Biol Invasions (2014) 16:329–339
DOI 10.1007/s10530-013-0521-0

ORIGINAL PAPER

Temperature explains variable spread rates of the invasive woodwasp *Sirex noctilio* in the Southern Hemisphere

M. Victoria Lantschner · José M. Villacide · Jeffrey R. Garnas · Philip Croft · Angus J. Carnegie · Andrew M. Liebhold · Juan C. Corley

Received: 15 February 2013 / Accepted: 11 July 2013 / Published online: 13 September 2013

Abstract The frequency of introductions of non-indigenous forest insects into new habitats is increasing worldwide, often with profoundly adverse consequences on natural and plantation forest ecosystems. Understanding rates and patterns of spread of invasive forest insects is important for predicting when and where these species will expand their geographical range, with the potential to improve mitigation strategies. The woodwasp *Sirex noctilio* is a damaging invasive forest insect that kills numerous species of *Pinus*. Despite encountering highly variable eco-climatic conditions, *S. noctilio* has arrived and established in exotic pine forest production areas throughout the Southern Hemisphere. In this study, we compiled historical records of *S. noctilio* invasion to compare spread rates among eight contrasting eco-climatic regions in the Southern Hemisphere and to explore how spread rate is predicted by landscape variation in climate, habitat characteristics and anthropogenic effects. Spread rates for *S. noctilio* varied considerably among the invaded regions, ranging from 12 to 82 km per year. Among regions, spread rates of *S. noctilio* increased with increasing mean annual temperature and isothermality. We hypothesize that temperature may directly or indirectly influence *S. noctilio* population growth and dispersal, thereby influencing spread rates.

Keywords Exotic pests · Invasion ecology · Range expansion · Landscape ecology · Climate

Introduction

Invasion by non-indigenous forest insects is increasing worldwide, often with strong negative economic and ecologic impacts on both natural and plantation forest ecosystems (Langor et al. 2009; Liebhold 2012). The invasion of species into a novel area is a sequential process that involves arrival, establishment and spread with each phase influenced by its own suite of ecological and evolutionary factors. For example, the arrival of non-native organisms is closely linked to

---

M. V. Lantschner (✉) · J. M. Villacide · J. C. Corley
Grupo de Ecología de Poblaciones de Insectos, INTA
EEA Bariloche, 8400 Bariloche, Argentina
e-mail: lantschner.v@inta.gob.ar

J. R. Garnas
Department of Zoology and Entomology, Forestry and
Agricultural Biotechnology Institute, University of
Pretoria, Pretoria, South Africa

P. Croft
Institute for Commercial Forestry Research,
Pietermaritzburg, South Africa

A. J. Carnegie
NSW Department of Primary Industries, Forest Science
Centre, PO Box 100, Beecroft, NSW 2119, Australia

A. M. Liebhold
Northern Research Station, USDA Forest Service, 180
Canfield Street, Morgantown, WV 26505, USA

human transport and commerce, and may occur repeatedly prior to establishment, irrespective of the biology or ecology of the organism or novel habitat (Lockwood et al. 2007). Establishment, which we define as the point at which introduced populations are no longer at high risk of extinction due to environmental or demographic stochasticity, is mediated by life history traits of introduced organisms as well as the suitability of the novel biotic and abiotic environment (Liebhold and Tobin 2008).

Spread, arguably the most tractable target for the management of invasion process, is influenced by the broadest array of ecological, evolutionary and anthropogenic factors. An important driver of invasion spread is natural dispersal, governed by the ecology and life history of the invader in the introduced range. Innate dispersal behavior (e.g., frequency, mode and distance)—and its interaction with population growth—is perhaps the most fundamental driver of natural spread (Liebhold and Tobin 2008). Environmental factors may be important to spread, either as drivers of variation in population growth or via effects on movement behavior (Shigesada and Kawasaki 1997). Habitat characteristics at local, landscape and regional scales can also be relevant, including the density and distribution of suitable hosts, as well as the suitability and/or permeability of matrix habitat (With 2002; Liebhold and Tobin 2008). Finally, spread is often greatly accelerated by human behavior as many invaders are transported well beyond their natural dispersal range via human transport and trade. Propagules transported over such long distances (whether human-aided or not) can form satellite populations, which grow and ultimately coalesce with the main advancing front, greatly enhancing spread (Shigesada and Kawasaki 1997; Liebhold and Tobin 2008). Understanding the factors and mechanisms operating during the spread stage has strong potential to inform or enhance strategies to contain or reduce the impact of invasive species.

Local and regional climate and weather conditions can have strong direct and indirect effects on movement and growth of insect populations. Temperature is the primary driver of insect developmental rates, diapause and voltinism but also has a strong direct influence on larval and adult behavior, including flight (Speight et al. 2008). For herbivorous insect species, temperature and precipitation may also indirectly affect population growth rates via its influence on the abundance, growth and susceptibility of hosts (Hanks et al. 1991). Geographical variation in these and other habitat characteristics can affect forest insect reproduction and dispersal, and thereby influence the spread of invading insect populations (Liebhold and Tobin 2008). For example, lower densities of host trees and higher fragmentation of forests have been found to be associated with slower rates of spread of forest pest species (Sharov et al. 1999).

The woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae) is a forest pest native to Eurasia and northern Africa and a successful invader in several countries of the Southern Hemisphere and North America. It was first reported in New Zealand around 1900 (Miller and Clark 1935), Tasmania in 1951 (Gilbert and Miller 1952), mainland Australia in 1961 (Irvine 1962), Uruguay in 1980 (Maderni 1998), Argentina in 1985 (Klasmer et al. 1998), Brazil in 1988 (Iede et al. 1988), South Africa in 1994 (Tribe 1995), Chile in 2001 (Ahumada 2002), USA in 2004 (Hoebeke et al. 2005) and Canada in 2005 (de Groot et al. 2006). *Sirex noctilio* is a wood-boring, solitary wasp that in association with a symbiotic fungus, *Amylostereum areolatum*, and a phytotoxic mucus kills host trees (Madden 1988).

Sirex noctilio has high dispersal capacities, moving naturally by adult flight or assisted by human activities through the movement of infested wood (Madden 1988; Bruzzone et al. 2009; Corley and Villacide 2012; Villacide and Corley 2012; Ryan and Hurley 2012). While considered a secondary pest in its native range, *S. noctilio* has become one of the most important threats to *Pinus* spp. plantations in many places where it has established (Madden 1988; Tribe 1995; Villacide and Corley 2012). *Sirex noctilio* populations occasionally reach epidemic levels resulting in significant economic losses in the Southern Hemisphere. Such outbreaks have been reported in almost all the invaded regions, causing up to 60 to 80 % tree mortality in some stands (Neumann et al. 1987; Haugen et al. 1990; Bedding 1993; Maderni 1998; Iede and Zanetti 2007; Corley and Villacide 2012; Villacide and Corley 2012).

For most invasive forest insects, there is generally a lack of data to enable the comparison of spread of the same species in different regions and to explore the factors influencing this process. The extensive data available for *S. noctilio* in the Southern Hemisphere allow for such a study, which furthers understanding of the drivers of spread rate in invasive insects at a broad spatial scale and contributes to the management of new and established populations of *S. noctilio*. Thus, the aim of this study was to compare historical spread rates of *S. noctilio* among contrasting eco-climatic environments invaded by this species across the Southern Hemisphere and to explore how differences in spread rates are related to climate, habitat and anthropogenic factors.

Methods

Study area

We estimated spread rates of *S. noctilio* in eight geographical regions of its distribution in the Southern Hemisphere: three in South America, two in Africa and three in Oceania (Table 1; Fig. 1). These regions represent a wide range of bioclimatic conditions, including temperate Mediterranean climates (e.g., mainland Australia and Western Cape, South Africa) similar to southern parts of the species' native range in Europe and northern Africa, but also covers colder climates (e.g., Southern Argentina, Chile and Tasmania) as well as warm semi-tropical areas (e.g., the rest of South Africa and Brazil). In all of these regions, *Pinus* species are exotic and are established mainly in plantations over relatively large areas. Pine plantations within regions are often homogenous, both with respect to species (though several species may be planted in close proximity within any given region) and with respect to management protocols (e.g., primarily pulp production or mixed pulp and saw log production). The dominant pine species planted varies both among and within regions; pine species most frequently utilized in temperate and cold climates are *Pinus radiata, Pinus pinaster*, *Pinus ponderosa* and *Pinus contorta*. *Pinus patula*, *Pinus elliotti* and *Pinus taeda* are most common in warmer climates (Table 1).

Estimation of *Sirex noctilio* spread rates

Historical records of the first local *S. noctilio* detections for each region were obtained from diverse sources that correspond to several different surveys, including ground and aerial surveys, as well as casual detections, carried out as the wasp was actively spreading in each region. For detailed information about specific detection methods used in different surveys, refer to original works (Table 1). It must be clarified that the data analyzed were collected after the initial detection in each region and therefore after land managers became aware of the invasion. Spatiotemporally referenced historical detection points were compiled in a GIS database, using ArcGIS 9.2 (ESRI, Redlands, California, USA), and were projected to the Universal Transverse Mercator (UTM) projection. The spatial resolution of detection data varied across different regions. Therefore, to homogenize spatial resolutions, we considered an area of 4 km around each point as the smallest unit for describing the annual distribution of *S. noctilio* in each region. Points separated by less than 4 km were merged, and in cases where points were from different years, the oldest observation was used. It must be noted that although the data sets included detection records for most years during which *S. noctilio* spread was monitored in each region, some years within a range had missing data.

Records of initial *S. noctilio* detections were used to estimate spread rates in each region using the distance regression approach described by Gilbert and Liebhold (2010). Specifically, the distance from the point of the first detection in the region to each new detection location is measured. Then, the average radial rate of spread is estimated as the slope from the least-square regression of distance as a function of time since first regional detection. The intercepts of these linear models were set to zero, corresponding to an initial point source of the invasion upon first detection. We used the distance regression method because it provides the most reliable estimate of spread rates, in comparison with other methods such as the square root area and the boundary displacement methods, when the invaded area has an irregular shape or when sample sizes are small (Gilbert and Liebhold 2010).

Relationship between spread rates and environmental variables

We considered a set of eight variables as potential predictors of variation in *S. noctilio* spread rate over the eight regions of the Southern Hemisphere. We chose these variables based on an a priori assessment of their biological relevance to reproduction and dispersal in *S. noctilio*. Variables examined included measures of climate (historic mean annual

Table 1 Characteristics of the eight geographical regions invaded by *Sirex noctilio* in the Southern Hemisphere, included in this study

Region	Country	States/Provinces	Latitude/Longitude	Planted *Pinus* spp.	Data sources
R1	Argentina	Neuquén, Río Negro, Chubut	36°–45°S, 70°–72°O	*P. ponderosa*, *P. contorta*	Klasmer et al. (1998), Villacide and Klasmer (2002), SENASA and SAG (2007), DGByP (2009)
R2	Chile	Aisén, Los Lagos, Los Ríos, Araucanía, BioBio, Maule	36°–47°S, 71°–74°O	*P. radiata*	Ahumada (2002), Beèche et al. (2005), SAG (2006, 2009, 2010, 2011, 2012)
R3	Brasil	Rio Grande do Sul, Santa Catarina, Paraná, Sao Paulo, Minas Gerais	21°–30°S, 44°–54°O	*P. taeda*, *P. elliottii*	Iede et al. (1988), Ribas Júnior (1993), Carvalho (1992), Iede et al. (2000), Gaiad (2001), Iede and Zanetti (2007)
R4	South Africa	Western Cape	31°–35°S, 18°–24°E	*P. radiata*, *P. pinaster*	Tribe (1995), Tribe and Cillie (2004)
R5	South Africa	Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo	23°–31°S, 23°–32°E	*P. patula*, *P. elliotti*, *P. taeda*	Tribe and Cillie (2004), Hurley et al. (2012), P. Croft (unpublished data)
R6	Australia	Tasmania	41°–44°S, 145°–149°E	*P. radiata*	Gilbert and Miller (1952), Mucha (1967)
R7	Australia	New South Wales, Queensland	28°–38°S, 146°–153°E	*P. radiata*, *P. taeda*, *P. elliotii*	Carnegie et al. (2005), Carnegie and Bashford (2012), Michael Ramsden (unpublished data)
R8	Australia	Victoria, South Australia	36°–39°S, 138°–148°E	*P. radiata*	Morgan (1989), Haugen (1990), Collett and Elms (2009)

temperature, isothermality = mean diurnal range divided by annual temperature range, annual maximum temperature, annual minimum temperature, annual precipitation and precipitation seasonality), human population density (which we hypothesize is correlated with the frequency of anthropogenic movement) and host density (percentage of area covered by pine) for each region (see Table 2 for descriptions of these variables). Climatic variables were estimated on 30 arc-second resolution grids, obtained from WorldClim (Hijmans et al. 2005). Human population data were derived from the 2.5-min resolution Gridded Population of the World (GPW) version 2 data set (CIESIN 2000). Both climate and human population density variables were calculated as the mean of all cells from the gridded data that fall within each region. Pine density was estimated as the percentage of land area in each region that consisted of *Pinus* spp. forest during the period of spread of *S. noctilio* in each region and therefore is not contemporaneous among the different regions studied (Carver 1960; O'Neill 1973; Cameron 1985; Castles 1990; SAGPyA 2001; BRACELPA 2004; Mayaux et al. 2004; INFOR 2009).

We used multiple linear regressions to assess how spread rates relate to mean temperature and precipitation, host density and human population density. We used spread rate in each region as the dependent variable and included environmental variables as independent variables. To understand the correlational structure in our data, and to pre-select variables for model comparison, we performed Spearman's correlations in a pairwise fashion between all predictor variables and with estimated spread rate. Variables that showed at least moderate correlation with spread ($p < 0.15$) were entered into an all possible regressions model and compared using Akaike's Information Criterion for small sample sizes (AICc) (Anderson 2008). Predictor variable pre-selection was necessary to allow us to employ an all possible regressions approach due to small sample size. Each region was considered as an independent replicate ($n = 8$).

Results

We compiled a total of 721 historical detection records of *S. noctilio* from the eight regions (this was reduced

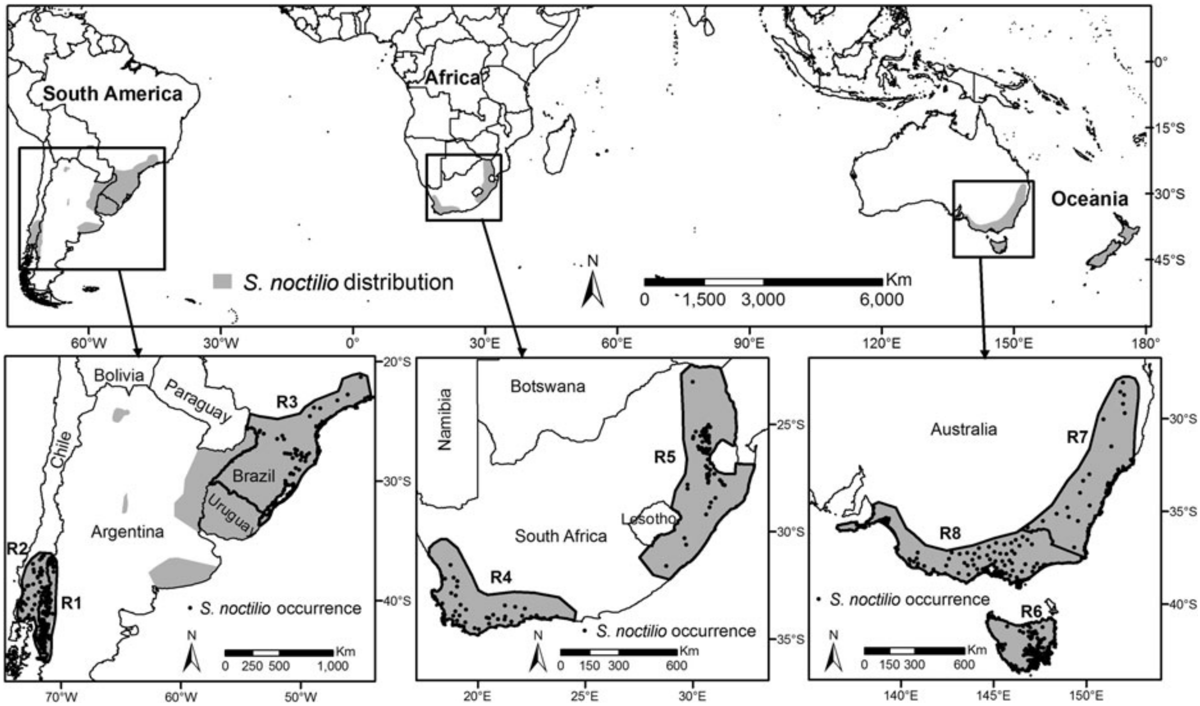

Fig. 1 Location of the eight study regions invaded by *Sirex noctilio* in the Southern Hemisphere with detection points. See Table 1 for detailed description of each region

Table 2 Mean value (standard deviation) of eight environmental variables across each region (R1–R8)

Variables	Abrev.	R1	R2	R3	R4	R5	R6	R7	R8
Mean annual temperature	MAT	7.2 (1.9)	9.8 (2.6)	18.3 (1.5)	16.3 (1.7)	18.0 (3.0)	10.1 (1.9)	14.2 (2.5)	13.3 (1.8)
Isothermality[a]	Iso	52.2 (2.7)	53.2 (2.3)	54.4 (5.2)	55.6 (2.4)	57.6 (2.2)	49.5 (1.5)	48.3 (1.9)	48.9 (2.6)
Annual maximum Temperature	AMaxT	21.3 (2.9)	22.8 (3.3)	28.4 (2.2)	28.8 (2.8)	27.5 (2.9)	20.0 (1.9)	27.3 (2.5)	26.0 (2.3)
Annual minimum temperature	AMinT	−2.8 (1.6)	1.2 (2.8)	8.3 (1.7)	4.4 (2.2)	5.3 (3.9)	2.3 (1.9)	1.5 (2.3)	3.5 (2.3)
Annual precipitation	AP	725 (296)	1,576 (434)	1,592 (231)	396 (211)	804 (164)	1,342 (593)	920 (225)	804 (278)
Precipitation seasonality[b]	PS	60 (11)	63 (14)	25 (19)	40 (21)	67 (12)	24 (7)	27 (10)	29 (11)
Human population density[c]	HPD	4.9 (0.5)	27.5 (5.6)	50.1 (21.7)	91.2 (63.2)	18.0 (2.5)	15.8 (4.5)	43.0 (27.2)	97.0 (50.8)
Percentage of pine by land area[d]	%Pine	0.658	5.153	1.076	0.882	1.793	0.107	0.911	0.827

Climatic variables were calculated over the period 1950–2000 (Hijmans et al. 2005)

[a] Isothermality = Mean diurnal range/Temperature annual range × 100

[b] Precipitation seasonality = Mean of the coefficient of variation of daily precipitation

[c] Human population density in year 2000 (CIESIN 2000)

[d] Sources of pine surface data, corresponding to the period of spread of *S. noctilio* in each region R1: SAGPyA (2001), R2: INFOR (2009), R3: BRACELPA (2004), R4 and R5: Mayaux et al. (2004), R6: Carver (1960), R7: Castles (1990), R8: O'Neill (1973) and Cameron (1985)

to 528 detections after merging all points separated by less than 4 km) to calculate spread (Table 3). The region with the greatest number of detection observations was Patagonia, Argentina (R1), while the fewest detection records were available from New South Wales, Australia (R7; Table 3). The duration of observed range expansion in our data varied from 8 years in Western Cape, South Africa (R4) to 28 years in Victoria and South Australia (R8). Maximum spread distances from the initial detection location in each region varied from 226 km in Tasmania (R6) to 1,077 km in Brazil (R3) (Table 3). The radial rates of spread varied more than sixfold among regions, ranging from 12 km per year in Tasmania (R6) to 78 km per year in southern South Africa (R5) (Table 3; Fig. 2).

We selected four variables as candidate predictors of rates of *S. noctilio* spread among regions, after taking into account their individual correlations with *S. noctilio* spread rates: mean annual temperature ($\rho = 0.738$, $p < 0.037$), annual maximum temperature ($\rho = 0.738$, $p < 0.037$), isothermality ($\rho = 0.857$, $p < 0.007$) and percentage of pine by land area ($\rho = 0.667, p < 0.071$). The model with the lowest AIC score contained two of these variables: mean annual temperature and isothermality, both positively related with and together describing 89 % of the variation in spread rate (Table 4). We obtained the following regression equation: *S. noctilio* spread rate $= -203.2 + 2.8 \times$ mean annual temperature $+ 3.9 \times$ isothermality (Table 5).

Discussion

There is considerable variability in the spread rates of *S. noctilio* among the different invaded regions in the Southern Hemisphere constituting a much greater range of values than previously known (30–50 km/year) (Haugen et al. 1990; Tribe and Cillie 2004). We also found that at a large scale, among environmental predictors considered, temperature best explained the differences in spread rates among different regions. Perhaps equally interesting, spread rate was not correlated with the remaining climatic variables or with human population density or percentage of pine in the region.

Abiotic conditions, and particularly temperature, are closely tied to developmental rate and the activity of most insect species (Speight et al. 2008). In the case of *S. noctilio*, higher temperatures may be facilitating its spread, either directly via increased metabolic rate and activity levels or indirectly by influencing its resource availability. The direct influence of temperature on activity levels could cause insects to be more active in regions with higher temperatures, causing them to disperse (and thus spread) longer distances.

Temperature also directly affects developmental rates of *S. noctilio* and may thereby influence their seasonal phenology (e.g., the timing and length of the flight and growing season) and voltinism (number of years required to complete development). As expected, emergence of *S. noctilio* starts earlier in the season in warmer climates. For example, in Brazil (R3) and KwaZulu-Natal, South Africa (R5), *S. noctilio* adult emergence starts around October (Iede et al. 1998; Hurley et al. 2008), while in Patagonia, Argentina (R1), Western Cape, South Africa (R4) and Tasmania, Australia (R6), adult flights are observed as from late December or even January (Taylor 1978; Tribe 1995; Klasmer et al. 2000). Voltinism may also be affected. In warmer climates, *S. noctilio* has been observed to

Table 3 Summary statistics of *Sirex noctilio* spread data (see Fig. 2) in the eight invaded regions analyzed in this study

Region	Time period	Total detections	Max. distance from 1st detection (km)	Spread rate (km/year^{-1})	SE[a]	R^2 [b]
R1	1993–2008	174	492.6	17.0	7.7	0.23
R2	2001–2012	38	643.9	32.6	19.5	0.41
R3	1988–2007	33	1,077.4	46.3	12.3	0.93
R4	1994–2002	40	486.9	53.4	6.7	0.88
R5	2002–2011	71	956.8	78.0	13.3	0.74
R6	1950–1963	81	226.1	11.7	3.3	0.60
R7	1980–2012	19	996.1	35.5	19.4	0.93
R8	1961–1989	72	682.0	15.8	8.9	0.68

[a] Standard error of spread rate estimate

[b] R^2 from the linear regression calculating spread rate

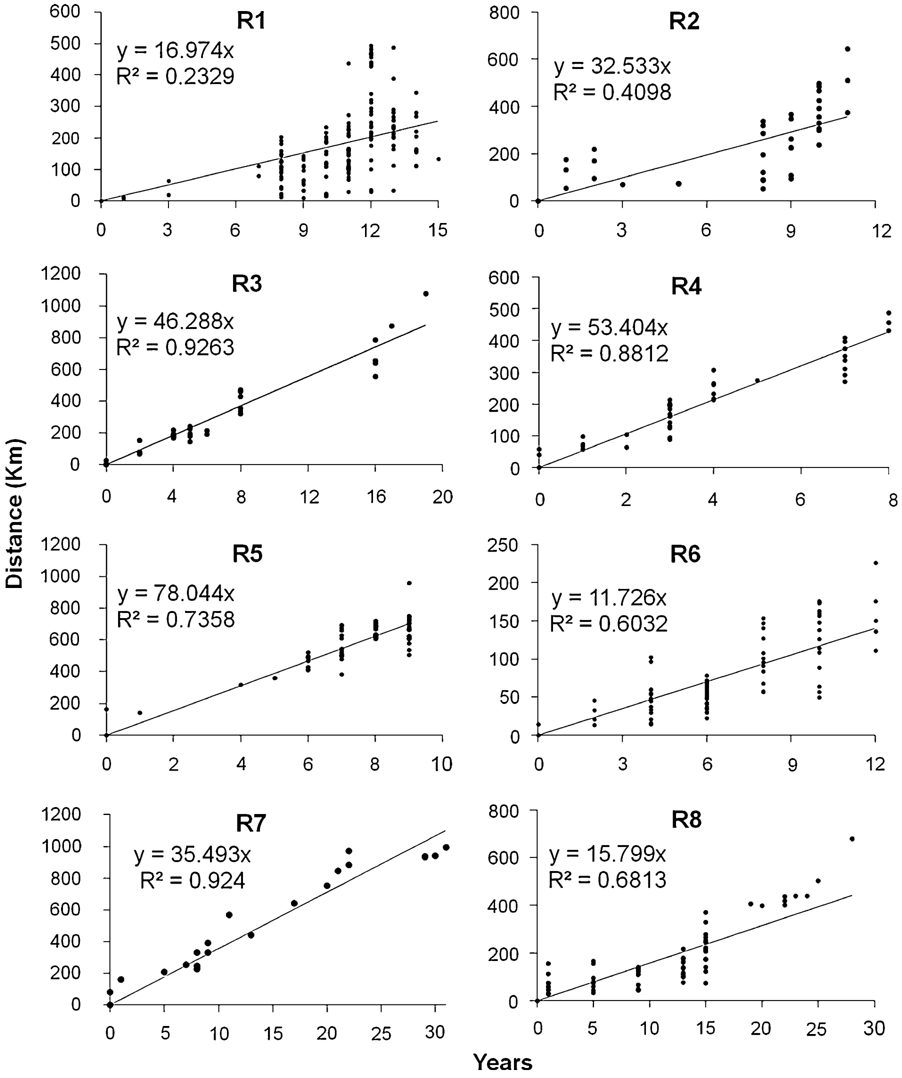

Fig. 2 Relationship between date of first detection of *S. noctilio* in each location and the distance to the location of the first detection for each region. Each point represents one location, and they are discriminated by region. Lines are the results of linear regressions forced through the origin. For description of the regions, refer to Table 1

exhibit up to two generations per year (Neumann et al. 1987), but in colder climates, completion of the life cycle may require several years. *Sirex noctilio* takes as little as three months to complete development in warmer regions (Neumann et al. 1987). In contrast in cold climates, low temperatures (lower than 6.8 °C) may delay egg hatch and prolong larval development in a portion of the population (e.g., those eggs laid later in the season) causing it to extend for up to 3 years (Madden 1981; Corley and Villacide 2012). The effects of higher temperatures on *S. noctilio* development may allow individuals to develop faster with the potential to result in higher population growth rates if voltinism, survivorship or fecundity is increased, which could in turn increase spread rates in warmer climates.

Several recent studies have indicated that temperature can influence the spread of other invasive forest insects. In other systems, spread may not necessarily be affected by mean annual temperature as observed here for *S. noctilio*, but instead may be associated other climatic characteristics, such as winter temperature. This is the case for the hemlock woolly adelgid (*Adelges tsugae*) and the gypsy moth (*Lymantria dispar*) in North America, for which spread rates have been reported to be faster in warmer climates (Liebhold et al. 1992; Evans and Gregoire 2007). In both cases, these patterns were hypothesized to have arisen from adverse impacts of cold winter temperatures on survival of overwintering populations.

In this study, we examined likely candidates to explain geographical variation in rates of spread of a

Table 4 Summary of variables included in the linear regression models

Models	K	AIC_c	ΔAIC_c	R^2
MAT + Iso	3	44.431	0	0.87
AMaxT + Iso	3	45.4	0.9	0.854
Iso	2	46	1.5	0.683
MAT	2	47.4	2.9	0.622
AMaxT	2	49.5	5	0.508
%Pine + MAT	3	50.7	6.2	0.717
%Pine + Iso	3	51.5	7.1	0.684
MAT + AMaxT	3	53	8.5	0.622
%Pine + MAT + Iso	4	52.9	8.5	0.883
MAT + Iso + AMaxT	4	53.5	9.1	0.874
%Pine + AMaxT	3	54	9.6	0.57
%Pine + Iso + AMaxT	4	54.5	10.1	0.857
%Pine	2	54.8	10.4	0.039
%Pine + MAT + AMaxT	4	60	15.5	0.718
%Pine + MAT + Iso + AMaxT	5	71.4	27	0.885

See Table 2 for descriptions of environmental variables

MAT mean annual temperature, *Iso* isothermality, *AMaxT* annual maximum temperature, *AMinT* annual minimum temperature, *AP* annual precipitation, *PS* precipitation seasonality, *HPD* human population density, *%Pine* percentage of pine by land area

Table 5 Parameters of the selected linear regression model

Parameters	β	SE	p value
Intercept	−203.2	59.9	0.019
Mean annual temperature	2.8	1.0	0.044
Isothermality	3.9	1.2	0.027

successful invading species at a broad spatial scale. Knowledge at regional and global scales is necessary to understand influences on invasion rates, and how preventative measures might be deployed. Only at this larger scale can invasion fronts and their movements be monitored and studied (Crowl et al. 2008). In contrast, at finer spatial scales (i.e., within a region), the factors determining variation in *S. noctilio* spread rates may be different and cannot be derived from this study. For example, Argentina and Chile (R1 and R2), or southwestern and eastern South Africa (R4 and R5), show similar mean temperatures but contrasting spread rates. These differences could be related to total area under cultivation (higher habitat connectivity), since spread rates were higher in regions with higher percentage of the territory covered by plantations, although data were not adequately replicated in this study to discern this. It might be fruitful for future studies to collect more detailed records of invasion spread within individual regions to further investigate the effects of habitat characteristics on spread.

Differences in management activities (for example, domestic quarantine regulations that restrict the movement of logs) and biological control efficacy among regions could also explain differences in spread rates. For example, inside South Africa, in the province of KwaZulu-Natal (R5), most plantations are cultivated for pulpwood, are planted at high density and are not pruned or thinned, leading to higher levels of tree stress and susceptibility to *S. noctilio* attack. In Western Cape, South Africa (R4), where the spread rate is lower, most plantations are managed for saw timber; these stands are subjected to more intense pruning, thinning and removal of suppressed trees which reduces stand density and promotes tree vigor (Hurley et al. 2007). These differences in management practices may explain the higher *S. noctilio* population growth rates, which would enhance spread rates, since population growth is an inherent driver of spread, as it has been demonstrated for other species, such as the gypsy moth in North America (Liebhold and Tobin 2008; Liebhold et al. 1992). Also, if natural dispersal is a density-dependent process (which remains unknown in this system), higher population growth and resultant higher population sizes could also increase spread via effects on dispersal.

Alternatively, the fact that some spread rates are quite large (e.g., 78 km per year in Western Cape, South Africa, R5) suggests that human-mediated movement is driving elevated spread rates, though we did not detect a relationship between spread rates and population density as might be expected if human-mediated dispersal was a dominant factor. Quarantine programs that restrict human movement of infested wood have been implemented to some degree in all invaded regions (Iede et al. 1998; Carnegie et al. 2005; SENASA and SAG 2007; Hurley et al. 2012), but information about the differences in efforts and effectiveness of control procedures among regions is poor or absent. Also, the implementation of biological control programs may reduce population growth rates and thereby reduce the spread of *S. noctilio*. Although various biological control agents have been introduced at different stages in the invasion history in the regions where populations of *S. noctilio* are established, it is not clear how the efficacy and timing of biological control programs have affected variation of *S. noctilio* populations observed among the regions (Hurley et al. 2007).

It should be noted that estimation of spread rate based on detections at various locations through time provides only an approximate quantification of the spread of *S. noctilio* populations at broad scales, in part because there may be a considerable time lag between *S. noctilio* entering an area and its first detections (Yemshanov et al. 2009). Furthermore, survey efforts may not have been uniform within or across regions, and this could introduce a bias in spread rate estimation. However, on the whole, it seems unlikely that systematic biases have substantially influenced our results, because in all regions studied, detections were based largely on the observation of established *S. noctilio* populations, rather than through early detection procedures. In this sense, as we described in methodology, data were collected after the first detection in each region and therefore after land managers became aware of the invasion. Also, regardless of the survey method, lags associated with the detection of established populations may be small, since the presence of dead trees is a conspicuous indicator.

Our findings suggest that climatic conditions correlate with observed differences in the rates of spread of an invading species in the Southern Hemisphere. Whether this correlation reflects a direct or indirect causal link awaits further investigation, though there are aspects of the physiology and behavior of *S. noctilio* and other insects that might support such a positive relationship. These results may have important implications in the context of climate change. Since climate change is expected to warm much of the Earth's surface (Houghton et al. 2001), increased temperatures in some regions may favor faster spread rates of *S. noctilio* in the future.

The improved understanding of spread in *S. noctilio* in relation to temperature may help facilitate the development of more rigorous models predicting rates of expansion of existing invasive populations (e.g., into eastern Australia, central Chile, Paraguay, southern Africa, North America, China, Zimbabwe) as well as into susceptible regions where *S. noctilio* has not yet arrived. In this way, understanding the factors that affect *S. noctilio* and other invasive species spread rates at broad scales might be critical in optimizing efforts to slow the spread of these species or define quarantine regulations.

Acknowledgments We thank the "Dirección General de Bosques y Parques de Chubut, Argentina" and "Servicio Nacional de Sanidad y Calidad Agroalimentaria (SENASA), Argentina" for providing data used in this paper. This work was partially supported by grants: PICT-1775 (Agencia Nacional para la Promoción Científica y Tecnológica, Argentina); SaFo-109 (Componente Plantaciones Forestales Sustentables, BIRF LN 7520 AR, Argentina); and the US Forest Service International Programs. M. Ramsden (HQPlantations) provided unpublished data on *S. noctilio* detections in Queensland.

References

Ahumada R (2002) Diseases in commercial *Eucalyptus* plantations in Chile, with special reference to *Mycosphaerella* and *Botryosphaeria* species. University of Pretoria, Pretoria

Anderson D (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York

Bedding RA (1993) Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*. In: Bedding RA, Akhurst R, Kaya H (eds) Nematodes and the biological control of insect pests. CSIRO, Australia, pp 11–20

Beèche M, Gonzales P, Sandoval A, Mayorga SI, Murillo ME, Jaques L, Rothmann S, Gonzalez H, Estay S, Muñoz C, Ferrada R, Peralta M, Bravo C, Sievert H, Canales R, Torres V, Zapata M, Carrillo M (2005) Informe anual del Subdepartamento de Vigilancia y Control de Plagas Forestales y Exóticas Invasoras, año 2004. Servicio Agrícola y Ganadero, Santiago, Chile

BRACELPA (2004) Associação Brasileira de Celulose e Papel. BRACELPA, Sao Paulo

Bruzzone OA, Villacide JM, Bernstein C, Corley JC (2009) Flight polymorphism in the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae): an analysis of tethered flight data using wavelets. J Exp Biol 212(5):731–737

Cameron RJ (1985) Official year book of the Commonwealth of Australia. Australian Bureau of Statistics, Canberra

Carnegie AJ, Bashford R (2012) Sirex Woodwasp in Australia: current management strategies, research and emerging issues. In: Slippers B, de Groot P, Wingfield MJ (eds) The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Netherlands, pp 176–201

Carnegie AJ, Eldridge RH, Waterson DG (2005) History and management of Sirex wood wasp in pine plantations in New South Wales, Australia. NZ J Forest Sci 35(1):3–24

Carvalho AG (1992) Bioecologia de *Sirex noctilio* F., 1793 (Hymenoptera, Siricidae) em povoamentos de *Pinus taeda* L., Universidade Federal do Paraná, Curitiba

Carver S (1960) Official year book of the Commonwealth of Australia. Commonwealth Bureau of Census and Statistics, Canberra

Castles I (1990) Official year book of the Commonwealth of Australia. Australian Bureau of Statistics, Canberra

CIESIN (2000) Gridded population of the world (GPW), Version 2. Center for International Earth Science Information Network (CIESIN), Columbia University, International Food Policy Research Institute (IFPRI), World Resources Institute (WRI). http://sedac.ciesin.columbia.edu/plue/gpw

Collett NG, Elms S (2009) The control of sirex wood wasp using biological control agents in Victoria, Australia. Agric For Entomol 11:283–294

Corley JC, Villacide JM (2012) Population dynamics of *Sirex noctilio*: influence of diapause, spatial aggregation and flight potential on outbreaks and spread. In: Slippers B, de Groot P, Wingfield MJ (eds) The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Netherlands, pp 51–64

Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. Front Ecol Environ 6(5):238–246

de Groot P, Nystrom K, Scarr T (2006) Discovery of *Sirex noctilio* (Hymenoptera: Siricidae) in Ontario, Canada. Gt Lakes Entomol 39:49–53

DGByP (2009) Informe sobre las acciones de manejo de la avispa de los pinos *Sirex noctilio* en la provincia del Chubut. Dirección General de Bosques y Parques, Provincia de Chubut, Esquel

Evans A, Gregoire T (2007) A geographically variable model of hemlock woolly adelgid spread. Biol Invasions 9(4):369–382

Gaiad DC (2001) Efeitos de desbastes em povoamentos de *Pinus taeda* na ocorrencia da vespa-da-madeira, *Sirex noctilio* F., 1792. Universidade Federal do Paraná, Curitiba

Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading populations. Ecography 33(5):809–817

Gilbert JM, Miller LW (1952) An outbreak of *Sirex noctilio* F. in Tasmania. Aust For 16:63–69

Hanks LM, Paine TD, Millar JG (1991) Mechanisms of resistance in *Eucalyptus* against larvae of the *Eucalyptus* longhorned borer (Coleoptera: Cerambycidae). Environ Entomol 20(6):1583–1588

Haugen DA (1990) Control procedures for *Sirex noctilio* in the Green Triangle: review from detection to severe outbreak (1977–1987). Aust For 53(1):24–32

Haugen DA, Bedding RA, Underdown MG, Neumann FG (1990) National strategy for control of *Sirex noctilio* in Australia. Aust For Grow 13(2):1–8

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hoebeke ER, Haugen DA, Haack RA (2005) *Sirex noctilio*: discovery of a palearctic siricid woodwasp in New York. Newsl Mich Entomol Soc 50:24–25

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D (2001) Climate change 2001. The scientific basis. Cambridge University Press, Cambridge

Hurley B, Slippers B, Wingfield M (2007) A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. Agric For Entomol 9:159–171

Hurley BP, Slippers B, Croft PK, Hatting HJ, van der Linde M, Morris AR, Dyer C, Wingfield MJ (2008) Factors influencing parasitism of *Sirex noctilio* (Hymenoptera: Siricidae) by the nematode *Deladenus siricidicola* (Nematoda: Neotylenchidae) in summer rainfall areas of South Africa. Biol Control 45(3):450–459

Hurley B, Croft P, Verleur M, Wingfield MJ, Slippers G (2012) The control of the Sirex woodwasp in diverse environments: the South African experience. In: Slippers B, de Groot P, Wingfield MJ (eds) The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Netherlands, pp 247–264

Iede E, Zanetti R (2007) Ocorrência e recomendações para o manejo de *Sirex noctilio* Fabricius (Hymenoptera, Siricidae) em plantios de *Pinus patula* (Pinaceae) em Minas Gerais, Brasil. Rev Bras Entomol 51(4):529–531

Iede ET, Penteado SRC, Bisol JC (1988) Primeiro registro de ataque de *Sirex noctilio* em Pinus taeda no Brasil. Circular Técnica EMBRAPA-CNPF n. 20. Circular Técnica EMBRAPA-CNPF n. 20. EMBRAPA, Brazil

Iede E, Penteado SRC, Schaitza EG (1998) *Sirex noctilio* problem in Brazil: detection, evaluation, and control. In: Iede E, Schaitza EG, Penteado S, Reardon R, Murphy ST (eds) Proceedings of a Conference: Training in the Control of *Sirex noctilio* by Use of Natural Enemies, Colombo, Brazil, pp 45–52

Iede E, Penteado S, Reis Filho W, Gomes Schaitza E (2000) Situação atual do Programa de Manejo Integrado de *Sirex noctilio* no Brasil. SÉRIE TÉCNICA IPEF 13(33):11–20

INFOR (2009) Los Recursos Forestales en Chile, Informe Final: Inventacio continuo de bosques nativos y actualización de plantaciones forestales. Instituto Forestal, Ministerio de Agricultura, Gobierno de Chile, Santiago

Irvine CJ (1962) Forest and timber insects in Victoria. Vic Resour 4:40–43

Klasmer P, Fritz G, Corley JC, Botto E (1998) Current status of research on *Sirex noctilio* F. in the Andean - Patagonian region in Argentina. In: Iede E, Shaitza E, Penteado S, Reardon R, Murphy T (eds) Training in the Control of *Sirex noctilio* by use of natural enemies, Morgantown, MV. USDA Forest Service, pp 89–90

Klasmer P, Botto E, Corley J, Villacide J, Arhex F (2000) Avances en el control biológico de *Sirex noctilio* en la región Patagónica Argentina. In: 1° Simposio do Cone Sul sobre Manejo de Pragas e Doencas de Pinus, Brazil. Serie técnica IPEF Brasil, pp 21–30

Langor DW, DeHaas LJ, Foottit RG (2009) Diversity of non-native terrestrial arthropods on woody plants in Canada. Biol Invasions 11(1):5–19

Liebhold AM (2012) Forest pest management in a changing world. Int J Pest Manag 58(3):289–295

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408

Liebhold AM, Halverson JA, Elmes GA (1992) Quantitative analysis of the invasion of gypsy moth in North America. J Biogeogr 19:513–520

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology. Blackwell, Oxford

Madden J (1981) Egg and larval development in the woodwasp, *Sirex noctilio* F. Aust J Zool 29:493–506

Madden J (1988) *Sirex* in Australasia. In: Berryman AA (ed) Dynamics of forest insect populations. Plenum Press, New York, pp 407–429

Maderni JFP (1998) *Sirex noctilio* present status in Uruguay. In: Iede E, Shaitza E, Penteado S, Reardon R, Murphy T (eds) Training in the control of *Sirex noctilio* by use of natural enemies, Morgantown, MV. USDA Forest Services, pp 81–82

Mayaux P, Bartholomé E, Fritz S, Belward A (2004) A new land-cover map of Africa for the year 2000. J Biogeogr 31(6):861–877

Miller D, Clark AF (1935) *Sirex noctilio* (Hym.) and its parasites in New Zealand. Bull Entomol Res 26:149–154

Morgan FD (1989) Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. NZ J Forest Sci 19(2/3):198–209

Mucha S (1967) The establishment and spread of *Sirex noctilio* F. in Tasmania from 1950 to 1964. Aust For Res 3(1):3–23

Neumann F, Morey J, McKimm R (1987) The sirex wasp in Victoria. Victoria bulletin no. 29. Lands and Forests Division, Department of Conservation, Forest and Lands, Melbourne

O'Neill JP (1973) Official year book of the Commonwealth of Australia. Australian Bureau of Statistics, Canberra

Ribas Júnior U (1993) Prácticas de controle da Vespa-da-madeira em povoamentos de *Pinus* do sul do Brasil e efeitos de seu ataque nas propiedades da maeira de *Pinus taeda*. Série Técnica IPEF 9(27):47–55

Ryan K, Hurley B (2012) Life history and biology of *Sirex noctilio*. In: Slippers B, de Groot P, Wingfield MJ (eds) The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Netherlands, pp 15–30

SAG (2006) Resolucion N° 3099. Diario Oficial de la República de Chile. Servicio Agrícola y Ganadero, República de Chile, Santiago

SAG (2009) Resoluciones N° 458, 642, 853, 986, 1229, 1594, 2117. Diario Oficial de la República de Chile. Servicio Agrícola y Ganadero, República de Chile, Santiago

SAG (2010) Resoluciones N° 322, 491, 682, 695, 973. Diario Oficial de la República de Chile. Servicio Agrícola y Ganadero, República de Chile, Santiago

SAG (2011) Resoluciones N° 1278, 1576, 1772, 2153. Diario Oficial de la República de Chile. Servicio Agrícola y Ganadero, República de Chile, Santiago

SAG (2012) Resoluciones N° 84, 147, y 313. Diario Oficial de la República de Chile. Servicio Agrícola y Ganadero, República de Chile, Santiago

SAGPyA (2001) Inventario Nacional de Plantaciones Forestales. Dirección de Forestación, Secretaría de Agricultura, Ganadería, Pesca y Alimentos, Buenos Aires

SENASA, SAG (2007) Informe final de las actividades del plan de contingencia binacional para el control biológico de la avispa de los pinos *Sirex noctilio* F., en las provincias de Neuquén, Río Negro y Chubut. Temporada 2006–2007. Servicio Nacional de Sanidad y Calidad Agroalimentaria (Argentina), Servicio Agricola y Ganadero (Chile), Cordoba

Sharov AA, Pijanowski BC, Liebhold AM, Gage SH (1999) What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility? Agric For Entomol 1(1):37–45

Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press, Oxford

Speight MR, Hunter MD, Watt AD (2008) Ecology of insects: concepts and applications. Wiley-Blackwell, Oxford

Taylor KL (1978) Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. Oecologia 32(1):1–10

Tribe GD (1995) The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa. Afr Entomol 3:215–217

Tribe GD, Cillie JJ (2004) The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. Entomol Soc South Afr 12(1):9–17

Villacide JM, Corley JC (2012) Ecology of the woodwasp *Sirex noctilio*: tackling the challenge of successful pest management. Int J Pest Manag 58(3):249–256

Villacide JM, Klasmer P (2002) Primer registro de la avispa de los pinos, *Sirex noctilio* en la Comarca Andina del Paralelo 42°. Comunicación Técnica N°18. INTA EEA Bariloche, Bariloche

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16:1192–1203

Yemshanov D, McKenney DW, de Groot P, Haugen D, Sidders D, Joss B (2009) A bioeconomic approach to assess the impact of an alien invasive insect on timber supply and harvesting: a case study with *Sirex noctilio* in eastern Canada. Can J For Res 39(1):154–168