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Predicting North American Scolytinae invasions in the Southern Hemisphere

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Abstract. Scolytinae species are recognized as one of the most important tree mortality agents in coniferous forests worldwide, and many are known invaders because they are easily transported in wood products. Nonnative trees planted in novel habitats often exhibit exceptional growth, in part because they escape herbivore (such as Scolytinae) pressure from their native range. Increasing accidental introductions of forest pest species as a consequence of international trade, however, is expected to diminish enemy release of nonnative forest trees. In this context, there is need to characterize patterns of forest herbivore species invasion risks at global scales. In this study, we analyze the establishment potential of 64 North American Scolytinae species in the Southern Hemisphere. We use climate-based ecological niche models (MaxEnt) to spatially define the potential distribution of these Scolytinae species in regions of the Southern Hemisphere were pines are planted. Our model predicts that all of the pine-growing regions of the Southern Hemisphere are capable of supporting some species of North American Scolytinae, but there are certain "hotspot" regions, southeastern Argentina, Bolivia, Chile, Peru and southwestern Australia, that appear to be suitable for a particularly large number of species. The species with the highest predicted risk of establishment were *Dendroctonus valens*, *Xyleborus intrusus*, *Hylastes tenuis*, *Ips grandicollis*, *Gnathotrichus sulcatus*, and *Ips calligraphus.* Given that global commerce is anticipated to continue to increase, we can expect that more Scolytinae species will continue to establish outside their range. Our results provide information useful for identifying a global list of potential invasive species in pine plantations, and may assist in the design of comprehensive strategies aimed at reducing pest establishment in Southern Hemisphere forest plantations.

Key words: ambrosia beetles; bark beetles; climatic niche models; ecological niche models; enemy release; exotic species; forest pests; invasion; Maxent; pine afforestation.

Introduction

Nonnative plants introduced in novel habitats often exhibit elevated performance compared to that in their native range, i.e., they grow more vigorously and are more competitive (Blossey and Notzold 1995, Adams et al. 2009). A commonly accepted mechanism to explain this phenomenon is the enemy release hypothesis, which posits that exotic plants leave behind many diseases and herbivores when they are transferred to a nonnative range, resulting in a rapid increase in distribution and abundance (Keane and Crawley 2002). This phenomenon has been widely exploited in extensive commercial forestry plantations of nonnative trees. In the Southern Hemisphere, the extensive planting of exotic species, particularly *Pinus* and *Eucalyptus*, has dramatically increased during the last century, because of their exceptional growth and performance in new habitats (Sedjo 1999). These plantations are largely established for the production of timber, pulp, or fuel wood, and typically consist of intensively managed, even aged, and regularly spaced stands of a single-tree species usually with low levels of genetic variation (FAO 2010).

As international trade increases over time, however, enemy-release of nonnative forest plantations is expected to diminish. This is because the number of accidental introductions of their natural enemies, such as herbivorous insects and pathogens, is likely to increase (Hulme 2009, Roy et al. 2014). Over the past few decades, establishment of exotic forest pests has increased in planted forests located in various parts of the world, resulting in significant economic loses (Wingfield et al. 2015). Several studies have documented how globalization is driving the spread of forest pests into new territories and threatening forest sustainability (Brockerhoff et al. 2006, Aukema et al. 2010). Well-known examples of invasive pests that have globally spread and caused significant economic losses in Southern Hemisphere forest plantations include the Sirex woodwasp, *Sirex noctilio* (Slippers et al. 2015, Lantschner et al. 2014); the bronze bug, *Thaumastocoris*

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peregrinus; and the Ecualyptus weevil, *Gonipterus scutellatus* (Wingfield et al. 2008).

True bark beetles (Coleoptera: Curculionidae, Scolytinae) are a large and diverse group of insects commonly recognized as one of the most important tree mortality agents in coniferous forests worldwide (Raffa et al. 2008, Kirkendall and Faccoli 2010). This is an important group among invasive forest species because they are easily transported in raw wood, wood products, and wood packaging materials (Brockerhoff et al. 2006, 2013). Consequently, bark beetles hold great potential to exert heavy impacts on exotic forest plantations. Some species have already invaded planted forests in various parts of the world, i.e., *Dendroctonus valens* and *Ips grandicollis* in pine forests of China (Kelley and Farrell 1998) and Australia (Morgan 1989), respectively, but arrivals are increasing worldwide, and additional invasions are likely to occur in the future (Brockerhoff et al. 2006).

Predicting and understanding the processes driving invasions during each of the three dominant invasion phases (i.e., arrival, establishment, and spread) is critical to the assessment of risks and the development of strategies for minimizing future negative impacts (Liebhold and Tobin 2008). Furthermore, recent studies have highlighted the importance of focusing on the management of forest pest invasions from a global level, rather than individual countries approaching the problem independently (Garnas et al. 2012, Wingfield et al. 2015). Thus, there is a need to characterize patterns of forest pest species invasion risks at a global scale rather than addressing only localized areas.

In this study, we analyze the establishment potential of North American Scolytinae species in pine plantation regions of the Southern Hemisphere. Establishment of introduced organisms is affected by different factors such as their life history traits, propagule pressure, and habitat characteristics of the novel environment (Liebhold and Tobin 2008). However, climate is known to be a key factor limiting bark beetle growth potential (Bentz et al. 2010). Several studies have demonstrated direct influence of climate on bark beetle population dynamics, particularly through the influence of temperature on life-history traits such as developmental timing, cold tolerance and flight activity (Aukema et al. 2005, Jönsson et al. 2009, Bentz et al. 2010).

Considering this strong relationship of bark beetle population dynamics with climatic conditions, we use climate-based ecological niche models to spatially define the potential distribution of North American Scolytinae species in the Southern Hemisphere, based on the climatic correlations explaining native distributions. Additionally, since most of the planted pine species in the Southern Hemisphere are native to North America (i.e., *Pinus radiata*, *P. ellioti*, *P. taeda*, *P. patula*, *P. ponderosa*, *P. contorta*), we focused on the North American bark beetle assemblage as potential sources of invading forest pests. It should be noted however that North American species represent just a fraction of the pool of species capable of invading the Sothern Hemisphere since Europe and Asia also represent sources of invading conifer-feeding Scolytinae species.

Methods

North American bark beetle occurrence data and susceptible hosts in the Southern Hemisphere

We selected 64 species of bark and ambrosia beetles (Coleoptera: Scolytinae) that are both native to North America and specialists using *Pinus* as hosts. The beetle species where grouped into five guilds based upon taxonomic and life history similarity: (1) all North American *Ips* species (18 species; larvae of these species feed in boles and branches), (2) all North American *Dendroctonus* species (11 species; larvae feed in boles), (3) a subset of North American *Hylastes* species (10 species; larvae feed in roots), (4) a subset of North American *Pityophthorus* species (13 species; larvae feed in branches and twigs), and (5) a subset of North American ambrosia beetles in the genera *Gnathotrichus*, *Trypodendron*, and *Xyleborus* (12 species; host-specific ambrosia beetles).

The second author assembled from four sources a large database of occurrence point data for bark and ambrosia beetles in North America and Central America. First, some records came from regional monographs and catalogs (Bright 1981, Wood 1982, Wood and Bright 1992*a*, *b*). Second, some occurrence data originated from other taxonomic literature and checklists published after 1982. A third source was specimens collected by or seen by the second author in various collections, mostly unpublished. Finally, a large number of records were taken from the Early Detection Rapid Response (EDRR) trapping program conducted by the U.S. Forest Service from 2006 to 2014 (Rabaglia et al. 2008). Most collection records were georeferenced and maps for each species can be viewed (*available online*).[6] The website also includes a complete list of all publications from which records were taken (list *available online*).[7]

Prior to using these collection records for climatic envelope modeling, we created a more spatially uniform dispersion of sampling locations by "thinning" collection records that were highly aggregated. Such aggregated collection records can introduce biases in climatic envelope models (Veloz 2009). To accomplish this thinning, we buffered collection point locations by 5′ distance, removing adjacent occurrence points.

The geographical distribution of susceptible host pines in each country of the Southern Hemisphere was assembled from various bibliographic sources (Table 1). We used this information to compile a composite map of the entire region delineating the location of *Pinus* spp. plantations (Fig. 1). This map was then used to mask the potential distributions of each bark beetle generated from climate models.

Environmental variables

We considered climate conditions as potential predictors of the distribution of each bark beetle species. We used 19

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[6] http://www.barkbeetles.info

[7] http://www.barkbeetles.info/articles_w_records.php

TABLE 1. Description of countries and regions with *Pinus* spp. plantations in the Southern Hemisphere, and the major planted species in each (see Fig. 1).

Continent, country, and region	Major planted *Pinus* species	Area (squared degrees)	Source
South America			
Argentina, NE	*P. ellioti*, *P. taeda*	24	MAGyP (2011)
Argentina, NW	*P. ellioti*, *P. taeda*	3	MAGyP (2011)
Argentina, SW	*P. ponderosa*, *P. contorta*	8	MAGyP (2011)
Bolivia	*P. radiata*	3	López (2004)
Brazil, N	*P. oocarpa*, *P. caribaea*	39	BRACELPA (2004)
Brazil, S	*P. taeda*, *P. elliottii*	202	BRACELPA (2004)
Chile	*P. radiata*	16	INFOR (2014)
Colombia†	*P. patula*, *P. caribaea*, *P. oocarpa*	8	Gómez et al. (2012)
Ecuador	*P. radiata*, *P. patula*	4	García (2005)
Paraguay	*P. ellioti*, *P. taeda*	3	Paraguay (2009)
Peru	*P. patula*, *P. radiata*	2	García (2005)
Uruguay	*P. taeda*, *P. elliottii*	6	FAO (2002)
Venezuela†	*P. caribaea*	8	García (2005)
Oceana			
Australia, NE	*P. taeda*, *P. elliottii*	19	Australia (2014)
Australia, SE	*P. radiata*, *P. pinaster*	34	Australia (2014)
Australia, SW	*P. radiata*	5	Australia (2014)
New Zealand	*P. radiata*	24	Thompson et al. (2003)
Africa			
Angola	*P. patula*, *P. elliottii*	15	FAO (2010)
Kenya	*P. caribea*, *P. oocarpa*, *P. patula*	23	Mathu and Ng'ethe (2011)
Madagascar	*P. kesiya*, *P. patula*	7	WAVES (2015)
Malawi	*P. patula*	10	Malawi (2002)
Mozambique	*P. patula*, *P. elliottii*	34	FAO (2010)
South Africa, NE + Lesotho	*P. patula*, *P. elliottii*, *P. taeda*	34	DAFF (2009)
South Africa, W	*P. radiata*, *P. pinaster*	6	DAFF (2009)
Tanzania	*P. patula*, *P. elliottii*, *P. caribaea*	67	Ngaga (2011)
Uganda†	*P. caribaea*	2	Alder et al. (2003)
Zambia	*P. kesiya*, *P. oocarpa*	36	Sekeli and Phiri (2002)
Zimbabwe	*P. patula*, *P. taeda*, *P. elliottii*	3	Mabugu et al. (1998)

Notes: Abbreviations are N, north; NE, northeast; NW, northwest; S, south; SE, southeast; SW, southwest; W, west.
†Large portions of Venezuela, Colombia, and Uganda are in the Northern Hemisphere.

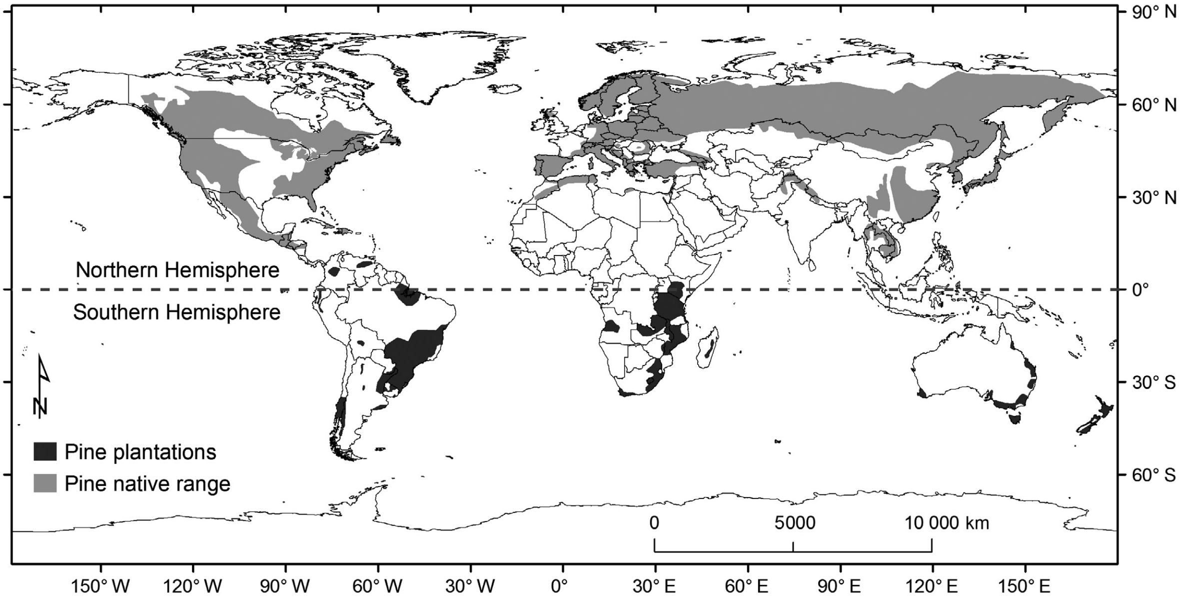

FIG. 1. Native range of pines, and distribution of pine plantations in the Southern Hemisphere.

bioclimatic variables acquired from the WorldClim database v1.4 (Hijmans et al. 2005). WorldClim data are interpolated climate surfaces for global land areas, and include surfaces for estimated monthly precipitation, and mean, minimum, and maximum temperature. Input data were obtained from weather stations restricted to records spanning 1950–2000 (Hijmans et al. 2005). Various bioclimatic variables are derived from the monthly temperature and rainfall values in order to generate more biologically meaningful variables. These include annual values (e.g., mean annual temperature, annual precipitation) seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest months, and precipitation of the wet and dry quarters) (Booth et al. 2014). We used WorldClim data grids of estimates at a resolution of 10′.

Models and data analyses

We predicted the potential distribution of the bark beetles species in the Southern Hemisphere, using the Maxent software v.3.3.1, which implements the maximum entropy algorithm for modeling species distributions with presence-only data (Phillips et al. 2004; software *available online*).[8] Maxent uses known occurrences of a species together with predictor environment variables, to quantify the species' ecological niche in the examined environmental dimensions. The Maxent model is nonlinear, nonparametric, and not sensitive to multicollinearity.

We generated minimum convex polygons (MCPs) around all occurrence points for all species combined to define the area for training the Maxent model. In this way, the background points for the Maxent model were drawn from within the MCPs to improve model performance (VanDerWal et al. 2009). For each species, we randomly divided species location data into two groups, each with 50% of samples; one subset was used to train models and the other subset was withheld for model validation. Each analysis consisted of 10 replicates using a different set of randomly drawn presence points for training and validating the model. The 10 model output replicates were averaged for a single model for each species. We used the area under the receiver-operating characteristic (ROC) curve (AUC) to assess the accuracy of the model. The spatial resolution of the output model grid was the same as that of the input environmental variables (10′).

To estimate the potential geographical distribution of each Scolytinae species in the pine-growing regions of the Southern Hemisphere, we designated a threshold probability to define habitat and non-habitat, such that probability values derived from Maxent models above that threshold were designated as suitable, while values at or below that threshold were designated as unsuitable. We used "equal training sensitivity and specificity logistic threshold" for each species to convert the continuous probability of occurrence maps from Maxent to a binary habitat/non-habitat map.

In order to identify groups of species with similar climatic requirements, we used nonmetric multidimensional scaling (NMDS) ordination to characterize the relationship among the potential distributions of the bark beetle species in the pine plantation zones of the Southern Hemisphere. NMDS is a robust unconstrained ordination method that makes no underlying assumptions about normality or linearity of the underlying data (Ludwig and Reynolds 1988), and is very effective in summarizing data into fewer dimensions (Legendre and Legendre 1998). NMDS was performed with the function metaMDS of the vegan library (Oksanen et al. 2006), in the statistical software R 3.0.2 (R Core Team 2016). For the ordination, we used the mean probability value (obtained from Maxent models) of each species in each 10′ grid cell located in Southern Hemisphere pine plantation regions (23257 cells). The NMDS ordination was based on a Bray-Curtis distance coefficient matrix (Legendre and Legendre 1998).

NMDS results were then mapped by assigning a color to each grid cell according to its position in the two-dimensional ordination space. We mapped the first two axes of the results, and performed an "Iso Cluster" clustering of these two grids. These analyses were performed using ArcGIS 9.3 (ESRI, Redlands, California, USA). The Iso Cluster Unsupervised Classification tool automatically finds the clusters in a raster and outputs a classified raster. The tool uses an iterative clustering procedure, also known as the migrating means technique, to find the natural grouping of cells. The algorithm separates each cell into one of these cluster/groupings by calculating an arbitrary mean for each and assigning a cell to the most suitable cluster based on the shortest Euclidean distance. The resulting signature file was used as the input to a Maximum Likelihood Classification that produced an unsupervised classification raster (Srivastava et al. 2014). This tool uses the variance and covariance of the class signature when assigning each cell to one of the classes. With the assumption that the distribution of a class sample is normal, a class can be characterized by the mean vector and the covariance matrix. The statistical probability is computed for each class to determine the membership of cells to a class, and each cell is assigned to the class to which it has the highest probability of being a member.

In order to rank species according to their overall likelihood of establishment, we created an index that we call the "Index of Establishment." This index accounts for both propagule pressure and habitat invisibility by. This was accomplished by multiplying propagule pressure, quantified by relative abundance in the species' native range (100 × original number of observations represented by the species/total number of observations) by habitat invasibility, quantified by the percentage of the area with pine plantations in the Southern Hemisphere where each species is predicted to establish. Though such an index has never been suggested in previous studies, we developed it here based on what we considered the most relevant

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[8] http://www.cs.princeton.edu/~schapire/maxent

available variables (environmental suitability and propagule pressure) to predict overall establishment risk.

Results

The Maxent models performed well for all the analyzed species, with average test AUC between 0.87 and 0.99 (see supporting information). Although each of the 19 bioclimatic variables used to predict potential distribution of the Scolytinae species in pine plantations regions of the Southern Hemisphere contributed differently for each species, in general, annual mean temperature (BIO1), isothermality (mean diurnal range, temperature annual range, BIO3), temperature seasonality (standard deviation, BIO4), mean temperature of the coldest quarter (BIO11), and precipitation of the warmest quarter (BIO16) showed the greatest contributions to the Maxent models (with mean contributions of 8.4%, 10.1%, 10.0%, 11.3%, and 7.9%, respectively; see Data S1: Table S1).

Predicted distributions for individual pine feeding Scolytinae species in pine plantation regions of the Southern Hemisphere are shown in Appendix S1: Fig. S1. The models predicted a likelihood that the climatic conditions allow each of the analyzed Scolytinae species to survive and reproduce in at least some of the pine plantations zones in the Southern Hemisphere, except for *Ips perroti,* which was not predicted to occur in any of the regions. Predicted ranges for each species varied from 0% to 68.9% of the total area of all regions (Table 2). The potential richness of these species varied among regions and among species groups (Table 3, Fig. 2). The regions with the highest median and 95th percentile total number of predicted species were southeast Argentina, Bolivia, Chile, Peru, Ecuador, Kenya, and southwest Australia, while the regions with the lowest predicted number of species were northeast Argentina, northern Brazil, Paraguay, and Mozambique (Table 3, Fig. 2; Data S1: Table S1).

Predicted numbers of *Ips* species were highest in southwest Argentina, Chile, Bolivia, southwest Australia, west and northeast South Africa, and Lesotho. The highest numbers of *Dendroctonus* species were predicted in Kenya, Uganda, Colombia, Ecuador, and Peru. The highest predicted numbers of *Hylastes* species were in southwest and southeast Australia, southern Argentina, Chile, and western South Africa. The highest predicted numbers of *Pityophthorus* species were in southern Argentina, Bolivia, and Peru; in the case of ambrosia beetles, the highest predicted numbers of species were in Bolivia, Chile, Peru, and Kenya (Appendix S2: Fig. S2).

The species with the highest Index of establishment risk in pine plantations of the Southern Hemisphere were *Dendroctonus valens*, *Xyleborus intrusus*, *Hylastes tenuis*, *Ips grandicollis*, *Gnathotrichus sulcatus*, and *Ips calligraphus* (Fig. 3). This index accounts both for habitat invasibility, based upon the predicted percentage of the pine plantation areas where the species can potentially establish, and propagule pressure, which is based on the species' abundance in their native ranges.

NMDS ordination showed an acceptable stress value of 0.154. Based on the Maximum Likelihood Classification of the NMDS axes, we classified pine plantation regions in the Southern Hemisphere into five groups based on their predicted species distributions (Fig. 4A). Several groups of Scolytinae species that are predicted to have similar potential distributions in Southern Hemisphere pine plantations can be identified in the ordination (Fig. 4B). Classes show a latitudinal pattern reflecting climatic similarity, with regions of similar latitudes exhibiting similar predicted invading Scolytinae assemblages.

Discussion

Given that rates of global commerce are anticipated to continue to increase, we expect that more Scolytinae species will continue to establish outside their native ranges, including locations in the Southern Hemisphere. New phytosanitary standards for wood packaging material (ISPM-15) appear to be reducing rates of movement of insects such as Scolytinae in wood packing material, but they are apparently less than 50% effective, so it is likely that this pathway will continue to facilitate new invasions (Haack et al. 2014). As a consequence, the implementation of early detection systems for alien bark- and wood-boring species may be advisable in order to facilitate eradication of these species before they become established. However, due to limited resources for such surveillance systems, it may be necessary to identify which species may be most likely to establish in specific regions and use this information to target surveillance efforts (Rassati et al. 2015).

Our model predicts that all of the pine-growing regions of the Southern Hemisphere are capable of supporting some species of North American Scolytinae, but certain regions appear to be suitable for a particularly large number of species (Table 2, Fig. 2). Such regions that are "hotspots" for Scolytinae invasions include southeast Argentina, Bolivia, Chile, Peru, Ecuador, Kenya, and southwest Australia. Table 2 suggests that, according to our climate-based models, heterogeneity in predicted invasive Scolytinae species richness is similar among all five species taxonomic groups indicating that there are no distinct differences in the climatic requirements among these groups. The NMDS analysis did identify groups of species with similar climatic requirements (Fig. 4), however these groups each include mixtures of species from various Scolytinae taxa.

The fact that North American pines are grown successfully in the Southern Hemisphere indicates that in a broad sense these regions are climatically similar to pine-growing regions of North America. However, the predicted hotspots for Scolytinae invasions must be particularly similar to specific North American climates. In South America, the predicted hotspots are located across the Andes mountain chain in South America, Kenya's highlands (between 1500 and 2500 m above sea level) in Africa, and in the Australian Alps in Oceania, which indicates that mountainous areas in the Southern

TABLE 2. Species of North American pine-feeding Scolytinae included in the analysis.

Group	Species	ID no.	Obs O	Obs R	PASH (%)	IER
1	*Ips apache*	1	30	26	64.8	17.7
1	*Ips avulsus*	2	201	154	12.8	23.4
1	*Ips bonanseai*	3	46	32	52.3	22.0
1	*Ips calligraphus*	4	414	329	17.3	65.5
1	*Ips confusus*	5	76	73	2.1	1.5
1	*Ips cribricollis*	6	62	48	39.4	22.3
1	*Ips emarginatus*	7	59	58	5.0	2.7
1	*Ips grandicollis*	8	837	625	10.2	78.1
1	*Ips hoppingi*	9	17	15	37.4	5.8
1	*Ips integer*	10	166	145	15.0	22.7
1	*Ips knausi*	11	29	26	4.3	1.1
1	*Ips lecontei*	12	17	17	29.5	4.6
1	*Ips montanus*	13	49	43	4.6	2.1
1	*Ips paraconfusus*	14	85	67	5.0	3.8
1	*Ips perroti*	15	33	30	0.0	0.0
1	*Ips pini*	16	661	525	0.5	3.3
1	*Ips plastographus*	17	55	51	7.7	3.8
1	*Ips woodi*	18	14	13	5.0	0.6
2	*Dendroctonus adjunctus*	19	85	66	41.6	32.3
2	*Dendroctonus approximatus*	20	72	60	41.6	27.3
2	*Dendroctonus brevicomis*	21	231	191	3.3	7.0
2	*Dendroctonus frontalis*	22	104	83	26.2	24.9
2	*Dendroctonus jeffreyi*	23	37	34	1.3	0.4
2	*Dendroctonus mexicanus*	24	61	39	44.5	24.7
2	*Dendroctonus murrayanae*	25	44	42	0.2	0.1
2	*Dendroctonus parallelocollis*	26	25	19	62.8	14.3
2	*Dendroctonus ponderosae*	27	322	286	4.1	12.1
2	*Dendroctonus terebrans*	28	456	304	8.5	35.2
2	*Dendroctonus valens*	29	803	658	24.1	176.6
3	*Hylastes flohri*	30	14	11	31.5	4.0
3	*Hylastes fulgidus*	31	53	14	68.9	33.3
3	*Hylastes gracilis*	32	222	196	12.4	25.2
3	*Hylastes longicollis*	33	49	42	7.8	3.5
3	*Hylastes macer*	34	213	178	4.4	8.5
3	*Hylastes nigrinus*	35	209	184	8.8	16.8
3	*Hylastes porculus*	36	620	456	0.7	3.9
3	*Hylastes ruber*	37	51	47	10.9	5.0
3	*Hylastes salebrosus*	38	270	204	9.4	23.2
3	*Hylastes tenuis*	39	557	408	17.0	86.3
4	*Pityophthorus annectens*	40	67	58	53.9	32.9
4	*Pityophthorus aztecus*	41	20	14	42.3	7.7
4	*Pityophthorus boycei*	42	29	29	2.8	0.8
4	*Pityophthorus confusus*	43	144	115	38.1	50.1
4	*Pityophthorus consimilis*	44	70	63	1.4	0.9
4	*Pityophthorus immanis*	45	13	11	5.0	0.6
4	*Pityophthorus nitidulus*	46	93	82	17.4	14.8
4	*Pityophthorus pinguis*	47	15	14	4.4	0.6
4	*Pityophthorus pulchellus*	48	294	140	4.9	13.2
4	*Pityophthorus pulicarius*	49	174	240	15.0	40.1
4	*Pityophthorus ramiperda*	50	19	18	0.1	0.0
4	*Pityophthorus schwerdtfegeri*	51	27	22	40.9	10.1
4	*Pityophthorus tuberculatus*	52	201	177	4.5	8.3
5	*Gnathotrichus deleoni*	53	13	12	35.6	4.2
5	*Gnathotrichus denticulatus*	54	74	62	9.6	6.5
5	*Gnathotrichus materiarius*	55	774	562	0.3	2.2
5	*Gnathotrichus nitidifrons*	56	18	13	30.6	5.0
5	*Gnathotrichus perniciosus*	57	35	28	46.9	15.0
5	*Gnathotrichus retusus*	58	134	113	12.2	14.9
5	*Gnathotrichus sulcatus*	59	217	172	35.5	70.2
5	*Trypodendron lineatum*	60	200	166	1.7	3.1
5	*Trypodendron rufitarsus*	61	60	52	3.4	1.9
5	*Trypodendron scabricollis*	62	80	71	5.6	4.1
5	*Xyleborus intrusus*	63	175	150	55.9	89.2
5	*Xyleborus pubescens*	64	555	366	11.1	56.2

Notes: Obs O, original number of locations with presence data; Obs R, number of locations with presence data obtained after randomly removing samples with locations closer than 5 min latitude/longitude from each other; PASH, percentage of the area with pine plantations in the Southern Hemisphere where each species is predicted to establish; IER, index of establishment risk in pine plantations of the Southern Hemisphere (higher value corresponds to higher risk).

TABLE 3. Median (Med) and 95th percentile (95%) of the number of predicted species for each bark beetle group in each pine plantation region of the Southern Hemisphere.

Continent, country, and region	*Ips* (18)		*Dendroctonus* (11)		*Hylastes* (10)		*Pityophthorus* (13)		Ambrosia beetles (12)		Total (64)	
	Med	95%	Med	95%	Med	95%	Med	95%	Med	95%	Med	95%
South America												
Argentina, NE	3	3	2	3	2	2	3	3	1	4	11	13
Argentina, NW	3	7	3	4	1	2	3	4	2	3	11	20
Argentina, SW	9	10	2	4	6	6	5	6	4	5	27	29
Bolivia	5	8	5	6	2	3	2	6	6	7	21	28
Brazil, N	1	4	1	2	1	3	1	2	1	2	5	11
Brazil, S	3	5	2	5	1	2	3	4	2	5	12	19
Chile	5	9	1	4	4	6	2	5	4	6	18	27
Colombia	1	5	3	7	1	3	1	3	1	4	7	20
Ecuador	4	6	6	7	3	4	2	3	4	5	19	23
Paraguay	1	3	2	2	2	2	3	3	1	2	9	11
Peru	5	7	6	7	3	3	3	6	6	6	23	27
Uruguay	3	3	2	2	2	3	3	5	2	4	13	17
Venezuela	2	4	1	4	2	3	1	2	2	2	9	13
Oceana												
Australia, NE	2	5	1	4	1	2	2	4	1	4	7	18
Australia, SE	3	7	2	4	3	6	2	4	3	5	13	22
Australia, SW	6	8	3	4	6	7	2	3	3	4	20	22
New Zealand	1	5	1	4	1	3	3	5	2	4	7	20
Africa												
Angola	4	5	5	6	2	3	3	4	4	5	18	20
Kenya	4	6	5	8	2	3	2	3	4	6	17	23
Madagascar	4	5	2	5	1	2	2	3	3	5	13	18
Malawi	4	5	4	5	1	2	2	4	2	5	12	19
Mozambique	3	4	2	4	1	1	2	3	1	3	9	14
South Africa, NE + Lesotho	4	8	3	4	1	2	3	5	3	5	14	22
South Africa, W	4	8	1	4	3	6	2	3	3	5	14	21
Tanzania	4	6	4	6	2	3	2	3	3	5	15	21
Uganda	1	5	2	7	2	3	2	3	4	5	12	19
Zambia	3	5	4	5	1	2	2	3	2	4	12	17
Zimbabwe	4	6	3	5	1	2	3	4	2	5	14	20

Note: Number of species in each bark beetle group are shown in parenthesis.

Hemisphere are particularly suitable for these North American Scolytinae species. Additionally, there is a clear latitudinal pattern reflecting climatic similarity in predicted Scolytinae assemblages in the Southern Hemisphere (Fig. 4). For example, temperate regions such as southern Argentina, southern Chile, southwest South Africa, southern Australia, and New Zealand are predicted to have comparable risks of invasion for a specific cohort of N. American Scolytinae species.

The index of establishment risk (Table 3) combines information about habitat suitability in the Southern Hemisphere with propagule pressure from North America and can be used to identify overall invasion risk for individual species. Of all of the species studied here, only one, *I. grandicolis*, has already established in the Southern Hemisphere (in Australia since 1934; Morgan 1989) and it also has the fourth highest index of establishment (out of 64 species). The utility of this index for predicting invasion is also supported by the fact that the species with the highest (*D. valens*) and sixth highest (*I. calligraphus*) have successfully invaded outside of the Southern Hemisphere. *Dendroctonus valens* established in China in the early 1980s (Yan et al. 2005) and *I. calligraphus* has established in the Philippines since 1959 (Lapis 1985). Taken together, this information suggests that the species with the five greatest index values are particularly likely to establish in the Southern Hemisphere. These species are *D. valens*, *Xyleborus intrusus*, *Hylastes tenuis*, *Ips grandicollis*, *Gnathotrichus sulcatus*, and *I. calligraphus*. Although it is difficult to predict the potential impact of these species in the different pine plantation regions of the Southern Hemisphere, these species could have substantial effects should they become established. For example, *I. grandicollis* has been shown to cause substantial tree mortality ranging from 15% to 100% in some stands in Australia (Morgan 1989); in China, *D. valens* has caused extensive tree mortality in pine plantations, estimated at more than 10 million trees (Yan et al. 2005). It should be acknowledged that abundance in the native range (quantified here from the number of occurrence records) is only one characteristic that contributes to propagule pressure, and thus these predictions based on our establishment risk index have limitations. Certain life history traits, such as higher growth rates or behavioral plasticity, may lead some species to become more strongly associated with pathways such as solid wood packing material, but we did not consider these because of the lack of information on these relationships.

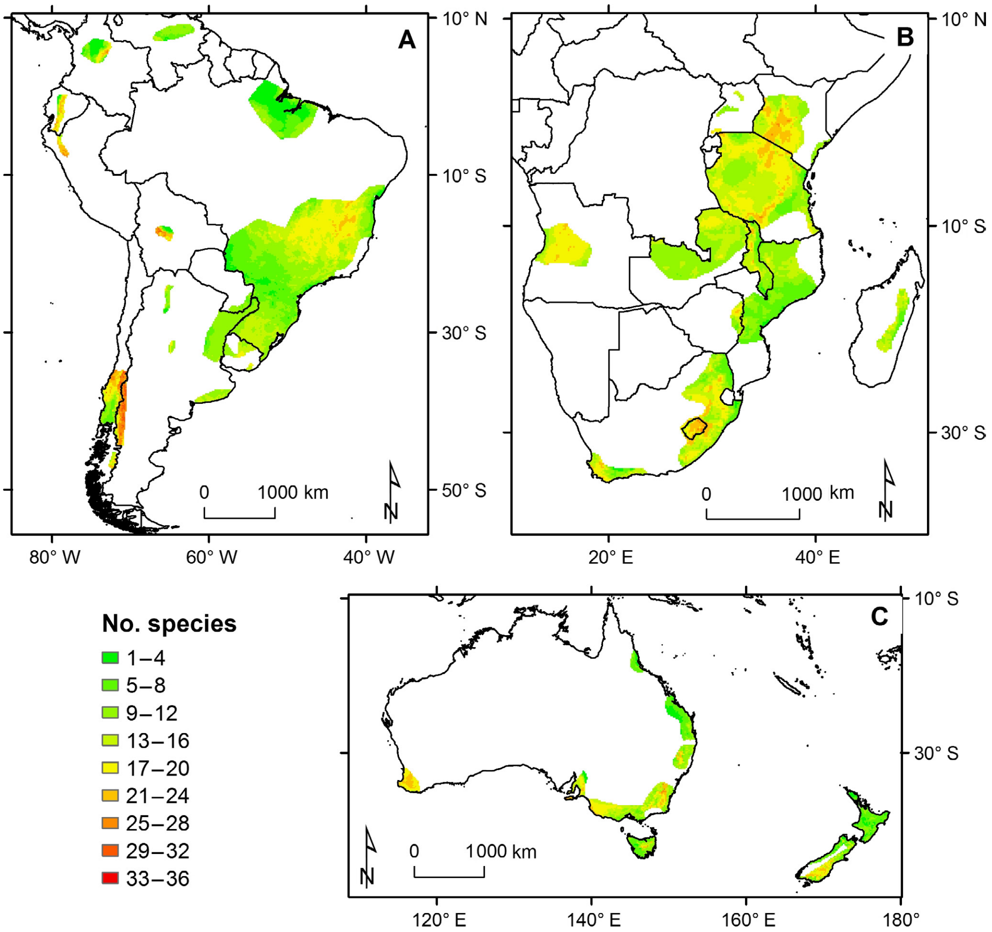

FIG. 2. Sum of the number of species with overlapping potential distributions for all Scolytinae species together, in the pine plantations zones of the Southern Hemisphere: (A) South America, (B) Africa, (C) Oceania. (Color figure can be viewed at wileyonlinelibrary.com.)

Despite the apparent close fit of the Maxent model used here, there are some reasons why predictions based on it may be constrained. Consequently, these results should also be interpreted with caution. First, the geographic distribution of Scolytinae species in their native range may be limited by factors other than climate and these may prevent species from occupying larger ranges. Such other possible factors include biotic constraints including the presence of competitors, parasites, and pathogens, as well as the availability of hosts and historical and current land use patterns (Beaumont et al. 2009). There are also biogeographic constraints that limit the native ranges of species; for example several Scolytinae species may be limited to either eastern or western North America because of the existence of geographical barriers that historically limited the movement of these species across the continent. It also must be acknowledged that, when distributional data are used to model a herbivore species' climatic envelope, part of the climatic limits may arise from the direct effects of climate on host plants in addition to direct effects on the herbivore (Evangelista et al. 2011). Some of these limitations associated with correlative ecological niche models (i.e., Maxent) could be overcome in future studies by developing models based on explicit biological processes (morphological and physiological traits) based upon species-specific measurements to predict potential species distribution (Morin and Thuiller 2009). Furthermore, information is also needed on plasticity of climatic requirements in Scolytinae species (Carroll et al. 2004, Bentz et al. 2010). Species with higher phenotypic plasticity can be expected to have greater establishment risk. It must also be considered that part of the occurrence point data for bark beetles in North America used in this study are records from trapping, and trapping alone does not necessarily mean that a species is established and reproducing at that specific location. However, the use of traps is considered a good approximation for surveying species ranges for insects, and in the case of the EDRR program, traps were placed in naturally forested areas to detect species that have become established (Rabaglia et al. 2008).

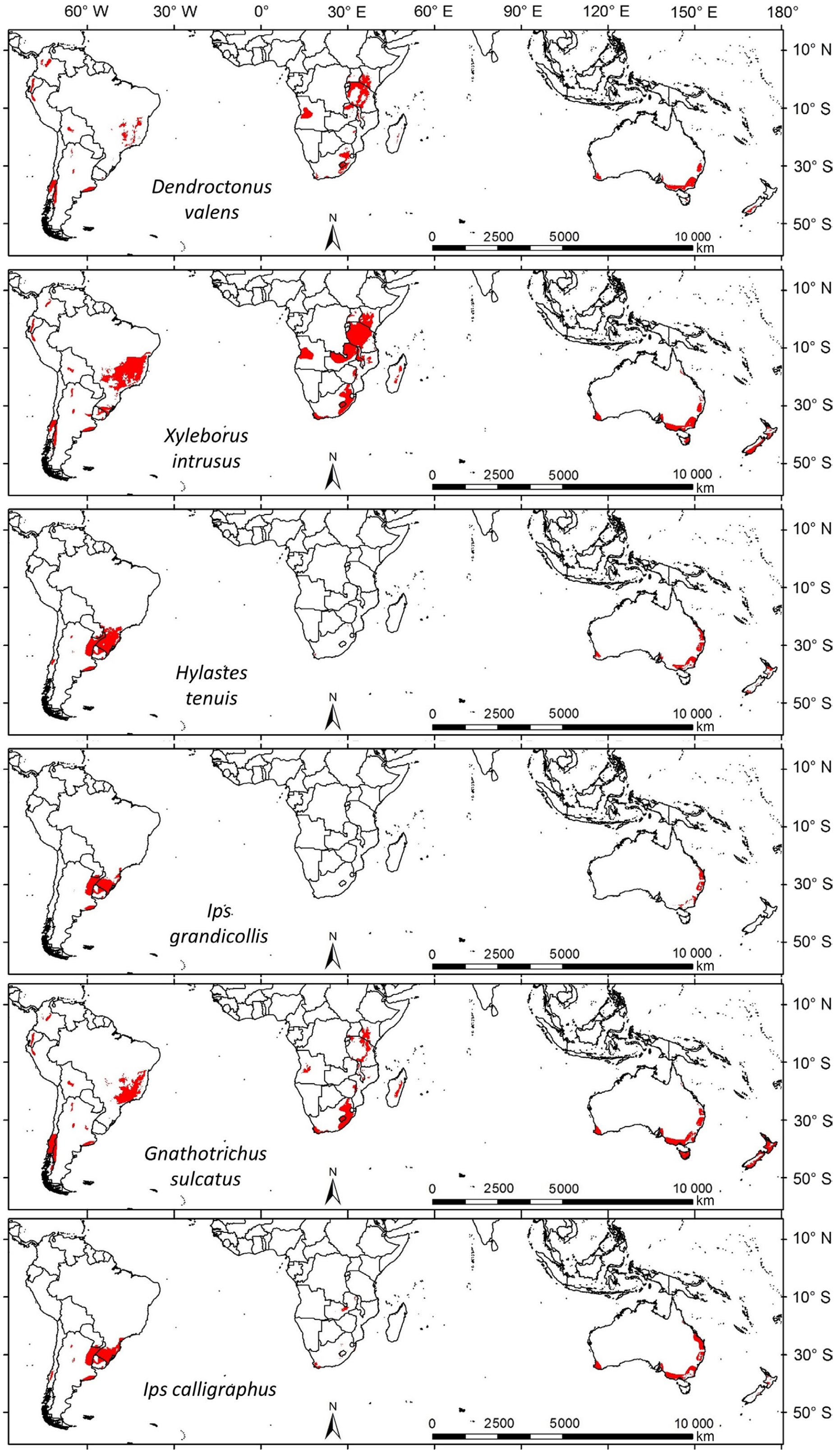

FIG. 3. Predicted range of the six species of North American pine-feeding Scolytinae with the highest index of establishment risk in pine plantations of the Southern Hemisphere. (Color figure can be viewed at wileyonlinelibrary.com.)

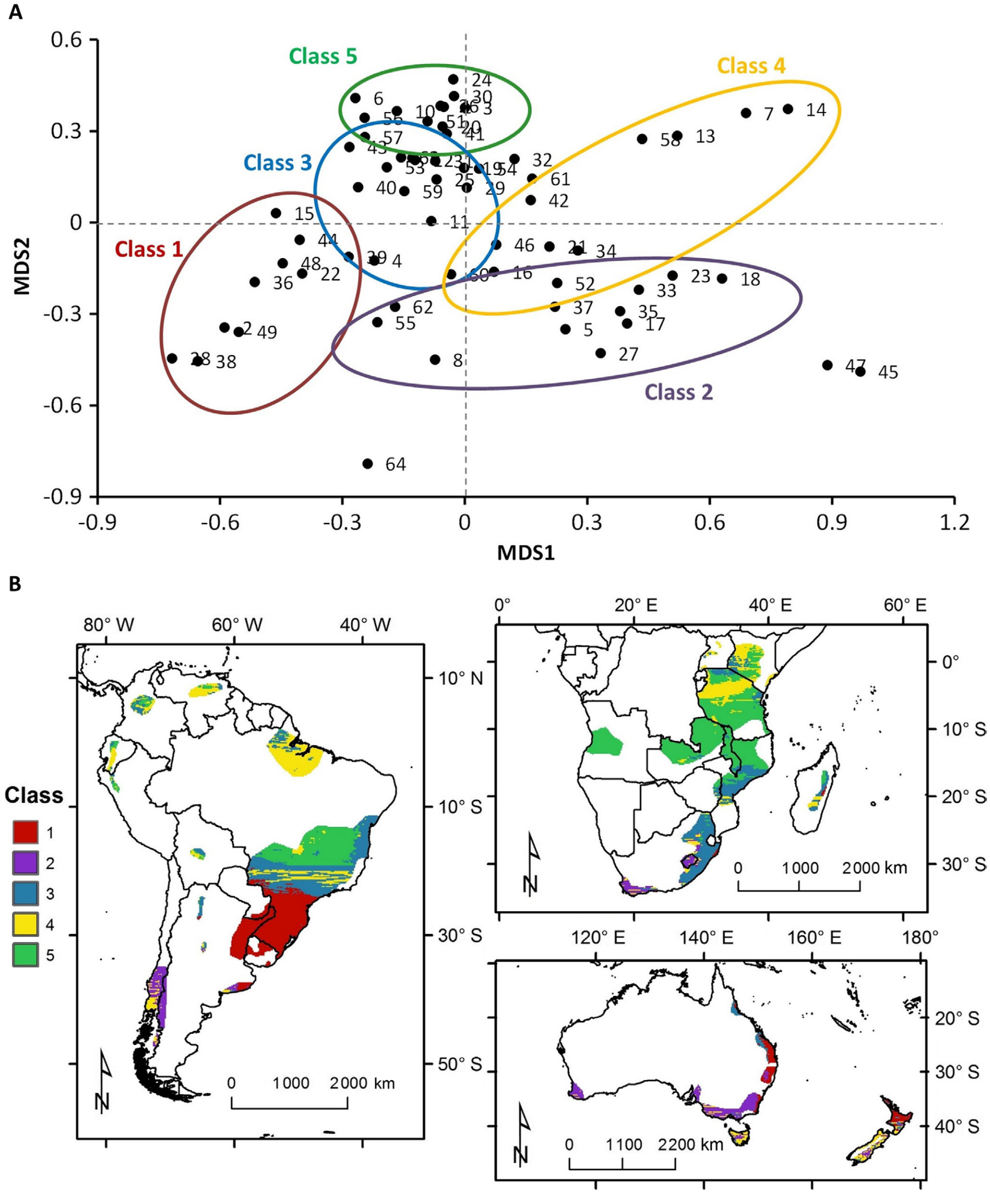

FIG. 4. Patterns of the predicted distribution of North American Scolytinae species in pine plantation regions of the Southern Hemisphere based on nonmetric multidimensional scaling (NMDS) results. (A) NMDS ordination of species. Color ovals indicate groups of similar species. See Table 2 for species ID numbers. (B) Map resulting from the Maximum Likelihood Classification of the NMDS results for grid cell assemblages. (Color figure can be viewed at wileyonlinelibrary.com.)

Future distributions of bark beetles in the Southern Hemisphere may also be limited by their host preferences. While most of the species used in our analysis have very wide host associations within the genus *Pinus*, and are able to attack and breed in any species of pine that occurs within their respective geographic ranges (Wood 1982), some of the species may exhibit varying preference or performance on different *Pinus* species. However such host associations are not fully known for most species, so it was not possible to include host preferences in our analysis. In many cases, novel host associations are difficult to predict; for example there are numerous records of North American bark beetle species known to breed in pine species (e.g., Scots pine, *Pinus sylvestris*) that are exotic to the ranges of these beetle species. In another example, *Ips grandicollis*, is native to southeastern North America yet it is a pest in Australia on *Pinus radiata*, a species with a native range that does not overlap with *I. grandicollis* (Critchfield and Little 1966, Yousuf et al. 2014). Nevertheless, there probably are some groups (e.g., some of the *Dendroctonus* species) for which performance may be markedly poorer on some pine species than others and this may limit the probability that such species establish in plantations of individual pine species (Kelley and Farrell 1998).

Our study is novel in that it considers invasion risks for a large pool of species at an intercontinental scale. This is of great relevance for the identification of potential pest species of forest plantations, which may be critical in the design of global strategies aimed at reducing pest movement into susceptible regions and improved targeting of pest surveillance (Wingfield et al. 2015). Future research, in addition to integrating spatial data on climatic suitability and habitat availability, should also include information about pathways, as well as species life history characteristics that may associate them with specific invasion pathways (Hulme 2015). Alternatively, the abundance of individual species may be quantified from data on interceptions at ports and used as a proxy for propagule pressure (Brockerhoff et al. 2013).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1451/full