LIFE HISTORY TRAITS OF *SIREX NOCTILIO* **F.** (HYMENOPTERA: SIRICIDAE) CAN EXPLAIN OUTBREAKS INDEPENDENTLY OF ENVIRONMENTAL FACTORS

JUAN PABLO APARICIO

Instituto de Investigación en Energías no Convencionales, INENCO, CONICET
Universidad Nacional de Salta, Av. Bolivia 5150, 4400 Salta, Argentina.
And
Mathematical, Computational and Modeling Sciences Center
Arizona State University, PO Box 871904 Tempe, AZ 85287-1904, USA

JUAN CARLOS CORLEY

Grupo de Ecología de Poblaciones de Insectos, INTA EEA Bariloche
Modesta Victoria 1500, 8400 Bariloche, Argentina

JORGE EDUARDO RABINOVICH

Centro de Estudios Parasitológicos y de Vectores (CEPAVE)
Universidad Nacional de La Plata
Calle 2 No. 584, 1900 La Plata, Argentina

ABSTRACT. The woodwasp *Sirex noctilio* is a major pest of pine plantations worldwide. Economically significant damage is however limited to outbreak populations. To understand what determines outbreaks dynamics in this species, we developed an individual based model for a wasp population developing within a pine plantation. We show that outbreaks may be the result of the insect's life history. Specifically we show that limited dispersal may not only increase population persistence but also create the conditions for eruptive dynamics. When the probability of long distance dispersal is greater than zero, but relatively small ($P_{LDD} = 0.1$) large outbreaks are the norm, with all of the suitable trees dead at the end of the simulation. For $P_{LDD} = 0$ (only local dispersal allowed) outbreaks are smaller in size, and in some cases not well defined and spread over longer periods. For $P_{LDD} = 1$ (only long distance dispersal allowed), the frequency of local population extinction (without outbreaks) increases significantly. Aggregated attacks may induce physiological changes in the trees which could allow other wasps to detect them. These changes may in turn trigger an outbreak. In contrast, healthy, vigorous trees are not suitable for wasp oviposition. In our model the density of suitable trees (healthy trees but yet suitable for oviposition) are a key factor determining population persistence before outbreaks. From an applied perspective, our results emphasize the importance of adequate plantation management in preventing woodwasp infestation.

1. **Introduction.** The study of forest insects has been instrumental in the development of insect population ecology[46, 34]. Forest insects are attractive to researchers in part, because several species may undergo remarkable population

growth patterns, such as cycles or outbreaks. Population epidemics or outbreaks are defined by a dramatic increase in insect population density in one or a few generations. High densities may occur at regular time intervals or maybe abrupt and ostensibly random and may last for several years, or else may also rapidly collapse usually due to resource limitation or natural enemy control. Such extraordinary density changes may be abrupt and ostensibly random, or population peaks may occur in a more or less cyclic fashion. Whether the observed population behavior is a consequence of external forces, such as macro climatic conditions, or is underlined by local conditions and the life history of the species involved, still remains a key issue[1, 2, 21, 4, 17, 26].

Forest insect outbreaks are also of great interest because of their economic importance. During outbreaks, insects can damage forests severely, indirectly through defoliation or directly by killing trees[6]. Thus, predicting outbreaks in space and time has become essential for the management of pests of natural forests and plantations[37]. Well known examples of forest insect population modeling are Ludwig et al.[22], Cole and Amman[5], Kucherov[18], Sharov[37], Gansner et al.[12], Liebhold et al. [19], Logan et al. [20], Weseloh[48], Selikhovkin et al.[36], Mason et al.[28], Tenow et al.[44], Obedzinski et al.[30], and Peltonen et al.[31]. Through these models, the role of density dependent factors such as parasitism, disease or predation on insects at different stages, density dependent factors (weather) and dispersal in fragmented landscapes have been shown to influence outbreak dynamics in specific systems.

The woodwasp *Sirex noctilio* Fabricius (Hymenoptera, Siricidae) is a phytophagous insect that attacks conifers. Native to Eurasia and North Africa, *S. noctilio* has recently invaded several other regions of the world such as Australasia[25], South America[16], South Africa[45] and more recently North America[13]. Partly because *S. noctilio* is an invasive forest insect, it has become one of the most economically significant pests of softwood afforestation in most invaded areas[25, 15, 47].

S. noctilio is a solitary wasp with a univoltine life cycle (but see[8]). Females lay eggs by drilling holes through the bark of adult trees. Attraction to potential hosts is mediated mainly by mono-terpenes (alpha and betapinene) liberated by the trees as a consequence of physiological stress[25]. Characteristic of the species is the occurrence of severely damaging, pulse-like eruptive population outbreaks[2, 25, 8, 29]. During outbreaks, tree mortality may reach 80%, for under these conditions woodwasps also attack healthy trees.

The mechanisms underlying outbreaks in invasive *S. noctilio* populations remain an open question. Madden [25] proposed the "intermediate drought" hypothesis, which emphasized density independent factors to explain outbreak dynamics: intermediate drought levels occurring during woodwasp emergence increase tree susceptibility to woodwasp attacks. According to this hypothesis, drought causes tree stress and enhances their attractiveness to female wasps; when short rains interrupt the drought period, tree growth is reinitiated, which subsequently improves woodwasp development rates. More recently, Corley et al.[7] suggested that strong spatial aggregation, as consequence of limited female wasp dispersal behavior, could lead to increased insect performance through the concentration of attacks on trees.

It is our aim here is to explore by means of a spatially explicit individual based model, whether outbreak densities may be reached. Our working hypothesis is that population build-up is solely a consequence of insect life history and behavior. We

consequently predict that pulse-like eruptive outbreaks are produced in the absence of climatic or other density independent variables.

2. Methods.

2.1. **Life history of** *Sirex noctilio***.** Woodwasps or horntails are primitive, solitary hymenopteran insects. Larvae do not feed or grow directly on the wood, but rely on its prior alteration carried out by a symbiotic fungus. *S. noctilio* females carry spores of the *Amylostereum aerolatum Boidin* (Basidiomycotina: Corticiaceae) in mycangial sacs and, during oviposition inoculate them into a tree together with a phytotoxic mucus[9]. *S. noctilio* females are attracted to physiologically stressed trees where they oviposit, drilling the bark in 1 to 6 shafts at a single drilling point[23]. The number of shafts is determined by tree suitability but where multiple shafts are made, there is always a drill set aside for inoculating fungal spores only[24, 39]. Adult wasps emerge from trees during the warm season (December - March in the Southern Hemisphere) and in general an adult female lives around 10 days[35]. The complete life cycle of *S. noctilio* takes 12 months, but in temperate climates, it may extend for up to 36 months through prolonged diapause[8].

2.2. **The model.** We developed an individual based model for a wasp population developing in a Pinus spp stand. Individual trees are characterized by three properties: their spatial position, their physiological state (see below), and by the number of wasp eggs they may have received. Wasps, in turn, are characterized by their spatial position within the plantation and their egg load.

2.2.1. *Modeling the pine stand dynamics and S. noctilio life cycle within a tree.* The plantation was assumed to have a square layout composed of trees. Tree growth or removal was not considered in our model. We considered each tree to be in one of four states:

1. unsuitable for oviposition,
2. suitable for oviposition but not stressed,
3. stressed,
4. dead.

Unsuitable trees are vigorous, healthy trees (i.e., not sick nor damaged). Wasps avoid laying eggs in these trees, but may drill oviposition holes in which the phytotoxic mucus and fungal spores are inoculated and occasionally eggs are laid. Suitable trees are healthy trees in which wasps may lay eggs in a limited number due to their high moisture levels. Stressed trees are those that because of droughts, fire, wind-damage or previous attacks by *S. noctilio* or other pests, become "chemically labelled" and are easily detected by wasps[24]. Stressed trees are preferred for oviposition and as such receive a higher number of eggs than other types of trees. In our model, dead trees do not receive any new eggs, but adult wasp emergence may occur from eggs laid previously and after prolonged diapause.

In the model, only wasp attacks may induce changes in tree category. We represent the number of eggs necessary to induce a change in a tree's state as N_{thi}, where $i = 1, 2, 3$ stands for unsuitable, suitable, and stressed, respectively. Unsuitable trees that in a given year receive more than N_{th1} eggs become suitable next year. Suitable tree receiving more than N_{th2} eggs become stressed. Stressed tree receiving more than N_{th3} eggs die. The threshold values for the N_{thi} transitions are listed in Table 1. The maximum number of eggs a tree can receive results from a number of factors (height and diameter of the tree, among others) and as the

maximum number of eggs a tree can receive is still unknown, we set this parameter to 500, independently of the tree's state.

We assumed a pooled egg and larval survival as a function of tree suitability (s_i in Table 1, [39]). Wasp offspring in each tree may correspond to the current season, or to any of the previous two warm (or flight) seasons.

2.2.2. *Simulation of wasp dispersal.* For each simulated day, *S. noctilio* females from a given tree emerge with two properties: their position (given by the position of the tree from which the wasp emerged), and their initial egg load, which was set to 100 eggs[27]. Trees within a radius R of a given tree is a short way for referring to all the $(2R + 1)^2 - 1$ first neighbor trees of the focal tree (Fig. 1). For simplicity we will call this the R-neighborhood. Each wasp visits τ trees during its lifetime, which are chosen using the following rules (see fig.2):

1. If there is at least one (chemically labelled) stressed tree in the R_s- neighborhood of the last visited tree, then that tree is detected with (usually high) probability P_s (Table 2). In such a case the wasp is moved to the spatial position of the stressed tree. If there is more than one stressed tree in the R_s-neighborhood, one stressed tree is chosen randomly (R_s was assigned a fixed value of 3 in all simulations);
2. If there are no stressed trees in the R_s-neighborhood, or if stressed trees are not detected (what occurs with probability 1- P_s), we simulated two scenarios:
   (a) long distance dispersal (with probability P_{LDD}), which consists in moving the wasp to a tree, of any category, chosen at random; or

   (b) local dispersal (with probability 1-P_{LDD}), which consists in moving the wasp to a tree chosen at random in a R-neighborhood (in general $R \neq R_s$) where R represents the radius for local dispersal (in the simulations we considered the values 2 and 4, see Table 1). This process is repeated τ times (the number of trees that female wasps may visit during their lifetime).
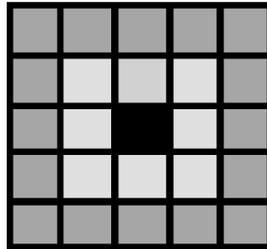
FIGURE 1. Schematic representation of R-neighborhood of a focal tree (black box in the center). The first eight neighboring cells represent the case $R=1$ (light gray boxes). Adding the outermost 16 cells (dark gray boxes) shows the case $R=2$.

TABLE 1. Model parameter's. Radiuses are implicit distances with no units (i.e., expressed in tree distances; see Fig. 1 and text). Subscript i represents tree state or condition (1= unsuitable, 2= suitable, 3= stressed, 4= dead).

| Parameter	Description	Value
N_{thi}	Threshold number of wasp eggs per tree necessary to induce a transition between tree states (from state i to i+1).	300 for i=1; 60 for i=2; 6 for i= 3;
H_i	Mean number of eggs laid in a tree type i	4 for i=1; 8 for i=2; 20 for i= 3; 0 for i= 4.
s_i	Annual egg and larval survival in a tree of state i	0.1 for i=1; 0.3 for i=2; 0.5 for i= 3; 0.5 for i= 4.
R_s	Radius around the position of a recently emerged wasp within which stressed trees can be detected	3
R	Radius for local dispersal	2, 4
P_{LDD}	Long distance dispersal probability	0, 0.1, 1
τ	Number of trees visited by each wasp during its lifetime	6, 12
P_S	Probability to find a stressed tree within the R_s-neighborhood.	0.85
P_{EU}	Probability of a wasp laying eggs in an unsuitable tree	0.10
N_{eMAX}	Maximum number of eggs a tree can receive in a given season	500
ρ	Initial proportion of suitable trees	0.025, 0.05
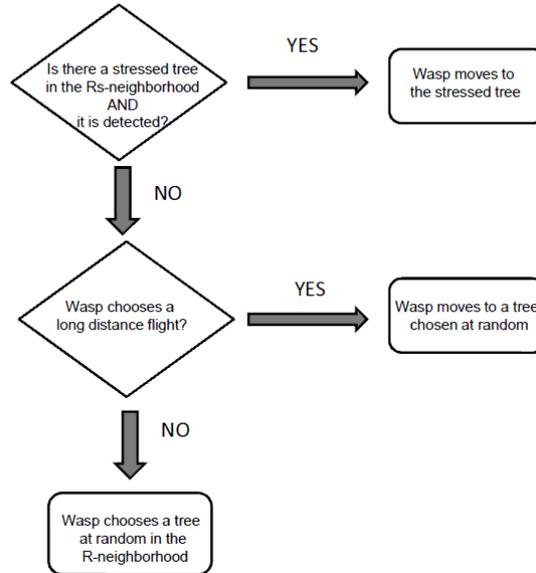
FIGURE 2. Flow-chart for the decision-making process used to simulate wasp dispersal.

2.2.3. *Simulation of oviposition behavior and wasp emergence patterns.* Wasps have a constant 1:1 male-female sex ratio at the time of adult emergence. Only females are considered in the model and it is assumed that all females are capable of laying eggs (all females are assumed to be mated with an initial load of 100 eggs[35]). In each visited tree, wasps may lay eggs but only if their egg load is greater than zero. We assume that there is a constant probability of oviposition per unit of type whose value depends solely on tree category. The mean daily value for this probability is denoted by H_i ($i =$1, 2, 3, 4, see Table 2). The laying activity per tree is carried out during one simulated day and therefore the number of eggs laid per tree (n) is a random variable with a Poisson distribution (with mean H_i). Eggs are laid in unsuitable trees with (a small) probability P_{EU}. In the model, the egg load of females is updated daily, decreasing as eggs are laid. That is, in a given day a wasp laid n eggs thus its egg load is decreased by n. This process continues until the end of the season or the egg load depletion, whatever occur first.

Wasp emergence was distributed uniformly during the fligth season. Each tree may have a stock of wasp eggs, laid in three successive years. The emergence of adult wasps lasts 90 days and takes place during the warm season (December to March in the Southern Hemisphere), and female adults start laying eggs immediately after emergence. Although biologically (and dependent upon climate) the life cycle of *S. noctilio* may last between 3 and 36 months, we simplified the emergence patterns in the following way: eggs laid in a given year (t) will produce wasps in the next season ($t + 1$) with probability 0.6, and with probability 0.4 in the following season ($t + 2$).[8] At the end of a simulated season we randomly determined which eggs emerge in the following two successive seasons (using the above probabilities), and the adult wasp population is set to zero. Egg and larval mortality inside trunks

(which are simulated as a single process) are assumed to occur simultaneously at the end of the season in which the eggs were laid.

In order to distribute the emergences uniformly, we computed the expected number of adult wasps emerging in a given day as the ratio of the egg stock (number of wasp eggs per tree) to the number of days until the end of the 90-days-long season. If this ratio is greater than one it is rounded to the nearest integer, and becomes the number of adults emerging in that day. If the ratio is smaller than one, one wasp emerges with a probability equal to that ratio. This process is summarized algebraically as follows:

$$A_e(k) = Round(N_e(k)/T(k)),$$
$$T(k) = S_l - k,$$
$$N_e(k + 1) = N_e(k) - A_e(k)$$

where $A_e(k)$ is the number of adults emerging in day k, *Round* is a rounding function, $N_e(k + 1)$ is the egg stock in a given tree on day k, $T(k)$ is a time function representing the number of days left until the end of the emergence season, S_l is the maximum number of emergence days of the season ($S_l = 90$), and k= 1,..., 90 days. All eggs which did not hatch before the end of a given season will be forced to emerge during the last day of that season.

For simplicity we assumed that each wasp visits a given stressed tree only once but in such a case it lays a larger number of eggs (H_1) than in suitable trees. In our model it is equivalent to allowing multiple visits with a smaller value of H_1 and therefore this assumption does not play any significant role in the population dynamics of *S. noctilio*.

We considered an isolated stand, so that no wasps could immigrate or emigrate from the plantation. Thus, for example, we considered that the 1-neighborhood of a tree in a corner is composed by its three first neighbors (instead of the eight as of a regular tree).

2.2.4. *Simulation scenarios*. The simulations were carried out considering a plantation with 10,000 trees (a square arrangement of size P= 100; under the assumption that trees are separated by 3 m each, the plantation covers a surface area of approximately 9 ha). Initially the plantation is composed by unsuitable trees and a small proportion of suitable trees (ρ); two values of ρ were used: 0.025 and 0.05. The simulations (each simulation is identified here as a 'run') start with a small number of wasps ($S_0 = 10$) randomly located in the plantation. Each scenario was run 100 times in order to obtain simulation statistics.

2.2.5. *Parameter uncertainty and output statistics*. Probability of suitable tree attacks, depends of the initial density of such trees (ρ) and the number of trees within the R-neighborhood, $(2R + 1)^2 - 1$. Probability of detecting stressed trees depends on the probability P_s and the size of the R_s-neighborhood. However, most wasps emerge from suitable trees and therefore their (local) density affects the probability of detecting stressed trees too. These two probabilities are crucial for population dynamics and the variations in their values were considered by using different values of ρ and R, in our simulations. Probability of choosing a long-distance flight varied in the full range by considering the values 0 (no long distance flights allowed), 0.1, and 1 (all flights are long-distance flights)

Number of trees visited by each wasp (τ) depends on wasp activity level (which, as for all insects, is temperature dependent) and wasp lifespan (10 days in average[35]). We considered two values of τ (6 and 12) in our simulations.

The mean number of eggs laid in different trees (H_i) was estimated from published data [24, 39]. Actual number of eggs laid by a given wasp in a given tree, was obtained using a Poisson distribution with mean H_i.

The threshold number of wasp eggs per tree, necessary to induce a transition between tree state (N_{thi}), is unknown. However it is related to tree initial condition. We captured this fact by assuming values of 300 for unsuitable, healthy trees; 60 for suitable trees; and 6 for stressed trees.

Egg survival varies from 0 to 50% but larvae mortality may be as high as 90% depending on tree category [39]. We used total survival probabilities (egg+larvae, s_i) ranging from 0.1 to 0.5.

We defined and computed a series of output statistics, depending on the presence or absence of outbreaks. When the wasp population was able to induce at least one tree transition from susceptible to stressed we considered that an outbreak took place. Most simulated outbreaks usually imply complete resource depletion due to the condition of an isolated forest stand we established from the outset. Thus, after an outbreak, the wasp population is lead to fast extinction. This case is different from the one in which the wasp population is driven to extinction without producing outbreaks, that is, when the wasp population fails to produce transitions from susceptible to stressed trees. Because in all cases the population will eventually become extinct, we simulated population dynamics using an open loop which were ended after population extinction.

The output statistics considered in this work are defined in the following.

- *Time until extinction* (T_{ext}) is the simulated time since the start of simulation until population extinction of the wasp in absence of outbreaks.
- *Peak* is the maximum value of wasp population after an outbreak.
- *Time until outbreak peak* (T_{out}) is defined as the time from the start of simulation until the wasp population reaches its maximum value (*Peak*) when outbreaks take place.
- *Persistence time* (T_{pers}) is the time since the start of the simulation until extinction when outbreaks take place.
- We also computed the *Frequency of extinction* (F_{ext}) as the number of runs where extinction without outbreak was observed over the total number of runs.

These statistics were calculated using 100 simulations for each combination of the parameter values considered. Variability of output statistics due to parameter uncertainty is summarized in Table 2. For each parameter combination the intrinsic variability due to stochasticity was quantified by the corresponding standard deviations.

3. **Results.** For the numerical parameter values explored (Table 2) we observed three types of regimes. Typical cases are shown in Figs. 3, 4 and 5. The differences are due mostly to the pattern of dispersal. When the probability of long distance dispersal is greater than zero (but relatively small, P_{LDD}= 0.1) large outbreaks are the norm, with all of the suitable trees dead at the end of the simulation (Fig. 4). For the same parameter values but with P_{LDD}= 0 (only local dispersal allowed) outbreaks are smaller in size, and in some cases not well defined and spread out over

TABLE 2. Frequency of extinction (F_{ext}, in %), time to extinction when there is no outbreak (T_{ext}, in years), time to outbreak (T_{out}, in years), time to extinction following outbreaks or time of persistence (T_{pers}, in years), and the maximum value of the wasp population (Peak). Results represent different simulation scenarios, corresponding to different combination of the values of ρ (initial proportion of suitable trees in the plantation), of P_{LDD} (probability of a wasp choosing long distance dispersal), of R (neighborhood of local dispersal), and of τ (number of trees visited by a wasp). In all cases Sd is the standard deviation. When outbreaks did not occur as well as when extinction without an outbreak did not occur the output variables T_{out} and T_{pers} or F_{ext} and T_{ext} and their respective standard deviations are reported with a dash.

ρ	P_{LDD}	R	τ	F_{ext}	T_{ext}	Sd	T_{out}	Sd	T_{pers}	Sd	Peak	Sd
0.25	0	2	6	94	10.0	11.7	19.7	6.1	34.5	10.62	661	325
0.25	0	2	12	12	10.1	5.8	32.8	8.9	70.7	16.02	8071	1644
0.25	0	4	6	100	8.8	4.7	-	-	-	-	-	-
0.25	0	4	12	15	12.3	11.6	35.3	7.4	60.4	7.61	12853	2604
0.25	0.1	2	6	100	9.6	7.7	-	-	-	-	-	-
0.25	0.1	2	12	12	9.4	3.5	29.4	5.9	51.4	6.64	34722	974
0.25	0.1	4	6	100	8.8	4.7	-	-	-	-	-	-
0.25	0.1	4	12	12	12.7	7.0	40.1	8	62.5	7.86	35244	1115
0.5	0	2	6	37	10	6.5	54.4	18.2	120.3	32.33	6496	1479
0.5	0	2	12	-	-	-	17.8	3.4	46.4	3.92	27560	5296
0.5	0	4	6	66	12.5	11.3	56.1	16.9	81.9	15.43	11063	2428
0.5	0	4	12	-	-	-	17.6	2	41.8	2.72	42320	8342
0.5	0.1	2	6	44	9	5.8	42.9	11	56.6	11.15	42570	1637
0.5	0.1	2	12	-	-	-	15.6	1.5	38.5	2.26	82262	2315
0.5	0.1	4	6	76	15.4	11	105.7	55.9	119.	55.66	43236	1805
0.5	0.1	4	12	-	-	-	17	1.4	40.5	2.5	83194	2464

TABLE 3. Similar to Table 2 but for $P_{LDD}= 1$. For this value of P_{LDD}, R is not present because it is irrelevant for the wasp will have no choice but a long dispersal flight. All abbreviations and symbols as in Table 2.

ρ	τ	$F_{ext}(\%)$	T_{ext}	Sd	T_{out}	Sd	T_{pers}	Sd	Peak	Sd
0.025	6	100	7.7	3.5	0	0	0	0	0	0
0.025	12	29	16	11	55	10	77	10.2	37894	1319
0.05	6	100	24	26	0	0	0	0	0	0
0.05	12	1	5	0	18	1.3	41	2.5	85201	2581

longer periods (Fig. 3, case D). Occasionally, a fraction of suitable trees may escape from becoming stressed trees (Fig. 3). When wasps are allowed only long distance dispersal ($P_{LDD}= 1$), the frequency of extinction (without outbreaks) increases significantly (Table 3). The system displays Allee effects, where aggregation of individuals (due to local dispersal rather than long distance dispersal), increases population survival. When the number of trees visited by each wasp during their lifetime, τ is large enough, outbreaks are well defined (Fig. 5 A) while for low values of τ the wasp population is unable to show large outbreaks but may persists in low numbers for long periods (Fig. 5 B).
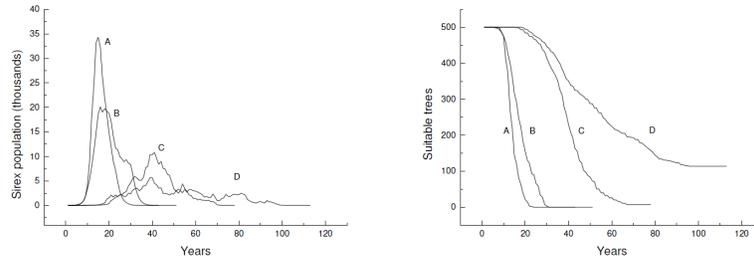
FIGURE 3. Left plate. Outbreaks obtained when long distance dispersal is precluded ($P_{LDD}= 0$). Curves A and B correspond to $\tau = 12$, and $R= 4$ and $R= 2$, respectively (where τ is the number of trees visited by each wasp during its lifetime, and R is the radius for local dispersal). Curves C and D correspond to $\tau= 6$, and $R= 4$ and $R= 2$, respectively. Right plate. Number of susceptible trees during the four simulations (A, B, C, and D). In all cases the initial proportion of susceptible trees (ρ) was set to 0.05.
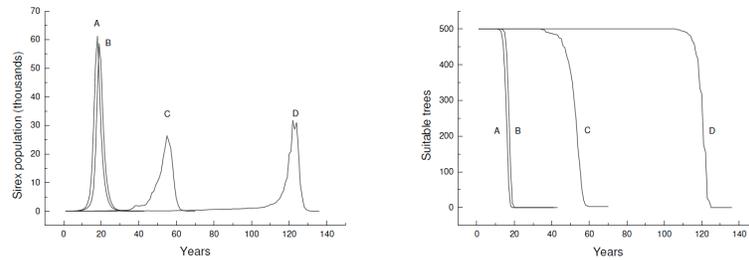
FIGURE 4. (a) Outbreaks obtained for a long distance dispersal probability $P_{LDD}= 0.1$. Curves A, B, C, and D are as defined in Fig. 3. (b) Dynamics of the population of susceptible trees in the four simulations (A, B, C, and D). In all cases the initial proportion of susceptible trees (ρ) was set to 0.05.
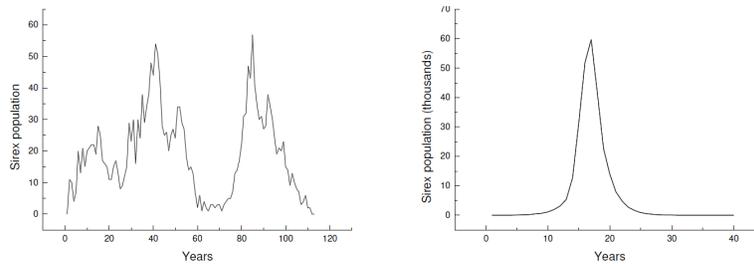

FIGURE 5. Wasp population when dispersal is at random ($P_{LDD}= 1$). For $\tau= 6$ (left plate, a) outbreaks are not observed, but the population cycles and may persist at very low numbers for long periods. For $\tau= 12$ (right plate, b) outbreaks take place soon after wasp introduction. In both cases the initial proportion of susceptible trees (ρ) was set to 0.05.
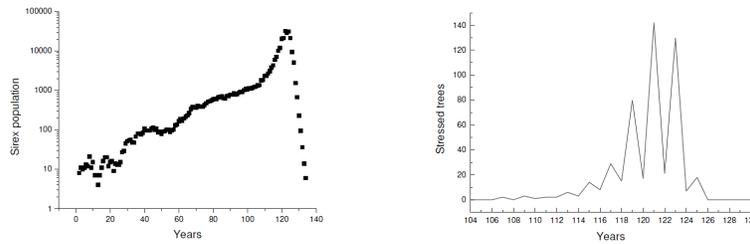
FIGURE 6. Wasp population growth with simulation conditions as in Fig. 3 D (P_{LDD}= 0.1, ρ= 0.05, τ= 6, R= 4). Later, a phase of slow exponential growth until year 107 is noted, when the first stressed tree appears in the plantation triggering the outbreak (note the large change in slope around this year). Total consumption of suitable trees leads to an abrupt extinction of the wasp population.

We may qualitatively understand the dynamics of large outbreaks as follows. The replacement rate R_0 (expected number of female progeny replacing in one generation each female wasp in the population) at the beginning of the outbreak is given approximately by (the contribution from unsuitable trees is disregarded):

$$R_0 = \rho \tau s H$$

where ρ is the initial proportion of suitable trees in the plantation, τ is the number of suitable trees visited per adult female wasp, s is egg survival in suitable trees, and H is the mean number of eggs laid in a suitable tree per wasp. Therefore, the expected population of *S. noctilio* in season (or year) t is given by

$$S(t) = S_0 R_0^t$$

where S_0 is the initial wasp population. For $R_0 > 1$ but close to one, a slow exponential growth is expected but strongly affected by demographic stochasticity during the first years, which in some cases may drive the population to extinction. An increase in the wasp population, significantly increases the probability of the appearance of the first stressed trees, which may in turn trigger a larger outbreak (Fig. 6) ($H_4 > H_i$)

4. **Discussion.** The model shows that *S. noctilio* population outbreaks may occur in the absence of density independent factors, such as droughts or other disturbances. Furthermore, our results suggest that eruptive dynamics may be related to limited wasp dispersal behavior and consequent aggregations of attacks (see also [8]). However, some long distance flights may be necessary. Outbreaks are more pronounced when most dispersal but not all, remains local (see also[7]). For example, when the average number of trees visited per wasp is set to six, and all (or none) of the flights are long distance flights, outbreaks are usually not observed although wasp population may survive for long periods. However, when long distance flights are allowed with a low probability, well defined outbreaks take place.

The relationship between strong clumping of insect attacks and population build-up is through the potential increase in individual performance associated with aggregation. While *S. noctilio* females are generally attracted to stressed trees, which may be spatially disperse, spatial concentration of attacks through reduced dispersal

behavior, implies that wasps may also be attracted to close-by healthy trees, eventually attacking these as well. It has been observed that through the repeated inoculations of fungal spores and mucus on such trees (even if no eggs are laid on them), healthy trees may rapidly (i.e.: within the same flight season) become attractive to other wasps as the liberation of mono-terpenes is induced by the attacks[23, 10, 40].

Recent flight-mill data has shown that female wasps are capable of sustained flights, which may exceed 50 km in a day[26, 3]. However, strong spatial aggregation of attacked trees is commonplace in the field, even increasing with increased wasp population numbers[7, 47]. According to the authors, the strong aggregated pattern shown by S. noctilio attacks is probably the result of a demographic process in which population growth rates exceed wasp dispersal rates within a pine plantation.

The role of external factors in determining population eruptions has received considerable attention. Many studies have attempted to correlate weather, host quality or natural enemies with outbreaks, but conclusions have been often limited to specific systems or influenced by the analytical approach used[38]. Still, external factors such as climate may be a major determinant of large scale outbreak synchronization[50, 11]. In our examples we considered constant parameters because we wanted to stress the influence of life history traits on population dynamics. However, external factors determine some parameter values. For example, two key parameters, the initial proportion of suitable trees (ρ) and the number of trees visited by each wasp (τ) are clearly affected by external factors. Climatic events as for instance droughts, may affect ρ, and it is well known that temperature is directly related with insect activity and therefore affecting τ.

Although some insect life history traits have also been singled-out as factors common in some outbreaking forest species [4], their study has received less attention. An exception is the work of Wilder and co-workers[49], who have shown that the gypsy moth populations in a two-dimensional, homogeneous stand of host trees can display an underlying dynamics that may be either periodic or chaotic. In an important cross-species analysis of forest Lepidoptera, Hunter[14] noted that there are differences between some outbreaking and non-outbreaking species in characters such as dispersal distances and offspring dispersal. In turn, spatial models have shown that sufficiently low dispersal rates can destabilize insect population dynamics[33].

For S. noctilio wasps, outbreaks are a mayor management concern for pine foresters, due to their magnitude and unpredictability[6]. Also, wasp population eruptions occur as pulses, after long periods of quiescence during which S. noctilio attacks seem to be largely limited to suppressed trees[32]. Partly because of the extended duration of an endemic population phase, the chance for climatic factors such as droughts occurring in pine-tree forestation is high. Such climatic events, through an instantaneous increase in tree susceptibility to wasp attacks, may undoubtedly favor population build-up.

Another interesting results stemming from our simulations, is the fact that certain dispersal rules may render small initial woodwasp populations to local extinction. Considering that S. noctilio is an invasive species, spreading populations may be more affected by local extinction through stochastic process and Allee effects, than otherwise noted. Specific studies on these aspects, as well as more in depth knowledge on effective dispersal rules in this species may not only add to our understanding of forest insect population dynamics by may also be important for the design and management of pine tree afforestation.

From an applied perspective, our results emphasize the importance of adequate plantation management in preventing woodwasp infestation. Simple practices leading to healthier plantations (such as timely thinning and pruning) that reduce the proportion of stressed (and/or suitable) trees, may lessen the chance of woodwasp outbreaks. It remains to be seen how catastrophic events may affect such dynamics.

Our main message is that some underlying life history traits of *S. noctilio* (mainly high fecundity and short dispersal behavior) may by themselves, independently of macro-climatic factors, lead to population eruptions. These characteristics and overlapping density independent factors that may haphazardly increase the number of attractive trees, may together explain the observed wood wasp pulse eruptions within pine stands[2, 25, 16, 43]. These characteristics should be considered when trying to understand the nature of invasive forest insect dynamics and when it comes to predicting severely damaging outbreaks of *S. noctilio* woodwasps in pine tree plantations.

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E-mail address: juan.p.aparicio@gmail.com
E-mail address: elmallin@gmail.com
E-mail address: jorge.rabinovich@gmail.com