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Predicting the Distribution of the Amphibian Pathogen *Batrachochytrium dendrobatidis* in the New World[1]

Santiago R. Ron[2,3]

Section of Integrative Biology, C0930, and Texas Memorial Museum, The University of Texas, Austin, Texas 78712, U.S.A.

ABSTRACT

One application of ecological niche modeling is predicting suitable areas for the establishment of invasive species. Herein, I model the fundamental niche of the chytrid fungus *Batrachochytrium dendrobatidis*, a pathogen linked to amphibian declines on several continents. Niche models were generated with the Genetic Algorithm of Rule-Set Prediction using point distribution data of the pathogen and digital maps of environmental variables integrated in a GIS environment. The distribution of regions suitable for *B. dendrobatidis* in the New World is extensive and includes significant portions of: (1) Sierra Madre Occidental pine-oak forest; (2) Sonoran and Sinaloan dry forest; (3) Veracruz moist forest; (4) Central America east from the Isthmus of Tehuantepec; (5) Caribbean Islands; (6) temperate forest in Chile and western Argentina south of latitude 30°S; (7) Andes above 1000 m of altitude in Venezuela, Colombia, and Ecuador; (8) eastern slopes of the Andes in Peru and Bolivia; (9) Brazilian Atlantic forest; (10) Uruguay, Paraguay, and northeastern Argentina; (11) southwestern and Madeira-Tapajós Amazonian tropical rainforests. The regions with the highest suitability for *B. dendrobatidis* include habitats that contain the world's most diverse amphibian faunas. Models were built with New World localities, but also showed strong predictability for *B. dendrobatidis* localities in the Old World. Out of a total of 59 reported Old World localities for *B. dendrobatidis*, 56 occurred within regions with high predicted suitability. I also present analyses of the environmental envelope of *B. dendrobatidis* and discuss the implications of the results for the conservation of amphibians in the neotropics.

RESUMEN

Una de las aplicaciones de los modelos de nicho ecológico es la predicción de áreas idóneas para el establecimiento de especies invasivas. En el presente trabajo modelo el nicho fundamental del hongo quítrido *Batrachochytrium dendrobatidis,* un patógeno que ha sido relacionado con disminuciones poblacionales de anfibios en varios continentes. Los modelos de nicho fueron generados con el Algoritmo Genético de Conjuntos de Reglas de Predicción, basado en datos de distribución puntual del patógeno y variables ambientales obtenidas de mapas digitales integrados por medio de sistemas de información geográfica. La distribución de regiones idóneas para el quítrido en el Nuevo Mundo es amplia e incluye: (1) bosque de pino y roble en la Sierra Madre Occidental; (2) bosque seco de Sonora y Sinaloa; (3) bosque húmedo de Veracruz; (4) América Central al este del Isthmus of Tehuantepec; (5) Islas del Caribe; (6) bosques temperados en Chile y el occidente de Argentina, al sur de 30°S; (7) Andes sobre 1000 m de altitud en Venezuela, Colombia, y Ecuador; (8) estribaciones orientales de los Andes en Perú y Bolivia; (9) bosque atlántico del Brasil; (10) Uruguay, Paraguay, y nororiente de Argentina; (11) bosques lluviosos tropicales de la Amazonía sur occidental y Madeira-Tapajós. Las regiones con las probabilidades más altas de presencia del nicho del quítrido incluyen los hábitats que tienen las faunas de anfibios más diversas del mundo. Los modelos fueron construidos en base a localidades del Nuevo Mundo solamente. Sin embargo, mostraron una alta predictividad de presencia del quítrido en el Viejo Mundo. De las 59 localidades de presencia conocida del patógeno en África, Australia, Europa, y Nueva Zelanda, 56 fueron incluidas en regiones de alta probabilidad de presencia del quítrido. Además de los mapas de distribución, presento análisis de la envoltura ambiental del quítrido y discuto las implicaciones de los resultados para la conservación de los anfibios del Neotrópico.

Key words: Amphibian population declines; Batrachochytrium dendrobatidis; *chytridiomycosis; ecological niche modeling; emerging infectious disease; GARP; Genetic Algorithm of Rule-Set Prediction; geographic range; neotropics.*

DURING THE LAST DECADES, SEVERAL EMERGENT INFECTIOUS DISEASES (*e.g.*, AIDS, Ebola) have been reported in humans, domestic animals, and/or wildlife species (Daszak *et al.* 2000). Often, the emergence of these diseases is coupled with a significant increase of the distributional range of the pathogen facilitated by anthropogenic introduction, with regions of potential colonization dependent on the ecological niche of the pathogen. One of the applications of ecological niche modeling is predicting ecologically suitable areas for the establishment of invasive species (Zalba *et al.* 2000, Peterson & Vieglais 2001, Peterson 2003). This methodology builds an ecological niche model based on the values of environmental variables (niche dimensions) at known localities of the target species. The niche model is then projected into geographic space to identify regions where the species is likely to be present but not yet discovered, or where it may become established after dispersal. This methodology has proven to be highly accurate in predicting the ranges in which invasive exotic species become established (Peterson *et al.* 2003).

Pathogens (especially viruses and fungi) are among the causes invoked to explain amphibian declines worldwide (Berger *et al.* 1998, Daszak *et al.* 1999, Lips 1999, Longcore *et al.* 1999, Carey 2000, Bosch *et al.* 2001, Green and Sherman 2001, Bradley *et al.* 2002, Bonaccorso *et al.* 2003, Daszak 2003, Jancovich *et al.* 2003, Muths *et al.* 2003, Kiesecker *et al.* 2004, Pasmans *et al.* 2004, La Marca *et al.* 2005). Although half of the world's amphibian species inhabit the neotropical region (Duellman 1999b) and reports of declines are widespread (*e.g.,* Pounds *et al.* 1999, Young *et al.* 2001), little is known about the taxonomic and geographic distribution of amphibian diseases in this region. One pathogen likely contributing to neotropical amphibian declines is *Batrachochytrium dendrobatidis* (Berger *et al.* 1998; Lips 1998, 1999; Ron and Merino-Viteri 2000; Bonaccorso *et al.* 2003; Lips *et al.* 2003a; Ron *et al.* 2003; Burrowes *et al.* 2004). This fungus is an emerging infectious disease of amphibians that invades keratinized areas of the skin

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[2] Museo de Zoología, Centro de Biodiversidad y Ambiente, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre y Roca, Aptdo. 17-01-2184, Quito, Ecuador.

[3] Corresponding author; e-mail: sron@mail.utexas.edu

of juveniles and adults, and the mouthparts of tadpoles. Amphibians are the only known hosts for *B. dendrobatidis*, but this disease shows low host specificity as indicated by a large number of infected species, most of them frogs (Daszak 2003; Appendix). The infection is restricted to the skin and recent evidence suggests that *B. dendrobatidis* can survive independently of a host (Johnson & Speare 2003).

Chytridiomycosis has been suggested as a causal agent of amphibian population declines (Lips 1998, 1999; Muths *et al.* 2003; La Marca *et al.* 2005). It has been found on all continents except Asia (Berger *et al.* 1998, Lips 1999, Ron & Merino-Viteri 2000, Green & Sherman 2001, Bonaccorso *et al.* 2003, Lane *et al.* 2003). Genetic variability among *B. dendrobatidis* samples from different regions of the world suggests that the spread of the disease has occurred recently (Daszak 2003, Morehouse *et al.* 2003). An assessment of the potential extent of the spread of this pathogen depends partly on the characteristics of its ecological niche. In this article, I model the fundamental niche (*sensu* Hutchinson 1957) of *B. dendrobatidis* to identify suitable regions for its establishment in the New World. These models can identify unidentified portions of the true geographic range of *B. dendrobatidis* and locations of uncolonized but suitable regions. The results can be used to implement preventive actions that can preclude the introduction of *B. dendrobatidis* or ameliorate the impact of its establishment. I also project the models worldwide as independent test of model quality and analyze environmental conditions at known *B. dendrobatidis* localities and within areas of niche predicted presence. Although my findings have worldwide implications, the primary focus of the analyses is the neotropical region.

METHODS

SPECIES RECORDS AND ENVIRONMENTAL LAYERS.—Niche modeling is based on locality data of the pathogen and environmental data from digital maps (*e.g.*, annual temperature, annual precipitation, and altitude) integrated in a GIS environment. To build models, environmental values at localities of known occurrence are determined and then used to identify geographic regions that have similar combinations of environmental values. Localities for *B. dendrobatidis* were gathered from the scientific literature (Appendix). A total of 44 New World wild amphibian populations' localities were reported with enough precision to allow georeferencing (Appendix).

Twenty digital environmental layers (resolution 2.5′) were obtained from WorldClim (Hijmans *et al.* 2004). I eliminated Environmental layers highly correlated to others. The included layers were: (1) altitude, (2) mean annual temperature, (3) isothermality, (4) temperature seasonality, (5) minimum temperature of coldest month, (6) maximum temperature of warmest month, (7) temperature annual range, (8) mean temperature of the driest quarter, (9) mean temperature of the wettest quarter, (10) mean diurnal range, (11) annual precipitation, (12) precipitation of the wettest month, (13) precipitation of driest month, (14) precipitation of the warmest quarter, (15) precipitation of coldest quarter, and (16) precipitation seasonality. Although encompassing relatively few of the possible fundamental niche dimensions (*sensu* Hutchinson 1957), the included digital environmental coverages are among the most important influencing species' macrodistributions. "Quarter" is a period of three consecutive months; see Hijmans *et al.* (2004) for computational details of environmental layers.

NICHE MODELING WITH GARP.—Niche models were generated with the Genetic Algorithm of Rule-Set Prediction (GARP) (http://biodi.sdsc.edu/bsw_home.html; Stockwell & Noble 1992; examples of GARP uses can be found in Peterson & Cohoon 1999, Godown & Peterson 2000, Anderson *et al.* 2002a, and Parra-Olea *et al.* 2005). Genetic algorithms develop rules to build niche models by a process analogous to natural selection. First, the performances of sets of rules (*e.g.*, ranges of environmental variables at a group of known localities) are evaluated. Only the rules with the highest performance (*i.e.*, rules that define a niche with high predictive accuracy for known localities) are maintained for the next generation. Then, processes analogous to genetic mutation, recombination, and crossing over modify the rules randomly. Finally, the modified rules are selected before the next generation based on their performance. The process is iterated until additional generations do not improve the performance of the set of rules (for details see Stockwell & Peters 1999). GARP modeling was carried out on DesktopGARP v. 1.1.4 (Scachetti-Pereira 2001). The output for each model in DesktopGARP is a binary digital map with regions of niche presence and absence (niche as defined by the environmental dimensions examined).

Because of random components of the GARP algorithm, each replicate model is different. Out of 300 replicates 10 optimal models were selected. To select the optimal models, localities were divided into two sets (with random assignment). One set (24 localities) was used to build the models in DesktopGARP (training data). The remaining 20 localities (test data) were used as a test of model quality: The proportion of test localities included within presence regions of each model was compared to the proportion expected under a random model (Anderson *et al.* 2003). The selected models were those with not more than one test locality outside the presence area and with the lowest commission values (Anderson *et al.* 2003).

ArcMap 8.3 (ESRI 2003) with the Spatial Analyst extension was used to integrate the output from ten models. Each model was projected as a binary map (0 = areas of niche absence; 1 = presence). The ten maps were added and then divided by 10 generating a final map with values ranging from 0 to 1 (1 for those regions where all the models predicted niche presence). The resulting value (hereafter referred to as overlap index, OI) is interpreted as a measure of the strength in the prediction of niche presence. Regions with high OI on the maps are those where confidence for the presence of *B. dendrobatidis* niche is higher (*e.g.,* Fig. 1).

It is possible that the localities used to test model quality are not truly independent from training localities because geographic proximity can lead to spatial autocorrelation. To address this issue, I projected the models based on just New World localities onto all continents to predict suitable regions (*i.e.,* niche presence) in the Eastern Hemisphere. I georeferenced positive localities for the chytrid in the Eastern Hemisphere (59 localities in Africa, Australia, Europe, and New Zealand; compiled from the literature and only including records from natural populations; Appendix) and then I determined the proportion of those localities falling within suitable regions. I compared that proportion to the expected proportion for a random model with the same niche presence area (*e.g.,* a random model with a presence area comprising 50% of the total area is

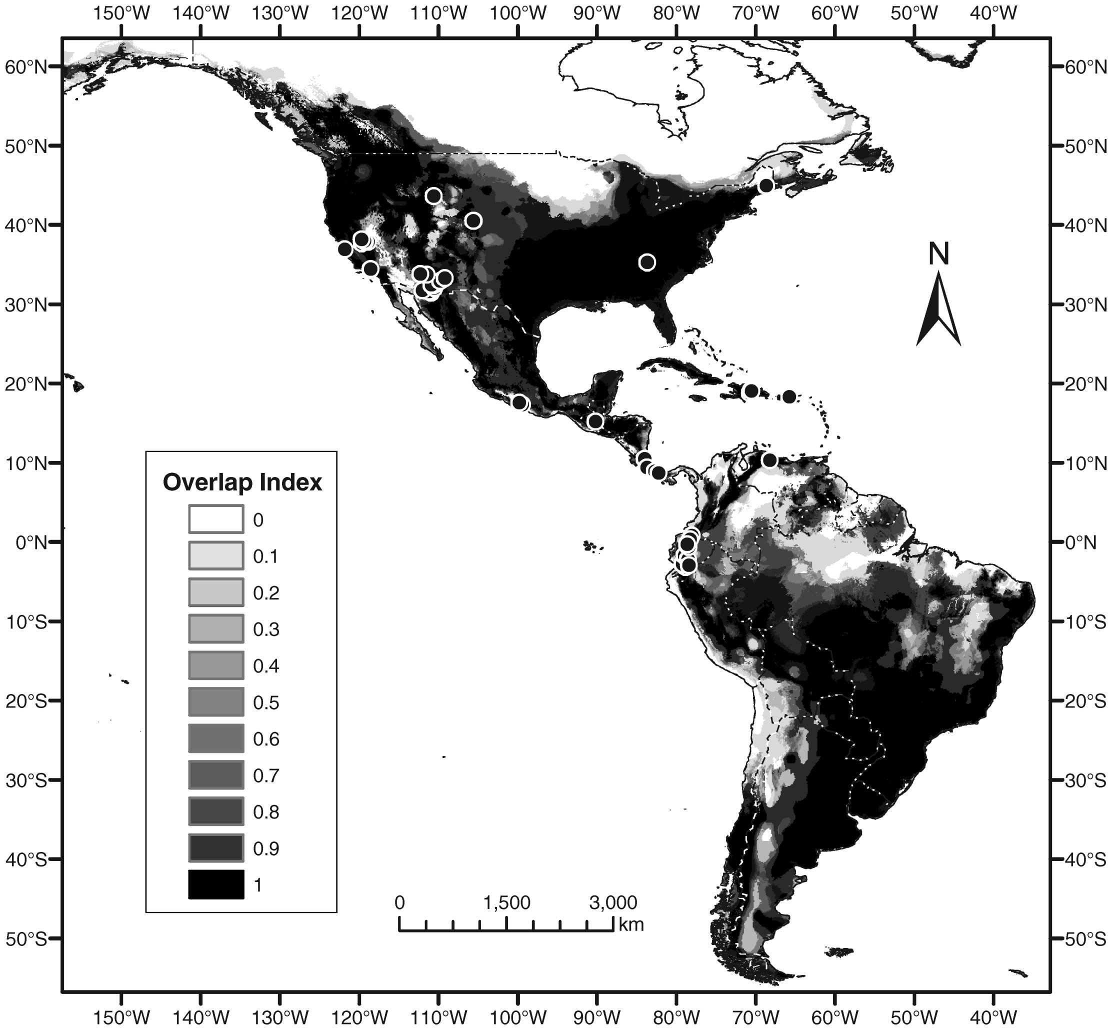

FIGURE 1. Predicted distribution of the fundamental niche of *Batrachochytrium dendrobatidis*. Darker regions are those where *B. dendrobatidis* niche presence was predicted by more models (*i.e.*, overlap index 1 means that ten out of ten models predicted presence; overlap index 0 means that none of the ten models did). The circles are localities of known occurrence of *B. dendrobatidis* used to build the predicted distribution. See Appendix for data sources.

expected to include 50% of the localities just by chance). Binomial tests (within the predicted area vs outside; $\alpha = 0.05$) were used to test for significance. The binomial probability was set as the presence area/total area. Inspection of localities on other continents and associated tests were carried out after the final maps were generated.

ENVIRONMENTAL ENVELOPE ANALYSES.—The zonal statistics routine (ArcMap 8.3, Spatial Analyst; ESRI 2003) was used to extract, from digital maps, values for 15 environmental variables (Hijmans *et al.* 2004) at the 44 New World localities for *B. dendrobatidis*. These values were used to run a principal components analysis (PCA; implemented in SPSS v. 11.5; SPSS 2002) to visualize the relative degree of clustering in environmental space among New World localities where *B. dendrobatidis* has been found.

To characterize the environmental envelope of the neotropical region, 4000 random locations were generated with a random point generator in ArcMap 8.3 (ESRI 2003). Values for 15 environmental variables were estimated at each location from digital maps (zonal statistics in ArcMap 8.3). The environmental values at each of the 4000 random locations and the 44 *B. dendrobatidis*-positive localities in the New World were used to run a PCA to visualize the position of the positive localities compared to the environmental space available in the neotropics (as defined by the two first PCs). Additionally, these data were contrasted with those from 2500 random locations within the neotropical areas where the models predicted the highest suitability for *B. dendrobatidis* occurrence.

RESULTS

NICHE DISTRIBUTION MODELS IN THE NEOTROPICAL REGION.—Regions of likely occurrence of *B. dendrobatidis* in the New World are extensive (Figs. 1–3). The highest suitability ($\text{OI} \geq 0.7$) areas in the neotropics include significant portions of (1) Sierra Madre Occidental pine-oak

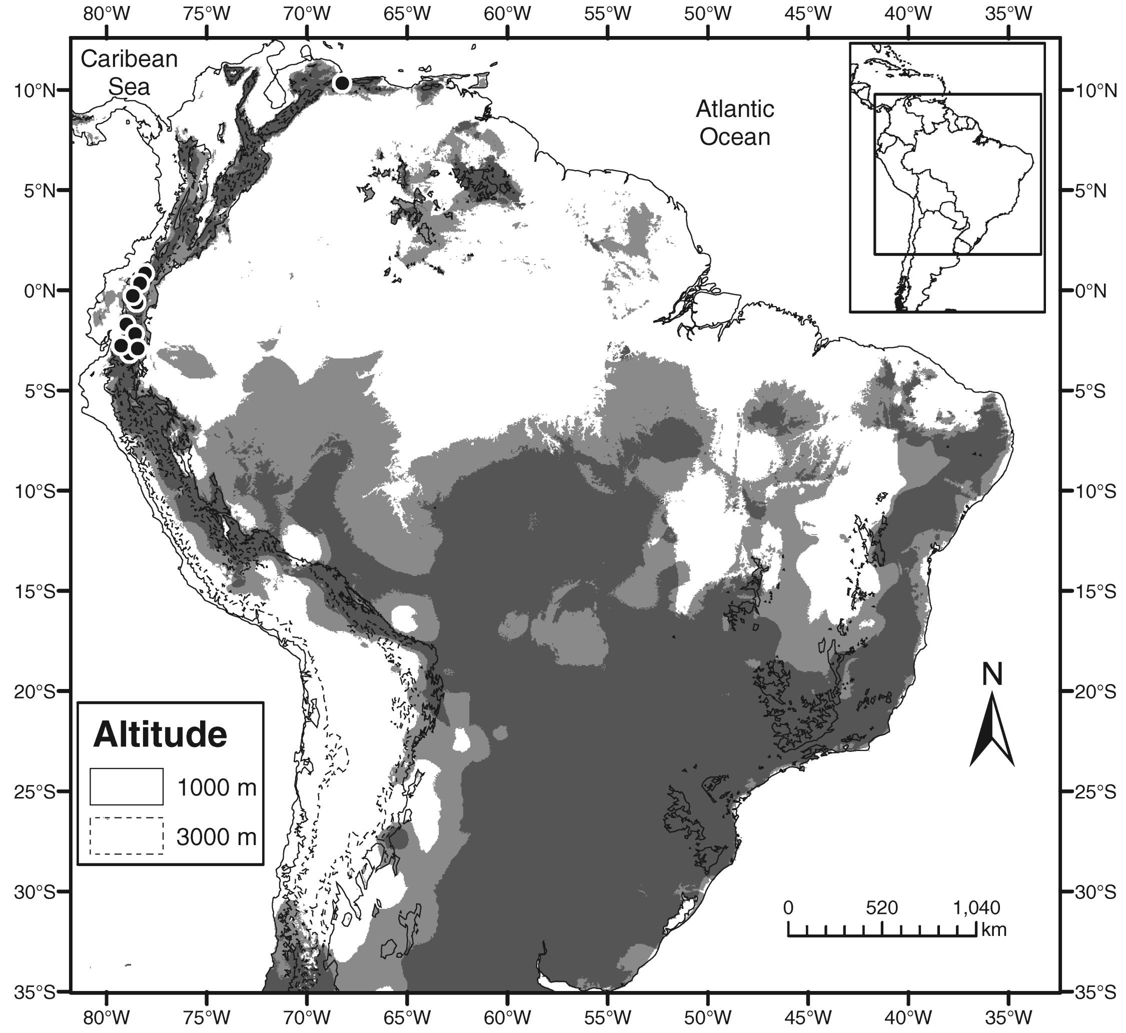

FIGURE 2. Predicted distribution of the fundamental niche of *Batrachochytrium dendrobatidis*. Dark gray regions are those where all ten models predicted niche presence; light gray areas = 7–9; white areas ≤6. The circles are localities of known occurrence of *B. dendrobatidis*. According to these predictions, suitable habitat for *B. dendrobatidis* occurrence is widespread in South America.

forest; (2) Sonoran and Sinaloan dry forest; (3) Veracruz moist forest; (4) Central America east from the Isthmus of Tehuantepec; (5) Caribbean Islands; (6) temperate forest in Chile and western Argentina south from latitude 30°S; (7) Andes above 1000 m of altitude in Venezuela, Colombia, and Ecuador; (8) eastern slopes of the Andes in Peru and Bolivia; (9) Brazilian Atlantic forest; (10) Uruguay, Paraguay, and northeastern Argentina; and (11) southwestern and Madeira-Tapajós Amazonian tropical rainforests.

Neotropical habitats with predicted low suitability ($\text{OI} \leq 0.2$; Fig. 1) include a diverse array of biomes and environmental conditions including: (1) Llanos in Colombia and Venezuela, (3) Chocoan tropical rainforest in Colombia, (4) Sechura and Atacama deserts, (2) Andean dry puna in southern Bolivian and northern Chile and Argentina, (5) Río Branco basin and Uatuma-Trombetas tropical rainforests in central Amazonia.

The New World models show a high predictability for *B. dendrobatidis* localities in the Old World (Fig. 4). Of the 59 known localities of the pathogen (14 in Africa, 39 in Australia, 3 in Europe, and 3 in New Zealand), 56 fall within regions that, according to the models, have high suitability for the occurrence of *B. dendrobatidis* ($\text{OI} \geq 0.7$). The exceptions are Bologna, Italy ($\text{OI} = 0.2$), Grobbelaars River, South Africa ($\text{OI} = 0.5$), and Big Tableland, Australia ($\text{OI} = 0.5$). Forty-seven localities fall within regions predicted by all models to have *B. dendrobatidis* ($\text{OI} = 1$). The proportion of localities predicted successfully is remarkably high considering that models were built from New World localities only, and suitable regions in the Eastern Hemisphere cover only a small portion of the total land area. Areas of $\text{OI} = 1$ cover only 11.8 percent and those with $\text{OI} \geq 0.7$ cover 23.5 percent of land area in this region. Location of the points within the predicted areas departed significantly from random expectations: for regions $\text{OI} = 1$, one-tailed binomial $P = 9.0 \times 10^{-33}$; for regions $P \geq 0.7$, binomial $P = 8.9 \times 10^{-32}$.

BATRACHOCHYTRIUM DENDROBATIDIS DISTRIBUTION IN NORTH AMERICA AND THE EASTERN HEMISPHERE.—According to the models (Fig. 1),

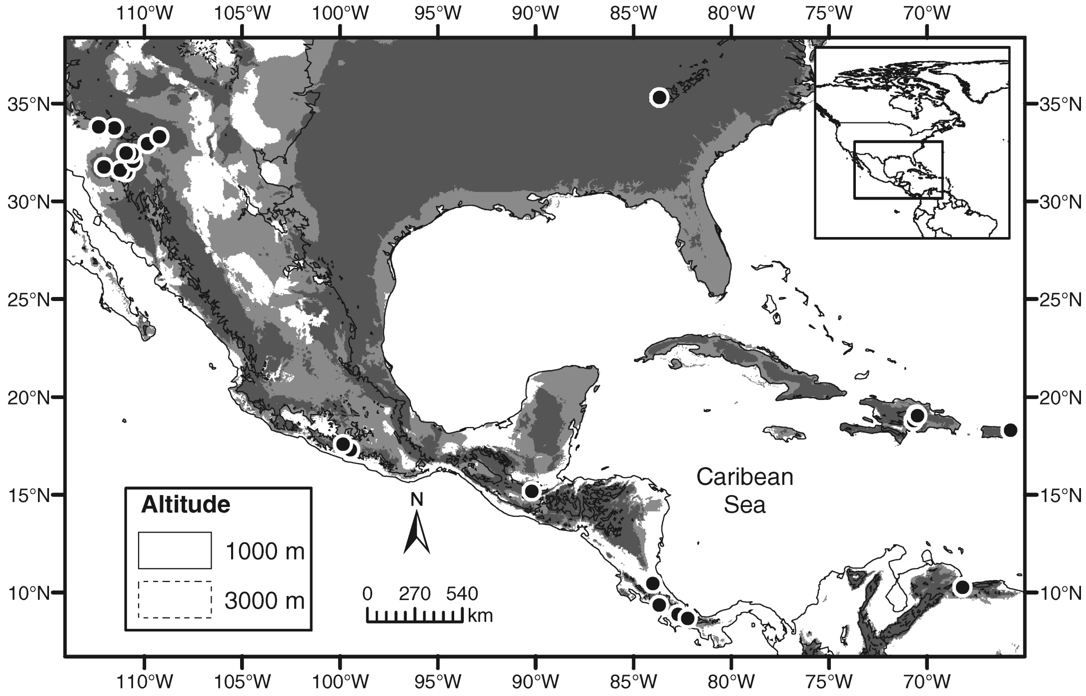

FIGURE 3. Predicted distribution of the fundamental niche of *Batrachochytrium dendrobatidis*. Dark gray regions are those where all ten models predicted niche presence; light gray areas = 7–9; white areas ≤6. The circles are localities of known occurrence of *B. dendrobatidis*. According to these predictions, suitable habitat for *B. dendrobatidis* occurrence is widespread in the region.

suitable areas for *B. dendrobatidis* in North America extend south from latitude 55°N on the western coast, from 40°N in the central Great Plains, and from 45°N on the eastern coast. The only habitats south of 50°N, where niche occurrence was predicted by two or fewer models, are parts of the Mojave and Sonoran deserts, and the shrub steppe in Wyoming and the Great Basin. In the Eastern Hemisphere, areas where *B. dendrobatidis* is predicted by all or most models include New Zealand, eastern, southern, and western Australia, New Guinea (especially along the Southeastern Papuan rainforest and parts of the Central Range montane forests), montane forests in Sumatra and Java, northern and southern Philippines, most of Japan, dry forests in central and eastern Indochina, subtropical forests in Vietnam and China, southern India, Anatolian forests and steppes, Europe south from about 55°N, United Kingdom, northwest Africa, tropical Africa between 10°N and 10°S, most of South Africa and eastern Mozambique, and eastern and central Madagascar.

ENVIRONMENTAL ENVELOPE.—The PCA of 4000 random locations in the neotropics shows that the *B. dendrobatidis*-positive localities in the New World are spread across a wide range of available environmental conditions (Table 1; Fig. 5A). The conditions under which *B. dendrobatidis* has been found in the neotropics represent a subset of the available conditions for the region (Fig. 5A). However, the bivariate environmental space unoccupied by neotropical localities is partly occupied by chytrid-positive localities in North America, suggesting that most environments in the neotropics may be suitable for *B. dendrobatidis* (Fig. 5A). Three principal components with eigenvalues > 1 were extracted from the PCA. Principal component I was positively correlated with mean temperature of coldest quarter of the year and minimum temperature of the coldest month of the year while principal component II was positively correlated with precipitation of the driest month and the driest quarter (Table 1; Fig. 5A).

According to the PCA of *B. dendrobatidis*-positive localities, there is considerable differentiation in environmental space between localities from the neotropical and neartic regions (Table 2; Fig. 5B). Three principal components with eigenvalues > 1 were extracted. Principal component I was positively correlated with precipitation (especially annual precipitation and precipitation of the wettest month), while principal component II was positively correlated with warmest temperatures (Table 2). Neotropical and neartic localities partly segregate in environmental space, especially along PC I (Fig. 5B) with the former having higher precipitation and higher temperature during the coldest month of the year (Fig. 5B).

Batrachochytrium dendrobatidis localities in the New World are characterized by a variety of temperature and precipitation regimes (Table 3). Mean annual air temperature ranges from −1.6°C (Wyoming) to 26.1°C (San Ramón de Saripiquí, Costa Rica). The five localities that reach the highest maximum temperatures (up to 39.6°C) are in Arizona; the five localities that reach the lowest coldest temperatures (down to −19.6°C) are in Wyoming, Maine, Colorado, and California. Annual precipitation ranged from 290 mm in Cottonwood Creek (Sonoran desert, Arizona) to 4383 mm in San Ramón de Saripiquí (Atlantic moist forest, Costa Rica). Most localities are in the highlands, 29 of 44 are above 1000 m in altitude.

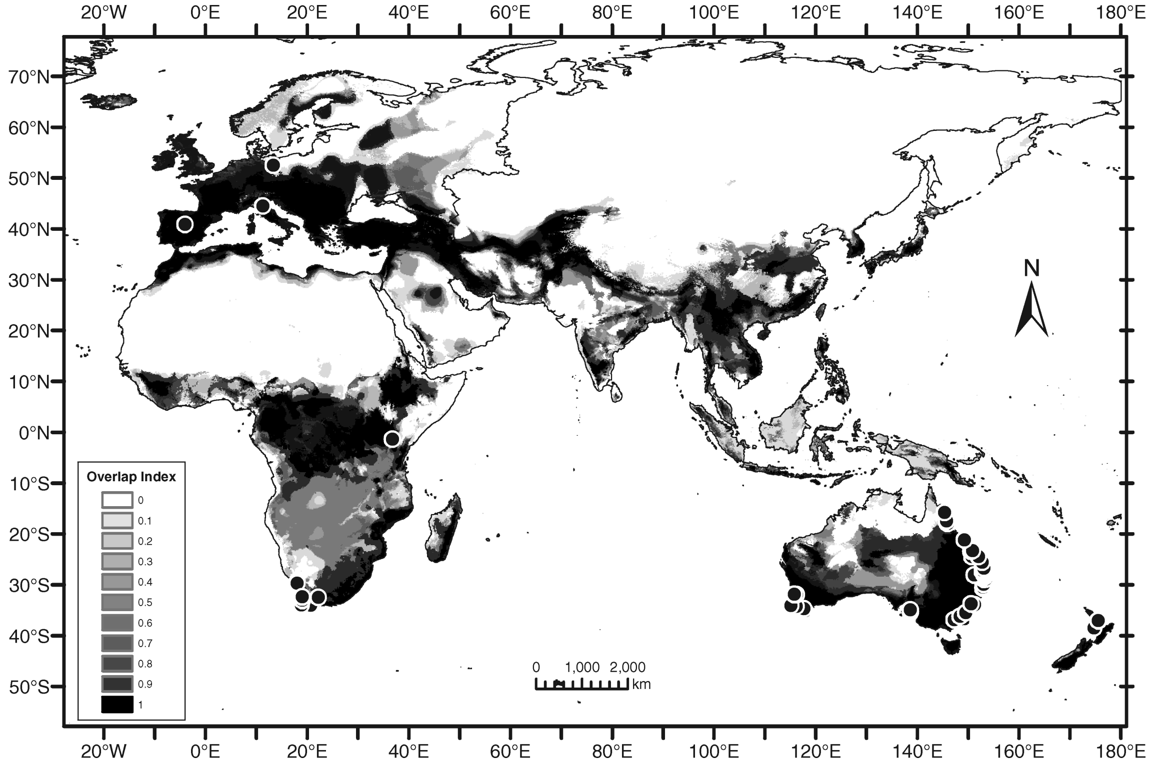

FIGURE 4. Predicted distribution of the fundamental niche of *Batrachochytrium dendrobatidis*. Darker regions are those where *B. dendrobatidis* niche presence was predicted by more models (*i.e.*, overlap index 1 means that ten out of ten models predicted presence; overlap index 0 means that none of ten models did). The predictions are based on *B. dendrobatidis* localities in the New World only (shown in Fig. 1). The circles are localities of known occurrence of *B. dendrobatidis* (see Appendix for data sources). Note that almost all the localities fall within high suitability regions indicating good model performance.

The relationship between mean annual temperature and annual precipitation at *B. dendrobatidis* localities and 4000 random locations within the neotropics is shown in Figure 6. None of the 21 neotropical localities of positive occurrence is in regions where annual precipitation is below 900 mm. However, mean annual precipitation at neotropical *B. dendrobatidis* localities (1836.9 mm; SD = 964.9) is not significantly different from the average at random localities (1671.0; SD = 969.3; Mann-Whitney $U = 39{,}564$, $P = 0.66$). Except at San Ramón de Saripiquí and Agua de Obispo (México), known neotropical *B. dendrobatidis* localities are not within regions with high mean annual temperature (>23°C), although those conditions are pervasive throughout the region (58% of the random localities have >23°C; Fig. 6). Mean annual temperature at known neotropical *B. dendrobatidis* localities (16.3; SD = 6.1) is below the average of random localities (21.4; SD = 6.3) and differences are significant (Mann-Whitney $U = 45{,}499$, $P < 0.001$).

A comparison of temperature and precipitation between the entire neotropical region and the subregions with niche presence OI = 1 shows that *B. dendrobatidis* is expected to occur under a wide variety of temperature and precipitation combinations. However, within the regions of predicted presence of *B. dendrobatidis*, the majority of habitats have mean annual temperature ranges between 20°C and 25°C and annual precipitation between 1500 and 2500 mm.

The relationship between maximum and minimum temperature shows that all neotropical *B. dendrobatidis* localities are arranged along the margin of this bivariate environmental space (Fig. 6). Neotropical-positive localities are characterized by lower warmest and higher coldest annual temperatures as compared to most random localities in the neotropics. The location of the neotropical-positive localities differs extensively from that of the localities in the more seasonal neartic region (Fig. 6).

DISCUSSION

SUITABLE REGIONS AND AMPHIBIAN DIVERSITY PATTERNS.—According to the niche models, neotropical amphibian faunas inhabit extensive regions with conditions suitable for the establishment of *B. dendrobatidis*. Available evidence, although still inconclusive, suggests that *B. dendrobatidis* can produce considerable reductions in the diversity of neotropical amphibian communities (Lips 1998, 1999; Lips *et al.* 2003a; Burrowes *et al.* 2004). If this is the case, the survival of a sizable portion of the world's amphibian species (half of which inhabit the neotropics) may be threatened by *B. dendrobatidis*.

Because not all species decline when exposed to *B. dendrobatidis*, its impact in the neotropics will depend on species-specific susceptibility. In Australia, *B. dendrobatidis* has infected 46 frog species of which 13 have declined and 3 are extinct (Collins & Storfer 2003). The impact may be even greater in neotropical faunas; monitoring of 99 species at four sites

TABLE 1. *Character loading and percentage of variance explained by principal components (PC) I–III for 15 environmental variables at 4000 random locations through the neotropics (Fig. 5A). Forty-four positive localities of* Batrachochytrium dendrobatidis *in the New World were also included. Bold figures indicate variables with the highest loadings.*

	PC I	PC II	PC III
Mean annual temperature	0.907	−0.407	0.031
Mean diurnal range	−0.583	−0.330	**0.511**
Maximum temperature of warmest month	0.702	−0.604	0.193
Minimum temperature of coldest month	**0.946**	−0.207	−0.162
Mean temperature of wettest quarter	0.804	−0.478	0.217
Mean temperature of driest quarter	0.899	−0.261	−0.201
Mean temperature of warmest quarter	0.816	−0.504	0.105
Mean temperature of coldest quarter	**0.929**	−0.300	−0.053
Annual precipitation	0.850	0.450	0.073
Precipitation of wettest month	0.838	0.262	−0.050
Precipitation of driest month	0.501	**0.720**	0.189
Precipitation of wettest quarter	0.842	0.276	−0.040
Precipitation of driest quarter	0.538	**0.718**	0.169
Precipitation of warmest quarter	0.532	0.430	**0.619**
Precipitation of coldest quarter	0.632	0.465	−0.386
Eigenvalue	8.893	3.106	1.032
Percentage of variance explained	59.28	20.70	6.88

in Central America showed declines in 96 of 166 populations (Lips *et al.* 2003b) and *B. dendrobatidis* was present during the declines in at least two of the sites.

The regions with the highest suitability for *B. dendrobatidis* include the habitat types that have the world's most diverse amphibian faunas. In Colombia, the country with the world's highest amphibian species richness, the habitats with the greatest regional diversities are Andean montane forests (Lynch 1997), precisely the regions where the occurrence of *B. dendrobatidis* is most likely. The same is true for neighboring Ecuador, where 62 percent of the amphibian species are found above 1300 m (S. R. Ron, pers. comm.). The combined diversity of Ecuador and Colombia is in excess of 800 species.

Other regions where high suitability for *B. dendrobatidis* occurrence overlaps with highly diverse faunas are the Brazilian Atlantic forest (334 species, 94% endemic), the Mexican Sierra Madre Oriental (118 species), the highlands of western Nuclear Central America (126 species), and the montane forests in Panama and Costa Rica (133 species; diversity figures from Campbell 1999, Duellman 1999a).

Despite the extensive distribution of habitat suitable for *B. dendrobatidis* in the neotropics, the pathogen has been reported from relatively few localities (Figs. 2 and 3; Appendix). The absence of records in the regions predicted to be suitable may be due to: (1) absence of *B. dendrobatidis* as a consequence of failure of colonization, (2) absence of *B. dendrobatidis* as a consequence of true habitat unsuitability or interactions with other species (model commission error; see below), (3) poor or nonexistent sampling.

The regions where searches for *B. dendrobatidis* are most likely to yield new positive localities are those of predicted niche presence where amphibian declines have occurred and in the vicinity of regions with chytrid-positive localities. This might be the case for the following regions:

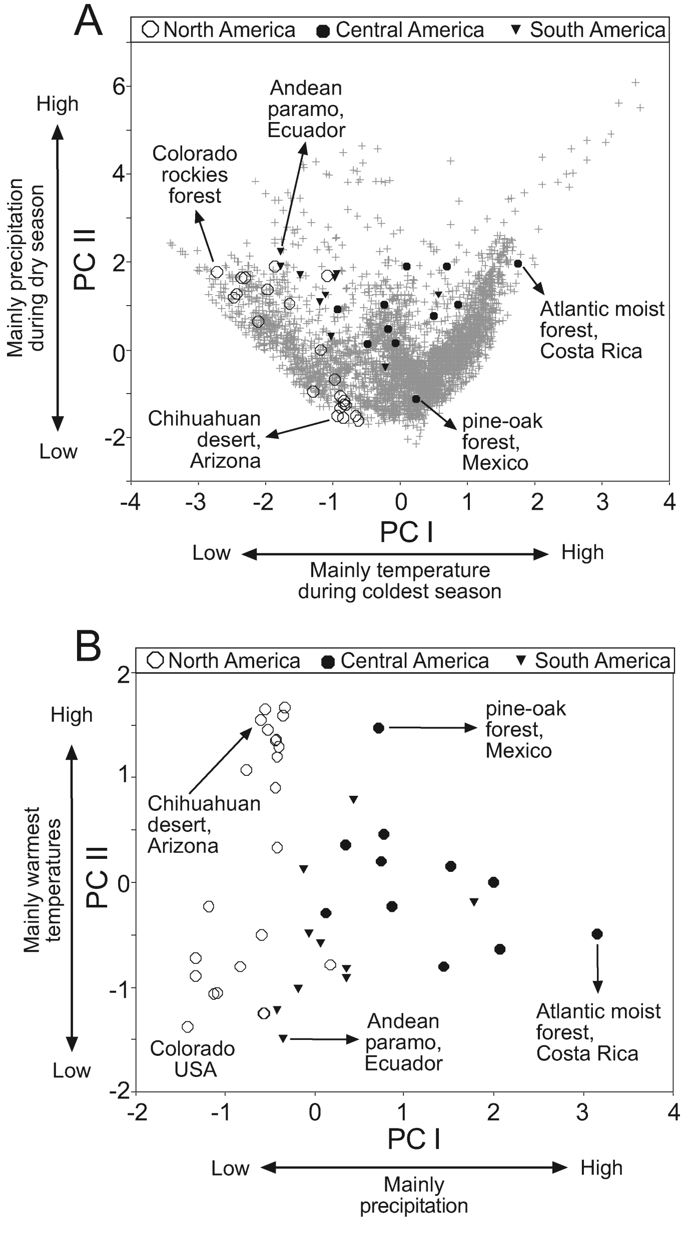

FIGURE 5. (A) Axes I and II from principal components analysis based on 15 environmental variables at 4000 random locations throughout the neotropics (gray symbols). Forty-four localities of known occurrence of *Batrachochytrium dendrobatidis* in the New World were also included in the PCA (black symbols). The distribution of the gray symbols represents the environmental space available in the neotropics (space as defined by the first two PCs). (B) Axes I and II from principal components analysis of the 44 localities of known occurrence of *Batrachochytrium dendrobatidis* only.

Brazilian Atlantic Forest.—Declines have been reported (Heyer *et al.* 1988), but causes are still unknown; the forest's southern edge lies at a distance of approximately 500 km from a *B. dendrobatidis*-positive

TABLE 2. *Character loading and percentage of variance explained by principal components (PC) I–III for 15 environmental variables at 44 known localities of* Batrachochytrium dendrobatidis *in the New World (Fig. 5B). Bold figures indicate variables with the highest loadings.*

	PC I	PC II	PC III
Mean annual temperature	0.723	0.673	−0.058
Mean diurnal range	−0.643	0.546	0.360
Maximum temperature of warmest month	0.084	**0.864**	**0.445**
Minimum temperature of coldest month	0.856	0.340	−0.306
Mean temperature of wettest quarter	0.522	0.704	−0.140
Mean temperature of driest quarter	0.473	0.746	0.030
Mean temperature of warmest quarter	0.305	**0.855**	0.348
Mean temperature of coldest quarter	0.821	0.449	−0.285
Annual precipitation	**0.905**	−0.359	0.087
Precipitation of wettest month	**0.881**	−0.221	−0.105
Precipitation of driest month	0.683	−0.482	0.430
Precipitation of wettest quarter	0.872	−0.242	−0.107
Precipitation of driest quarter	0.717	−0.478	0.401
Precipitation of warmest quarter	0.848	−0.292	−0.174
Precipitation of coldest quarter	0.597	−0.333	**0.602**
Eigenvalue	7.352	4.493	1.415
Percent of variance explained	49.01	29.95	9.43

TABLE 3. *Descriptive statistics for environmental conditions at 44 localities of known occurrence of* Batrachochytrium dendrobatidis *in the New World. Values are estimates obtained from digital maps (Hijmans et al. 2004). Temperature (air) is expressed in °C, precipitation in mm. A quarter is a period of 3 months.*

	Min	Max	Mean	SD
Altitude	23	4112	1714.4	1170.4
Mean annual temperature	−2.1	26.1	13.1	7.4
Mean diurnal range	8.3	20.0	13.0	3.0
Maximum temperature of warmest month	10.0	39.8	26.2	7.4
Minimum temperature of coldest month	−17.6	20.9	1.8	10.1
Mean temperature of wettest quarter	−8.1	28.3	13.5	10.4
Mean temperature of driest quarter	−10.6	26.7	14.5	8.8
Mean temperature of warmest quarter	5.4	30.2	18.7	6.9
Mean temperature of coldest quarter	−10.6	25.3	8.5	9.6
Annual precipitation	290	4383	1216.9	925.9
Precipitation of wettest month	37	557	170.3	126.0
Precipitation of driest month	0	149	35.3	36.5
Precipitation of wettest quarter	89	1455	449.4	333.6
Precipitation of driest quarter	3	536	122.4	120.0
Precipitation of warmest quarter	9	860	280.8	207.7
Precipitation of coldest quarter	17	1199	225.6	209.0

captive population of exotic *Rana catesbeiana* in Uruguay (Mazzoni *et al.* 2003).

Colombian Andes.—Declines have occurred (Lynch & Grant 1998, Young *et al.* 2001), but causes and extent are still unclear. Only 10 km separates this area from a positive locality in northern Ecuador, which belongs to the same biogeographic subregion of the Andes (Duellman 1999a).

Peruvian Andes.—Declines have been reported (Young *et al.* 2001) and positive localities in the Andes of southern Ecuador are 170 km from suitable areas in northern Peru (Merino-Viteri 2001).

Most neotropical regions where *B. dendrobatidis* has been found have experienced amphibian population declines. These are (1) highlands of Costa Rica and Panama, (2) Venezuelan Andes, (3) Ecuadorian Andes, (4) Puerto Rico, (5) highlands of western Nuclear Central America, and (6) Sierra Madre del Sur, Guerrero, Mexico (La Marca & Lötters 1997; Berger *et al.* 1998; Lips 1998, 1999; Campbell 1999; Ron & Merino-Viteri 2000; Merino-Viteri 2001; Bonaccorso *et al.* 2003; Lips *et al.* 2003a, 2004; Ron *et al.* 2003; Wilson & McCrane 2003; Burrowes *et al.* 2004; La Marca *et al.* 2005).

Although this correspondence suggests that the chytrid is a causal agent of amphibian declines in the neotropics, alternative explanations should not be ruled out. Searches for *B. dendrobatidis* have not been random, but have targeted regions where amphibian declines have occurred. The observed co-occurrence of *B. dendrobatidis* and amphibian declines would also be expected if *B. dendrobatidis* were a widely distributed, nearly innocuous pathogen with minor effects on amphibian population sizes. Overall, few efforts have been made to detect *B. dendrobatidis* in the neotropics (especially in South America), but virtually all have found positive localities (Berger *et al.* 1998, Merino-Viteri 2001, Bonaccorso *et al.* 2003, Lips *et al.* 2003a, Burrowes *et al.* 2004). The wide range of conditions under which *B. dendrobatidis* has been found and its high detection rate in the neotropics suggests that *B. dendrobatidis* may already occupy a significant part of the major natural regions in Central and South America.

ENVIRONMENTAL ENVELOPE AND PHYSIOLOGICAL TOLERANCE.—The environmental envelope analysis shows that *B. dendrobatidis* occurs under a wide variety of temperature and precipitation regimes. This wide environmental tolerance may explain the broad areal extent of suitable habitat for *B. dendrobatidis*. Our knowledge of the systematics of *B. dendrobatidis* is incomplete, and it may be composed of two or more evolutionarily independent lineages, each adapted to more restricted conditions. Morehouse *et al.* (2003) found extremely low genetic variability among isolates from North America, Africa, and Australia and argued that *B. dendrobatidis* was a recently emerged clone. However, Daszak (2003) reported genetic distances of about 10 percent among isolates from Australia, North, Central, and South America using the internally transcribed spacer region gene.

Recent studies have explored the physiological tolerances of *B. dendrobatidis* under various *ex situ* temperature regimes (Johnson *et al.* 2003, Johnson & Speare 2003, Woodhams *et al.* 2003, Piotrowski *et al.* 2004). Under laboratory conditions, optimal growth of *B. dendrobatidis* occurs between 17°C and 25°C (Piotrowski *et al.* 2004), which is also the temperature range most frequently found within the most suitable neotropical areas for *B. dendrobatidis*. Results also show that sustained exposures to temperatures in excess of 30°C reduce the survival of *B. dendrobatidis*. Several localities of known occurrence of *B. dendrobatidis*

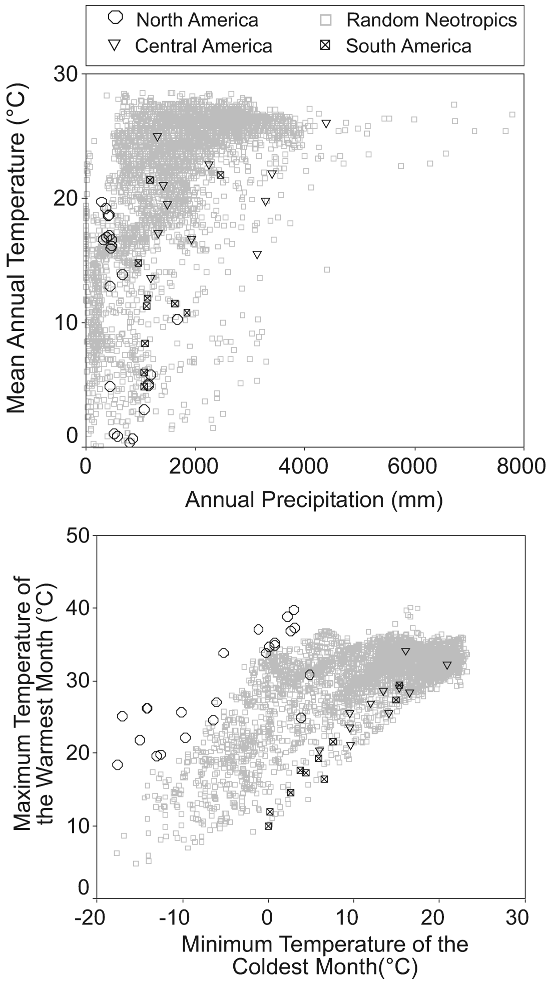

FIGURE 6. Bivariate plots of environmental variables at localities of known occurrence of *Batrachochytrium dendrobatidis* in the New World. Gray squares are from 4000 random locations in the neotropical region and represent the available set of conditions.

experience maximum temperatures above 30°C (Fig. 6), and the presence of *B. dendrobatidis* at those sites might be explained by active avoidance of high temperatures by the host, and/or sublethal temporal exposure.

CONSIDERATIONS ON MODEL QUALITY.—The ability to predict species' distributions relies on the quality of the occurrence data for the target species. I have used a wide array of information sources for *B. dendrobatidis* occurrence and, while experienced pathologists made most of the diagnoses (in several cases confirmed by genetic data), reliability of the reports of *B. dendrobatidis* varies. Therefore, the inclusion of false-positive localities is a possible source of error for the niche models.

The models are subject to two kinds of error, commission (inclusion of regions not actually inhabited) and omission (exclusion of regions inhabited); biased sampling will tend to increase model omission error, so real niche distribution may actually be larger than predicted. This is especially true for predictions in the Eastern Hemisphere (Fig. 4) because they were based on New World localities only. Significance of statistical tests also can be affected by this type of bias and should also be considered when interpreting these results. A potential source for both commission and omission errors in model building is the failure to include variables (*i.e.,* niche dimensions) important to define the species' fundamental and realized niches. For example, host absence or species interactions (*i.e.,* mutualism, competition, predation) can compress or even expand the suitable areas for *B. dendrobatidis*.

Sampling of *B. dendrobatidis* has not been carried out at random locations, and this is an additional source for model error. The regions where most of the sampling has occurred are those where scientists work and/or collections are available (especially North America and Australia). Sampling could also be biased by *a priori* perceptions of where *B. dendrobatidis* might occur (*e.g.,* locations at high elevation experiencing amphibian population declines).

The quality of the predictions also depends on the degree to which the pathogen responds to environmental factors beyond the body of the host. Because amphibians are ectotherms and *B. dendrobatidis* infection is epidermic, the environment is expected to have a strong influence on *B. dendrobatidis*. This is particularly true for temperature and humidity, two variables that are known to influence *B. dendrobatidis* survival (Johnson *et al.* 2003, Woodhams *et al.* 2003, Piotrowski *et al.* 2004).

Despite possible sources of error, the final model for *B. dendrobatidis* showed a high predictive power for localities in the Eastern Hemisphere. Although the predicted area in the Eastern Hemisphere was relatively small, it included most known localities for *B. dendrobatidis* suggesting low omission error. These results parallel those of other investigations that have shown a high predictive power of distribution ranges from niche modeling (*e.g.*, Anderson *et al.* 2002b, 2003; Peterson *et al.* 2002a, 2003, 2004; Peterson 2003; Ortega-Huerta & Peterson 2004). Two neotropical localities in Uruguay and the Venezuelan Andes (Mazzoni *et al.* 2003, Hanselmann *et al.* 2004), where *B. dendrobatidis* has been reported as a pathogen of the exotic *Rana catesbeiana* were predicted as present by all models (OI = 1).

MANAGEMENT RECOMMENDATIONS.—The predicted distributions for *B. dendrobatidis* are intended to be a management tool for conservation biologists and policy makers. The wide availability of suitable regions for the establishment of *B. dendrobatidis* and its presence in several types of amphibian trade (Daszak 2003) make necessary the implementation of severe trade regulations to avoid anthropogenic spread of *B. dendrobatidis*. In addition, pathological studies on amphibians from more regions are a priority.

Amphibian species with a low susceptibility to *B. dendrobatidis* can act as reservoirs for the disease in the wild (Collins & Storfer 2003). This evidence combined with the proven survival of *B. dendrobatidis* without an amphibian host, at least under sterile conditions (Johnson & Speare 2003), indicates that *B. dendrobatidis* eradication from its natural habitats may be difficult. Under those circumstances, one of the few effective strategies for the conservation of highly susceptible species might be the establishment of captive breeding colonies.

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Appendix. _Localities of known occurrence of the chytrid_ Batrachochytrium dendrobatidis _used to build or test chytrid niche models. The asterisk refers to sources cited in Speare and Berger (2002)._

Species	Country: State (or Province), Locality	Source
Litoria caerulea	Australia: New South Wales, Lanitza	Berger _et al._*
Adelotus brevis	Australia: Queensland, Lamington	Berger and Hines*
Adelotus brevis	Australia: Queensland, Mount Mee State Forest	Berger and Hines*
Adelotus brevis	Australia: Queensland, Buderim	Berger and Wilson*
Adelotus brevis, Litoria caerulea	Australia: Queensland, Brisbane	Berger and Hines*
Crinia georgiana, Heleioporus eyrei	Australia: Western Australia, Elleker, near Albany	Aplin and Kirkpatrick*
Geocrinia rosea	Australia: Western Australia, Big Brook	Aplin and Kirkpatrick*
Heleioporus australiacus	Australia: New South Wales, Springwood	Berger and Wotherspoon*
Limnodynastes dumerilii, Litoria lesueuri	Australia: Queensland, Goomburra	Berger and Hines*
Limnodynastes tasmaniensis	Australia: South Australia, Adelaide	Berger _et al._ (1998)
Litoria adelaidensis	Australia: Western Australia, Lake Gwelup, Gwelup	Aplin and Kirkpatrick*
Litoria adelaidensis, Litoria moorei	Australia: Western Australia, Perth	Main and Aplin; Berger and Smith*
Litoria aurea	Australia: New South Wales, Hoskinstown	Berger and Pietsch*
Litoria aurea	Australia: New South Wales, Homebush Bay, Sydney	Berger and Michelle Christy*
Litoria spp.	Australia: Queensland, Kroombit Tops	Berger and Clarke*; Berger and Hines*
Litoria caerulea	Australia: New South Wales, Bowraville	Berger _et al._*
Litoria caerulea	Australia: New South Wales, Bellingen	Berger and Williams*
Litoria caerulea	Australia: New South Wales, Casino	Berger _et al._ (1998)
Litoria caerulea	Australia: New South Wales, Alstonville	Berger and Miller*
Litoria caerulea	Australia: Queensland, Maryborough	Berger and Wilson*
Litoria caerulea	Australia: Queensland, Rockhampton	Berger*
Litoria caerulea	Australia: Queensland, Kinka Beach	Berger and Taylor*
Litoria caerulea	Australia: Queensland, Mackay	Berger and Wilson*
Litoria ewingi	Australia: South Australia, Woodville	Berger and Tyler*
Litoria genimaculata	Australia: Queensland, Topaz	Speare _et al._*
Litoria lesueuri	Australia: Queensland, Canungra Ck	Berger and Hero*
Litoria lesueuri	Australia: Queensland, Broadwater Creek	Mendez and Freeman*
Litoria moorei	Australia: Western Australia, Mount Barker	Speare and Aplin*
Litoria moorei	Australia: Western Australia, Manjimup	Speare and Aplin*
Litoria moorei	Australia: Western Australia, Witchcliffe	Speare and Aplin*
Litoria moorei	Australia: Western Australia, Mount Helena	Speare and Aplin*
Litoria moorei, Crinia pseudinsignifera	Australia: Western Australia, Sawyers Valley	Speare and Aplin*
Litoria spp., _Taudactylus acutirostris_	Australia: Queensland, Big Tableland	Berger _et al._ (1998)
Litoria pearsoniana	Australia: New South Wales, Mebbin State Forest	Berger and Mahony*
Litoria raniformis, Limnodynastes dumerilii	Australia: South Australia, Mount Compass	Berger and Tyler*
Litoria spenceri	Australia: Victoria, Bogong Creek	Berger and Gillespie*
Mixophyes fasciolatus	Australia: Queensland, Mount Glorious	Berger and Hines*
Nyctimystes dayi	Australia: Queensland, Tully	Berger _et al._*
Pseudophryne corroboree	Australia: New South Wales, Mount Jagungal, Koskiusko National Park	Speare _et al._*
Atelopus chiriquiensis, Eleutherodactylus melanostictus	Costa Rica: Punta Arenas, Las Tablas	Lips _et al._ (2003a, 2003b)
Atelopus varius	Costa Rica: San José, San Isidro del General	Puschendorf (2003) in Lips _et al._ (2003a, 2003b)
Atelopus varius	Costa Rica: Heredia, San Ramón de Sarapiquí	Puschendorf (2003) in Lips _et al._ (2003a, 2003b)
Atelopus sp. 1	Ecuador: Pichincha, Otongoro	Berger and Ron (pers. comm.)
Atelopus sp. 2	Ecuador: Imbabura, Cuicocha	Merino-Viteri (2001)
Atelopus sp. 2	Ecuador: Carchi, 42 km O Tulcán	Merino-Viteri (2001)
Atelopus bomolochos, Gastrotheca pseustes	Ecuador: Chimborazo, Lagunas de Atillo	Berger and Ron (pers. comm.)
Gastrotheca pseustes	Ecuador: Bolívar, Cashca-Totoras	Merino-Viteri (2001)
Gastrotheca pseustes	Ecuador: Cotopaxi, Limpiopungo	Berger and Ron (pers. comm.)

Appendix. *Continued.*

Species	Country: State (or Province), Locality	Source
Gastrotheca pseustes, Telmatobius niger	Ecuador: Azuay, Las Tres Cruces	Merino-Viteri (2001)
Hyalinobatrachium sp.	Ecuador: Morona Santiago, 6.6 km N Limon road to Macas	Merino-Viteri and Coloma (pers. comm.)
Telmatobius niger	Ecuador: Azuay, 10 km S from Cutchil	Merino-Viteri (2001)
Rana arvalis	Germany: Berlin, Berlin	Mutschmann 2002*
Ptychohyla hypomykter	Guatemala: Baja Verapaz, Sierra de las Minas, 3.0 km N of La Unión Barrios, Río Cafetal	Mendelson *et al.* (in press)
Bombina pachypus	Italy: Emilia-Romagna, Bologna	Stagni *et al.* 2002*
Ptychadena anchietae	Kenya: Nairobi, Langata, Nairobi	Berger and Parker*
Leiopelma archeyi	New Zealand: Waikato, Tapu	Bell *et al.* (2004)
Leiopelma archeyi	New Zealand: Waikato, Te Moehau	Bell *et al.* (2004)
Leiopelma archeyi	New Zealand: Waikato, Whareorino	Bell *et al.* (2004)
Atelopus varius, Bufo haematiticus, Cochranella spp., *Eleutherodactylus* spp.	Panama: Chiriqui, Fortuna	Berger *et al.* (1998)
Eleutherodactylus spp.	Puerto Rico: Río Grande, El Yunque	Burrowes *et al.* (2004)
Hyla vasta	República Dominicana: La Vega, Arroyazo	R. L. Joglar, P. A. Burrowes, and M. Hernandez (pers. comm.)
Eleutherodactylus pituinus	República Dominicana: La Vega, Casabito	R. L. Joglar, P. A. Burrowes, and M. Hernandez (pers. comm.)
Eleutherodactylus patriciae, Hyla vasta	República Dominicana: La Vega, Valle Nuevo	R. L. Joglar, P. A. Burrowes, and M. Hernandez (pers. comm.)
Afrana fuscigula	South Africa: Western Cape, Algeria, Cedeberg	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Northern Cape, Bloukerboom-water, Goegap Nature Reserve	Hopkins and Channing (2003)
Xenopus laevis	South Africa: Western Cape, Grabouw	Mendez, Speare, and Cunningham*
Afrana fuscigula	South Africa: Western Cape, Grobbelaars River	Hopkins and Channing (2003)
Afrana fuscigula, Strongylopus grayii	South Africa: Western Cape, Groot Winterhoek	Hopkins and Channing (2003)
Afrana fuscigula, Strongylopus grayii	South Africa: Western Cape, Groot Winterhoek(2)	Hopkins and Channing (2003)
Afrana fuscigula, Strongylopus grayii	South Africa: Western Cape, Jamaca farm pond, Cederberg	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Northern Cape, Kraaifontein, Goegap Nature Reserve	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Western Cape, Stellenbosch	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Western Cape, Swellendam	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Western Cape, Table Mountain	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Western Cape, Table Mountain(2)	Hopkins and Channing (2003)
Afrana fuscigula	South Africa: Western Cape, Tradouws pass	Hopkins and Channing (2003)
Alytes obtetricans	Spain: Madrid, Parque Natural Peñalara	Bosch *et al.* (2001)
Ambystoma macrodactylum	USA: California, Ellicot Slough	USGS (2003)
Ambystoma tigrinum	USA: Arizona, San Rafael Valley	E. Davidson (pers. comm.)
Bufo boreas	USA: Colorado, North Fork of Big Thompson River, Kettle Tarn	Muths *et al.* (2003)
Bufo boreas	USA: Colorado, North Fork of Big Thompson River, Lost Lake	Muths *et al.* (2003)
Bufo boreas	USA: Wyoming, National Elk Refuge	USGS (2003)
Hyla regilla	USA: California, San Francisquito Canyon	USGS (2003)