caused by *S. noctilio* (Neumann & Minko, 1981; Haugen et al., 1990; Haugen & Underdown, 1993; Villacide & Corley, 2006), rely on finding attacked trees within the forest, usually when these are rare such as during the endemic phase. Also, sampling protocols on which management decisions are based (e.g., sequential sampling) rely on prior knowledge of the spatial arrangement of attacked trees (Penteado, 1995).

We studied the spatial arrangement of an endemic population of the woodwasp *S. noctilio* within two pine forests, located in northwest Patagonia, Argentina, during three consecutive years since colonization. By censusing healthy and attacked trees, we obtained data on current and past yearly woodwasp infestations, which enabled us to assess: (i) the spatial pattern of attacked trees during the endemic phase of a woodwasp population, and (ii) the changes in the spatial arrangement over time and with an increasing woodwasp population (i.e., no intervention).

Materials and methods

Study site and tree censusing

We carried out our study in a 14-year-old pine tree plantation located approximately 20 km east of the city of

Bariloche, Argentina, (71°15'W–41°03'S), during the summer months of December 2002 and January 2003, before adult emergence. The study site is located within the Patagonian steppe, a temperate to cold area (8 °C annual mean temperature) with average rainfall just under 600 mm per year. The area is characterized by low scrub-like vegetation with pine plantations appearing as distinct woodland patches. The plantation studied consisted of 93 ha, distributed in two distinct patches (henceforth Forest A and Forest B), which were separated by more than 1200 m (minimum linear distance). Both patches are planted with *Pinus ponderosa* Douglas ex C. Lawson and *Pinus contorta* Douglas ex Loudon (Pinaceae), with a 3 × 3 m original plantation design. Forest limits were mapped by means of Geographic Resources Analysis Support System (GRASS), using Global Positioning System (GPS) data.

The forests studied were invaded by *S. noctilio* only recently (ca. 1999), and populations are still low. Because the site is relatively isolated from other plantations and separated by a clear steppe vegetation matrix, natural colonization is an unlikely event. Accidental introductions of infested wood did not occur during our study period.

We counted all trees (healthy and attacked) within the plantation by walking along the plantation lines, examining every single tree. Attacked trees were labelled and geographically located using a GPS (Garmin® GPS 12 Personal Navigator®, Taipei, Taiwan; average accuracy 3–5 m). Attacks were dated by looking at the hole cut out by the emerging adult. When an attack is recent, the holes are clean, sharp, and perfectly rounded. However, such holes turn dark and dirty after exposure to two or more winters. Furthermore, trees with older infestations completely lose their needles and the bark in sections of the trunk. Because woodwasps are univoltine, trees attacked during the most recent flight season bear no emergence holes until the following flight season. However, such trees display clear symptoms of attack, namely, wilting and chlorosis (i.e., loss of green pigmentation in needles), and bear distinctive resin droplets produced as a reaction to the wasps' oviposition. Additional evidence was obtained by scraping the bark at the oviposition holes and checking for typical fungal stains caused by growth of the fungus *A. aerolatum*. Thus, trees with symptoms but no holes were classified as attacked during year 2002; trees with clean emergence holes, as attacked in 2001; and, finally, trees with dark, old emergence holes together with other symptoms, as attacked during the year 2000 or before. As we had observational evidence that the woodwasp invaded the site in 1999, our records for the year 2000 also included attacks that occurred during the previous year (Villacide et al., 2004).

Data analysis

We performed two series of statistical analysis: first, we measured the overall spatial pattern of attacks, and second, after estimating the size of aggregates, we estimated changes in the spatial pattern with time. We assumed that the number of attacked trees relates to *S. noctilio* population size.

Yearly spatial pattern of attacks. We statistically tested and quantified the degree of aggregation of attacked tree patches by means of SADIE (Spatial Analysis by Distance Indices) for mapped data (Perry, 1995). SADIE algorithms calculate the shortest total distance to regularity for an observed sample, by moving the points to a completely regular distribution. Hypothesis testing is carried out through a number of simulations in which points are randomly distributed, to achieve a distribution of random distances to regularity. In this, an aggregation index (Ia) and a probability of aggregation are calculated from the comparison of the observed distances with the distribution of the randomized distances to regularity. Values of Ia in excess of the unity denote spatial aggregation, and those less than unity indicate regularity. The significance was calculated after 5000 randomizations.

Because SADIE assumes rectangular areas that are larger than the irregularly shaped forests, the indices probably overestimate aggregation in our study. Thus, we changed the critical P-value for significance from 0.025 ($P = 0.05$ two-tailed test) to 0.0125 ($P = 0.025$ in a two-tailed test).

While SADIE for point data provides information of the overall spatial pattern, the Ripley test (Ripley, 1981) provides the size of the spatial structures of the spatial array. The Ripley test is one of the most commonly used methods for second order point patterns of mapped data (Dale et al., 2002) and is widely used in plant ecology (Wiegand & Moloney, 2004). Second order statistics for mapped data are based on the distribution of distances of pairs of points (Ripley, 1981; Wiegand & Moloney, 2004). Ripley's K-function, or the pair correlation function g , uses the information of all interpoints distances, and consists of the calculation of the number of points tallied within a given distance or distance class. The univariate form is typically represented by the following equation:

$$K_{(d)} = A \frac{\sum \sum l_{ij} w_{ij} (x_i - x_j) \leq d}{n^2}, \quad (1)$$

where A is the area of the plot, n is the number of points, $(x_i - x_j)$ is the distance between the points i and j , d is the distance class, w is a weight factor used for edge correction, and l is an indicator function that takes on a value of 1 if the condition is true $[(x_i - x_j) \leq d]$ or 0 if the condition is false.

The alternative pair correlation function (the O-ring statistic) arises when circles are replaced by rings. Both statistics are complementary and it is best to use them together with the K-function, as O-ring is a probability density function, and K a cumulative measure (Wiegand & Moloney, 2004). We performed Ripley's univariate test and SADIE for yearly data sets (2000, 2001, and 2002) of both censused forests. Ripley statistics were calculated using a python programme with the numerical and scientific extension modules (Python Software Foundation, 2005) and, to perform SADIE analyses, we used the SADIEM programme for mapped data, available on the author's website (http://www.rothamsted.ac.uk/pie/sadie/SADIE_downloads_software_page_5_2.htm).

Dispersal of attacks with time. The basic assumption of this analysis is that trees attacked by *S. noctilio* in a given season are determined by the redistribution of woodwasps emerging from trees attacked during the previous flight season. We used a null model of antecedent conditions that consists in keeping the earlier pattern fixed (here, the distribution of attacked trees in the previous years), while randomizing the latter (the distribution of attacked trees in the following years; Wiegand & Moloney, 2004). As this null model is especially appropriate to investigate the relationship between adult trees and seedlings, the relationship studied here is analogous in that *S. noctilio* woodwasps emerging from an attacked tree are the 'seedlings' that create new attacked trees. For this test, we performed the bivariate Ripley test, in which the Ripley function is typically represented by the following equation:

$$K_{(d)} = A \frac{\sum \sum l_{ij} w_{ij} (x_i - x_j) \leq d}{n_1 n_2}, \quad (2)$$

where n_1 and n_2 are the number of points of patterns 1 and 2, respectively.

We performed a set of bivariate Ripley tests as follows: years 2000 to 2001, 2001 to 2002, and 2000+2001 to 2002, for each forest independently and considering the first year as the antecedent condition in all cases.

Both uni- and bivariate Ripley tests were performed with edge correction. For each series of the test, the confidence intervals were calculated after 20 000 randomizations with a $P = 0.05$ for a two-tailed test and a progressive Bonferroni correction (Legendre & Legendre, 1998). The size of the aggregation (univariate test) or the distance of dispersal (bivariate test) were measured as the last interval for which the correlation function was significantly higher than that expected by the null model. The edge correction was performed using a polygon with the shape of the

Table 1 Total number of trees attacked by *Sirex noctilio* each year and statistics calculated for census data obtained from two planted pine forests in northwest Patagonia, Argentina. Note that population size and all the spatial indices follow the same pattern in both forests, from 2000 to 2002. The population grew (to more than twice its original size) as did aggregation

Year	Forest A					Forest B				
	Attacked trees	Aggregation size (m)				Attacked trees	Aggregation size (m)			
		O-ring	K	Ia	P (Ia)		O-ring	K	Ia	P (Ia)
2000	38	100–125	200–225	1.936	0.0002	18	125–150	375–400	1.744	0.0028
2001	14	75–100	150–175	1.427	0.0264	4	0–25	75–100	–	–
2002	87	50–75	125–150	2.256	0.0002	57	50–75	200–225	1.755	0.0002

forests, and the points were weighted following Wiegand & Moloney (2004).

Results

Among a total of 53 649 trees tallied in both forests, attack rates were low during the study period (accumulated attack less than 0.5%). The overall spatial pattern of infestations was always aggregated, with SADIE indices equal to or higher than 1.5. Indices corresponding to the years 2000 and 2002 were significant except for Forest B during the first year of attack ($P < 0.0025$). The indices for the year 2001 were non-significant (albeit with a tendency towards aggregation) in Forest A, but it was not possible to calculate them for Forest B due to the small number of points (i.e., less than 10 attacked trees in that year). These results were consistent with the observed radius of the aggregates that were smaller than 150 m (O-ring statistic, Table 1).

The spatial pattern of attacked trees in both forests shows a tendency to increase its aggregation together with an increase in the number of attacked trees. While, for Forest A, we observe higher Ia values in 2002 compared to those of 2000 and 2001, for forest B, we estimated a slightly higher Ia in 2002, accompanied by a stronger significance level (Table 1). A similar tendency is observed with the

Ripley statistics, where the radius of the aggregations decreased from above 100 m, to values below 75 m (O-ring, Table 1) in both forests with increasing attack levels.

Woodwasp attack dispersal, interpreted as the result of the redistribution of newly attacked trees as a function of those infested in previous season, was also limited. Recorded values for 2002 were smaller than the size of the original aggregates (less than 100 m, O-ring, Table 2), suggesting that woodwasp natural dispersal within the plantation also decreased during successive flight seasons. While in Forest A, for the first yearly interval, dispersal from attacked trees was limited to a range of 75–100 m (O-ring statistic, Table 2), during the second yearly interval, dispersal did not exceed 25 m. For Forest B, the spatial redistribution of attacked trees was never in excess of 50 m. Overall, for both forests and during the 3 years studied, woodwasp dispersal remained remarkably limited, within a range below 100 m per year, and less than the size of the aggregates (Tables 1 and 2), suggesting that woodwasp redistribution occurred within but not outside the area of original aggregation.

Discussion

Spatial aggregation of *S. noctilio* infestations within a pine tree plantation during the early stages of pest colonization

Table 2 *Sirex noctilio*-attacked trees increase at yearly time intervals (growth rate) and results of the bivariate Ripley statistics estimated from the census data obtained from two planted pine forests in northwest Patagonia, Argentina. Empty cells indicate that statistics were not estimated, due to the small sample size (see text for details)

Year interval	Forest A			Forest B		
	Growth rate	Dispersal (m)		Growth rate	Dispersal (m)	
		O-ring	K		O-ring	K
2000 to 2001	(–) 0.63	75–100	200–225	(–) 0.78	–	–
2001 to 2002	(+) 5.21	0–25	0–25	(+) 13.25	25–50	75–100
2000+2001 to 2002	(+) 0.67	–	–	(+) 1.59	25–50	225–250

was strong. Also, the spatial pattern of attacked trees showed a tendency to increase its aggregation together with an increase in the number of attacked trees, throughout three consecutive years.

The strong aggregated pattern shown by the attacks was probably the result of a demographic process in which population growth rates exceeded wasps dispersal capabilities within the pine plantation (Rosenheim et al., 1989; Van Baalen & Hochberg, 2001). Considering that in these pine plantations there are no apparent barriers for dispersal and that they represent a somewhat homogeneous habitat (i.e., all trees are potential hosts, of the same age, and planted in a regular spatial array), the observed dispersal range between parental trees and new hosts is remarkably low.

The spatial concentration of attacks by *S. noctilio* females could contribute to observed population dynamics. Recently, using a spatially explicit model of *S. noctilio*, some of us found that spatial aggregation of attacked trees increases the probability of outbreak occurrence (Bruzzone & Corley, 2004). The underlying explanation is that aggregation of attacks on healthy trees, through the inoculation of the phytotoxic mucus and fungal spores, may rapidly turn them into individuals in which woodwasp performance is enhanced (Coutts & Dolezal, 1969; Madden, 1974; Spradbery, 1977). Through repeated inoculations of spores and mucus, wood conditions that favour fungal growth are created. This is important because feeding by immature stages depends on the fungal decomposition of wood.

For herbivorous insects in general, the advantages of aggregation imply a connection between individual variance in performance (Capuccino et al., 1995). Although there is no hard data for *S. noctilio* in this respect, evidence obtained from laboratory rearing of woodwasps shows a connection between wood moisture content (i.e., tree physiological status) and wasp size. Aggregation by *S. noctilio* females on trees or tree patches may favour tree conditions for fungal growth though repeated attacks, which could lead to larger offspring and ultimately enhance population performance. Note that adult females vary significantly in size (maximum weight: 0.6348 g, minimum weight: 0.0438 g, mean = 0.3235 g; $n = 19$) and consequently in the number of eggs they carry at emergence (maximum number of eggs: 466, minimum number of eggs: 40, mean = 262; $n = 19$; see also Madden, 1974).

Strong aggregation of *S. noctilio* can also influence success in both biological and mechanical control measures. Sampling and monitoring programmes for classification purposes (i.e., to establish specific control interventions) or density estimations require information on the underlying spatial distribution of attacks (Penteado, 1995). Also,

control measures that depend on finding attacked individual host trees can benefit from knowledge on their spatial arrangement. Finally, some work has shown that aggregation can play an important role in the dynamics of host–parasitoid interaction (Hassell & Wilson, 1997). Current *S. noctilio* integrated pest management (IPM) programmes include several parasitoid species (i.e., *Ibalia leucospoides*, *Rhyssa persuasoria*, and *Megarhyssa nortoni nortoni*) as biological control agents.

Because *S. noctilio* is a major pest, understanding the mechanisms leading to eruptive outbreaks in this species is central to managing its populations. In this study, we present data on the woodwasps' spatial redistribution under field conditions that show that, as in other outbreaking forest insects, spatial aggregation of *S. noctilio* infestations can be strong, despite the fact that they lack aggregation pheromones. However, to show how the observed spatial clumping may relate to outbreaks in this species, experimental work on increased woodwasp performance related to aggregation is still needed.

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