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ORIGINAL PAPER

Estimating the potential geographical range of *Sirex noctilio*: comparison with an existing model and relationship with field severity

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Abstract The Sirex woodwasp, *Sirex noctilio*, is a significant pest of exotic stands of *Pinus* species in the southern hemisphere, and an emerging threat in north-eastern America. The potential global distribution of *S. noctilio* was assessed using the process-oriented niche modelling software CLIMEX. Model parameters were inferred from *S. noctilio*'s known native distribution in Eurasia and northern Africa, its exotic range in Brazil, New Zealand and South Africa, and from ecophysiological laboratory observations of both *S. noctilio* and its symbiotic wood-decay fungus, *Amylostereum areolatum*. Model predictions were validated using independent distribution data from Australia, New Zealand, South Africa and the Americas. Damage significance and spatial distribution data of *S. noctilio* infestations in New Zealand were compared with growth and suitability outputs of the model, to explore if the impact of *S. noctilio* could be related to climate. However, no correlation between modelled climate suitability and field infestation severity were found. The resulting model indicated that *S. noctilio* is currently occupying a fraction of its potential climatic niche in the regions it has invaded. Taking into account areas where suitable hosts occur, results suggest that *S. noctilio* could further extend its range into additional plantations in southern Queensland in Australia and central Brazil, and into native and exotic stands of *Pinus* throughout north-east America. Stands of *Pinus* that are isolated at present from current *S. noctilio* infestations, such as those in California, Central America and Western Australia, may also be at risk if control measures are ineffective

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in preventing its spread. Differences in parameter selection and risk projections of our model and a previously published CLIMEX model of *S. noctilio* are discussed.

Keywords Climate · European wood wasp · Forest pest · Invasive species

Introduction

Sirex noctilio (colloquially, European or Sirex woodwasp) is a significant pest of exotic pine plantations in the southern hemisphere (Hurley et al. 2007) and an emerging biosecurity threat to both exotic and native stands of *Pinus* spp. in North America (Borchert 2006). It has a wide host range within *Pinus*, with *P. radiata*, *P. taeda* and *P. patula* being particularly susceptible (Carnegie et al. 2005; Morgan and Stewart 1966; Spradbery and Kirk 1978). *Sirex noctilio* is native to Eurasia and northern Africa (Spradbery and Kirk 1978), where it is not known to adversely affect plantations or amenity trees (Hall 1968; Wermelinger and Thomsen 2012), and outbreaks rarely occur (Tarasco and la Notte 2003). Within its exotic range, *S. noctilio* is considered a major pest of pine plantations, and has been known to cause widespread tree mortality (Haugen and Underdown 1990) and significant economic losses (Cameron et al. 2018; Slippers et al. 2012).

Female *S. noctilio* cause tree mortality when they oviposit their eggs, along with a phytotoxic mucus and spores of the symbiotic wood decay fungus *Amylostereum areolatum* (Coutts 1969a, b), into stressed or suppressed trees (Madden 1971; Rawlings 1948). Tree stress may be induced by abiotic stressors such as drought (Rawlings 1948), or occur as a result of excessive competition or inadequate nutrition—factors that are amenable to silvicultural management (Haugen et al. 1990). *Sirex noctilio* carries *A. areolatum* to new trees where, in the process of decaying the wood (in concert with cell death caused by the phytotoxic mucous) it provides a favourable environment for *S. noctilio* eggs and larvae to develop, contributing to tree mortality (Morgan 1968). Given this close association, optimal growth of the fungus is closely related to optimal growth of *S. noctilio*.

Sirex noctilio was first identified as an exotic pest in pine plantations in New Zealand in the early 1900s (Rawlings 1948). It subsequently spread into all major pine producing countries in the southern hemisphere by 2001 (Carnegie et al. 2005) and North America by 2004 (Hoebeke et al. 2005). All pine growing regions of New Zealand, the south-eastern states of Australia (Tasmania, South Australia, Victoria and New South Wales), Uruguay and Argentina are now infested with *S. noctilio* (Carnegie and Bashford 2012; Carnegie et al. 2005; Eldridge and Taylor 1989a; Irvine 1962; Klasmer and Botto 2012; Klasmer et al. 1998; Maderni 1998; Neumann et al. 1987). The potential for further spread of *S. noctilio* into non-infested susceptible pine-growing regions of Australia and the Americas remains a concern (Carnegie et al. 2017; Nahrung et al. 2016a; Slippers et al. 2012). Native and exotic *Pinus* stands in China may also be threatened by incursions of *S. noctilio*, assuming that it is not native to the area (Carnegie et al. 2006; Li et al. 2015; Sun et al. 2016). It is likely that the threat of new incursions by *S. noctilio* will continue, particularly given that *Sirex* species are among the most commonly intercepted pests in wood at ports of entry in the United States (Scott 2003). This threat of spread through international trade may now be moderated, however, by the implementation of ISPM 15 (International Standard for Phytosanitary Measures for the regulation of wood packaging material in international trade) (FAO 2006; Haack et al. 2014).

Despite recognition of *S. noctilio* as a major damaging pest of pine plantations (Corley et al. 2007; Haugen et al. 1990; Hurley et al. 2007), only one model defining *S. noctilio*'s bioclimatic niche and potential global distribution has been published. Carnegie et al. (2006) utilised climate station data and the Compare Locations function in the process-oriented distribution modelling software, CLIMEX (Kriticos et al. 2015; Sutherst and Maywald 1985), to model *S. noctilio*'s potential distribution. One other model employed the use of the Climate Matching function in CLIMEX for the *S. noctilio* biological control parasitoid, *Ibalia leucospoides* (Villacide and Corley 2003), for a limited area of interest in Argentina; while Kirk (1974) examined bioclimatic homologues of the native distribution of *S. noctilio* within Australian *P. radiata* plantations using less sophisticated methods in the early 1970s. Together, the aforementioned models reflect the extent of bioclimatic niche modelling in the published literature for *S. noctilio*.

Bioclimatic niche models such as CLIMEX are often used to examine potential geographic range of invasive species as they are considered to reliably project a species response to novel situations, such as introduction to a new region (Sutherst and Bourne 2009; Webber et al. 2011). Additionally, in contrast to correlative species distribution models, the Compare Locations module in CLIMEX is not restricted to using distribution data to train the model, but is able to assimilate information from many knowledge domains (Kriticos et al. 2015). This allows gaps in one domain, such as distribution, to be compensated for, and challenged by knowledge in other domains, such as eco-physiological laboratory data. The model can also be useful for identifying errors in the available information where different knowledge elements are applied in the model and produce results that conflict with other data or beliefs. Despite it being such a significant pest threat, many unknowns remain regarding knowledge of the full distribution and climatic requirements of *S. noctilio*. As such, CLIMEX is expected to perform well as a niche modelling tool for estimating pest risk for this species.

A useful application of bioclimatic niche models is to estimate the potential impacts of invasive pest species by deriving a climate-related damage function and applying it within the area of interest. Such projections can be particularly useful to policymakers and land managers, allowing them to direct resources prudently to activities such as: (1) managing invasion pathways and surveys, (2) investing in the development of resistant crop cultivars and (3) controlling pest abundance or spread in areas projected to be most at risk of outbreaks and production/biodiversity loss. Climate-damage functions have successfully been modelled, and validated, using CLIMEX for two forest pests, the pine processionary moth (*Thaumetopoea pityocampa* sensu lato) (Kriticos et al. 2013) and mycosphaerella leaf disease [caused primarily by *Teratosphaeria cryptica* (syn. *Mycosphaerella cryptica*) and *T. nubilosa* (syn. *M. nubilosa*)] (Pinkard et al. 2010), and two wheat diseases, stem rust caused by *Puccinia graminis* f. sp. *tritici* (Pardey et al. 2013) and stripe rust caused by *P. striiformis* f. sp. *tritici* (Beddow et al. 2015). Linkages between field severity and climatic suitability outputs from CLIMEX may therefore be possible for other pest-host interactions.

Knowledge of the potential global distribution and climate suitability patterns for pests such as *S. noctilio* are useful to forest managers and biosecurity officers when planning surveys, control methods and regulatory guidelines (Venette et al. 2010). It is important that models reflect the best available information about a particular pest at that point in time, and that these models are re-evaluated and updated when necessary. The objective of this study was to refine the *S. noctilio* CLIMEX model developed by Carnegie et al. (2006), producing a more accurate and finer-grained risk map for the wasp. We then relate this predicted risk of *S. noctilio* establishment and persistence with known host distributions. This finer spatial resolution and intersection of pest risk with host distribution is likely to be more useful for forest managers and risk assessment professionals, who require a more site-specific understanding of risk when managing stands and pest spread across the landscape. Additionally, we attempt to link measures of field severity for *S. noctilio* in New Zealand with projections of climatic suitability from our CLIMEX model. Differences with the previous Carnegie et al. (2006) model and implications for forest biosecurity are discussed.

Materials and methods

The CLIMEX model

The Compare Locations function in CLIMEX 4.0 (Kriticos et al. 2015; Sutherst and Maywald 1985) was used to develop a climate suitability model for *S. noctilio*. The CliMond CM10_1975H_V1 interpolated global climate surface (Kriticos et al. 2012) was used for all modelling. As described previously (Ireland et al. 2013), the Compare Locations function in CLIMEX calculates an annual index of climatic suitability, the Ecoclimatic Index (EI), which reflects the combined potential for population growth during favourable periods and survival during stressful periods. This is achieved by firstly calculating a baseline annual growth index (GI_A) which describes the potential for growth of the host and pathogen as a function of average weekly soil moisture (Moisture Index; MI) and temperature (Temperature Index; TI) during favourable conditions. This GI_A is then moderated by factoring in stress and stress interaction indices [including cold stress (CS), wet stress (WS), heat stress (HS) and dry stress (DS), and a stress interactions such as cold–dry stress (CDX), cold–wet stress (CWX), hot–dry stress (HDX) and hot–wet stress (HWX)] to calculate the EI (see Kriticos et al. 2015 and Ireland et al. 2013 for equations, extended summary and further detail). The EI ranges from 0 for locations at which the species is not able to persist to 100 at locations that are optimal for the species year-round.

New model parameters

Native distribution records (Boissin et al. 2012; CABI 2006, 2016; GBIF Secretariat: GBIF Backbone Taxonomy 2016; Goldarazena 2015; Kirk 1974; Norwegian Biodiversity Information Centre 2010; Spradbery and Kirk 1978; Stroganova 1968; Tarasco and la Notte 2003; Viitasaari 1984; Wermelinger and Thomsen 2012) (Fig. 1), exotic distribution records from South Africa (Boissin et al. 2012; Hurley et al. 2008; Ismail et al. 2010; Lantschner et al. 2014 and references therein; Tribe and Cillie 2004) (Fig. 2b) and New Zealand (Boissin et al. 2012; 1960–2009, Scion and New Zealand Forest Owners Association Forest Health Database, supplementary material 1) (Fig. 3a) and relevant laboratory data (see parameter selection below) were used to inform the selection of relevant parameters for growth and stress of *S. noctilio* (Table 1). Given that *A. areolatum* creates conditions conducive to *S. noctilio* growth (Slippers et al. 2003), temperature and moisture requirements of *A. areolatum* were also included when defining these parameters. The stress indices were fitted in such a way as to conform to the guidance of Kriticos et al. (2005), so that the stresses and growth should not occur at the same time, and hence the thresholds for stresses were adjusted to occur outside the limits for growth.

Temperature indices were refined to reflect laboratory-derived limitations to egg and larval development of *S. noctilio* and *A. areolatum* growth requirements (King 1966; Madden 1981). The lower (DV1) and upper (DV2) optimal temperatures were set to 23 and 27 °C, in order to encompass the estimated optimal temperature of 25 °C for growth of *S. noctilio* eggs and *A. areolatum* mycelia (Madden 1981). The limiting lower temperature for growth (DV0) was set to 5 °C, which is just below the lower temperature threshold recently recalculated by Nahrung (2017). This recalculation is based on prior observations for both *S. noctilio* and fungus (6.2–6.8 °C) by Madden (1981). The limiting high temperature was set to 33 °C, which reflects the upper limit of growth of *S. noctilio* and *A. areolatum* (Madden 1981; M. Ramsden, HQPlantations, unpublished data).

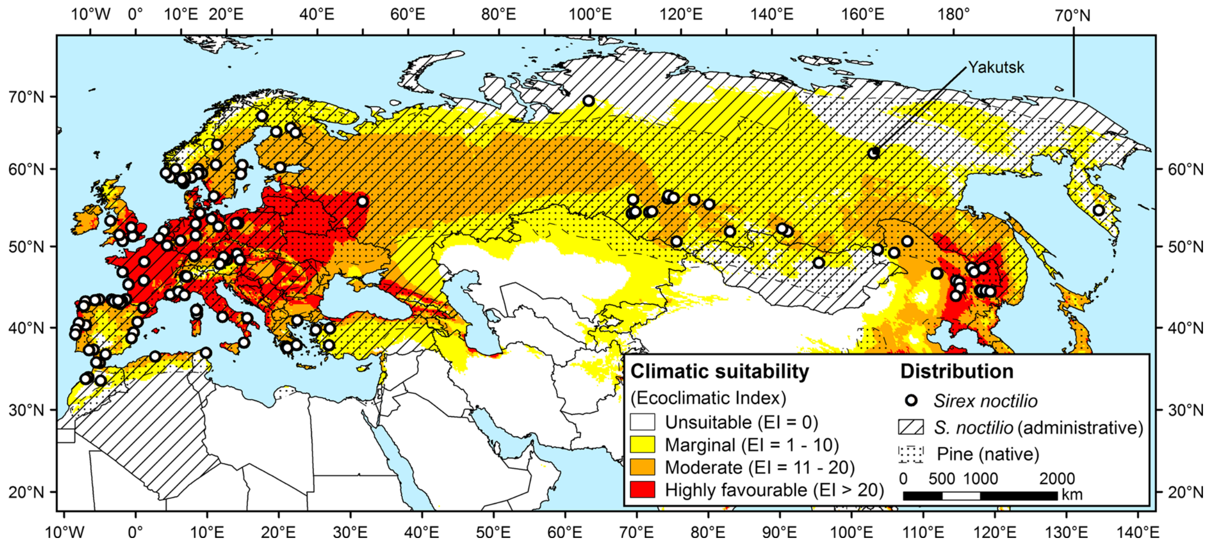


Fig. 1 Projected climatic suitability for *Sirex noctilio* and observed native *S. noctilio* and pine distributions in the Palaearctic region and North Africa. The projection is under the 1961–1990 climate normals, as modelled using CLIMEX. Administrative level distribution indicates *S. noctilio* presence being recorded on a whole of country or region basis

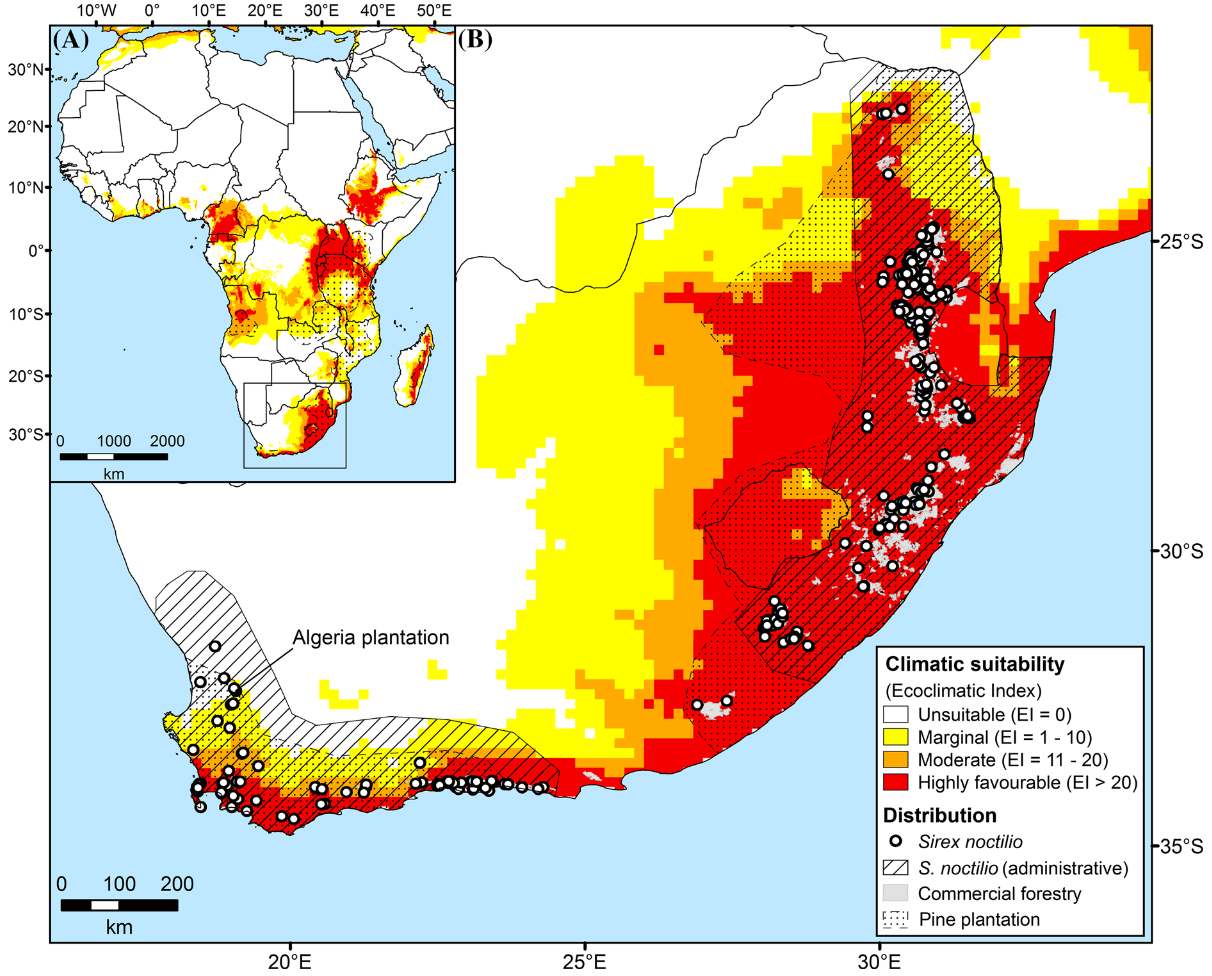


Fig. 2 Projected climatic suitability for *S. noctilio* and observed pine plantation distributions in Africa (**a**) and enlargement of the observed *S. noctilio* and commercial forestry distributions in South Africa (**b**). The projection is under the 1961–1990 climate normals, as modelled using CLIMEX. Administrative level distribution indicates geographical regions considered infested by *S. noctilio* as per Lantschner et al. (2014)

Moisture indices were adjusted to reflect the fact that ovipositing wasps are attracted to stressed trees and that fungal growth and wasp development is impeded by an excess or scarcity of water (Madden 1981; Taylor 1981). Given that a value of 0.1 is approximately permanent wilting point, the minimum soil moisture index value for population growth (SM0) was set at this value. The lower (SM1) and upper (SM2) optimal soil moistures were set to 0.5 and 0.8, respectively, to model conditions that are neither too dry nor too wet. The limiting high soil moisture was set to 1.8 in order to incorporate the moistest locations that *S. noctilio* is known to occur, east of the city of Greymouth, along the west coast of the South Island of New Zealand (Fig. 3a).

The threshold for the onset of cold stress (temperature threshold for cold stress, TTCS) was set to − 42 °C with an accumulation rate (THCS) of − 0.005 week^{-1}. This incorporated the coldest location that *S. noctilio* has been recorded, the city of Yakutsk, Sakha (Yakutia) republic, Siberia (Stroganova 1968) (Fig. 1), as being a barely suitable location for persistence of *S. noctilio*.

Heat stress was set to accumulate above 33 °C (TTHS), as *S. noctilio* has been recorded as not surviving temperatures greater than 33.5 °C (Madden 1981) and constant temperatures above 36 °C are

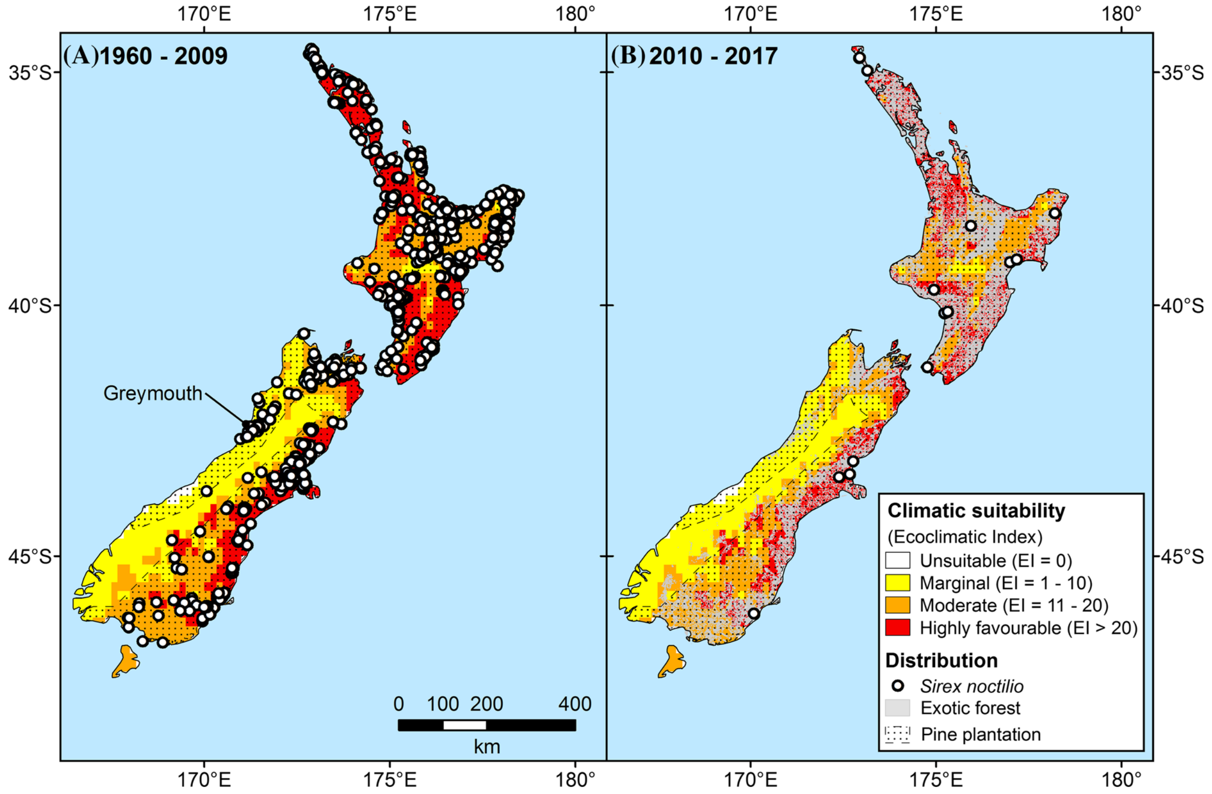


Fig. 3 Projected climatic suitability for *S. noctilio,* observed *S. noctilio* distributions for 1960–2009 (**a**) and 2010–2017 (**b**), and pine plantation (**a**) and exotic forest (**b**) distributions in New Zealand. The projection is under the 1961–1990 climate normals, as modelled using CLIMEX

known to kill the fungus within one to seven days (King 1966; M. Ramsden, HQPlantations, unpublished data). A Heat Stress accumulation rate of 0.05 week^{-1} (THHS) was deemed biologically reasonable, though we have no suitable primary data with which to fit this parameter.

Dry stress was set to accumulate below the permanent wilting point of the host and the lower soil moisture threshold for growth (SM0 and SMDS = 0.1), at a rate of − 0.05 week^{-1} (HDS) to incorporate the driest location where *S. noctilio* is known to persist, at the Algeria plantation in South Africa (Tribe and Cillie 2004) (Fig. 2). Potentially drier regions north of the Algeria plantation have been infested with *S. noctilio* (Tribe and Cillie 2004), but these are in moist microclimates, not representative of the overall eco-climatic landscape (Geoff D. Tribe, ARC-Plant Protection Research Institute, personal communication) and were therefore excluded from model fitting.

Wet stress was excluded from the model as adequate data were not available to define this index and experimental model fitting indicated that the inclusion of wet stress accumulating above the upper soil moisture threshold (SM3) of 1.8 had little impact on the results. Hot–dry stress was also excluded from the model as adequate data were not available, particularly in regards to inland distribution of *S. noctilio* along the north-African coast (Spradbery and Kirk 1978). Hot-wet stress was set to begin accumulating at a rate of 0.025 week^{-1} (PHW) above 27 °C (TTHW) and a soil moisture threshold (MTH) of 1, in order to exclude *S. noctilio* from tropical locations, where it has not been observed.

The minimum length of the growing season (PDD) was set to a threshold of 415 degree days above the lower temperature threshold (DV0) of 5 °C. This was derived from *S. noctilio* generation times estimated by the model at the coldest location in Siberia (Stroganova 1968), used to infer the cold stress parameters for *S. noctilio* (as outlined above). Because *S. noctilio* is semi-voltine the PDD parameter represents the minimum annual heat sum required for persistence at a

Table 1 CLIMEX parameter values used to model eco-climatic suitability of *Sirex noctilio*

Parameter	Description	Value and model	
		Old (Carnegie)[a]	New (Ireland)[b]
Temperature			
DV0	Lower temperature threshold for growth	0 °C	5 °C
DV1	Lower optimum for growth	5 °C	23 °C
DV2	Upper optimum for growth	24 °C	27 °C
DV3	Upper temperature threshold for growth	30 °C	33 °C
Moisture			
SM0	Lower soil moisture threshold for growth	0.1[c]	0.1[c]
SM1	Lower optimum for growth	0.3[c]	0.5[c]
SM2	Upper optimum for growth	1.0[c]	0.8[c]
SM3	Upper soil moisture threshold for growth	2.5[c]	1.8[c]
Cold stress			
TTCS	Temperature threshold for cold stress	0 °C	− 42 °C
THCS	Cold stress accumulation rate	0 week^{-1}	− 0.005 week^{-1}
Heat stress			
TTHS	Temperature threshold for heat stress	35 °C	33 °C
THHS	Heat stress accumulation rate	0.05 week^{-1}	0.05 week^{-1}
Dry stress			
SMDS	Soil moisture threshold for dry stress	0.1[c]	0.1[c]
HDS	Dry stress accumulation rate	− 0.01 week^{-1}	− 0.05 week^{-1}
Wet stress			
SMWS	Soil moisture threshold for wet stress	2.5[c]	–
HWS	Wet stress accumulation rate	0.002 week^{-1}	–
Hot–dry stress			
TTHD	Hot–dry temperature threshold	23 °C	–
MTHD	Hot–dry moisture threshold	0.1[c]	–
PHD	Hot–dry stress rate	0.1 week^{-1}	–
Hot–wet stress			
TTHW	Hot–wet temperature threshold	32 °C	27 °C
MTHW	Hot–wet moisture threshold	1.5[c]	1.0[c]
PHW	Hot–wet stress rate	0.5 week^{-1}	0.025 week^{-1}
Annual heat sum			
PDD	Degree-day threshold	–	415 °C days

[a] Model published by Carnegie et al. (2006)

[b] Model presented in this paper

[c] Expressed as a proportion of soil moisture holding capacity, where 0 = oven dry and 1 = field capacity (saturation)

location, rather than the heat sum required to complete a generation. This parameter value was also consistent with the recent reanalysis of Madden's 1981 data set by Nahrung (2017), which estimated a lower thermal threshold of 5.1 °C and lower cumulative day-degree requirements of 1973. These estimates are more consistent with field observations, and fit with the notion that *S. noctilio* may take up to 6 years to complete a generation under sub-optimal cold conditions (Escherich 1942, as cited by Långström et al. 2004).

Model validation

The model was validated against independent datasets of *S. noctilio* point location distribution in Argentina (Patagonia) (Boissin et al. 2012; Klasmer and Botto 2012; Klasmer et al. 1998; Lantschner et al. 2014 and references therein) (Fig. 4), Australia (R. Bashford and T. Wardlaw, Forestry Tasmania, pers. comm.; A. Carnegie and M. Nagel, New South Wales Department of Primary Industries, pers. comm.; Carnegie et al. 2006; Lantschner et al. 2014 and references therein;

Nahrung et al. 2016a; H. Nahrung and S. Lawson, Queensland Department of Agriculture and Fisheries, pers. comm.; C. Phillips, South Australian Forestry, pers. comm.; Plant Health Australia 2017) (Fig. 5),

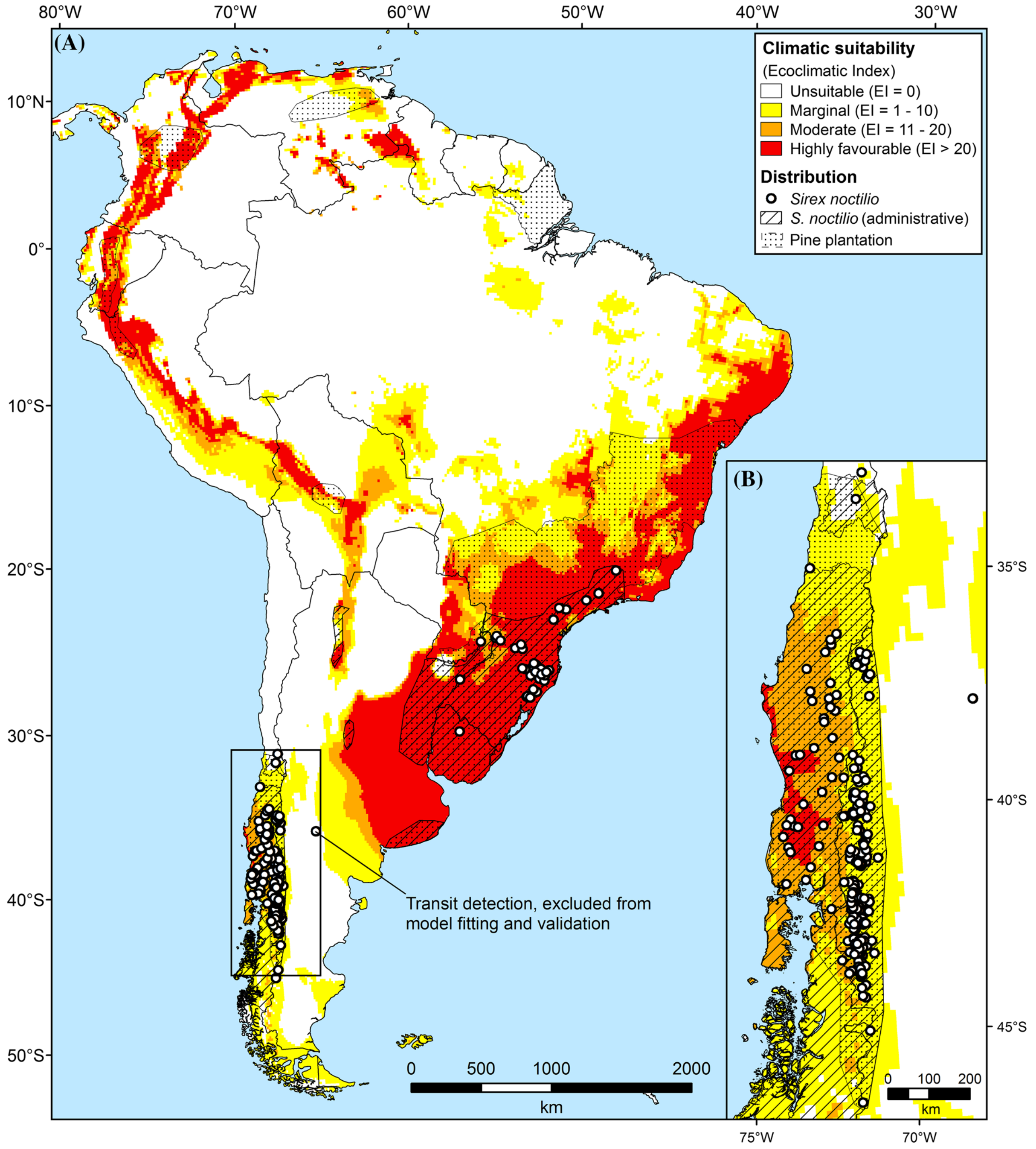


Fig. 4 Projected climatic suitability for *Sirex noctilio* and observed *S. noctilio* and pine plantation distributions in South America (**a**) and enlargement of the observed distribution in Chile and southern Argentina (**b**). The projection is under the 1961–1990 climate normals, as modelled using CLIMEX. Administrative level distribution indicates geographical regions considered infested by *S. noctilio* as per Lantschner et al. (2014), Poisson et al. (2016) for Chile and for all pine plantation regions in Argentina

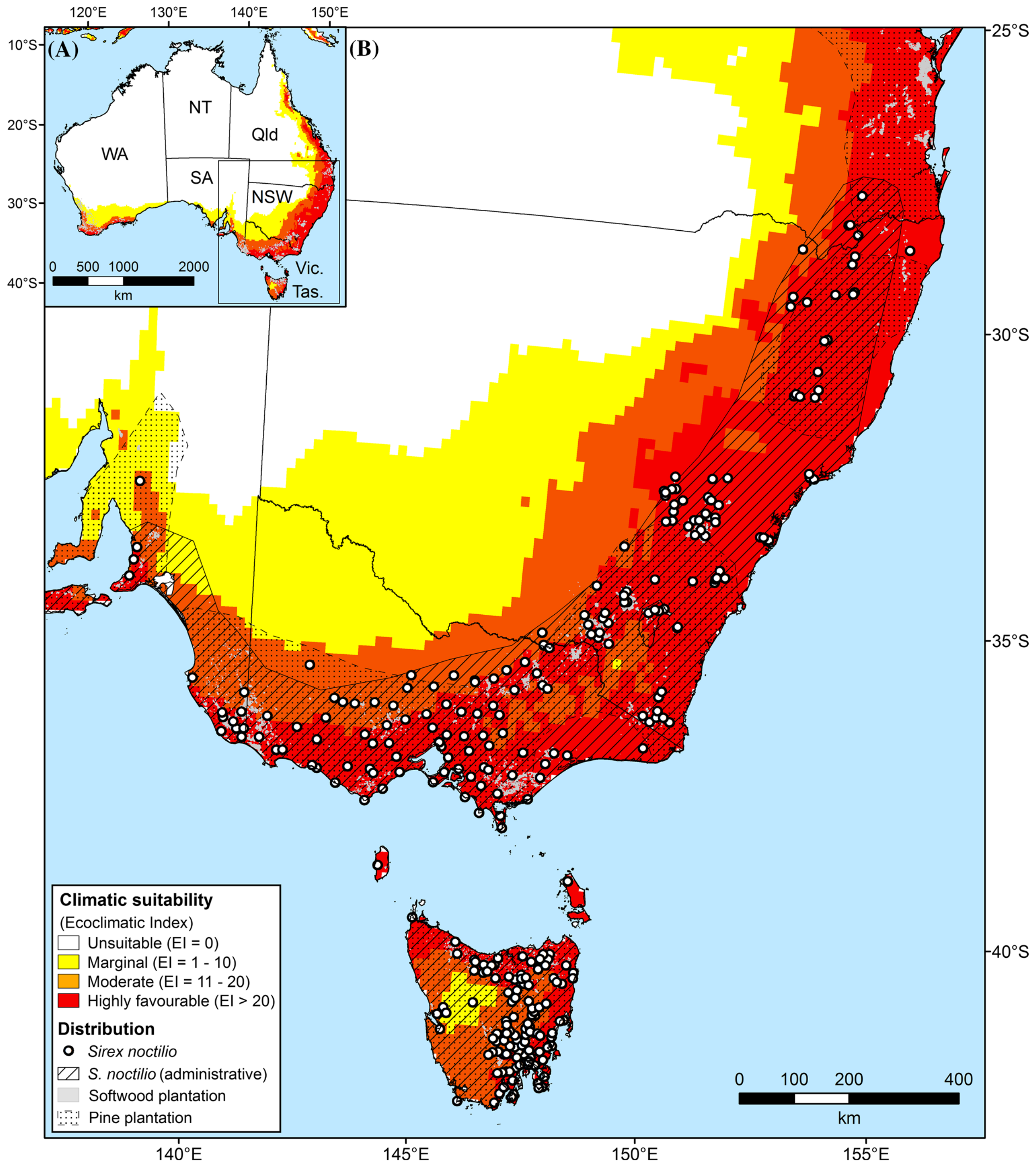


Fig. 5 Projected climatic suitability for *Sirex noctilio* and softwood plantation distributions in Australia (**a**) and enlargement of the observed *S. noctilio*, softwood and pine plantation distributions in South-East Australia (**b**). The projection is under the 1961–1990 climate normals, as modelled using CLIMEX. Administrative level distribution indicates geographical regions considered infested by *S. noctilio* as per Lantschner et al. (2014). States and territories are identified as New South Wales (NSW), Northern Territory (NT), Queensland (Qld), South Australia (SA), Tasmania (Tas.), Victoria (Vic.) and WA (Western Australia) (A)

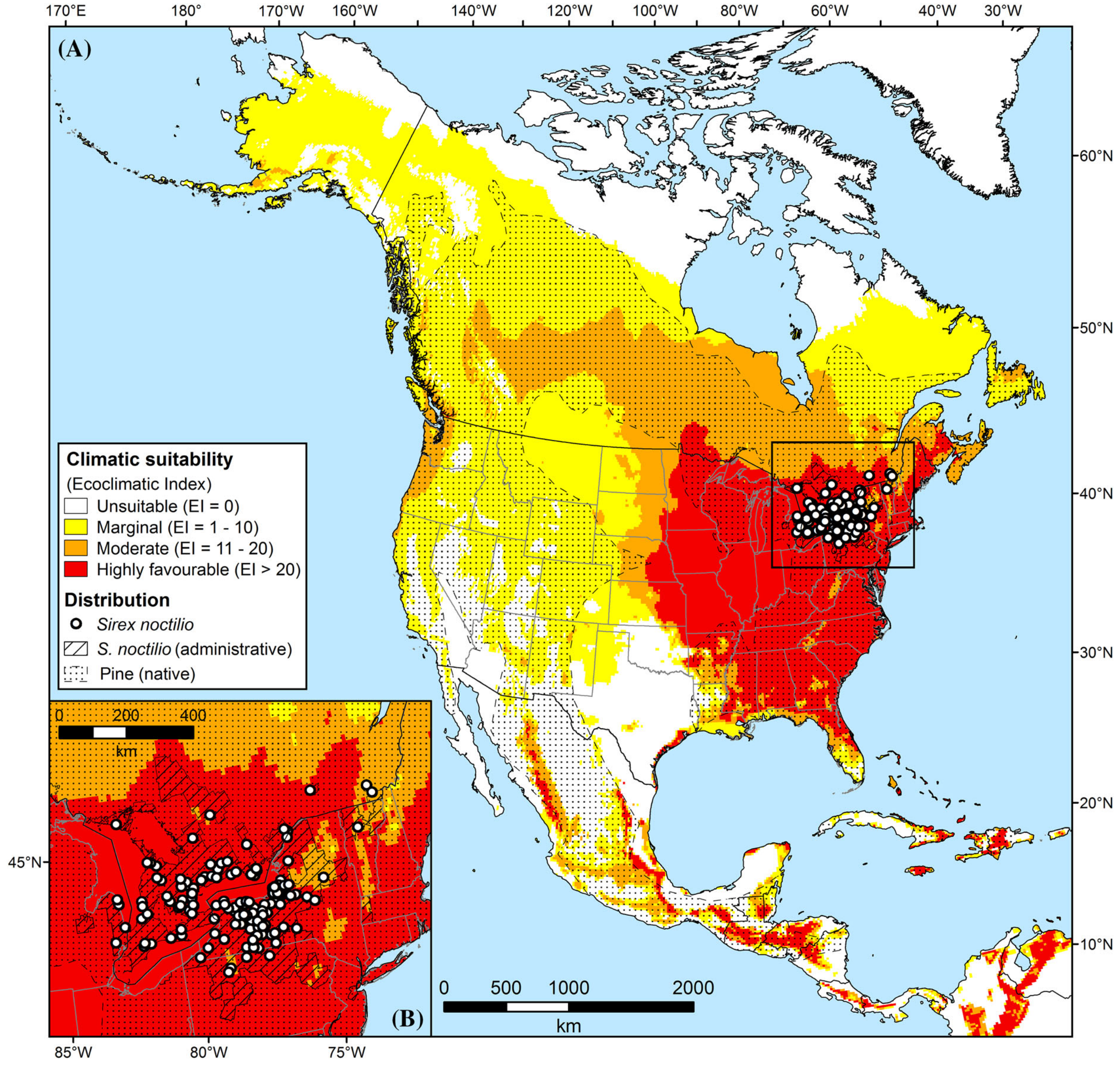


Fig. 6 Projected climatic suitability for *Sirex noctilio*, observed *S. noctilio* and native pine distributions in North America (**a**) and enlargement of the observed distribution surrounding the great lakes region of the North-East USA and Canada (**b**). USA state boundaries area overlain with grey outlines. The projection is under the 1961–1990 climate normals, as modelled using CLIMEX. Administrative level distribution indicates *S. noctilio* presence recorded on a county basis

Brazil (Lantschner et al. 2014 and references therein) (Fig. 4), Canada (Canadian Food Inspection Agency, unpublished positive trap data 2005–2009) (Fig. 6), Chile (Boissin et al. 2012; Lantschner et al. 2014 and references therein) (Fig. 4), China (Li et al. 2015; Sun et al. 2016) (Fig. 7), New Zealand (2010–2017, Scion and New Zealand Forest Owners Association Forest Health Database), South Africa (Institute for Commercial Forestry Research, positive survey data 2017) (Fig. 2b) and Uruguay (Boissin et al. 2012) (Fig. 4), and point location and infested county data from the USA (CERIS 2017; United States Forest Service, unpublished positive trap data 2005–2008) (Fig. 6).

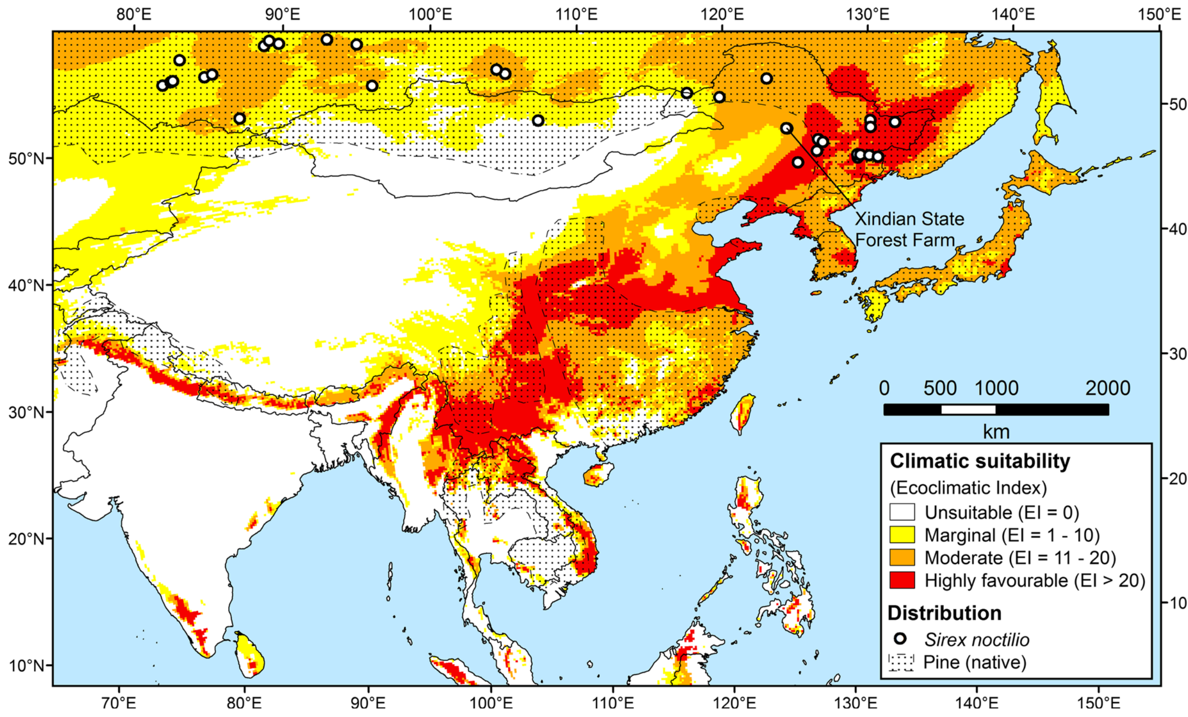


Fig. 7 Projected climatic suitability for *Sirex noctilio* and observed *S. noctilio* and pine distributions in Asia and southern Siberia. The projection is under the 1961–1990 climate normals, as modelled using CLIMEX

Relating potential geographical range of *Sirex noctilio* to host distribution

The native range of *Pinus* species in the northern hemisphere and distribution of pine plantations in the southern hemisphere as defined by Lantschner et al. (2017) (Figs. 1, 2, 3a, 4, 5b, 6, and 7) and areas of softwood plantations in Australia (ABARES 2017) (Fig. 5), exotic forest in New Zealand (Landcare Research New Zealand Ltd 2015) (Fig. 3b) and commercial forest in South Africa (Institute for Commercial Forestry Research, unpublished data) (Fig. 2b), were spatially intersected with *S. noctilio* distribution and the relevant EI estimated in CLIMEX for the 10′ grid cell that that location exists in using Arc GIS 10.3 (ESRI, Redlands CA). These areas were then related to the proportion of these areas considered to be climatically suitable for *S. noctilio* establishment and persistence.

Relating Ecoclimatic Index to *Sirex noctilio* impact

As described above, the EI and GI_A are relative scales of climate suitability for the modelled organism, and as such are not a direct measure of the potential impact of *S. noctilio* infestation in the field. A dataset of *S. noctilio* distribution (i.e. presence only data) with measures of infestation damage and spatial distribution at the stand level from New Zealand (1960–2009, Scion and New Zealand Forest Owners Association Forest Health Database, supplementary material 1) were spatially intersected with the relevant EI estimated in CLIMEX for the 10′ grid cell that that location exists in, using Arc GIS 10.3 (ESRI, Redlands CA) (supplementary material 1). Damage significance of *S. noctilio* infestations were assessed qualitatively by L. Bulman as negligible, low, moderate, high, secondary (i.e. primary cause for tree decline not *S. noctilio* infestation), debris (i.e. *S. noctilio* infesting logging slash) and abortive (i.e. evidence of *S. noctilio* drill holes which were abandoned) (sensu Bain et al. 2012). Spatial distribution of *S. noctilio* infestations at the stand level are assessed as clustered, isolated, localised, scattered or widespread (Fig. S1).

All data analyses, beyond fitting of the CLIMEX models, were conducted in the R statistical Environment version 3.4.0 (R Core Team 2015). A regression modelling approach was used to investigate the relationships between *S. noctilio* damage significance and distribution at the stand level with EI and GI from the CLIMEX models by using ordinal logistic regression (package MASS ver. 7.3-47; Venables and Ripley 2002). After testing for suitability of model assumptions, statistical significance was tested by calculating *p* values (assuming a standard normal distribution) and by profiling the likelihood surface to investigate confidence at the 95% confidence level. Decadal period of the record was also investigated as a factor influencing the above relationships. Bar graphs and scatterplots were also produced to plot frequency of occurrence and field impact of *S. noctilio* at certain EIs and to examine the relationship between EI and damage significance of *S. noctilio* infestation. The results of these visualisations were then used to help define boundaries for marginal, moderate and highly favourable climatic suitability envelopes for *S. noctilio*, and applied to the model outputs.

Differences between CLIMEX models

Comparisons of parameters and projections between the prior Carnegie et al. (2006) and our *S. noctilio* CLIMEX models were made. The parameters from the Carnegie et al. (2006) model were run with the climate surface described above, with boundaries for climatic suitability envelopes projected identically to our model (i.e. according to the results found in the EI-severity relationship study). This allowed for direct comparison of the projections of the models and expanded the original projection of the Carnegie et al. (2006) model. The original Carnegie et al. (2006) model was run on weather station data in an earlier version of CLIMEX, which was therefore limited in its ability to project beyond those specific weather station locations. Model validation using our updated distribution dataset (as described above) was also undertaken.

Results

Model fit and projections

Almost all moderate (coastal, Mediterranean and humid subtropical) and continental (humid and subarctic) climates were projected to be favourable for *S. noctilio* establishment and persistence (Fig. 8a), though it poses a transient invasion threat to a much larger area where conditions are suitable for population growth during only part of the year (Fig. S2). The model projected that *S. noctilio* would be restricted from arid, tropical and polar climatic zones (Fig. 8a), predominantly due to heat and dry stress (Figs S3 and S4) and some measure of hot-wet stress (Fig. S5). Our results indicate that *S. noctilio* could extend its range into humid subtropical climates of Australia (Fig. 5), China (Fig. 7), and the south-eastern USA (Fig. 6a), and continental and subarctic climates of north-eastern America (Fig. 6a). The projected potential distribution shows that isolated regions with native and exotic *Pinus* spp. in Western Australia (Fig. 5), the Pacific northwest of the USA (Fig. 6), and the highlands of Ethiopia and the Rwanda–Kenya–Uganda border (Fig. 2a), may also be at risk. Very few locations were projected to be too cold for *S. noctilio* (Fig. S6).

Three locations along the inner west coast of South Africa (north-west of Algeria Plantation), were specifically excluded when fitting the model's dry stress parameters (Fig. 2b; Fig. S4), as the location of these infestations are not representative of the climate of surrounding area, particularly on a 10′ grid. Consequently, these locations were deemed to be unsuitable for *S. noctilio* persistence, while the remaining distribution points from South Africa used to fit the model fell predominantly into areas projected to be of moderate (6.9%, 10/144) and highly favourable (85.4%, 123/144) climatic suitability (Fig. 2b).

Distribution points from the west coast of the South Island of New Zealand (near Greymouth) were used to fit the model's upper soil moisture threshold (SM3), and as such were projected as being of marginal suitability, though the vast majority of distribution points from New Zealand used to fit the model (97.7%, 1068/1093) fell into areas projected to be of moderate to highly favourable climatic suitability (Fig. 3a).

Globally, only 0.2% (6/2711) of all *S. noctilio* distribution points gathered in this study fell into areas considered to be climatically unsuitable for

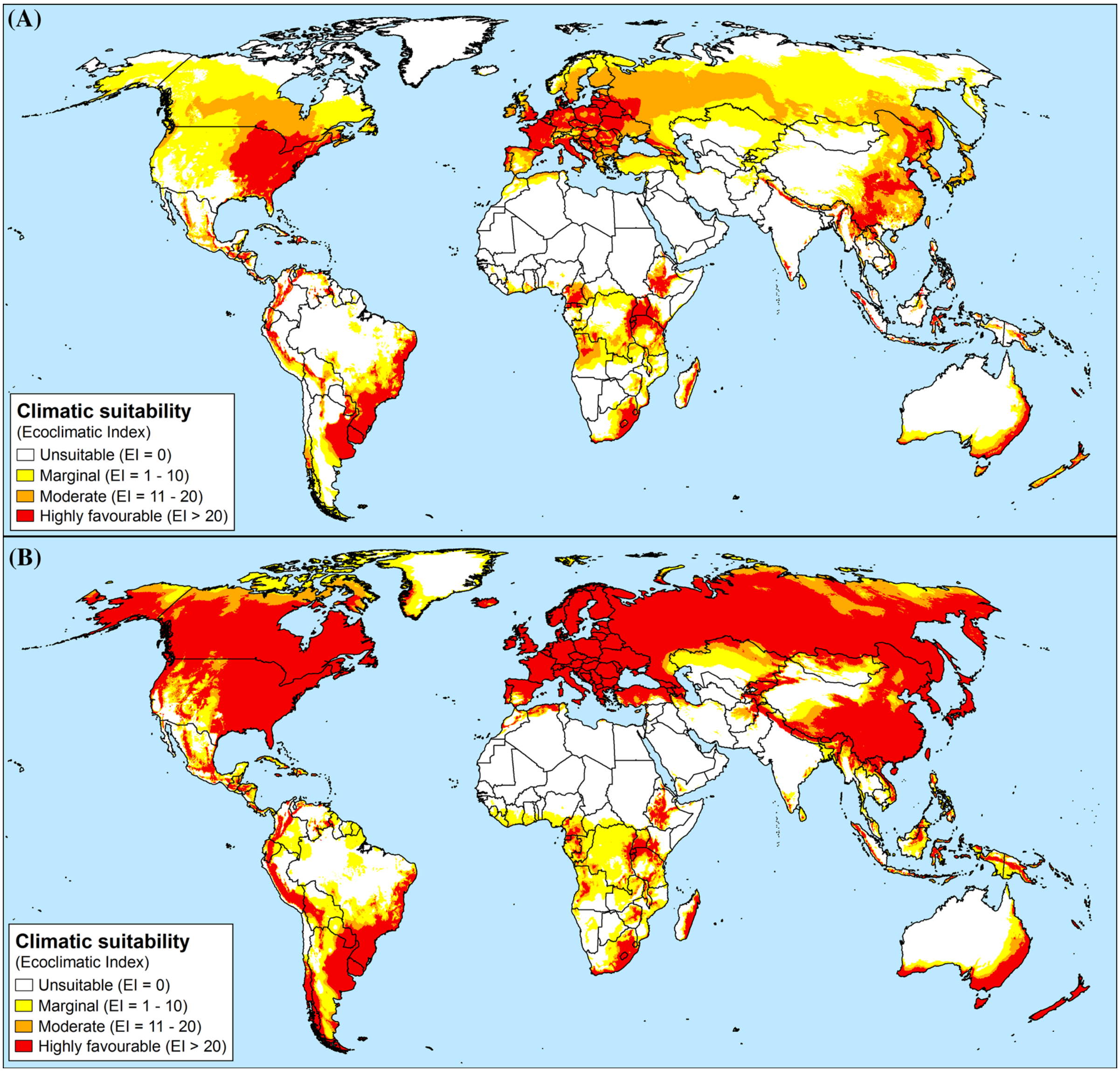


Fig. 8 Global projected climatic suitability for *Sirex noctilio*. The projection is under the 1961–1990 climate normals, as modelled using CLIMEX and using the parameters presented in this paper by Ireland et al. (**a**) and those of Carnegie et al. (2006) (**b**)

S. noctilio. These points included those excluded from model fitting and validation, as discussed previously for South Africa (3) and discussed below from Argentina (1). In the case of South Africa, these points are considered to be evidence of *S. noctilio* existing in microclimates not representative of the surrounding climate on the 10′ climate grid (South Africa), and in the case of Argentina, represent reports of *S. noctilio* in goods that were in transit (discussed below). One native distribution point from Norway gathered from the GBIF Data Portal (GBIF Secretariat: GBIF Backbone Taxonomy 2016) was also mapped into an area projected to be unsuitable for *S. noctilio*. When interrogated using Google earth (2016) and investigating the data point (GBIF Secretariat: GBIF Backbone Taxonomy 2016), this point falls into an urban area with a high margin of error in the GPS reading (± 1000 m), leading us to believe this is most likely not an accurate distribution point for *S. noctilio*. One final alien distribution point from Chile used in the validation data set also mapped into an unsuitable area, and is discussed below. Of the other 2705 qualified distribution points, 8.7% were projected to be in areas of marginal climatic suitability, 18.9% in areas of moderately suitable climate and 72.2% in areas of highly favourable climate. All areas identified on an administrative scale as having detections of *S. noctilio* were dominated by areas projected to be of moderate to highly favourable climatic suitability (Figs. 1, 2b, 4, 5b, and 6).

Model validation

The projected climatic suitability of the model fits all known *S. noctilio* occurrences within Argentina, Australia, Brazil, Canada, Uruguay and the USA, and all occurrences recorded in New Zealand from 2010 to 2017 and South Africa in 2017 (both reserved from model fitting), extending significantly beyond the known current distribution (Figs. 1, 2, 3, 4, 5, 6, and 7). One distribution point from Argentina, associated with timber in transit (V. Klasmer, INTA Bariloche, pers. comm.), fell into a climatically arid region (Fig. 4; Fig. S4) modelled as unsuitable for *S. noctilio* persistence and was therefore removed from model validation. Only one other distribution point from the Metropolitan region of Chile (as reported by Poisson et al. 2016) fell into a climatically arid area (Fig. 4, Fig. S4) modelled as unsuitable for *S. noctilio* persistence. This distribution point falls within a grid with a GI_A of 12, indicating some potential for *S. noctilio* growth throughout the year, and was surrounded by marginally suitable climatic grids to the north (just 9.1 km away), north-east, east and south-east of this grid (Fig. 4). It may also be a misrepresented data point as it could be reflecting the centroid of the region, rather than the actual locality at which *S. noctilio* was detected.

In Australia, the known distribution of *S. noctilio* was found to fall predominantly into areas of moderate to highly favourable climatic suitability, with only nine locations (1.3%, 9/678) in western Tasmania falling into areas of marginally suitable climates (Fig. 5b). Distribution points located in pine plantations of the Mesopotamian region of north-east Argentina, all of which are regarded as infested (Klasmer and Botto 2012), were all projected to be in areas of moderate to highly favourable climatic suitability (Fig. 4a). All distribution points within the Argentinian Patagonian Andes fell into predominantly marginally suitable climatic areas, while the adjoining area in Chile fell predominantly into areas predicted to be of moderate climatic suitability (Fig. 4b). All regions infested with *S. noctilio* in Brazil and Uruguay fell into predominantly highly favourable climatic suitability areas (Fig. 4a). Distribution data points located in China fell predominantly into areas of moderate (23.5%, 4/17) and high (70.6%, 12/17) suitability (Fig. 7). Almost all validation distribution points from New Zealand (94.1%, 16/17) (Fig. 3b) and South Africa (99.3%, 144/145) (Fig. 2b) fell into areas of high suitability, with the single remaining points from both countries falling into areas of moderate suitability.

Relating potential geographical range of *Sirex noctilio* to host distribution

The majority of pine plantations in the southern hemisphere (89% suitable, Table 2, Figs. 2, 3, 4, and 5) and the vast majority of the native distribution of pines in the northern hemisphere (86% suitable, Table 2, Figs. 1, 6, and 7), as defined by Lantschner et al. (2017), occur in areas considered to be climatically suitable for *S. noctilio*. Softwood plantations in Australia (ABARES 2017) predominantly fell into areas projected to be of high and moderate climatic suitability for *S. noctilio*, with only 1.4% of softwood plantation projected to be in areas considered to be climatically unsuitable (Table 2, Fig. 5). All exotic forests (Landcare Research New Zealand Ltd 2015) in New Zealand were found to occur in areas considered climatically suitable for *S. noctilio*, comprised mostly of high and moderate climatic suitability envelopes (Table 2, Fig. 3b). Similarly, all commercial forests in South Africa (Institute for Commercial Forestry Research, unpublished data) were found to occur in areas considered climatically suitable for *S. noctilio*, comprised of predominantly high climatic suitability envelopes (Table 2, Fig. 2b).

Relating Ecoclimatic Index to *Sirex noctilio* impact

We identified no significant relationships between EI or GI_A and *S. noctilio* damage significance or distribution at the stand level, or the interaction of these variables with each other and decade of inspection in New Zealand (p values > 0.05 and confidence intervals all crossed 0 at the 95% confidence level in all

Table 2 Relating potential geographical range of *Sirex noctilio* to host distribution

Host distribution	Climatic suitability[a] (%)[b]			
	Unsuitable	Marginal	Moderate	High
Pine distribution[c]				
Northern Hemisphere (Native Pine)	14.0	40.3	31.6	14.2
Southern Hemisphere (Pine Plantations)	11.0	24.1	19.6	45.3
Australian Softwood Plantations[d]	1.4	11.0	29.1	58.5
New Zealand Exotic Forests[e]	–	12.6	37.7	49.7
South Africa Commercial Forests[f]	–	–	2.4	97.6

[a] Projection outputs are as those modelled using CLIMEX using 1961–1990 climate normals. Climatic suitability is classified as: unsuitable (EI = 0), marginally favourable (EI = 1–10), moderately favourable (EI = 11–20), and highly favourable (EI > 20)

[b] Host distributions were spatially intersected with the relevant EI estimated in CLIMEX for the 10′ grid cell that that location exists in using Arc GIS 10.3 (ESRI, Redlands CA), then presented as percentages of these areas falling into the four CLIMEX climate suitability envelopes

[c] As defined by Lantschner et al. (2017)

[d] ABARES (2017)

[e] Landcare Research New Zealand Ltd (2015)

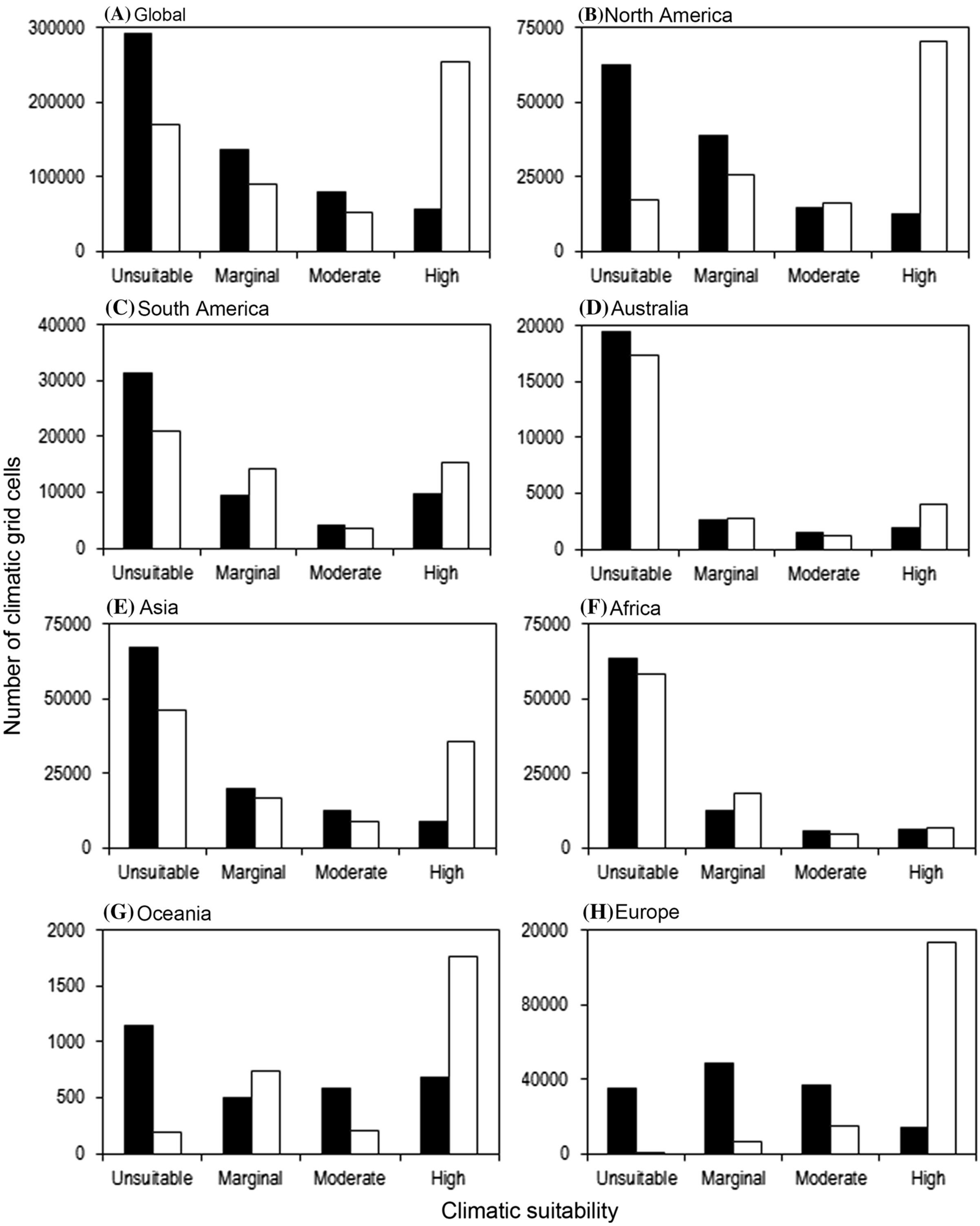
[f] Institute for Commercial Forestry Research, unpublished data

cases). EI and GI_A were found to be equivalent at all known distribution points, indicating that *S. noctilio* is not under a great amount of stress at these locations. *Sirex noctilio* was found to occur in areas with EIs ranging from 1 to 44 throughout New Zealand (Fig. 3). It was most frequently recorded in areas where the EI was greater than 10. Only 4.4% of the 1960–2009 distribution records (Fig. 3A) were located where the EI $\leq$ 10, 29.3% where the EI = 11–10 and 66.3% where EI > 20. All sites identified as having low to high damage significance occurred at and above the EI value of 10. Given this, EI was categorised by the classifications of Vera et al. (2002) to capture this result, and to allow for comparability between these models. Climatic suitability was therefore classified and projected as marginal (EI = 1–10), moderate (EI = 11–20) and highly favourable (EI > 20) for *S. noctilio* establishment and persistence.

Differences between CLIMEX models

Globally, the refitted model has significantly greater specificity. The area of risk of *S. noctilio* establishment according to the Carnegie et al. (2006) model was 22% greater than our model, with more than four times the amount of highly favourable climates projected (Figs. 8 and 9a). Regionally the difference of the projected suitable ranges between the models was greatest in North America (35.5%), followed by Oceania (excluding Australia; 32.9%), Europe (26%), Asia (19.2%), South America (18.8%), Australia (8.2%) and Africa (6.2%) (Fig. 9b–h).

In relation to model fit and validation, a much greater proportion of the distribution points gathered in this study fell into areas projected to be of high suitability in the Carnegie et al. (2006) model (99.1%, 2686/2711) compared to our model (72.2%, 1956/2711). The number of distribution points falling into moderate [0.4% of Carnegie et al. (2006) and 18.9% in our model] and marginal [0.3% of Carnegie et al. (2006) and 8.7% in our model] climatic suitability envelopes were similarly markedly different, with a more measured spread of potential risk projected and validated in our model. Only five distribution points (0.2%) (compared to 6 for our model), fell into areas considered climatically unsuitable in the Carnegie et al.(2006) model. Only three of the distribution points projected to exist in climatically unsuitable areas in our model were the same, two of the distribution points from South Africa that were specifically excluded from model fitting (with the third projected into an area of marginal suitability) and the transit detection from Argentina that was excluded from model validation (see above). The other two


(A) Global
300000
200000
100000
0
(B) North America
75000
50000
25000
0
(C) South America
40000
30000
20000
10000
0
(D) Australia
20000
15000
10000
5000
0
(E) Asia
75000
50000
25000
0
(F) Africa
75000
50000
25000
0
(G) Oceania
2000
1500
1000
500
0
(H) Europe
20000
80000
40000
0
Unsuitable
Marginal
Moderate
High
Number of climatic grid cells
Climatic suitability

◀**Fig. 9** Differences between the climatic suitability (Ecoclimatic Index) envelopes of the Ireland model (black bars) and Carnegie model (Carnegie et al. 2006) (white bars) for the potential distribution of *Sirex noctilio*. Projection outputs are as those modelled using CLIMEX using 1961–1990 climate normals. Climatic suitability is classified as: unsuitable (EI = 0), marginally favourable (EI = 1–10), moderately favourable (EI = 11–20), and highly favourable (EI > 20)

distribution points projected to fall into climatically unsuitable areas in the Carnegie et al. (2006) model were located in the south of Spain, are well established historical reference points from Kirk (1974) and Spradbery and Kirk (1978), and were used in our model development and projected as occurring in areas of moderate climatic suitability in our model. The Metropolitan region data point from Chile projected to exist in an area of unsuitable climate in our model (see above) was projected to exist in a marginal climate according to the Carnegie et al. (2006) model, while the Norwegian GBIF data point projected to exist in an area of unsuitable climate in our model (see above) was projected to exist in a highly suitable climate according to the Carnegie et al.(2006) model.

The parameters of our model presented in this paper and that of Carnegie et al. (2006) are shown in Table 1. The differences are a result of both interpretation and utilisation of different resources to inform parameter selection. We were able to source specific location data to define the cold stress limitations of *S. noctilio*, rather than relying on positive detections at the country level, while also making use of laboratory derived data. Carnegie et al. (2006) defined 8 climate response functions, with 22 individual parameters within these, while we only defined 6 climate response functions, with 17 individual parameters and an annual heat sum (Table 1). Of the 17 parameters that were included into both models, three remained the same in our new model: the lower soil moisture threshold for growth (SM0), the soil moisture threshold for dry stress (SMDS) and the heat stress accumulation rate (THHS). Carnegie et al. (2006) fitted parameters by defining a threshold EI value of 30 as indicating suitability for persistence. This does not accord with common practice in fitting CLIMEX models, nor with the User's Guide (Kriticos et al. 2015), where an EI value of 1 or greater indicates an ability to persist (during an average year at least). A consequence of this is that the EI maps of Carnegie et al. (2006) are distorted, with the known distribution of *S. noctilio* falling into only moderate and highly suitable climatic envelopes.

Discussion

The CLIMEX model developed in this paper suggests that *S. noctilio* could spread beyond its current global range, particularly onto susceptible amenity, native and plantation *Pinus* bordering on the newly invaded areas of north-eastern America and southern Queensland in Australia. While our model agrees broadly with previous modelling in Carnegie et al. (2006), the models differ considerably in their formulation and representation of potential invasion risk. Given the new information we have incorporated into our model, and more nuanced modelling approach, we believe our model is a more accurate representation of potential *S. noctilio* distribution and should be considered as the most reliable representation of climatic suitability risk to date. The parameters in the present model are better justified and are more parsimonious than the previous model. Further, the resulting model accords better with an expanded set of known distribution data.

Our model indicates that *S. noctilio* has spread to occupy the vast majority of its potential ecoclimatic niche, particularly in Australia, New Zealand, South Africa and South America, where almost all pine plantations, which are predominantly in favourable climates for *S. noctilio*, are already infested (Carnegie et al. 2006; Lantschner et al. 2014). Where suitable hosts are present and control measures and ecological competitors or constraints do not exist, it is likely that *S. noctilio* will continue to spread, particularly in areas projected to be climatically favourable in Australia and the Americas. The majority of host distributions assessed in this study (86–100%, Table 2) were predicted to be at some risk of *S. noctilio* establishment and persistence, with pine plantations in the southern hemisphere at considerable more risk than native pine plantations in the northern hemisphere (45.3% compared to 14.2% highly favourable climatic suitability). A major limitation of the host data we used in our study was the discrimination of suitable and susceptible hosts, which varies across plantations in the southern hemisphere (Lantschner and Corley 2015), is markedly different to the host susceptibility landscape in the newly invaded North American distribution in the northern hemisphere (Haavik et al. 2016, 2017) [and may be somewhat similar to host use patterns in the native range (Ayres et al. 2014)] and is complicated by complex interactions of biological control and other plant pest and pathogen interactions with the host (Nahrung et al. 2016b; Williams and Hajek 2017). Further work intersecting potential climatic risk with host availability and suitability may shed further light on the true area at risk of *S. noctilio* establishment and persistence globally.

It is crucial to manage *S. noctilio* using integrated pest management techniques. Outbreaks of *S. noctilio* historically follow particular abiotic stress events such as drought (Rawlings 1948), or occur as a result of accumulated stress, i.e. plant stress following failure to thin susceptible stands (Haugen et al. 1990). In this study we found no correlation between measures of damage significance of plantation infestations of *S. noctilio* in New Zealand and related climatic suitability (EI), other than infestations generally occurring at EIs greater than 10. Given that timely silvicultural regimes to reduce tree stress in susceptible stands, combined with biological control methods are argued to be one of the most effective means of reducing the severity of outbreaks and impact of *S. noctilio* (Madden 1975; Neumann and Minko 1981), and that these management regimes have been implemented for some time in New Zealand with success (Bain et al. 2012), a lack of correlation between severity and EI or GI_A is not surprising. This has been further supported by a recent population dynamics modelling exercise, which demonstrated how life history traits of *S. noctilio* may explain outbreaks independently of environmental factors (Aparicio et al. 2013). While Aparicio et al. (2013) did not explicitly test the effects of environmental or climatic factors in their model, they concede that external factors such as climate and weather (extreme weather events in particular) may be a major determinant of large scale outbreak synchronization for forest pests such as *S. noctilio* by influencing and increasing tree susceptibility. Therefore, we would expect that *S. noctilio* incidence and severity should appear fairly random within our climatic suitability envelopes (as observed in our data analysis), as the host response is confounded by these strongly influential patterns of anthropogenic stand management and heterogeneity. Mapping of marginal areas for pine growth and overlaying of such maps with the one presented here may help to prioritise areas for immediate management concern or those areas on which pines should not be planted, in order to reduce outbreak severity.

The CLIMEX EI estimates the potential for population persistence and the GI_A estimates the potential for population growth respectively at each location *with respect to climate*. The factors that influence a species persistence and abundance operate in a hierarchical manner, with climate operating at the broadest level (Allen and Starr 1982). Because of co-evolution, pests need to have ranges that overlap their hosts, and so their climatic preferences also need to overlap. However, within that constraint, the climatic conditions that favour pest impacts do not need to coincide with climatic favourability for pest abundance. In the case of *S. noctilio*, the insect must overcome plant defences before it can oviposit and the larvae thrive. We tested whether we could discern a positive relationship between the favourability of climatic conditions for population growth for *S. noctilio* and its impacts on host trees. Our inability to discern any compelling relationship suggests that within the overlapping range of the *Pinus* tree hosts and *S. noctilio*, the patterns of tree stress are not related to climate factors (as distinct from weather events, which have been shown to induce tree stress as a precursor to *S. noctilio* attack, as noted above). This contrasts with previous findings for *T. pityocampa* (Kriticos et al. 2013). Further analysis considering more detailed and consistent *S. noctilio* impact and severity datasets (such as that proposed by Krivak-Tetley et al. (2016)) which take into account relative host susceptibility, stand age, management and other conditions conducive to *S. noctilio* attack may be able to expose the factors that exacerbate or mitigate *S. noctilio* impacts within its potential distribution, as indicated by the CLIMEX EI.

In both the subtropical regions of southern Queensland in Australia and central Brazil it is somewhat surprising that *S. noctilio* has not spread further, despite ample time to do so based on average spread rates and ample bridgeheads (Figs. 4 and 5) (Carnegie et al. 2005; Eldridge and Taylor 1989b; Lantschner et al. 2014; Nahrung et al. 2016a). Indeed, it is remarkable that the spread of *S. noctilio* has been restricted in the exotic range to latitudes lower than 20° and in the native range to latitudes lower than

40°N (Figs. 1, 2, 3, 4, 5, 6, and 7). In the native Palearctic range, suitable contiguous host availability may be the primary limiting factor for the limited spread of the wasp beyond these latitudes, with native pine forests in these subtropical and tropical Northern African and Asian latitudes separated by great distances from their temperate pine relatives (Figs. 1, 2a, and 7). However, in the exotic range, these available host barriers to spread largely do not exist, particularly on the east coast of Australia and in Brazil where pine plantations are largely contiguous to approximately 25°S in eastern Australia (Fig. 5a) and close to 10°S in Brazil (Fig. 4a) (Lantschner et al. 2017). While the wasp has readily established and spread in pine plantations in the southern hemisphere at latitudes between 20 and 40°S, to the best of our knowledge the wasp has not spread further than approximately 20°S in Brazil (Fig. 4a) and 28°S in Australia (Fig. 5b). Whether this is an artefact of the wasp reaching the limits of its climatic niche or a complex reaction to one or many factors (and potentially their interactions) such as less suitable hosts or reduced host availability and connectivity, presence of biotic competitors such as blue stain fungi and/or other wood borers, presence and performance of natural enemies and biological control organisms, or anthropogenic management factors at these sites (all of which may be exacerbated or mitigated by climatic factors) (Hurley et al. 2012a, b; Lantschner et al. 2014; Nahrung et al. 2016a; Yousuf et al. 2014), remains to be thoroughly interrogated. In further support of what we stated previously, analysis of these factors in a climatic and pest severity context would be beneficial to disentangle complex biotic and abiotic relationships related to the wasp's success, with a view to contribute to better monitoring, management and prioritisation of resources for managing *S. noctilio* at these invasion fronts.

In North America we expect *S. noctilio* to spread some distance from where it has been found around the Great Lakes. Risk models published by the USFS (United States Forest Service) projected the most susceptible areas to be in the south-east of the country, based upon likelihoods of introduction and establishment on suitable hosts (FHTET 2006; Gandhi et al. 2011) (Fig. S7B). Our model differs most significantly from that of the FHTET models in the projected reduced risk of *S. noctilio* establishment, particularly for the north-east to mid-west regions of the USA (Fig. S7A and S7B). Given *S. noctilio*'s spread into and around the Great Lakes area of Canada and the USA, we argue that our model is likely a more accurate estimate of potential risk because it is not confounded by entry pathway considerations. Examination of the entry risk model produced by the USFS indicates that these regions are considered to be at a high risk of entry potential, and that the differences between our models may lie primarily in the assessment of establishment potential on suitable hosts (FHTET 2006; Gandhi et al. 2011) (Fig. S7C).

The impact in the north-east of the USA and eastern Canada may be great if *S. noctilio* spreads to homogenous stands of *Pinus* spp. similar to the environments where it has caused widespread tree mortality in the southern hemisphere, or into stands or individual trees of exotic *Pinus* planted on lands marginally suitable for tree growth. In the case that the 20° latitude meridian is identified as a potential barrier to *S. noctilio* spread (as discussed above), then independent of host suitability and other biotic factors there is certainly plenty of room for the wasp to spread within contiguous forests of native pines in North America, which effectively end prior to 20°N in southern Florida. Of course, should the wasp first spread west and then south, this would provide another natural experiment to test if the 20° meridian is indeed a spread limiting factor for the wasp. The potential impact of *S. noctilio* in North America is likely to be moderated however by the heterogeneous forested landscapes with diverse species compositions and management practices (Dodds and de Groot 2012). Native populations of *Pinus* are likely to have broader genetic diversity, which may support greater population level resistance to *S. noctilio*. These North American native *Pinus* species already have their own suite of native siricids (Schiff et al. 2006) and associated natural enemies. Coevolution may have resulted in the trees developing greater resistance mechanisms to fend off *S. noctilio* outbreaks (Gandhi et al. 2011). Whilst the native siricids may provide competition for *S. noctilio*, they may be having similar negative impacts on *Pinus* hosts or their impacts may be mitigated by their own suites of natural enemies keeping their populations in check. Given the large number of native siricids, misidentification of *S. noctilio* is also a concern for managing the invasion, as *S. noctilio* may spread without accurate detection (Schiff et al. 2006; Wilson and Schiff 2010).

While it is unclear whether the initial lack of reports of *S. noctilio* in China was due to a failure of detection or reporting processes, or *S. noctilio* spreading only slowly within this region (Carnegie et al. 2006), the wasp now appears to be spreading from an initial site in north-eastern China in 2015 (Li et al. 2015) to other forests in the area (Sun et al. 2016). Siricids exist as native components of the forest fauna in China (Wu 1985; Xiao 1992), and it is possible that this suite of other siricids may compete with *S. noctilio*, leading to exclusion or control of populations at levels that are difficult to detect. Our model suggests that large areas of eastern China are climatically favourable for *S. noctilio* establishment and persistence, with all distribution records falling into areas projected to be of moderate and high climatic suitability (Fig. 7). Using the results of their model, Carnegie et al. (2006) argued that *S. noctilio* may have had many opportunities to spread to China given the climatically suitable areas it could spread through, but that it may be limited by the natural barrier of the high elevation Gobi desert, which has few host trees and an inhospitable climate. Given the current known distribution of *S. noctilio*, available suitable hosts may be a limiting factor to *S noctilio* spread throughout China and the Asian region (Fig. 7). The wasp may spread further and more readily however, should large scale plantings in climatically suitable areas for *S. noctilio* establishment and persistence (and potentially most importantly north of the 20°N meridian, as discussed above) be undertaken. Our model was more conservative when identifying climatically suitable areas in China when compared to Carnegie et al. (2006), and given that marginally suitable climates in our model were rarely infested in Australia or New Zealand (Figs. 3 and 5b), it may also be likely that *S. noctilio*'s spread in China is limited by climatic conditions, or because they are outcompeted by other siricids that are better adapted to these climates.

Pest risk maps are important visual representations of potential risk for use by policy makers and managers to plan biosecurity efforts to contain pest spread (Baker et al. 2012; Venette et al. 2010). In comparison to Carnegie et al. (2006), our model projects a much more conservative global potential distribution for *S. noctilio*. The Carnegie et al. (2006) model overestimates the potential risk. Basing management plans on that model could have spread surveillance effort too widely. By attaching higher EIs to areas known to have *S. noctilio* in exotic locations, we believe Carnegie et al. (2006) overestimated the area at risk and misconstrued the underlying climatic parameters defining the pest's ecoclimatic niche in the process.

We strove to only use parameters in this model that we felt we could comfortably estimate from the available evidence. For this reason, wet stress and hot-dry stress were removed from the model, but could easily be reincorporated later should reliable data become available. Heat stress limits of *S. noctilio* are currently being studied in Southeast Queensland and have been highlighted as a key knowledge gap in managing *S. noctilio* effectively in the sub-tropics (Carnegie and Bashford 2012). Once this data is readily available, these parameters may be adjusted accordingly. So far, unpublished reports indicate that constant temperatures of 30 °C *in planta* do not kill *S. noctilio* (Carnegie and Bashford 2012), which accords with our current model formulation. Loss of fitness of emerging *S. noctilio* larvae has been found above these temperatures, similar to results obtained by Madden (1981), who reported on reduced fitness at temperatures of 33.5 °C (it is important to note however, that Madden did not test above this temperature). As reported in our methods, temperatures above 36 °C, have been found to be detrimental to the symbiotic wood-decay fungus, *A. areolatum* (King 1966; M. Ramsden, HQPlantations, unpublished data). Given the uncertainty of this high temperature data, we remain confident that accumulation of heat stress above 33 °C at the rate described is justified, and conservative enough to allow for a reasonable estimation of the ecoclimatic envelope of *S. noctilio*. We recognise that this uncertainty highlights an important area of future research for *S. noctilio*, in order to plan for management and control of the wood wasp in the newly invaded sub-tropics of southern Queensland and South America, which will have potentially important implications in non-invaded regions such as the south-eastern USA.

While the continued spread of *S. noctilio* confirms it as a prevalent biosecurity threat to non-infested pine-growing regions, the results of our model suggest that the pest may have reached the limits of its spread in other locations. Opportunities exist to plan future plantations and biological control efforts using the results of our model, particularly if potential distribution models of biological control agents were used in concert with our model to apply the best method in either the riskiest locations or at the margins of such locations to prevent additional spread.

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