Received: 12 June 2025 | Accepted: 7 November 2025

DOI: 10.1111/afe.70023

RESEARCH ARTICLE

Agricultural and Forest Entomology

Royal Entomological Society

Linking spatiotemporal and demographic patterns in modulating local population outbreak of invasive forest insect

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Funding information
INTA, Grant/Award Numbers: PDI074-2023, PEI033-2023; USDA Forest Service International Programs, Grant/Award Number: IcoS

Abstract

1. Understanding the spatial and demographic structure of local outbreaks is critical for identifying the ecological mechanisms underlying invasive forest insect dynamics.
2. We investigated a population outbreak of *Sirex noctilio* within a pine plantation in Patagonia by integrating spatial analyses of infestation patterns with quantification of oviposition behaviour and adult performance.
3. At the plot level, the distribution of infested trees shifted from a highly clustered pattern in previous seasons to a more spatially dispersed one of newly attacked trees
4. Logs sampled from *S. noctilio*-infested trees located in the outbreak epicentre and periphery showed no significant differences in total oviposition drills or estimated egg numbers; however, single (non-reproductive) drills were more frequent in the periphery.
5. Emergence of *S. noctilio* adults were higher in the periphery, though individuals were smaller, suggesting spatial variation in offspring performance within the outbreak area.
6. These findings highlight spatial variation in oviposition behaviour and larval performance, suggesting the role of localized feedback and host availability in shaping outbreak trajectories.
7. Our study emphasizes the importance of spatial structure in modulating demographic responses during a population outbreak, offering insights into context-dependent regulatory mechanisms of invasive forest insect populations in simplified plantation systems.

KEYWORDS
body size, forest pest, population dynamics, preference–performance, regulation mechanisms, *Sirex noctilio*, spatial autocorrelation

INTRODUCTION

Outbreaks of herbivorous insects, defined as abrupt increases in population density over short periods, represent major disturbance processes in forest ecosystems (Berryman, 1986, 1987; Garnas et al., 2023). These events can drastically reduce host resource availability, cause extensive tree mortality and consequently alter forest productivity, ecosystem functioning and associated ecosystem services (Dale et al., 2001; van Lierop et al., 2015). As a result, herbivorous insect outbreaks can have significant impacts on both commercial forest resources and on values related to forest ecosystem conservation (Garnas et al., 2023).

The transitions of forest insect populations between endemic and epidemic phases are influenced by a complex interplay of life-history traits and environmental conditions (Berryman, 1986; Isaev et al., 2017; Royama, 1992). Processes involved in the transition may include density-dependent mechanisms, such as intraspecific competition and natural enemy responses, as well as density-independent factors, including climate-related and other environmental stressors (Garnas et al., 2023; Lantschner et al., 2019; Raffa et al., 2008; Seidl et al., 2017). Despite considerable research efforts to improve our understanding of the dynamics of forest insect outbreaks, the mechanisms that trigger changes between different population phases in general and for noteworthy specific systems often remain uncertain.

Forest insect population can display outbreak dynamics that typically follow cyclical or pulse-like patterns, with variations in amplitude, duration, stochasticity and spatial extent that differ considerably among insect species and forest conditions (Berryman, 1987; Corley & Villacide, 2025). The expression of these dynamics can lead to severe impacts when invasive forest insects establish novel associations with exotic trees, as commonly observed in plantation forests. In such non-equilibrium contexts, population regulation is weakened and populations are more likely to reach epidemic levels (Garnas et al., 2023; Stazione et al., 2025; Villacide & Fuentealba, 2025; Wingfield et al., 2015). Therefore, understanding the mechanisms that determine whether insect pest populations exhibit positive or negative growth is essential for developing effective management strategies (Krebs, 2002).

Plantation forests composed of exotic tree species are ecologically simplified systems that function as living laboratories for studying mechanisms driving phase transitions in insect population dynamics. These human-made environments are typically comprised of even-aged tree monocultures planted at regular spacing, covering vast areas (Payn et al., 2015; Villacide & Fuentealba, 2025). The reduced biological complexity observed in these systems may create ideal conditions for the establishment and spread of alien insect species (Wingfield et al., 2015). Often under these conditions, alien forest insects become pests, given the weak influence of both top-down and bottom-up regulating forces related to the development of new insect-tree associations (Corley & Villacide, 2025; Stazione et al., 2025; Villacide et al., 2023; Villacide & Fuentealba, 2025).

A notorious example of global alien pests of commercial pine plantations is the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae). This forest insect is native to Eurasia and North Africa, and it is recognized as one of the most damaging insect pests of pines worldwide (Corley et al., 2019; Villacide et al., 2023). The global spread of *S. noctilio* to novel regions over the past century has been highly impactful because severe population outbreaks have been observed in many portions of the invaded range, resulting in considerable tree mortality in planted pine forests, especially in the Southern Hemisphere where pines are also non-native (Corley et al., 2019; Slippers et al., 2015; Villacide & Corley, 2012).

The life cycle of *Sirex noctilio* is strongly conditioned by host tree physiology and by its obligate association with the symbiotic fungus *Amylostereum areolatum* (Corley et al., 2019; Slippers et al., 2012). Females typically oviposit in physiologically stressed or suppressed pines, where host susceptibility is enhanced by stress factors such as water deficit or competition and further intensified by the physiological alterations triggered by female attacks (Masagué et al., 2023). During oviposition, females deposit eggs together with spores of the fungal symbiont and a phytotoxic venom synthesized in secretory glands (Madden, 1988). The combined action of venom and fungus rapidly compromises host physiology, increasing volatile emissions that attract conspecifics and frequently lead to host death (Bordeaux & Dean, 2012; Fernández Ajó et al., 2015; Masagué et al., 2023; Spradbery, 1973).

Hosts strongly influence the body size of *Sirex noctilio*, a central life-history trait that shapes other key traits, including reproduction and dispersal capabilities. Larger females emerge with markedly higher egg loads, ranging from about 30 to more than 450 eggs, and produce larger eggs (Krivak-Tetley et al., 2022; Madden, 1974; Neumann et al., 1987). Dispersal ability is likewise size-dependent, with larger females sustaining long and continuous flights with mean distances of approximately 31 km, whereas smaller individuals are restricted to shorter flights averaging only 3 km (Bruzzone et al., 2009; Corley et al., 2019; Corley & Villacide, 2012). Because *S. noctilio* adults are short-lived and do not feed, body size determines both reproductive potential and dispersal capacity, which in turn can impact the demographic processes that drive population dynamics.

Sirex noctilio populations typically persist at low densities for extended periods (Spradbery & Kirk, 1978). In its native range, *S. noctilio* has co-evolved with local pine species and is known as a benign scavenger, primarily colonizing dead or dying trees (Ayres et al., 2014; Krivak-Tetley et al., 2021; Lombardero et al., 2016). Within these forest ecosystems, *S. noctilio* population densities are likely regulated by a complex interplay of modifying and regulating factors (Berryman, 1986; Corley & Villacide, 2025; Garnas et al., 2023; Isaev et al., 2017). However, the invasion of *S. noctilio* into non-native regions has led to the establishment of new associations. For example, throughout the Southern Hemisphere, where pine trees are exotic and often planted for commercial purposes in high densities (Payn et al., 2015; Villacide et al., 2023), a number of the ecological factors found in the woodwasps' native range are absent or are less effective (Corley & Villacide, 2025). The absence of stable, co-evolved communities in these forest plantations can lead to lower biological complexity and weakened (or absent) top-down regulatory pressures, which in turn may facilitate the establishment of non-native pests and promote the occurrence of insect population outbreaks.

Population peaks of *Sirex noctilio* have been described as eruptive and pulse-like (Berryman, 1987). Local eruptions are followed by a continuum of population growth phases, where tree mortality serves as a proxy for population size over time. During the low-density phases, host selection by *S. noctilio* females is strongly biased towards weakened, spatially dispersed trees. However, spatial aggregation increases over time, even as the number of attacked trees increases (Corley et al., 2007, 2019; Villacide & Corley, 2012). While such low population phases may extend over long periods, some newly established populations have shown the capacity to increase in size over a short period. These eruptive patterns often involve strong spatial structuring within stands and may give rise to feedback mechanisms—such as host resource depletion or variation in offspring

performance—that influence overall outbreak trajectories over time. Such feedback, operating at local scales, can generate spatial heterogeneity in population responses, and thereby influence both the intensity and the spatial progression of outbreaks in scale-structured systems (Pichon et al., 2024).

As *S. noctilio* populations grow and transition to an epidemic phase, host selection by females often extends to healthy and vigorous trees. Such changes in host selection behaviour lead to extensive tree mortality and progressive spatial spread (Corley et al., 2019; Garnas et al., 2023; Madden, 1988; Villacide & Corley, 2012). Outbreaks eventually subside, and *S. noctilio*-induced tree mortality subsequently declines, even when uninfected trees are still widely available in the affected plots and adjacent areas. The progression towards epidemic phases has been attributed to a combination of environmental drivers (e.g., drought events that increase the availability of suitable hosts), biotic pressures (e.g., reduced regulation by parasitoid wasps such as *Ibalia leucospoides* and *Megarhyssa nortoni*, or by the parasitic nematode *Beddingia siricidicola*) and demographic processes (e.g., spatial aggregation of attacked trees) (Corley et al., 2007, 2019; Lantschner & Corley, 2015, 2023; Villacide & Corley, 2012). By contrast, the mechanisms operating during *S. noctilio* outbreaks and contributing to their eventual collapse remain poorly understood.

We studied the population ecology of the invasive woodwasp *Sirex noctilio* in northwestern Patagonia, Argentina, focusing on outbreak dynamics. Our aim was to understand how spatial and demographic patterns modulate the local dynamics of *S. noctilio* during population peaks. Our working hypothesis was, that changes in the spatial distribution of *S. noctilio*-infested trees influenced female host selection and adult offspring performance, shaping the trajectory of outbreak development. We predict that, as an outbreak progresses, the initial aggregation of weakened, spatially clustered trees will give way to a more diffuse infestation pattern as females expand to hosts across the stand. At the same time, we expect local demographic feedbacks to emerge across the outbreak area, with heavily infested patches experiencing stronger competition and reduced offspring performance, while peripheral areas with lower infestation maintain higher reproductive success. These processes would generate spatially structured dynamics that modulate outbreak development and decline. Nonetheless, alternative scenarios are plausible—persistent spatial aggregation of attacked trees if host selection by females remains highly clustered, or weak demographic feedbacks are possible, if regulation is primarily driven by natural enemies. Understanding the mechanisms driving these spatial dynamics may improve our knowledge of invasive insect outbreak behaviour and regulation and consequently inform the design of more effective management strategies for forest pests.

MATERIALS AND METHODS

We selected a large pine plantation (223 ha large) hosting high population levels of the woodwasp *S. noctilio*. The site is located close to the town of Junín de los Andes, in the southern region of Neuquén Province, Argentina. This commercial plantation has 28-year-old lodgepole pines (*Pinus contorta*), with some small patches of ponderosa pine (*Pinus ponderosa*), and had only partially undergone recommended pruning and thinning practices, resulting in relatively high stem density and basal area. According to the *S. noctilio* status classification scale generated in 2023 by the official "*Sirex noctilio Monitoring and Control Program*" established by the *General Directorate of Plant Health and Agricultural Emergency*, *Ministry of Production and Industry*, *Neuquén Province*, *Argentina* (see open data in: https://produccioneindustria.neuquen.gov.ar/programa-de-control-de-avispa-sirex/; accessed on April 24, 2024), the plantation was categorized as severely attacked, with tree mortality rates greater than 50% (see Figure 1). Although no quantitative data were available for this plantation prior to the study, local observations confirm the presence of natural enemies of *S. noctilio*, including the parasitoid wasps *Ibalia leucospoides* and *Megarhyssa nortoni*, and the parasitic nematode *Deladenus siricidicola*.

Ortho-mosaic imagery of the pine plantation was compiled from UAV-based georeferenced multispectral images captured to ensure comprehensive coverage of the entire stand. The images were acquired in April 2024, at the end of the *S. noctilio* adult flight season. During this period, trees colonized by *S. noctilio* in the previous season exhibit pronounced crown chlorosis and browning, or are defoliated showing greyish tones. These characteristics allowed for a clear distinction between Sirex-infected trees and healthy pine trees with green foliage (see Figure 1). Using QGIS (QGIS.org, 2021), we generated a uniform 100-m grid in WGS 84/UTM Zone 19S (metres). Around each of the 140 grid points, we drew 400 m^2 circular plots (11.2 m radius), a size and shape commonly used in the region for forest and sanitary surveys of pine plantations. All plots combined covered approximately 2.5% of the total plantation area and were used to visually identify and count all trees within them.

Sirex-attacked trees were classified as "new" or "old", if attacks had occurred in 2023 or in prior wasp flight seasons, respectively. This classification relied on visual symptoms observable at the end of the 2023 flight season, where recently attacked trees displayed crown chlorosis and browning tones while previously attacked trees appeared defoliated with greyish tones. These distinct features ensured a clear separation between categories and minimized the likelihood of misclassification, allowing us to reliably differentiate between new and old *S. noctilio*-attacked trees. Because trees attacked by *S. noctilio* typically die within a single season, they are no longer available for re-attack in subsequent years, further supporting the robustness of this classification. According to this criterion, we estimated the proportion of affected trees per plot and inferred the temporal pattern of attacks. It is important to note that in the study region, *S. noctilio* is the only species present capable of producing these characteristic symptoms in affected trees, which reduces uncertainty about other potential causes of tree mortality.

Spatial pattern

To assess the spatial distribution pattern of attacked trees (i.e., the proportion of both new and old attacks within each sampling plot),

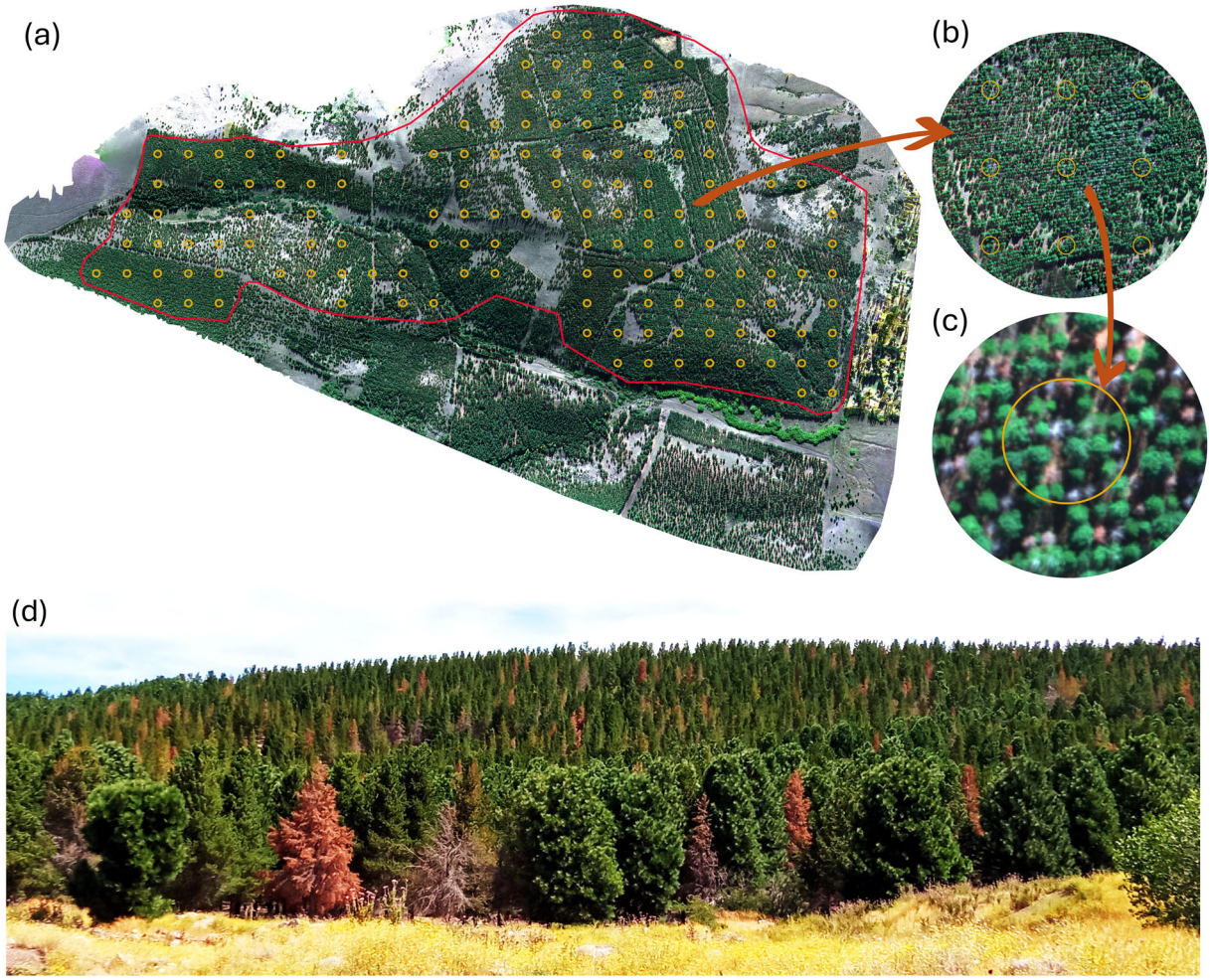

FIGURE 1 Pine plantation hosting a *Sirex noctilio* outbreak located in NW Patagonia, Argentina. (a) Ortho-mosaic projection of the pine plantation generated using UAV-based georeferenced multispectral images; (b) uniform grid of 129 circular sample plots of 400 m^2 each used to visually identify and count all trees (*Sirex noctilio*-infested and healthy); (c) zoom-in of sample plots showing the visual criteria used to distinguish recently attacked trees (pronounced crown chlorosis and browning), previously attacked trees (defoliated with greyish tones) and healthy pine trees (green foliage); (d) general view of the plantation illustrating the magnitude of the *S. noctilio* outbreak.

we computed local and global Moran's I spatial indices (Fortin & Dale, 2005). Spatial proximity among sampling plots was defined using a k-nearest neighbours (KNN) approach (k = 8), set to balance sensitivity and stability in Moran's I estimation. Connectivity was established among the eight closest neighbours, and a row-standardized spatial weights matrix was constructed to normalize the influence across neighbours. The global Moran's I index evaluates overall spatial autocorrelation across all sampling plots, where positive values (I > 0) indicate positive spatial autocorrelation, with similar values clustering together and forming aggregated patterns; values near zero (I ≈ 0) indicate random spatial distributions with no spatial autocorrelation; and negative values (I < 0) indicate negative spatial autocorrelation, where dissimilar values are segregated, resulting in dispersed patterns. In contrast, the local Moran's I index identifies specific areas within the study where significant clusters of spatial autocorrelations occur, providing a more detailed characterization of spatial patterns. Moran's I values were computed using the moran. Test() function from the *spdep* package, which assesses significance using an asymptotic normal approximation. Sampling plots showing the highest local Moran's I values, representing the zones of strongest spatial clustering of attacks, were designated as the *epicentre*, while adjacent plots with lower values were defined as *peripheral*.

Additionally, we generated auto-correlograms to examine how spatial autocorrelation varied with distance, facilitating the visualization and interpretation of spatial clustering patterns (Fortin & Dale, 2005). Spatial correlograms were generated by calculating global Moran's I across successive distance classes (100–800 m, 50-m increments) using distance-based neighbour lists and row-standardized weights. Here, the term "epicentre" is used as a descriptive label for the area of strongest spatial clustering, rather than as an inference about the initial infestation point. All spatial analyses were conducted in R, and visualizations were created with ggplot2 (Pebesma & Bivand, 2023; R Core Team, 2020).

Host tree selection and adult performance

Early in the 2024 *S. noctilio* flight season, new *Sirex*-attacked trees located at the epicentre and periphery zone of the outbreak distribution were selected for sampling. Within each zone, candidate trees were identified through systematic inspection of the stand and those fulfilling the criteria were chosen haphazardly. Selected individuals exhibited typical symptoms of recent *S. noctilio* attack, including resin drops, oviposition drills and crown foliage chlorosis, but without adult emergence holes. A total of 11 and 7 selected *Pinus contorta* trees were felled from the epicentre and periphery, respectively (DBH = 18.7 ± 0.6 and 16.0 ± 1.3 cm, mean ± standard error [SE]). For each tree, one sample log (0.80 m long, a stem segment collected for oviposition drill quantification and insect rearing) was cut at 1.3 m above the base, a standard reference height used to ensure comparability across trees. Each log was stored individually in cages under ambient conditions for one insect emergence season. The volume of each sample log (m^3) was estimated assuming a cylindrical shape, using log diameter and length. From December to May, all emerging adults from each sample log (including *Sirex noctilio* and the parasitoid wasps *Ibalia leucospoides* and *Megarhyssa nortoni*) were daily collected to reduce the probability of log reinfestation, then individually labelled and stored. All *S. noctilio* adults were sexed, and the thorax width was measured as a proxy for body size.

After the end of the adult emergence season, we carefully debarked each sample log to quantify and classify *S. noctilio* oviposition drills (i.e., single, double, triple or quadruple tunnels). The number and type of drill tunnels made by females during oviposition on trees indicate host suitability and preference and are closely related to the number of eggs laid by females (Ayres et al., 2014; Haavik et al., 2017; Madden, 1974; Wermelinger & Thomsen, 2012). While double, triple and quadruple tunnels usually receive one or more eggs, single drills typically lack eggs and likely reflect less suitable oviposition sites for female wasps. Also, single drills could play a key role in triggering positive density-dependent feedback mechanisms that contribute to *S. noctilio* population build-up by collectively enhancing fungal inoculation and that of phytotoxic compounds, thereby improving substrate quality and larval performance (Villacide et al., in production). Finally, we used the function fitted by Krivak-Tetley et al. (2022) to estimate the total number of eggs deposited in each sampled log, based on the number and type of oviposition drills made by females.

We used generalized linear mixed models (GLMMs) to analyse a set of related response variables concerning host tree preference and adult offspring performance, with *location* (*epicentre* vs. *periphery*) as the main predictor variable (Zuur et al., 2009). All models included *tree* as a random effect to account for variation among individual trees and the nested structure of the data, while the *volume of each sample log* (sampling unit) was included as an offset to account for differences in log size (Gelman & Hill, 2006). To assess host tree preference, we modelled the *total number of oviposition drills*, *number of single drills* and *total number of eggs laid* as response variables using a negative binomial error distribution with a log-link function. For adult offspring performance, we modelled the total *number of adult emergences* (including *Sirex noctilio* and its parasitoids, *Ibalia leucospoides* and *Megarhyssa nortoni*) and the *number of emerged S. noctilio* with a negative binomial error distribution and a log-link function, while *adult Sirex body* size was modelled using a Gamma distribution with an identity link function. To compare the mortality mediated by parasitoid wasps, we modelled the parasitism rate — defined as the proportion of parasitoid emergences relative to total emergences (*S. noctilio* plus parasitoids) — using a binomial error distribution with a logit link function. Estimates are presented on the corresponding link scale: log (oviposition drills, egg counts, adult emergences), logit (parasitism rate) and identity in millimetres (thorax width) (for a detailed description of the statistical models used, see Supp. Mat. - Table 1).

All models were fitted using the *glmer* and *glmer*.nb functions from the *lme4* package (version 1.1–27.1), and model selection was based on the Akaike information criterion corrected for small sample sizes (AICc), comparing alternative error distributions and model structures, with competitive models within ΔAICc ≤2 (Bates et al., 2015). Model residuals were assessed using the *DHARMa* package (version 0.4.6) (Hartig, 2018), while overall model performance was assessed using the *performance* package (version 0.11.0) (Lüdecke et al., 2021). Data visualization was conducted with the *ggplot2* package (version 3.3.5) (Wickham, 2009), and all analyses were conducted in R (version 4.2.2) (R Core Team, 2020). All estimates and p-values reported are derived directly from the fitted GLMMs, without additional *post hoc* comparisons.

RESULTS

Spatial patterns

Plot-level data on *Sirex noctilio* attack intensity shows spatial variation in the proportion of infested trees across the stand (Figure 2, upper panels). In previous seasons, high attack rates were largely

TABLE 1 Comparative summary of infestation patterns and *Sirex noctilio* performance across outbreak zones.

Variable	Epicentre versus periphery (E vs. P)
Sirex noctilio attack history of sampled plot	E: mostly old attacks (previous seasons), high intensity versus P: recent attacks (2023), moderate intensity
Spatial pattern of sampled plot	E: strong clustering (high local Moran's I) versus P: weaker clustering (lower Moran's I)
Total oviposition drills and estimated eggs per sample log	Similar number of oviposition drills and estimated eggs between zones
Single oviposition drills per sample log	E: fewer single drills versus P: higher frequency of single drills
Sirex noctilio adult emergence per sample log	E: fewer emerging adults versus P: higher number of emerging adults
Sirex noctilio adult body size per sample log	E: larger adults (both sexes) versus P: smaller adults (both sexes)

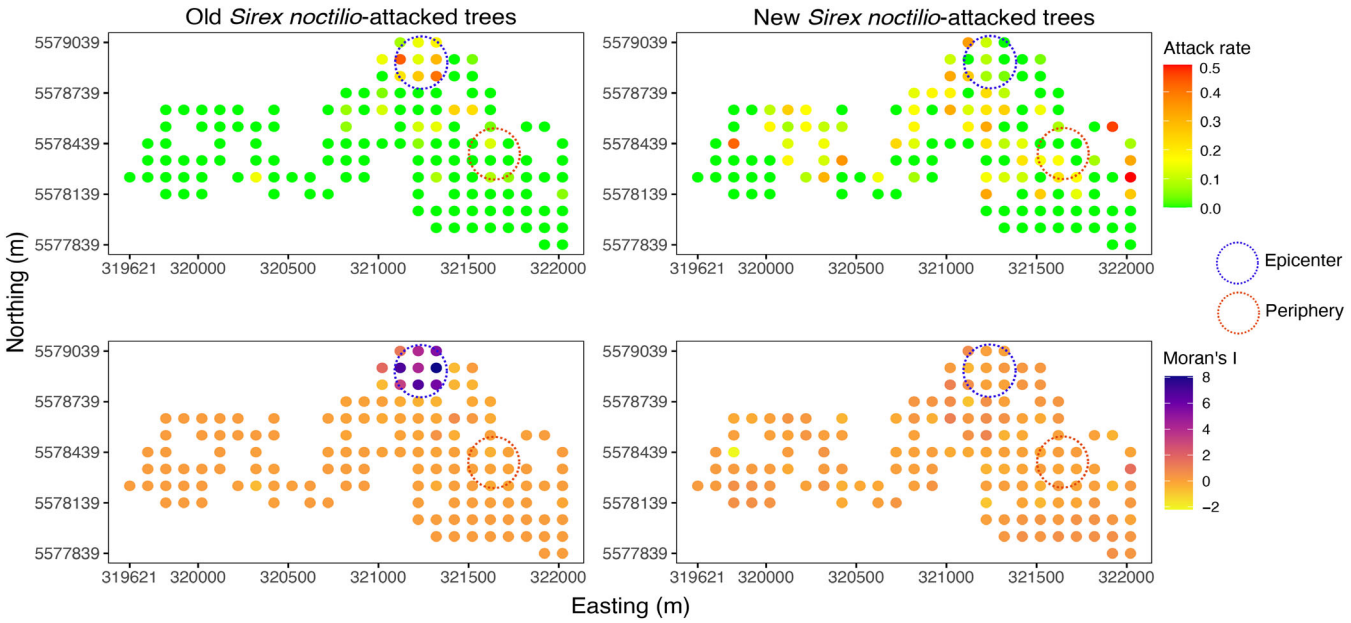

FIGURE 2 Attack intensity and local spatial autocorrelation of *Sirex noctilio*-attacked trees within a stand. Upper panels show the proportion of infested trees per sampling plot, and lower panels display local Moran's I values. Colours indicate the magnitude of attack rate and spatial clustering, respectively. Dashed blue and orange circles denote the epicentre and periphery zones of the outbreak from where sample logs were collected to evaluate host tree selection and adult performance. Axes are in WGS 84/UTM Zone 19S (metres).

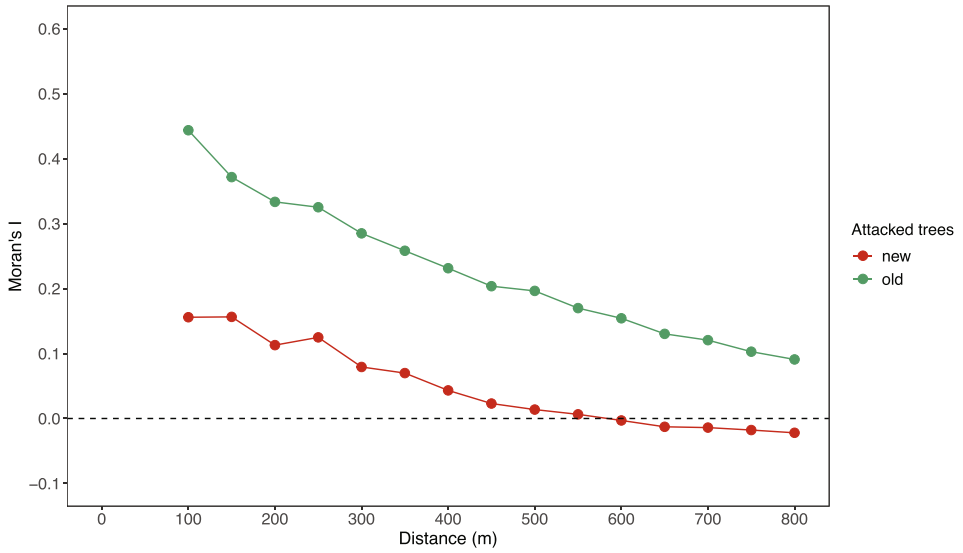

FIGURE 3 Spatial correlograms illustrating the spatial autocorrelation of *Sirex noctilio*-attacked trees as a function of distance. The correlograms show Moran's I index for old (green line) and new (red line) attacks across increasing distance intervals (m). The horizontal dotted line represents the expected Moran's I value under the null hypothesis of spatially random distribution.

concentrated in a localized area. In contrast, new attacks (in 2023) exhibited more variable intensities that were broadly distributed throughout the plantation. In addition, the distribution of *S. noctilio*-infested trees exhibits a spatially aggregated pattern within the outbreak area (Figure 2, lower panels). The global Moran's I index indicates significant spatial autocorrelation, with notable differences between newly infested (2023) trees ($I = 0.1209$; $SD = 3.2796$; $p = 0.001$) and those infested in 2022 or earlier ($I = 0.3741$; $SD = 10.1620$; $p < 0.001$). This autocorrelation remains positive up to 600 metres, beyond which it shifts to negative values, indicating a decay of spatial aggregation at larger distances (Figure 3). Mapping of local Moran's I indices reveals that older Sirex-infested trees are strongly clustered, while more recent infestations exhibit a more diffuse pattern. These results also identify the spatial structure of the outbreak, distinguishing an epicentre or focal area where attacks originated and a peripheral zone where the newer attacks are expanding.

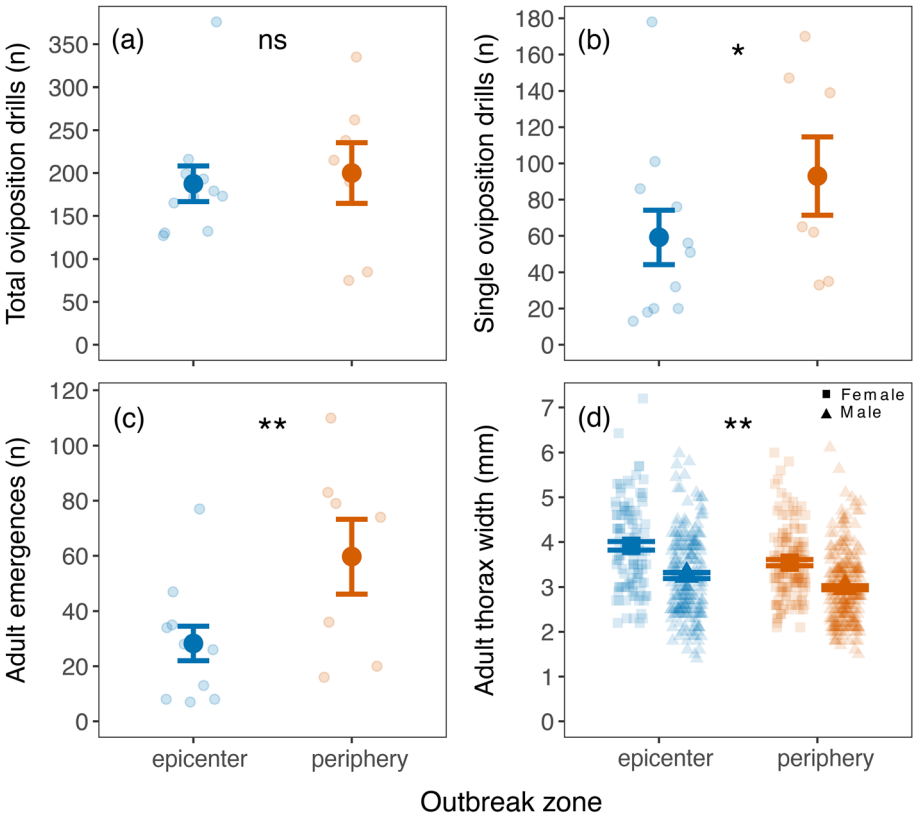

FIGURE 4 Host tree selection and *Sirex noctilio* adult performance at the outbreak epicentre and periphery. (a) total number of oviposition drills (including single, double, triple and quadruple drills), (b) number of single oviposition drills, (c) number of *S. noctilio* adult emergences and (d) *S. noctilio* adult body size, measured as thorax width (mm). Data are displayed as mean ± standard error (SE), with different colours in (a–c) representing individual trees and symbols in (d) representing *S. noctilio* females (squares) and males (triangles). Significance of differences between outbreak zones is indicated by asterisks (*$p < 0.05$; **$p < 0.01$; ns, non-significant).

Host preference and adult emergences

Sirex noctilio-infested trees sampled from the epicentre and periphery zones of the outbreak were used to assess oviposition behaviour and offspring performance. The total number of oviposition drills per sample log (estimate = 0.1615; SE = 0.1915; z = 0.8430; $p = 0.399$; Figure 4a) and the estimated number of eggs laid by females was not significantly different between the location of the attacked trees within the outbreak distribution (estimate = 0.0302; SE = 0.1691; z = 0.1790; $p = 0.858$). However, sample trees located at the outbreak periphery received a significantly higher number of single oviposition drills than those attacked at the epicentre (estimate = 0.7274; SE = 0.3559; z = 2.0430; $p = 0.041$; Figure 4b).

The number of emerging adults differed significantly between the two outbreak zones. At the outbreak periphery, both the total number of emerging adults (*S. noctilio* plus parasitoids) and the number of *S. noctilio* emergences per tree were significantly higher than at the epicentre (total emergences: estimate = 0.8510; SE = 0.3301; z = 2.578; $p = 0.010$; *S. noctilio* emergences: estimate = 0.9137; SE = 0.3232; z = 2.827; $p = 0.005$; see Figure 4c). Consistently, no significant differences were detected in mortality mediated by parasitoid wasps between zones (estimate = −0.4974; SE = 0.3459; z = −1.438; $p = 0.150$). Additionally, a significant reduction in body size was observed in *S. noctilio* adults of both sexes emerging from trees at the outbreak periphery compared to those from the epicentre (estimate = −0.1799; SE = 0.0662; z = −2.717; $p = 0.007$). As expected, thorax width was significantly smaller in males than in females (estimate = −0.5382; SE = 0.0636; z = −8.459; $p < 0.001$; see Figure 4d). The sex ratio of emerging *S. noctilio* adults was consistently male-biased, averaging ∼1:2.0 and ∼ 1:2.2 (♀:♂) in the outbreak epicentre and periphery, respectively.

A comparative summary of the observed differences between outbreak zones is provided in Table 1, detailing key variables associated with stand infestation history, as well as *S. noctilio* oviposition behaviour and adult performance measured per sampled log.

DISCUSSION

Understanding the drivers of insect population dynamics remains central to forest pest management (Biedermann et al., 2019; Garnas et al., 2023; Liebhold & Tobin, 2008). On the one hand, insect outbreaks are common forest disturbances that are expected to become more frequent, widespread and severe with climate change (Jactel

et al., 2019; Pureswaran et al., 2018; Seidl et al., 2017). Additionally, the accelerating pace at which alien species are becoming established in commercial and natural forests globally leads to new associations that can have unpredictable impacts on forest resources (Brockerhoff & Liebhold, 2017; Stastny et al., 2024; Wingfield et al., 2015).

Our study focused on the *S. noctilio* woodwasp, a global and economically significant insect pest of pines that in many parts of the invaded range, such as NW Patagonia (Argentina), displays erratic and severely damaging outbreaks (Corley et al., 2019; Villacide & Corley, 2012). Our results indicate that, in our study area and during an outbreak event, the spatial dynamics of *S. noctilio* attacks shifted from an initially highly aggregated to a more diffuse pattern, with a positive spatial autocorrelation persisting up to 600 meters before transitioning to negative values. Since trees attacked by *S. noctilio* typically die within a single season, these spatial changes reflect the progression of infestations onto new hosts rather than repeated attacks on previously infested trees. This spatial pattern may reflect the limited local dispersal behaviour of *S. noctilio* females, as they usually remain near emergence sites within plantations despite their potential for long-distance flights. Modelling studies suggest that outbreaks tend to be more pronounced when dispersal is predominantly local with occasional long-distance movements, which enable colonization of new hosts while maintaining aggregation within focal areas (Aparicio et al., 2013; Bruzzone et al., 2009; Corley et al., 2007; Corley & Villacide, 2012; Villacide, 2015).

Consistent with the observed spatial trends, plot-level attack rates suggested a higher number of new infested trees in the outbreak periphery, indicating an increase in infestation intensity across the stand during the second year of attacks. This temporal shift in the spatial pattern, from an initially strong localized aggregation to a more uniform distribution of attacked trees, is consistent with processes observed across a range of other forest insect taxa. For instance, aggressive bark beetles, such as tree-killing *Dendroctonus* species, exhibit strongly aggregated attack patterns driven by pheromone-mediated positive feedback loops during initial attack phases where aggregation plays a central role in triggering eruptive dynamics that then lead to rapid population growth and spatial outbreak expansion (Aukema et al., 2006; Raffa et al., 2008).

Our results suggest that host selection behaviour may change with outbreak progression. We observed that *S. noctilio* female oviposition was likely influenced by tree location within the outbreak zoning. While the total number of oviposition drills and the estimated number of eggs laid per tree did not differ significantly between the epicentre and the periphery, the number of single drills was markedly higher in the periphery. Single drills, which typically do not involve egg laying, are done to test stem suitability or quality and are known to involve the introduction of symbiotic fungal spores and wasp venom into the host tree (Madden, 1968, 1974; Madden & Irvine, 1971; Spradbery, 1977). Fungal growth together with the venom may contribute to tree decline, enhancing attraction to foraging female wasps.

Our results also indicate that insect performance may not be homogenous across the landscape. *Sirex noctilio* larvae, measured by both the number of emerging individuals and their body size, differed between zones with differing outbreak trajectories. We observed that more adults emerged from infested trees at the outbreak periphery, despite similar parasitoid-induced mortality rates in both epicentre and peripheral locations. However, we found a contrasting pattern in the body size of adult insects, with individuals emerging at the outbreak periphery being smaller than those emerging from trees located at the aggregated epicentre. Given that *S. noctilio* adults do not feed, their body size is determined by resource acquisition during larval development inside the host tree. Body size strongly influences adult performance, as it is positively associated with survival rates and flight capacity in both sexes, as well as with the reproductive output of females (Bruzzone et al., 2009; Corley et al., 2019; Garnas et al., 2020; Krivak-Tetley et al., 2022; Lombardero et al., 2016; Villacide & Corley, 2008; Villacide & Corley, 2012). Consequently, these differences in larval performance may give rise to subpopulation dynamic behaviour across the outbreak area, driven by adult condition and functional capacity. This heterogeneity may reflect localized ecological feedbacks operating at fine spatial scales, which can modulate population structure and influence outbreak trajectories (Pichon et al., 2024).

The occurrence of both density-dependent and density-independent mechanisms has been suggested as a key factor in the transition between different phases of *S. noctilio* population dynamics (Villacide et al., submitted). While density-independent stressors such as drought can influence host selection by females (Lantschner et al., 2019), local increases in population density may enhance host susceptibility and promote positive feedback loops that facilitate the low-to-high population transition. However, our findings suggest that these processes vary spatially. In the outbreak epicentre, oviposition effort per tree was comparable to that at the periphery, although adult emergence was significantly lower but unrelated to parasitoid-mediated mortality. The decoupling between oviposition and successful emergence may reflect a decline in the availability and detectability of suitable hosts, limited by female host-search efficiency in areas previously affected by high tree mortality. Together, these patterns may indicate the occurrence of localized negative density-dependent processes, likely driven by host depletion in severely infested stand zones. Such mechanisms may limit further population growth and contribute to the eventual attenuation or collapse of the outbreak epicentre, even when numerous healthy trees remain available within the stand (Garnas et al., 2023; Royama, 1992; Turchin, 1995).

Earlier studies have described how spatial aggregation of *S. noctilio*-attacked trees relates to the transition from low density to outbreak phases (Aparicio et al., 2013; Corley et al., 2007; Villacide & Corley, 2012). Our findings suggest that additional spatial patterns can emerge within a given stand, resulting in a dynamic and heterogeneous outbreak spatial structure over time. These results can contribute to a broader framework for understanding the mechanisms that drive and modulate transitions in *S. noctilio* local population dynamics within non-native environments. However, the ecological context often observed for forest insects in an invaded area appears to be a critical factor in shaping these dynamics. For instance, in invaded

regions such as North America (Ayres et al., 2014; Krivak-Tetley et al., 2022), where native pine forests coexist with a diverse assemblage of native woodboring insects and resident natural enemies, the resulting ecological matrix likely imposes distinct pressures on *S. noctilio* populations. This scenario may result in different population dynamics and even limit the occurrence, severity and extent of outbreaks. Context-dependent dynamics highlight the need for regional or local studies of alien insect species in novel regions. Such work will allow a better understanding of the drivers of insect outbreaks and importantly, may improve pest management (Stastny et al., 2024).

Our study highlights the potential role of spatial and density-dependent processes in shaping the population dynamics of an invasive forest insect. For *S. noctilio*, the contrasting patterns of offspring performance between the outbreak epicentre and periphery indicate how localized ecological feedbacks may modulate demographic trajectories and contribute to the spatial heterogeneity of eruptive outbreaks. These findings emphasize the importance of considering spatial structure and demographic responses when investigating the mechanisms behind insect population regulation (Bjørnstad et al., 1999; Haynes & Walter, 2022; Liebhold et al., 2004).

While our study is based on a single-site outbreak event, the consistency and resolution of the observed spatial and demographic patterns provide valuable insights into the local dynamics of *S. noctilio* populations and contribute to our understanding of forest insect population ecology. However, given that sampling was restricted to a single epicentre and periphery within a pine plantation where the outbreak occurred, the differences observed between zones should be interpreted with caution. Although commercial plantations are generally structurally homogeneous, fine-scale variation —such as differences in host tree condition or microsite characteristics— may still have influenced oviposition behaviour and the performance of emerging *S. noctilio* adults. Despite these limitations, this study provides the first detailed description of an outbreak of this invasive forest insect in non-native commercial forestry plantations. Future studies incorporating replicated sampling across multiple outbreak sites would be valuable to assess the generality of these patterns.

Given the global increase in the establishment of non-native forest insects, which often develop novel tree-insect associations, integrating ecological theory into pest management strategies is becoming increasingly important (Ramsfield et al., 2016; Stastny et al., 2024; Trumbore et al., 2015; Wingfield et al., 2015). Locally adapted, ecologically informed approaches offer promising avenues for promoting more resilient and sustainable forest landscapes. To improve the effectiveness of prevention and mitigation strategies for invasive forest insect outbreaks, site-specific knowledge on the drivers of population dynamics is increasingly needed (Biedermann et al., 2019; Corley & Villacide, 2025; Stastny et al., 2024; Villacide et al., 2023; Williams et al., 2023).

AUTHOR CONTRIBUTIONS

José Villacide: Conceptualization; data curation; formal analysis; funding acquisition; investigation; writing – original draft; writing – review and editing. **Andrew Liebhold:** Funding acquisition; writing – original draft; writing – review and editing. **Axel von Müller:** Data curation. **Santiago Behr:** Data curation. **Juan Corley:** Conceptualization; funding acquisition; methodology; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

We would like to thank Lucio Illescas, Agustin Ruiz Díaz and Francisco Azzaro for their help with site selection, as well as Joaquín Villacide Ferrero, Fabian Jaque and Esteban Pizzio for their assistance in collecting and debarking Sirex-affected sample billets and measuring emerged adults. We are also grateful to the anonymous reviewers for their constructive and valuable suggestions, which greatly improved the quality of this manuscript. This work was partially supported by grants: IcoS - FS-USDA International Programmes and PDI074-2023 and PEI033-2023 projects (INTA, Argentina).

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.17207767.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplemental Table S1: Structure of the statistical models used for host tree selection and adult performance analysis

How to cite this article: Villacide, J., Liebhold, A., von Müller, A., Behr, S. & Corley, J. (2026) Linking spatiotemporal and demographic patterns in modulating local population outbreak of invasive forest insect. *Agricultural and Forest Entomology*, 28(2), 201–212. Available from: https://doi.org/10.1111/afe.70023