Predicting the distribution of a novel bark beetle and its pine hosts under future climate conditions

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Abstract

1 Understanding the distribution of key biotic elements of forest ecosystems is essential in contemporary forest management and in planning to meet future management needs. Habitat distribution (niche) models based on known occurrences provide geographical structure for such management as the environmental factors change.

2 Bark beetles play critical roles in coniferous forest dynamics in western North America. Among these insects, *Dendroctonus rhizophagus* Thomas and Bright, which occurs in the Sierra Madre Occidental in Mexico, is unique in that it attacks only immature trees (*Pinus* spp.) and therefore represents a threat to forest regeneration. We developed current habitat distribution models for *D. rhizophagus* and its *Pinus* hosts and projected these to future climate scenarios.

3 Predicted suitable habitat of *D. rhizophagus* currently covers approximately 119 000 km^2 of which approximately 11% is occupied, and overlap with suitable habitat for all *Pinus* hosts exceeds 99.5%. Some suitable habitat occurs isolated from known *D. rhizophagus* occurrences in Mexico and the south-western U.S.A.

4 Habitat distribution models were projected to four potential climate scenarios for the period 2040–2060 and this predicted the gains and losses of suitable *D. rhizophagus* habitat throughout the region. Areas of north-western Mexico maintain large areas of suitable *D. rhizophagus* and *Pinus* host habitat in all scenarios. Dispersal to isolated areas of *D. rhizophagus* habitat appears unlikely.

5 The results of the present study can be used to target *D. rhizophagus* monitoring and management activities and may serve as a model for the management of other invasive species.

Keywords Curculionidae, *Dendroctonus rhizophagus*, Madrean Archipelago, niche model, Scolytinae, Sierra Madre Oriental.

Introduction

Bark beetles in the genus *Dendroctonus* Erichson (Curculionidae, Scolytinae) play an important role in coniferous forest dynamics in Central and North America (Bentz *et al*., 2010; Salinas-Moreno *et al*., 2010; Evangelista *et al*., 2011). Under certain conditions, such as extreme drought and where stands are relatively dense (Raffa *et al*., 2005; Negron *et al*., 2009), some species in this genus have caused extensive tree mortality (Bentz *et al*., 2010) substantially altering forest structure, composition and function (Raffa *et al*., 2008). In recent years, the magnitude of bark beetle outbreaks have increased and have occurred in habitats that were apparently unaffected historically (Raffa *et al*., 2008).

Changes in bark beetle distribution have been linked mainly to increases in temperature, which have had a dramatic impact on insect survival, reproduction (Dale *et al*., 2001; Lange *et al*., 2006) and dispersal. Host species condition has also been affected significantly by changes in temperature and precipitation (Lindner *et al*., 2010; Williams *et al*., 2010). Even

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small increases in mean temperature may affect fire frequency or intensity and pathogen and insect outbreaks (McNulty & Aber, 2001; Lange *et al*., 2006).

Many examples exist of how recent climate change has transformed species distributions and abundance (Kelly & Goulden, 2008; Walther, 2010). Predicting the course of future climate-associated changes of this sort has become a central objective in much biogeographical research (Dormann, 2007; Elith & Leathwick, 2009; Sommer *et al*., 2010; Dawson *et al*., 2011; Hill *et al*., 2012). A variety of modelling methods have been developed to predict suitable habitat that can be projected to future conditions. Such predictions are dominated by the results obtained from correlative modelling techniques. These approaches generally involve the construction of multivariate models using contemporary patterns of known species occurrence (and sometimes absence) and environmental variables (Elith *et al*., 2011) that are then often projected to future environments as predicted by global climate models (GCM) (Rehfeldt *et al*., 2006; Saenz-Romero *et al*., 2010). Little is known of the temperature-dependent physiological processes of the hundreds of bark beetle species that are native to forests of western North America, including the majority of the species occurring in south-western U.S.A. and Mexico. Given the very limited understanding of the basic biology of *Dendroctonus* (Sanchez-Martinez & Wagner, 2009), correlative modelling may represent the most tractable method with respect to the identification of target environments for monitoring invasive species and planning responses to it.

The bark beetle *D. rhizophagus* Thomas and Bright is considered endemic to Mexico, occurring in the Sierra Madre Occidental (SMOc) from northern Jalisco to northern Chihuahua and Sonora, primarily at elevations between 2000 and 2600 m (Mendoza *et al*., 2011). This species is unique in that it attacks only immature trees (height <3 m), which is in direct contrast to other bark beetles that prefer large-diameter mature host trees (Raffa *et al*., 2005; Negron *et al*., 2009). It is found on various *Pinus* species from section Trifoliae (Sanchez-Martinez & Wagner, 2009; Mendoza *et al*., 2011). Because of its ability to cause significant seedling mortality (Estrada-Murrieta, 1983; Cibrián-Tovar *et al*., 1995) *D. rhizophagus* may represent a major threat to pine regeneration. This is in a region where stand-replacing fires are common and seedling establishment is a critical component of post-fire recovery (Allen *et al*., 2010).

The current range of *D. rhizophagus* may be more related to environmental variables affecting the insect or host regeneration rather than to the presence of hosts because several of the host species have apparently much larger distributions (Little, 1971; Mendoza *et al*., 2011). Importantly, large areas of potential *D. rhizophagus* habitat are very remote and have not been surveyed for its presence. Given the possible devastating effects on host seedling establishment (Sanchez-Martinez & Wagner, 2009), forest managers could benefit from a better understanding of *D. rhizophagus* biology, including habitats where it may exist (Mendoza *et al*., 2011) or could become established in the face of climate change and host shifts (Swetnam & Betancourt, 1998; Allen *et al*., 2010). The development of science-based monitoring and management of *D. rhizophagus* could be greatly facilitated by an understanding of pending changes within host-pest communities as climate changes occur (Lindner *et al*., 2010).

The presence of *D. rhizophagus* could complicate efforts to introduce more natural regeneration regimes in forests of Mexico and the south-western U.S.A. (Sabo *et al*., 2009; Allen *et al*., 2010). The present study aimed to refine strategies for the development of management tools based on habitat distribution modelling that could be used in species for which we have limited detailed phenological knowledge such as *D. rhizophagus*. This included refinement of correlative models as presented by (Mendoza *et al*., 2011) to improve our understanding of the geographical characteristics of the *D. rhizophagus* habitat. These models were also used to project the potential range of suitable habitat beyond the SMOc in Mexico, and in the south-western U.S.A. In addition, we modelled habitat suitability over this range for mature individuals from eight taxa of *Pinus* that have been recorded as hosts for *D. rhizophagus*. Insect and pine models were then projected to four potential future climate scenarios to provide guidance for future monitoring and management of affected forest environments.

Materials and methods

Study area

Our research addresses areas of potential *D. rhizophagus* and pine habitat in north-western Mexico and adjoining regions in the south-western U.S.A. (area bounded by 21.0–34.5°N, 102.5–112.0°W; total area: 1 097 337 km^2; Fig. 1). The primary focus is on the SMOc in north-western Mexico that is entirely within the study area. This range is almost 1200 km in length, is topographically and environmentally complex, and has large continuous areas of high-elevation pine-dominated forests (Bye, 1994; Ferrusquía-Villafranca *et al*., 2005). Precipitation generally increases with elevation, and oak-pine forests occur in the SMOc at elevations between 900 and 2300 m, with pines dominant above approximately 1600 m (Rzedowski, 1981; Felger *et al*., 2001). Mixed-conifer forests with representatives of *Abies*, *Picea*, *Pseudotsuga* and *Pinus* can occur above 2000 m (Rzedowski, 1981). The SMOc represents a region of high biological diversity generally, and especially high genetic diversification within the genus *Pinus* (Bye, 1994; Farjon & Styles, 1997). This region is also an area where timber harvest has been extensive, although management practices have been applied unevenly, often because forest stands are remote (Fulé & Covington, 1997; Thoms & Betters, 1998; Guerrero *et al*., 2000; Weaver, 2000; Escárpita, 2002; Hernández-Díaz *et al*., 2008).

Of particular interest in this research are high-elevation habitats within the Madrean Archipelago of northern Mexico and the south-western U.S.A. that are associated with the SMOc biogeographically (Peet, 2000) and where *D. rhizophagus* has not been observed. The relatively small 'Sky Island' mountain ranges of this archipelago occur in the Mexican states of Sonora and Chihuahua (north of approximately 30°N), and in southern Arizona, and New Mexico (south of approximately 33°N) in the U.S.A. (Peet, 2000). These ranges are isolated by 20–50 km from each other often by large expanses of
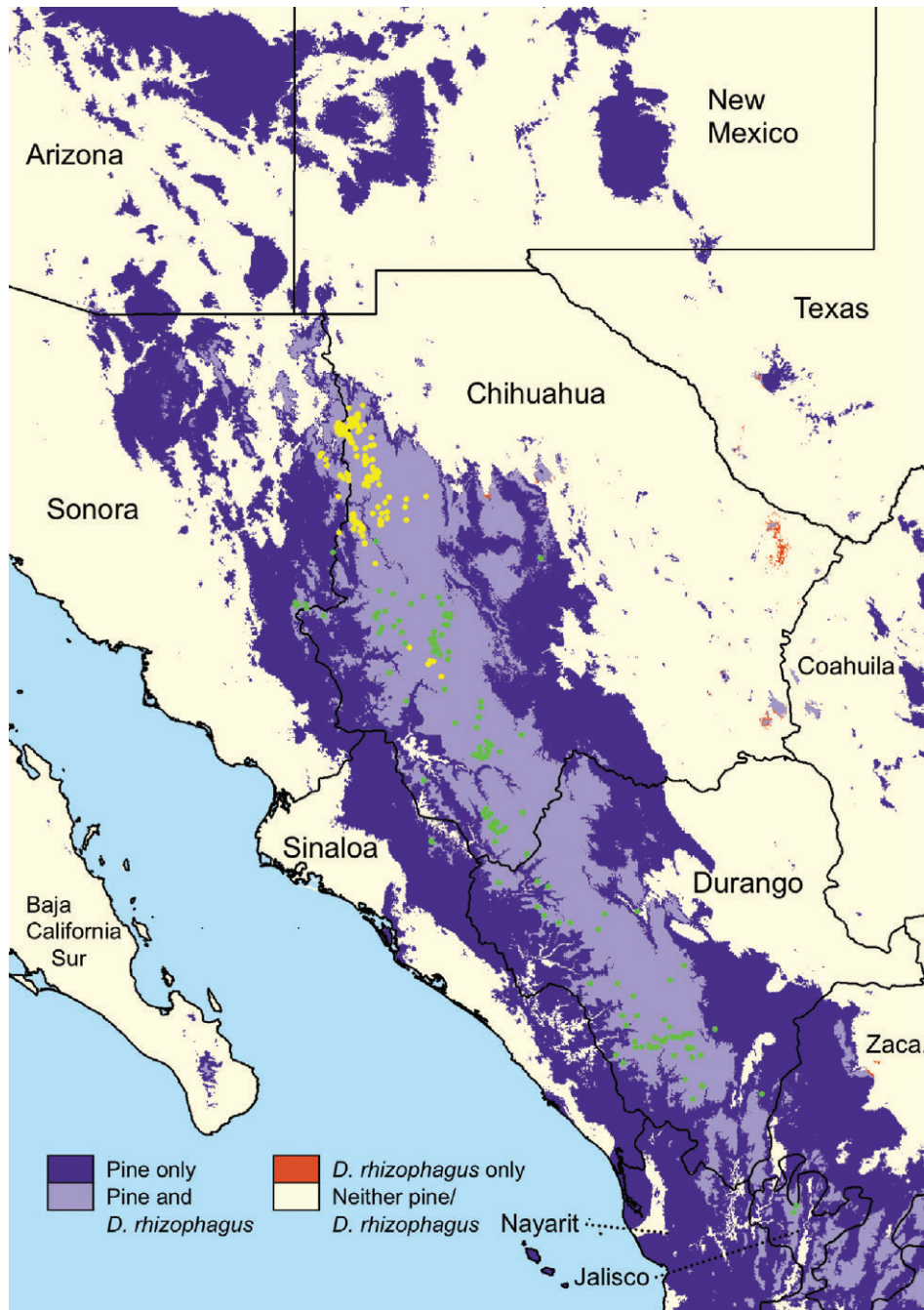
Figure 1 Predicted suitable habitat for *Dendroctonus rhizophagus* and combined predicted suitable habitat for eight modelled *Pinus* host species under current conditions (1950–2000). Yellow and green polygons represent the occurrence locations for *D. rhizophagus* used in the modelling. Yellow, north cluster; Green, south cluster (some polygons overlap). The extent of the Sierra Madre Occidental corresponds well with suitable *Pinus* habitat in western Chihuahua and Durango, and in eastern Sonora, Sinaloa and Nayarit, as well as northern Jalisco.

grassland or, at lower elevations, Sonoran or Chihuahuan Desert shrublands (Warshall, 1994). At elevations above approximately 1800 m, many of the ranges have significant pine habitat similar in species composition to that of the SMOc (Bye, 1994). Diversity in the archipelago is high as a result of their location at the intersection of the SMOc and Rocky Mountains, and the Sonoran and Chihuahuan Deserts.

Accordingly, they may represent critical targets for management efforts to maintain regional ecosystem function (Spector, 2002). These ranges also represent high-elevation habitat that could serve as dispersal corridors between the SMOc and the extensive forests of the Rocky Mountains that are present in the northern portion of our study area in Arizona and New Mexico.

Study species occurrences

We derived occurrence data for *D. rhizophagus* (from 1964 to 2011) from the major natural history and entomological collections in Mexico and Canada and technical reports of state and national forest management agencies in Mexico (see Supporting information, Table S1). In addition, we included records gathered in the course of several field studies conducted by the Laboratorio de Variación Biológica y Evolución, Escuela Nacional de Ciencias Biológicas del Instituto Politécnico Nacional from 2000 to 2011 in the SMOc. We eliminated duplicate or imprecisely placed occurrences, leaving a total of 329 locations. Three estimates of total area occupied by *D. rhizophagus* were produced using buffers with radii of 0.5, 1 and 5 km around the occurrence locations. These were generated using the Buffer tool within ARCGIS (ESRI, 2011).

A list of *Pinus* species ('host taxa') that *D. rhizophagus* has been known to infest was compiled from Salinas-Moreno *et al.* (2010) and Mendoza *et al.* (2011). Host taxa (*n* = 8) were included if more than 30 independent and verified occurrences of *D. rhizophagus* have been recorded on the species (Table 1) (Hernandez *et al.*, 2006). The primary occurrence data for host taxa were obtained mainly from the Global Biodiversity Information Facility (accessed through the GBIF Data Portal; http://data.gbif.org; accessed 1 December 2010). Occurrences were assumed to represent mature trees because cones are generally required for identification in these taxa. We eliminated duplicate or obviously unreasonable or imprecisely placed occurrences based on analysis of information within the collection records and Google Earth imagery (accessed 1 December 2010). We also included our observation records for individuals in the host taxa as occurrences. Because the identification of seedling trees is difficult, many of the *D. rhizophagus* occurrences (52%) were not definitively associated with a single *Pinus* host taxon. We therefore did not include *D. rhizophagus* occurrences as occurrences of host trees. *Pinus* classification follows that described by Gernandt *et al.* (2005), except for *Pinus ponderosa* where we adopted the interpretation of Kral (1993).

Environmental variables

The environmental data used in habitat distribution models (HDM) included elevation and the 19 bioclimatic (BIO) variables from the WorldClim 1.4 dataset for the period 1950–2000 (= 'Current conditions') at a resolution of 30 × 30 asec. Individual records from this dataset are referred to as grids (Hijmans *et al.*, 2005) (approximately 820 × 923 m at 28°N) and values within this database are based on predicted monthly means. Final HDMs were also projected to publically available statistically downscaled future environmental layers (Ramirez & Jarvis, 2008) based on two global climate models: UKMO-HadCM3 (Pope *et al.*, 2000) and MRI-CGCM2.3.2a (Yukimoto *et al.*, 2001) run under two different emissions scenarios (A2a and B1). The choice of climate models can have significant effects on predicted distributions in habitat distribution modelling (Ziter *et al.*, 2012). We therefore purposefully chose models that have been shown to perform well in predicting precipitation associated with the North

American monsoon (Liang *et al.*, 2008), which is a major factor affecting ecosystem functions in the region of interest (Sheppard *et al.*, 2002; Higgins *et al.*, 2003).

We conducted predictions for the period 2040–2069. This period represents a compromise between our desire to provide biogeographical information within a timescale where climate predictions are more reliable (earlier) and opportunities for expansion of insect habitat are greater (later)(Dessai *et al.*, 2009). The period selected also represents the approximate range of one complete minimum generation for pine hosts of *D. rhizophagus* from the time that this research was conducted (Krugman & Jenkinson, 1974).

Previous research has shown a close linkage between occurrences of *D. rhizophagus* and *Pinus engelmannii* (Salinas-Moreno *et al.*, 2010; Mendoza *et al.*, 2011). This *Pinus* taxon is also distributed along the full extent of the SMOc and in the Madrean Archipelago. We therefore chose to describe general changes in environmental conditions predicted using GCMs over the grids with current *P. engelmannii* occurrences (*n* = 271; see Supporting information, Fig. S1). We consider these grids representative of current high-elevation (mean 2125 m) SMOc and Madrean Archipelago pine habitat. Ten environmental variables (BIO 1, 4, 10–12 and 15–19; Table 2) were selected to describe general changes in environmental conditions under future climate projections at these locations. Mean values for these variables were calculated using PROC MEANS in SAS (SAS Institute Inc., 2009). The significance of differences between paired means for current conditions and future climate predictions over these locations was determined using a Wilcoxon signed rank-sum test (*P* ≤ 0.05) in PROC UNIVARIATE in SAS.

Habitat distribution modelling and analysis

Individual HDMs under current conditions were developed for *D. rhizophagus* and the selected *Pinus* hosts using MAXENT, version 3.3.3a (Phillips *et al.*, 2006). MAXENT represents one of the best performing HDM platforms using 'presence-only' data (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Mateo *et al.*, 2010) and has been utilized extensively for this purpose (Elith *et al.*, 2011). We assumed that the size of sampling units represented by occurrence records equaled that of an individual environmental grid. Before model development, we insured that no more than one occurrence record existed for each taxon within each environmental grid in the study area. This was accomplished using the 'Grid' method in the Trim Duplicate Occurrences tool within ENMTOOLS (Warren *et al.*, 2010). Occurrences are spatially biased because collectors do not move randomly. To better account for this bias, MAXENT modelling was peformed using target-group background occurrences (pseudo-absences) rather than randomly selected background locations (Phillips *et al.*, 2009; Elith *et al.*, 2011). For *Pinus* taxa and *D. rhizophagus*, this involved 10 000 randomly selected occurrence records from GBIF (Accessed through GBIF Data Portal; http//data.gbif.org; accessed 2 January 2011). As with data for the modelled taxa, the Trim Duplicate Occurrences tool (Warren *et al.*, 2010) was used to insure that only a single occurrence was included in each environmental

Table 1 Number of occurrences, approximate area occupied, and overall mean values for elevation, latitude, annual temperature, temperature for the warmest and coldest quarters, and annual precipitation at occurrence locations for *Dendroctonus rhizophagus* (in bold) and *Pinus* host species/intraspecies cluster

Taxon (cluster)[a]	Number of occurrences	Area occupied (×1000 km²)[b]	Elevation (m)[c,d]	Latitude (°N)	Mean annual temperature (°C)	Mean temperature warmest quarter (°C)	Mean temperature coldest quarter (°C)	Mean annual precipitation (mm)	Mean precipitation warmest quarter (mm)	Mean precipitation in coldest quarter (mm)
Pinus ponderosa Douglas ex C. *Lawson* (North cluster)	243	93.1	2136cd	32.4a	10.9g	19.1cd	3.1g	608fg	243f	145a
Pinus strobiformis Engelm.	133	64.0	2289ab	32.0ab	10.3g	18.0e	2.9g	638f	283e	135abc
Pinus leiophylla Schiede ex Schltdl. & Cham. (North cluster)	120	50.3	1877e	31.5b	13.1ef	21.2a	5.3f	535h	240f	116d
***Dendroctonus rhizophagus* Thomas and Bright (North cluster)**	**180**	**4.7**	**2129cd**	**29.8c**	**12.4f**	**19.7c**	**5.1f**	**570gh**	**299e**	**93f**
Pinus engelmannii Carrière	271	147.4	2125cd	27.9d	13.5de	19.4c	7.3e	726e	385d	112ed
Pinus ponderosa (South cluster)	140	80.6	2331a	26.1e	13.1ef	17.9e	7.9de	880c	481b	124cd
***Dendroctonus rhizophagus* (South cluster)**	**149**	**8.4**	**2343a**	**26.1e**	**13.2e**	**18.0e**	**8.1d**	**885c**	**490b**	**122cd**
Pinus oocarpa Schiede	44	27.4	1474f	26.0ef	18.3a	22.7a	13.3a	957ab	494b	131bc
Pinus lumholtzii B.L. Rob. & Fernald	71	49.1	2140cd	25.9efg	14.5c	19.1cd	9.3c	895c	475b	123cd
Pinus herrerae Martinez	47	30.8	2198bc	25.6efg	15.2b	19.5c	10.3b	1003a	543a	138ab
Pinus leiophylla (South cluster)	217	124.4	2198bc	25.5fg	14.4c	19.0cd	9.3c	782d	415c	100ef
Pinus durangensis Martinez	120	76.1	2234abc	25.4g	14.1cd	18.4de	9.2c	928bc	488b	131bc
All taxa	1679	–	2162	28.2	13.2	19.1	6.9	745	381	119

[a]*Pinus* taxonomy follows Gernandt et al. (2005) except for *P. ponderosa sensu lato*, where we adopted the interpretation of Kral (1993). All but *P. strobiformis* are members of Section Trifoliae (Gernandt et al., 2005). All taxa have >30 georeferenced collection locations in the study area.

[b]Approximate area represented by occurrences based on a 5-km buffer surrounding each occurrence, with buffer area overlaps excluded.

[c]Environmental grids with multiple occurrences are included only once in all mean calculations.

[d]Means within a column followed by different lowercase letters are significantly different ($P < 0.05$) based on a multiple comparison test (Dunn, 1964) generated using the results from a Kruskal–Wallis single-factor analysis of variance by ranks.

Table 2 Mean values for selected environmental variables at 271 current occurrence locations for *Pinus engelmannii* and the percentage change in these variables predicted using two global climate models (UKMO-HadCM3, MRI-CGCM2.3.2a) and two emissions scenarios (A2a, B1)

| Environmental variables | BIO variable number | Mean under current conditions | Percent change predicted, 2040–2069 relative to current conditions | | | |
| | | | UKMO-HadCM3 | | MRI-CGCM2.3.2a | |
			A2a	B1	A2a	B1
Annual mean temperature	1	13.5 °C	+18.2	+15.9	+16.9	+11.0
Temperature seasonality[a]	4	47.6%	+5.6	+2.4	+6.4	+7.6
Mean temperature warmest quarter	10	19.4 °C	+14.4	+11.7	+12.4	+9.3
Mean temperature coldest quarter	11	7.3 °C	+34.8	+32.7	+29.7	+15.5
Annual precipitation	12	726.5 mm	+7.6	+0.7	−11.5	−5.0
Precipitation seasonality[b]	15	88.7%	−3.5	+5.0	+17.1	+3.6
Precipitation wettest quarter	16	436.1 mm	+4.9	+4.5	−3.2	−3.3
Precipitation driest quarter	17	41.8 mm	−8.6	−20.6	−31.0	−18.5
Precipitation warmest quarter	18	384.4 mm	+1.7	−0.5[c]	+0.8	−4.0
Precipitation coldest quarter	19	111.9 mm	−6.7	−10.6	−37.0	−5.8

[a]Temperature seasonality = coefficient of variation of mean monthly temperatures.
[b]Precipitation seasonality = coefficient of variation of monthly mean precipitation.
[c]Mean difference between current and predicted values not significantly different from zero based on Wilcoxon signed rank sum test ($P < 0.05$).

grid before selection of the target-group background began. Occurrences for the Kingdom *Plantae* within the study area were used for the target-group background for *Pinus* taxa and those for Class *Insecta* were used for *D. rhizophagus*.

Values for environmental data for use in species distribution modelling are often highly correlated and the inclusion of redundant traits may reduce accuracy of predictions (van Zonneveld *et al*., 2009; Comas *et al*., 2011). We attempted to objectively identify redundancies among environmental variables using hierarchical clustering of environmental variables on oblique centroid components (PROC VARCLUS in SAS under default settings). This procedure attempts to identify non-overlapping clusters of variables and to maximize total variation across clusters explained by cluster components. (Total variation explained by clusters exceeded 0.9 in all cases in this research.) Initial MAXENT model development began with a single variable from each cluster from the VARCLUS output. In multiple-variable clusters, this primary variable was the one most highly correlated with other members of that cluster and most weakly correlated with other clusters (i.e. the smallest ratio of correlation within the cluster to next closest cluster). Correlation coefficients were also calculated among all variables for each grid of the study area using the Correlation tool in ENMTOOLS (Warren *et al*., 2010) and no two variables were included within any model if $|r| \geq 0.7$ between them. Selection of the variable used among such pairs was accomplished employing the same procedure used to identify primary variables described above.

Certain taxa examined in this research occupy a wide variety of environments, have discontinuous distributions, (Felger *et al*., 2001) and may occur in fundamentally different environments in different portions of their range (Nakazato *et al*., 2010). If this occurs, then differences in the most accurate HDMs might be expected across the range. We examined patterns of environmental variability within a taxon's range by conducting a hierarchical cluster analysis (PROC CLUSTER,

Ward's minimum-variance method in SAS). In this analysis, each occurrence represented an observation and clustering was performed using the primary variables from each intrataxon cluster derived from the VARCLUS analysis described above (standardized to mean = 0 and SD = 1). In the cluster analysis, examination of the cubic clustering criterion, and the pseudo F and t^2 statistics ($P \leq 0.01$) was used to determine whether there was evidence of distinguishable intrataxon clusters (Cooper & Milligan, 1988). Cluster analysis was performed omitting 2% of observations with the lowest estimated probability density. If multiple clusters were established for a taxon, omitted observations were placed in the geographically nearest cluster. When significant support for multiple clusters within a taxon was established, separate HDMs were developed for occurrences within each cluster, which were named based on their relative locations (i.e. 'North', 'South').

MAXENT was run using default settings for features, convergence threshold, regularization, clamping, extrapolation and maximum iterations. To reduce bias associated with training-testing fold selection, final model results represented means of 10 replicate runs from cross-validation where all occurrences were present within a single test fold (Marmion *et al*., 2009). As the model selection proceeded, removal or substitution of environmental variables within models was perfomed based on the VARCLUS cluster groups. When decisions regarding variable inclusion were made, a variety of sources of information were used. Most often, this included results of jackknife tests and response curves for environmental variables produced by MAXENT (Phillips *et al*., 2006). In some cases, we also used existing knowledge of the natural history, physiology and apparent environmental requirements of the taxon involved (van Zonneveld *et al*., 2009). The final models selected were those with the lowest mean values for the Akaike information criterion (AIC_c) (Warren & Seifert, 2011) as calculated in the Model Selection tool within ENMTOOLS over 10 replicate runs (Warren *et al*., 2010).

Continuous probability maps for final models produced by MAXENT in logistic output format were converted into binary maps presenting suitable-unsuitable habitat. This was performed using the mean maximum training sensitivity (true predicted presences) and specificity (true predicted absences) threshold from the 10 replicate runs in DIVA-GIS, version 7.3.0 (http://diva-gis.org; accessed 1 August 2010). This procedure has demonstrated high accuracy in validation tests comparing multiple procedures (Liu *et al*., 2005; Jimenez-Valverde & Lobo, 2007). We report the mean receiver operating characteristic curve (AUC) values (Lobo *et al*., 2008) over 10 cross-validation replicates.

For taxa where cluster analysis justified generation of separate north and south models (Table 1), whole-taxon suitable habitat maps (rasters) were generated by overlaying the two binary maps to display the maximum value per pixel from the individual maps in the overlay map. These and all species or present-future comparison maps were similarly produced using Grid Overlay options in DIVA-GIS. Areas of suitable habitat in all maps were calculated using Albers equal-area conic projections of the model-derived rasters within ARCMAP in accordance with standard procedures for such projections. Nearest-neighbour analysis was conducted using Euclidian distances and the Spatial Statistics toolset in ARCGIS on Albers equal-area conic projections of *D. rhizophagus* occurrence locations. When comparing predicted ranges of two taxa, approximate range overlap values were calculated as the combined area of suitable habitat for both taxa divided by the total area of suitable habitat for the taxon with the smaller range (Nakazato *et al*., 2010). All maps are presented using a geographical coordinate system WGS 1984.

We used nonparametric one-way analysis of variance to determine whether environmental values for core variables at occurrence locations (Table 1) differed significantly among taxa or intrataxon clusters (Nakazato *et al*., 2010). This was performed using PROC NPAR1WAY (Kruskal–Wallis test) in SAS. Significance of differences among means was determined using a multiple comparison test, as previously described by Dunn (1964).

Results

Geographical characteristics of occurrence locations

Occurrences of *D. rhizophagus* were not distributed randomly across the study area (Nearest-neighbour ratio: 0.421, Z-score: -20.106, $P \leq 0.01$). Mean distance to the nearest occurrence was 5.8 km, although two isolated occurrences (7.4 km apart) at the southern limit of all occurrences in Jalisco were over 130 km from the nearest occurrence in southern Durango (Fig. 1). Another single isolated occurrence location in central Chihuahua was 111 km from its nearest neighbour. The distance between the most northerly and southerly occurrences is approximately 1050 km when measured along the approximate crest of the SMOc.

Cluster analysis of environmental variation demonstrated evidence of two significantly different multivariate relationships among environmental variables (i.e. multiple clusters separated in space) at occurrence locations for three taxa: *D. rhizophagus*

(Fig. 1), *Pinus leiophylla*, and *P. ponderosa*. Examination of environmental values for each of these cluster pairs showed that clusters within taxa were clearly differentiated in mean altitude, latitude and in primary climate variables (Table 1). All occurrences within the South cluster of *D. rhizophagus* were located within $22.07-29.00°$N primarily in south-western Chihuahua and western Durango (Fig. 1). North cluster occurrences were within $27.50-30.40°$N in north-western Chihuahua and north-eastern Sonora. Mean geographical correspondence was significant between the South clusters of *D. rhizophagus* and *P. ponderosa* based on comparisons of mean values for key environmental variables (Table 1). Similar direct geographical correspondence with a *Pinus* taxon/intrataxon cluster was not evident for the North cluster of *D. rhizophagus*. Environmental characteristics of this cluster did not differ from *P. engelmannii* in mean elevation or mean temperature in the warmest quarter. However, insects in this cluster were associated with sites having lower temperatures in the coldest quarter and lower annual and quarterly precipitation than in *P. engelmannii*. Mean precipitation was significantly lower in the coldest quarter at North-cluster occurrences of *D. rhizophagus* than in any sympatric *Pinus* hosts (Salinas-Moreno *et al*., 2010).

Habitat distribution models

All final models identified based on minimum AIC_c values exhibited mean training and testing AUC values in excess of 0.89 (mean 0.960) (see Supporting information, Table S2). Training and testing omission rates under a maximum sensitivity plus specificity threshold for all models were generally less than 0.1 (mean 0.054). Omission rates for *D. rhizophagus* were less than 0.06. Binomial tests of omission for all final models using this threshold showed that test occurrences were predicted significantly better ($P \leq 0.001$) than a random prediction of the same fractional area.

Final MAXENT models contained two to five variables and all included at least one temperature variable (see Supporting information, Table S3). All models, except that for the low-elevation host taxon *Pinus oocarpa*, also included at least one precipitation variable. Models for *D. rhizophagus* had approximately equal combined permutation importance for temperature and precipitation variables. The highest permutation importance values were associated with temperature in models for *Pinus* taxa with a mean elevation above approximately 1700 m and a latitude of occurrence (in either cluster) north of approximately $26°$N. By contrast, precipitation variables had the highest permutation importance values in models for *Pinus* taxa with a mean latitude south of $26°$N and for *P. oocarpa*.

Predicted suitable habitat: current conditions

Predicted suitable habitat (hereafter 'suitable habitat') for *D. rhizophagus* under current conditions represented approximately 11% of the entire study area, whereas that for all *Pinus* host taxa was approximately 32% of this area (Fig. 1 and Table 3). Predicted range overlap of *D. rhizophagus* and at least one host taxon exceeded 99.5%. Among individual *Pinus*

taxa, predicted range overlap with *D. rhizophagus* was highest for *P. engelmannii* and *P. leiophylla* and lowest for *P. oocarpa* (Table 3; see Supporting information, Fig. S2). Suitable habitat for *D. rhizophagus* approximately follows the spine of the SMOc from its intersection with the Tran-Mexican Volcanic Belt of central Mexico in the eastern portion of the state of Nayarit, southern Zacatecas and northern Jalisco to the northern end of the range in Sonora and Chihuahua (Fig. 1). The majority of suitable habitat is in the states of Durango and Chihuahua.

Significant suitable habitat also occurs over approximately 2374 km^2, primarily > 2000 m in 14 Sky Island mountain ranges of the Madrean Archipelago in Sonora, Chihuahua, Arizona and New Mexico (see Supporting information, Table S4) where no occurrences of *D. rhizophagus* have been recorded. Our results also indicate suitable habitat exists in the north-western portions of the Sierra Madre Oriental in Mexico and in southern Texas (Fig. 1; see also Supporting information, Table S4).

Estimates of the total area currently represented by occurrences of *D. rhizophagus* ranged from less than 1% of the total suitable habitat with a 0.5- or 1.0-km buffer (0.21%, 255 km^2; 0.75%, 895 km^2) to approximately 11% of the suitable habitat with a 5-km buffer (11.0%, 13 118 km^2). Occurrences of *D. rhizophagus* on the margins of suitable habitat in the SMOc can all be connected to large contiguous areas of suitable habitat in the central region of the range over *D. rhizophagus* habitat gaps less than 10 km. These areas occur in eastern Sonora, central and western Chihuahua, southern Durango, and northern Jalisco (Fig. 1). Connecting the two occurrences in northern Jalisco requires crossing a gap of approximately 2 km that is classified as unsuitable habitat for both *D. rhizophagus* and pine. Similarly, a gap of 23 km in *D. rhizophagus* habitat separates two occurrences in northern Sinaloa with the central SMOc habitat. This gap also contains patches of nonpine habitat but these are all less than 2 km in diameter.

Predicted future environmental conditions

Predicted values for all selected measures of temperature increased significantly at *P. engelmannii* occurrence locations for both GCMs and emissions scenarios for the period 2040–2069 relative to current conditions (Table 2). Annual mean temperature was predicted to increase by a mean of 2.1 °C with the highest proportional increases in mean temperature in the coldest quarter. Temperature seasonality (coefficient of variation for mean monthly temperature) was also predicted to increase under all future scenarios as a result of greater increases in winter temperature compared with the increases in summer temperature.

Relative changes in precipitation predicted for 2040–2069 were generally less consistent among GCMs and emissions scenarios than were temperature changes (Table 2). Precipitation in the driest quarter was predicted to decrease significantly under all scenarios. Change in precipitation seasonality was also inversely related to the change in cold-quarter precipitation. Relative to current conditions, HadCM3 (A2a) conditions would result in an increased annual precipitation that is more uniformly distributed throughout the year with increased precipitation in both the wettest and coldest quarters. There would be relatively little change in annual precipitation under HadCM3 (B1) conditions, although precipitation would be less uniformly distributed with increases in the wettest quarter and decreases in the coldest quarter. Annual precipitation would decrease under CGCM2.3.2a conditions with both emissions scenarios. With this GCM, precipitation would be less uniformly distributed and would decline in the wettest, driest and coldest quarters. For each of these variables with this GCM, changes in A2a conditions relative to current conditions are predicted to be larger than under the B1 scenario. Note that our data do not directly measure plant available moisture, which has been estimated from the difference between precipitation and evaporation (Seager *et al*., 2007).

Predicted suitable habitat: future climate conditions

The total area predicted to be suitable for *D. rhizophagus* declined under three of the four future climate scenarios modelled (Fig. 2 and Table 3). All projections predict a loss of *D. rhizophagus* habitat in the southern SMOc. The largest total decline in suitable habitat was predicted for HadCM3 (A2a) with much of this loss in habitat in the Madrean Archipelago of Sonora and at lower elevations of the SMOc in Chihuahua (Fig. 2A). A loss of suitable habitat is also seen in north-western Chihuahua under HadCM3 (B1) but this is accompanied by gain of habitat at lower elevations in the SMOc in east central Sonora, central Chihuahua and north central Durango. This scenario is also associated with gain of significant habitat in north-western Zacatecas and south-western New Mexico (Fig. 2B). A loss of habitat in Sonora and Chihuahua predicted with CGCM2.3.2a (A2a) (Fig. 2C) closely mirrors that seen with HadCM3 (A2a). However, under this scenario, significant areas of relatively isolated habitat occur in south-eastern Arizona, as well as south central and south-western New Mexico. Under CGCM2.3.2a (B1), there would be less habitat loss in the northern portions of the current range than under the other scenarios (Fig. 2D). Small areas of habitat gain would also occur in south central Chihuahua and north central Durango, whereas a large area of habitat gain would occur in north-western Zacatecas. In all scenarios, novel habitat predicted to occur in areas isolated from the SMOc are uniformly > 130 km from any known *D. rhizophagus* occurrence location (Figs 1 and 2).

Certain areas would contain predicted suitable habitat for *D. rhizophagus* regardless of future climate projection. For example, high-elevation areas in western Chihuahua and Durango contain large contiguous areas of predicted suitable habitat under all model scenarios (see Supporting information, Fig. S3). Smaller somewhat isolated patches of consistent suitable habitat would also occur in eastern Sonora, north-western Chihuahua, southern Arizona, northern Coahuila and southern Texas.

The total combined area of suitable habitat for *Pinus* hosts increased or remained nearly constant with HadCM3 scenarios for 2040–2069 but declined overall under CGCM2.3.2a scenarios (Table 3; see also Supporting information, Fig. S4).

Table 3 Area of predicted suitable habitat for *Dendroctonus rhizophagus* and *Pinus* host species under current conditions (1950–2000) and under four future climate scenarios over the entire study area[a]

Taxon/combination of taxa	Current conditions		Percent change in 2040–2069 relative to current conditions							
			UKMO-HadCM3				MRI-CGCM2.3.2a			
			A2a		B1		A2a		B1	
	Area (×1000 km²)	Range overlap (%)[b]	Area	Range overlap[b]	Area	Range overlap	Area	Range overlap	Area	Range overlap
All host *Pinus* taxa[c]	393.1	99.6	+0.2	+0.4	+12.4	−2.7	−8.5	0	−5.7	−1.0
Pinus engelmannii	204.8	96.6	−44.6	−0.4	−39.3	−25.1	−37.2	−12.4	−31.7	−7.3
Pinus leiophylla	230.6	96.6	+41.1	+3.3	+48.1	−4.5	+15.4	+0.2	+6.5	−0.1
Pinus ponderosa	213.8	89.9	+6.2	+1.8	−36.6	−50.4	−35.5	−6.2	−21.6	−8.2
Pinus durangensis	228.3	89.4	−18.2	+10.9	−2.1	−6.0	−17.7	+1.6	−8.5	+6.7
Pinus oocarpa	151.5	56.1	−3.4	+21.9	−15.0	−2.5	−19.4	+21.4	−16.1	+0.9
Pinus herrerae	118.1	60.6	+4.3	+47.2	+8.5	+2.5	−20.5	+3.3	−18.1	−2.1
Pinus lumholtzii	185.0	85.3	−4.1	+14.5	+31.4	+3.5	−5.6	+6.6	+5.8	+10.7
Pinus strobiformis	107	70.4	−9.9	+15.3	−48.0	+16.8	−82.8	+7.5	−52.8	+25.1
Dendroctonus rhizophagus	119.0	–	−42.5	–	+21.3	–	−23.7	–	−18.1	–
Dendroctonus rhizophagus and host *Pinus*	118.6	99.6	−42.3	+0.4	+17.9	−2.7	−23.7	0	−19.0	−1.0
Pinus host and not *Dendroctonus rhizophagus*	274.6	–	+15.5	–	+10.0	–	−2.0	–	+0.1	–
Dendroctonus rhizophagus and not host *Pinus*	0.46	–	−100.0 (0)[d]	–	+884.8 (4.53)	–	−36.0 (0.32)	–	+200.0 (138)	–

[a]Area bounded by 21.0 to 33.5°N, −112.0 to −102.5°W. Areas were derived from mean MAXENT derived habitat suitability maps based on maximum training sensitivity plus specificity threshold in 10 replicate runs visualized in Albers equal-area projections with standard parallels at one sixth of the latitudinal range from the northern and southern limits of the area of interest.
[b]Range overlap = [area suitable for pine taxon (taxa) and *D. rhizophagus*]/(area suitable for taxon with smaller range).
[c]All but *P. strobiformis* are members of Section Trifoliae (Gernandt *et al.*, 2005) and with > 30 georeferenced collection locations in the study area.
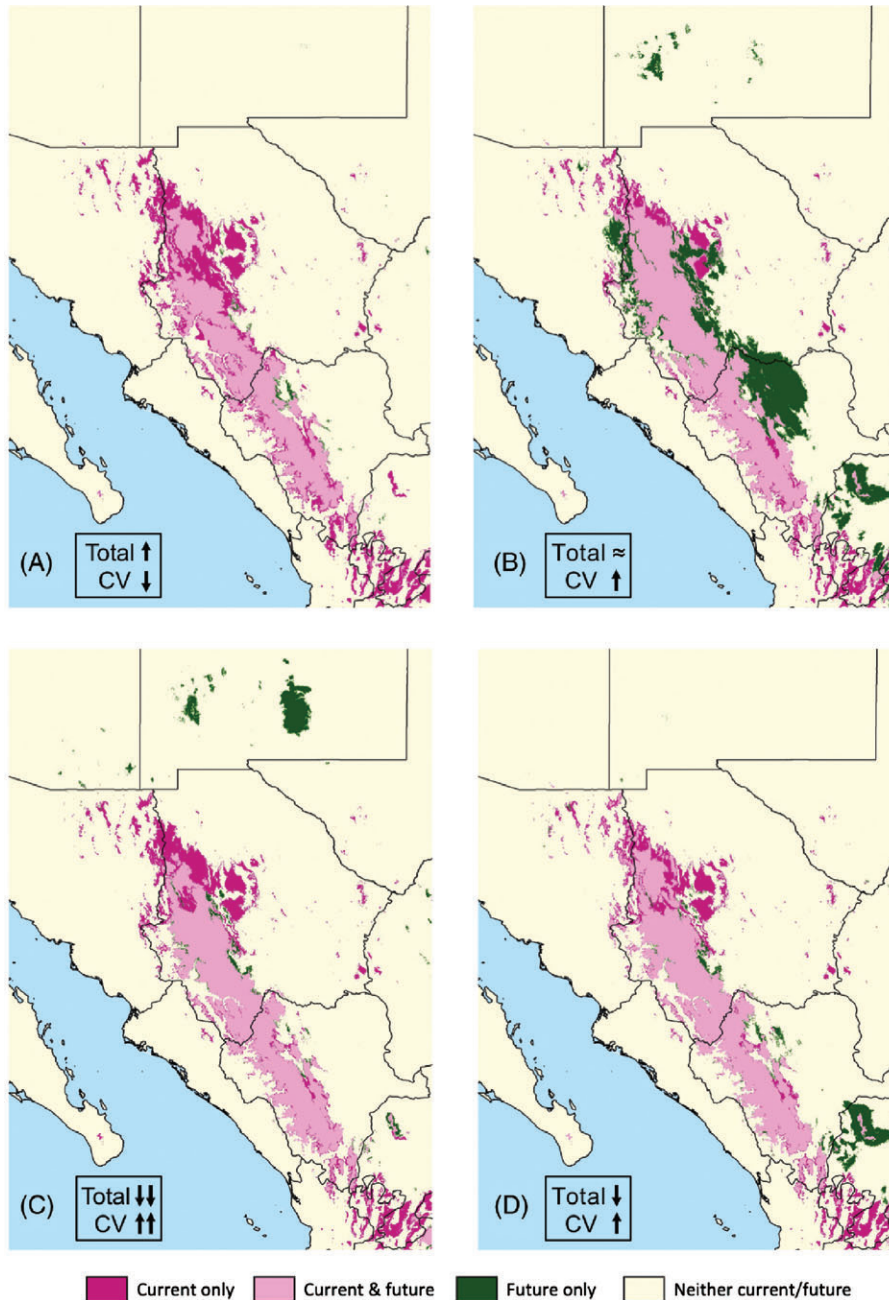[d]Values in parenthesis represent the predicted area × times 1000 km².

Figure 2 Predicted suitable habitat for *Dendroctonus rhizophagus* under current conditions (1950–2000) and four scenarios based on global climate models for the period 2040–2069. (A) HadCM3 (A2a), (B) HadCM3 (B1), (C) CGCM2.3.2a (A2a), (D) CGCM2.3.2a (B1). Total, total annual precipitation; CV, coefficient of variation in monthly precipitation, with both expressed relative to current conditions at current locations of *Pinus engelmannii* (see Supporting information, Fig. S1).

Under both emissions scenarios for HadCM3, pine habitat gains would occur on the margins of current habitat in the eastern Madrean Archipelago of Sonora, in central Arizona and New Mexico, the north-east margins of the SMOc in Chihuahua, and in north central Durango and central Zacatecas (see Supporting information, Fig. S4a, b). Gain of suitable habitat was also predicted for central Zacatecas and southern Baja California Sur with HadCM3 (B1). No significant loss of suitable habitat

was predicted with HadCM3 (A2a) but significant habitat losses are predicted with HadCM3 (B1) in extreme northern Sonora, central Arizona, western Texas and New Mexico, southern Chihuahua, west central Coahuila, extreme western Durango, southern Sinaloa, and coastal Nayarit (see Supporting information, Fig. S4a, b). Under CGCM2.3.2a conditions, large suitable habitat losses would be predicted in south-eastern Arizona, south-western and south central New Mexico, south

central Chihuahua, west central Coahuila, southern Sinaloa, and coastal Nayarit (see Supporting information, Fig. S4c, d). Additional habitat gains would occur in west central Texas. With this GCM and emissions scenario A2a, additional habitat losses would be predicted in central Arizona and western Texas (see Supporting information, Fig. S4c), whereas, with a B1 scenario, both habitat gains and losses would be predicted in western Texas, and gains would be seen in central coastal Sinaloa (see Supporting information, Fig. S4d).

Regardless of the future climate projections modelled, areas of contiguous suitable habitat for at least one *Pinus* host taxon of *D. rhizophagus* would be predicted to occur under all four future climate scenarios over large areas along the length of the SMOc, the northern Sierra Madre Oriental, the Madrean Archipelago, and mountainous areas of central Arizona and New Mexico (see Supporting information, Fig. S5). However, a variety of patterns were seen in changes in the areas of suitable habitat for individual *Pinus* taxa under future climate scenarios. The area of suitable habitat for *P. leiophylla* increased under all scenarios with especially large gains in northern Sonora, as well as central Arizona and New Mexico (Table 3; see also Supporting information, Figs S6–S9). The area of suitable habitat also consistently decreased for *P. engelmannii*, *P. durangensis*, *P. oocarpa*, and *P. strobiformis* in all scenarios.

Under current conditions, only 0.4% of predicted *D. rhizophagus* suitable habitat was predicted to be currently unsuitable for *Pinus* hosts (Table 3). This percentage ranged from 0% to 3.2% (mean 1.3%) over the four future climate scenarios. However, range overlap between *D. rhizophagus* and all *Pinus* host taxa showed relatively little change (< 2.8%) under all future climate scenarios (Table 3; see also Supporting information, Fig. S10). Modelled range overlap between *D. rhizophagus* and individual *Pinus* taxa did show some significant changes (Table 3; see also Supporting information, Figs S11–S14). Reflecting changes in area of suitable habitat, the range overlap of *D. rhizophagus* declined with *P. engelmannii* and increased with *P. strobiformis* and *P. lumholtzii* under all scenarios.

Discussion

Our HDMs indicate that suitable habitat for *D. rhizophagus* may currently extend across wide contiguous areas of the SMOc and bordering mountain ranges (Fig. 1). As would be expected, we have also shown that the vast majority of this habitat co-occurs with modelled suitable habitat for mature individuals of known *Pinus* hosts of this insect (Table 2). These analyses provide an approximate outline of the geographical boundaries for areas of potential *D. rhizophagus* occurrence. Correlative modelling techniques offer the opportunity to utilize occurrence and environmental data in the absence of more extensive response data to analyze and project distribution in unexplored and future environments.

Geographical analysis of occurrence records shows that *D. rhizophagus* has occurred across a remarkably variable range of environmental conditions within the SMOc and that two different multivariate and largely non-overlapping descriptions of environmental variation (and suitable habitat) apply in two main regions of its range (Table 1). Examination of occurrence

records and our HDMs presents a hypothesis regarding the natural history and habitat preference of *D. rhizophagus*. In the northern part of its current range (North cluster), pine regeneration events, and therefore seedling hosts, are probably less common than farther south where precipitation is higher and regeneration may be more frequent (Puhlick *et al.*, 2012). However, in the northern SMOc, *D. rhizophagus* occurs on sites that are remarkably arid (over the period 1950–2000) relative to the mean values for *Pinus* taxa that may be sympatric with it (Table 1). It is possible that *D. rhizophagus* occurs on these sites because the relative aridity there slows seedling growth such that susceptible hosts from a given regeneration event are available for attack over much longer periods of time.

Occurrences of *D. rhizophagus* are necessarily associated with antecedent environmental conditions that resulted in the establishment of seedlings of host taxa (Sanchez-Martinez & Wagner, 2009). Accordingly, the suitable habitat for this insect approximates the host regeneration niche (Grubb, 1977; McKenzie *et al.*, 2003; Sillero, 2011). Outside of plantations, regeneration requires that mature seed trees of host species be present. Our models of habitat suitability for host pine taxa describe this essential component of *D. rhizophagus* habitat. However, a suitable insect habitat would also require seed production on these trees and conditions leading to relatively high densities of seedling trees (Thomas, 1970; Sanchez-Martinez & Wagner, 2009) within flight distance of adult insects. The successful regeneration of coniferous trees in the Madrean Archipelago (and likely at least in the northern SMOc) is episodic and linked with periods of comparatively higher annual precipitation (Swetnam & Betancourt, 1998; Fulé & Covington, 1999; Barton *et al.*, 2001; Park, 2003; Brown & Wu, 2005; Fulé *et al.*, 2005; Puhlick *et al.*, 2012). The relatively warm and wet period between 1978 and 1998, which has been associated with increased seedling regeneration in the south-western U.S.A. (Savage *et al.*, 1996; Mast *et al.*, 1999) and generally reduced wildfire (Mouillot & Field, 2005), is coincident with a large *D. rhizophagus* infestation in north-western Chihuahua when >2 000 000 seedling trees were reported to be killed (Estrada-Murrieta, 1983). Although not all *D. rhizophagus* occurrences are dated, 66% (North cluster) and 35% (South cluster) of dated occurrence records trace to the period from 1999 to 2010, suggesting that many of these may represent seedlings from the 1978–1998 regeneration. Some evidence (Fulé & Covington, 1997; Rodriguez-Trejo & Fulé, 2003) suggests that recent fire absence may also be associated with increased seedling densities in the SMOc. Incorporating historical contingencies such as these within HDMs may improve their predictive power (Jackson *et al.*, 2009; Bateman *et al.*, 2011).

Although *D. rhizophagus* occurrences are generally clustered, the confirmed species range covers a potential dispersal path of more than 1000 km. Occurrence locations are also spread fairly uniformly along the spine of the SMOc but some marginal occurrences within this range are isolated by >100 km (Fig. 1). These observations suggest that *D. rhizophagus* has been able to disperse quite widely into new habitat patches, although the rate at which this may have occurred is unknown. However, a comparison of occurrence locations and suitable habitat patches indicates no evidence for dispersal of *D.*

rhizophagus having occurred over distances of nonsuitable (*D. rhizophagus*) habitat greater than 23 km and, generally, these distances are less than 10 km. There is also no evidence that the dispersal of *D. rhizophagus* has occurred through patches of habitat greater than 2 km in diameter, which is considered unsuitable for both *D. rhizophagus* and a *Pinus* host. Our analysis would indicate that natural dispersal from the SMOc into habitat in peripheral isolated mountain ranges separated by 10–40 km of pine-free habitat is unlikely. It should be noted that natural dispersal from areas of current predicted habitat to some areas of presently isolated predicted future habitat of *D. rhizophagus* and its pine hosts would require long-distance dispersal (> 60 km) over areas of currently nonsuitable habitat (Fig. 2B, C) (Trakhtenbrot *et al*., 2005). Reforestation projects have been conducted in pine forests of the SMOc (Mexal, 1996; CONAFOR, 2002; Powers *et al*., 2005) using nursery grown seedlings. If *D. rhizophagus* had infested nurseries, then it is possible that at least some dispersal may have been associated with reforestation activities.

The four future climate scenarios that we examined suggest generally warmer and either wetter or similar (HadCM3) or drier (CGCM2.3.2a) conditions at high elevations in the SMOc and Madrean Archipelago for the period 2040–2069 (Table 2). Our habitat suitability models applied to these scenarios suggest that *D. rhizophagus* habitat will typically coincide with that of mature *Pinus* hosts in the future (Table 3; see also Supporting information, Fig. S10), although the most commonly encountered host species may differ from that under current conditions. This represents one of the first descriptions of possible changes in habitat distribution among *Pinus* taxa in this region under projected future climate scenarios. Importantly, core areas of *D. rhizophagus* and *Pinus* host habitat are predicted to persist regardless of the climate scenario along the western crest of the SMOc in western Chihuahua and Durango (see Supporting information, Fig. S3).

Acknowledgements

Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12007

 Figure S1. Occurrence locations for *Pinus engelmannii* (N = 271). Used here as a representative of pine habitat in the Sierra Madre Occidental and Madrean Archipelago for the description of current and predicted climate conditions.

Figure S2. Predicted suitable habitat for *Dendroctonus rhizophagus* and each of eight modelled *Pinus* hosts under current conditions (1950–2000). (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S3. Predicted suitable habitat for *Dendroctonus rhizophagus* over four scenarios based on global climate models for the period 2040–2069. The areas identified are based on the number of scenarios with predicted suitable habitat.

Figure S4. Combined predicted suitable habitat for eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* under current conditions (1950–2000) and four scenarios based on global climate models for the period 2040–2069. (a) HadCM3 (A2a), (b) HadCM3 (B1), (c) CGCM2.3.2a (A2a), (d) CGCM2.3.2a (B1). Total, total annual precipitation; CV, coefficient of variation in monthly precipitation, with both expressed relative to current conditions at current locations of *Pinus engelmannii* (see Supporting information, Fig. S1).

Figure S5. Predicted suitable habitat for eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* over four scenarios based on global climate models for the period 2040–2069. The areas identified are based on the number of scenarios with predicted suitable habitat.

Figure S6. Predicted suitable habitat for each of eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* under current conditions (1950–2000) and based on the HadCM3 (A2a) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S7. Predicted suitable habitat for each of eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* under current conditions (1950–2000) and based on the HadCM3 (B1) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S8. Predicted suitable habitat for each of eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* under current conditions and based on the CGCM2.3.2a (A2a) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S9. Predicted suitable habitat for each of eight modelled *Pinus* hosts of *Dendroctonus rhizophagus* under current conditions and based on the CGCM2.3.2a (B1) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*,

(e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S10. Predicted suitable habitat for *Dendroctonus rhizophagus* and combined suitable habitat for eight modelled *Pinus* hosts under four scenarios based on global climate models for the period 2040–2069. (a) HadCM3 (A2a), (b) HadCM3 (B1), (c) CGCM2.3.2a (A2a), (d) CGCM2.3.2a (B1). Total, total annual precipitation; CV, coefficient of variation in monthly precipitation, with both expressed relative to current conditions at current locations of *Pinus engelmannii* (see Supporting information, Fig. S1).

Figure S11. Predicted suitable habitat for *Dendroctonus rhizophagus* and eight modelled *Pinus* hosts under the HadCM3 (A2a) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S12. Predicted suitable habitat for *Dendroctonus rhizophagus* and eight modelled *Pinus* hosts under the HadCM3 (B1) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S13. Predicted suitable habitat for *Dendroctonus rhizophagus* and eight modelled *Pinus* hosts under the CGCM2.3.2a (A2a) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Figure S14. Predicted suitable habitat for *Dendroctonus rhizophagus* and eight modelled *Pinus* hosts under the CGCM2.3.2a (B1) global climate model for the period 2040–2069. (a) *Pinus engelmannii*, (b) *Pinus leiophylla*, (c) *Pinus ponderosa*, (d) *Pinus durangensis*, (e) *Pinus oocarpa*, (f) *Pinus herrerae*, (g) *Pinus lumholtzii*, (h) *Pinus strobiformis*.

Table S1. Source and number of *Dendroctonus rhizophagus* occurrences used in habitat suitability modelling.

Table S2. Mean area under the operating curve (AUC) and mean ± SE of omission fractions for training and testing of final MAXENT models over 10 replicate runs for *Dendroctonus rhizophagus* (in bold) and *Pinus* host species/intraspecies cluster.

Table S3. Mean ± SE normalized permutation importance values for environmental variables within final MAXENT models for *Dendroctonus rhizophagus* (in bold) and *Pinus* host species/cluster groups over 10 replicate (cross-validation) runs.

Table S4. Area of predicted current suitable habitat for *Dendroctonus rhizophagus* and at least one taxon of *Pinus* identified as a host in mountain ranges within our study area in Mexico and the U.S.A. that are not considered part of the Sierra Madre Occidental.

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