

High environmental niche overlap between the fungus *Batrachochytrium dendrobatidis* and invasive bullfrogs (*Lithobates catesbeianus*) enhance the potential of disease transmission in the Americas

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Abstract. Chytridiomycosis is linked to several amphibian population declines, including local extinctions. Besides this, it is already widespread over the globe, and one of the possible carriers is believed to be the American bullfrog. In order to assess whether the successful establishment of invasive bullfrog populations is associated with environmental suitability for *Batrachochytrium dendrobatidis* (Bd), we evaluated the close linkage between the fungus (Bd) and bullfrogs by measuring their environmental niche overlap. Our results indicate that Bd and bullfrogs largely overlap in their realized niches, wherein Bd occupies a larger climate space in which the bullfrogs' niche is nested. Therefore, our results strengthen the bullfrog carrier hypothesis. Besides this, we suggest that Bd can colonize areas adjacent to the bullfrogs' realized niche, infecting other species of native wild frogs. Central and South American governments must be aware of such problem and the international frog trade must be controlled to avoid further disease spreading.

Key words: environmental tolerance, emerging infectious disease, amphibian decline, host-pathogen, carrier.

Introduction

Amphibian populations are declining at a global scale through anthropogenic habitat loss, biological invasions and emerging infectious diseases (e.g. Mendelson et al. 2006, Stuart et al. 2008). Among the latter, the most devastating agent is chytridiomycosis, caused by the zoosporic fungus *Batrachochytrium dendrobatidis* (Bd) (Berger et al. 1998, Pounds et al. 2006). The recent introduction of the fungus in large parts of the world may be associated with movements of migratory birds (Garmyn et al. 2012) and, maybe more important, with the global trade of amphibians as pets, food and bio-control (e.g. Schloegel et al. 2009, 2010a, Gratwicke et al. 2010) also including illegal trade (Pistoni & Toledo 2010). A close linkage between biological invasions and transmission of diseases has been suggested (Both et al. 2011, Daszak et al. 2004).

Such introduction pathways were also suggested for Bd, since within the three most widely introduced amphibian species, *Xenopus laevis*, *Lithobates catesbeianus* and *Rhinella marina*, numerous cases of Bd infections have been reported (Daszak et al. 2004, Fisher & Garner 2007). Out of these, the most efficient carrier of the disease in the Americas is the American bullfrog *L. catesbe-*

ianus (South America: Mazzoni et al. 2003, Ron & Merino 2000, Hanselmann et al. 2004, Schloegel et al. 2010b, 2012, Central America: Berger et al. 1998, USA: Peterson et al. 2007, Schloegel et al. 2009), as both wild and farmed populations show strong host resistance (e.g. Mazzoni et al. 2003, Daszak et al. 2004, Pearl & Green 2005) and often high infection loads (e.g. Mazzoni et al. 2003, Hanselmann et al. 2004, Garner et al. 2006).

As a result of their size, enormous growth rate, easy breeding and husbandry, American bullfrogs, native to eastern North America, are especially attractive for the food consumption market. Early introductions in Brazil occurred since the 1930s in association with aquaculture (Giovanelli et al. 2007), while the international trade of bullfrogs as a food source, especially in South America, has dramatically increased over the last few decades (Mazzoni et al. 2003, Schloegel et al. 2009, 2010b). Correspondingly, escaped farm individuals successfully spawn in many areas and have established dense and expanding invasive populations (Giovanelli et al. 2007, Both et al. 2011). Furthermore, the cleaning of farm tanks with drainage water containing zoospores can easily contaminate wetlands. Besides this, small wild frogs are able to enter bullfrog tanks carrying the fungus outside (LFT, person. obs.). In Uruguay,

for example, low economic gains induced a closing of bullfrog farms without an implementation to prevent unintentional escapes or releases (Laufer et al. 2008).

Nowadays, invasive bullfrog populations exist in 10 countries in South America (Argentina: Peyrera et al. 2006, Uruguay: Laufer et al. 2008, Brazil: Giovanelli et al. 2007, Both et al. 2011, Ecuador: Cisneros-Herdeia 2004, Colombia: Rueda-Almanocid 1999, and Venezuela: Hanselmann et al. 2004), as well as in Central America (Puerto Rico, Jamaica, Cuba, Dominican Republic, see Mahon & Aiken 1977, Lopez-Flores et al. 2003). Today, the American bullfrog has successfully established feral populations in major parts of South America, representing one of the hundred worst invasive species in the world (Nori et al. 2011).

There are several predictive species distribution models for the present and future distribution of bullfrogs within South America (e.g. Ficetola et al. 2007, Giovanelli et al. 2007, Loyola et al. 2012, Nori et al. 2011). Models for the present (Ron 2005, Rödder et al. 2009) and future (Rödder et al. 2010) global distribution of Bd are also available. However, none of these models took into account that bullfrogs are well known to be efficient carriers of the amphibian chytrid. Therefore, we herein evaluated the close linkage between the fungus and its probably most important vector in the Americas. We measured the ecological niche overlap between the two species in order to assess whether successful establishment of invasive bullfrog populations is always associated with environmental suitability for Bd and therefore accompanied by increased conservation concerns.

Material and methods

We compiled two sets of species records within the Americas for Bd and bullfrogs from online data bases, i.e. the Global Biodiversity Information Facility (GBIF, available at www.gbif.org), HerpNet (available at <http://www.herpnet.org/portal.html>) and the Global Bd-Mapping Project (available at <http://www.bd-maps.net/>), and supplemented them with published records (Mahon & Aiken 1977, Kupferberg 1997, Berger et al. 1998, Rueda-Almanocid 1999, Lopez-Flores et al. 2003, Cisneros-Herdeia 2004, Peyrera et al. 2006, Toledo et al. 2006, Ficetola et al. 2007, Giovanelli et al. 2007, Peterson et al. 2007, Laufer et al. 2008, Both et al. 2011, and references therein).

When assessing a species' environmental niche properties via climate data stored in a GIS framework, it is often necessary to reduce spatial clumping of the records in order to avoid pseudo-replication in highly densely sam-

pled areas. Therefore, we filtered both data sets in geographic space, wherein only one record per 10 arc-min was randomly chosen for further processing. Our final data sets comprised 1,060 bullfrog records and 574 records of Bd.

To compare the realized niches of the species, we downloaded monthly minimum and maximum temperature and precipitation GIS layers available through the WorldClim database version 1.4 (Hijmans et al. 2005). These layers represent interpolated monthly average weather conditions recorded between 1950-2000 with a spatial resolution of 2.5 arc-min. Using the monthly variables we derived a set of 19 bioclimatic variables (cf. Figures 1, 2) with DIVAGIS 7.4 (available at <http://www.divagis.org>, Hijmans et al. 2005), which have been suggested to sufficiently describe climatic conditions at a given site (Busby 1991, Beaumont et al. 2005). Based on bioclimatic conditions of the bullfrog and Bd records, we computed density estimations and a bootstrap hypothesis test of equality across the bioclimatic gradients occupied by each species using the `sm.density.compare` function of the `sm` package (Bowman & Azzalini 2010) for Cran R 2.13.2. The resulting graphs allow detailed comparison of both species' realized niches.

Several different methods to compute environmental niche overlaps based on species records and gridded environmental data have been proposed (for a recent review see Broennimann et al. 2012). According to these authors, niche overlaps derived from a climate space captured by a Principal Component Analysis (PCA) is the most reliable technique (termed PCA-env by the authors). In this framework, a PCA is trained with the entire environmental range available for both species - herein: the climatic conditions within a 250 km circular buffer around the species records. The records of both species are subsequently projected into the environmental space, which is spanned by the two most important principal components. For each species, a density kernel with a given resolution is computed ($R = 100$ herein) in order to compensate possible errors caused by unequal sampling efforts. Niche overlaps in terms of Schoener's D (Schoener 1968) as well as niche identity and similarity tests as proposed by Warren et al. (2008) and modified by Broennimann et al. (2012) are finally computed based on densities derived from the kernels. These randomization tests allow to assess (i) whether the niches of two species are actually distinguishable (niche equivalency) and (ii) whether the observed niche overlaps are likely to be a function of the available climatic conditions within the species' general area of occurrence, or can be attributed to active habitat choice (niche similarity).

Results and discussion

Our results indicate that Bd and bullfrogs largely overlap in their realized niches, wherein Bd occupies a larger climate space in which the bullfrogs' niche is nested. All univariate comparisons of their

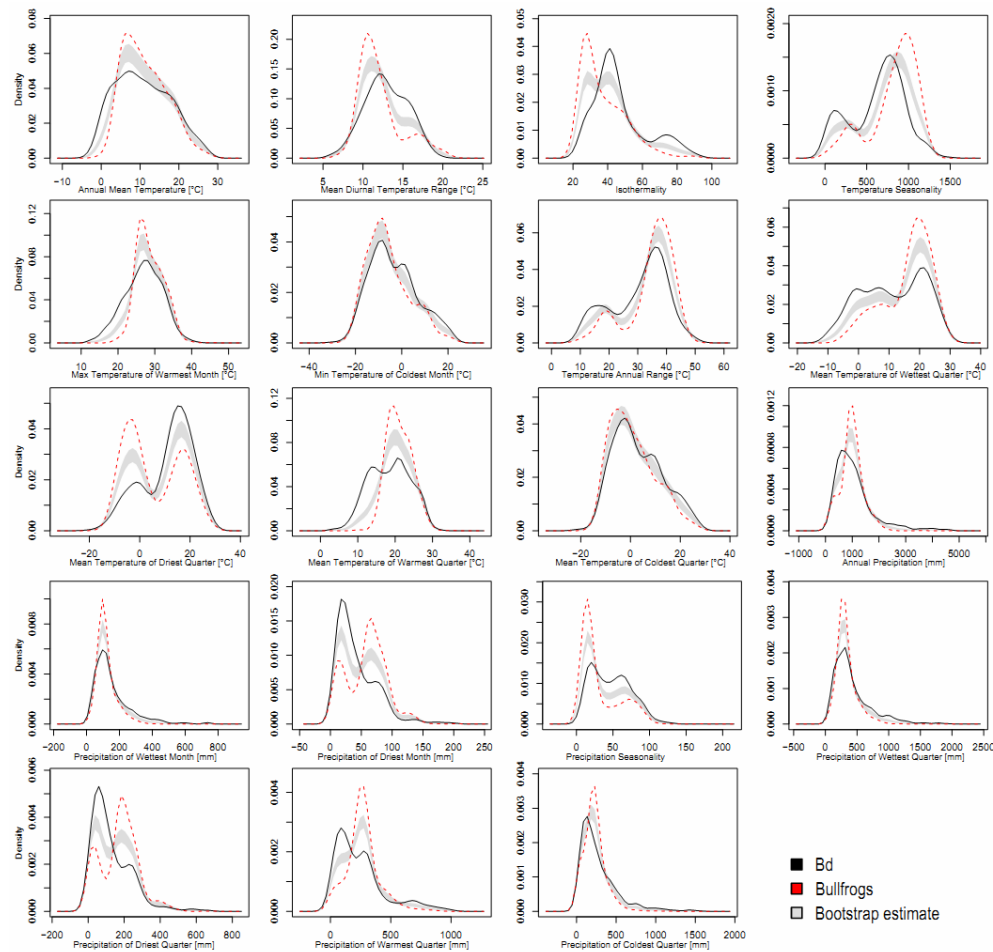


Figure 1. Comparison of density distributions of bullfrog and Bd records along 19 bioclimatic variables. The hypothesis of niche equivalency is rejected when both density distributions (black and dashed red lines) exceed the confidence limits of the respective bootstrap estimates (grey bands).

realized climatic niches revealed high overlaps in the occupied parameter spans, but with varying density maxima (Fig. 1). This indicates that all areas where native and invasive bullfrogs are known, generally provide suitable bioclimatic conditions for Bd as well. However, the relative frequencies of both species in environmental space differ at least in some niche axes, wherein the density distributions are more similar for temperature gradients than for precipitation gradients (Fig. 1). It needs to be noted that, although none of the very conservative bootstrap hypothesis tests of equivalency of the density distributions was significant across any of the complete bioclimatic gradients, the density distributions are at least

equivalent across some parts (Fig. 1).

Summarizing the occupied bioclimatic spaces of both species in a PCA indicates a similar pattern: the bullfrogs' realized niche is completely nested in the Bd's realized niche. Therefore, it is reasonable to state that the multivariate determined niche overlap is only *moderate* ($D = 0.437$) according to the classification of Rödder & Engler (2011) and the hypothesis of niche equivalency is rejected. As the niche similarity test was significant in both directions (each $p = 0.0198$), the bioclimatic spaces occupied by both Bd and bullfrogs are well differentiated from the general available bioclimatic space captured within the 250 km circular buffer around the records. These significant

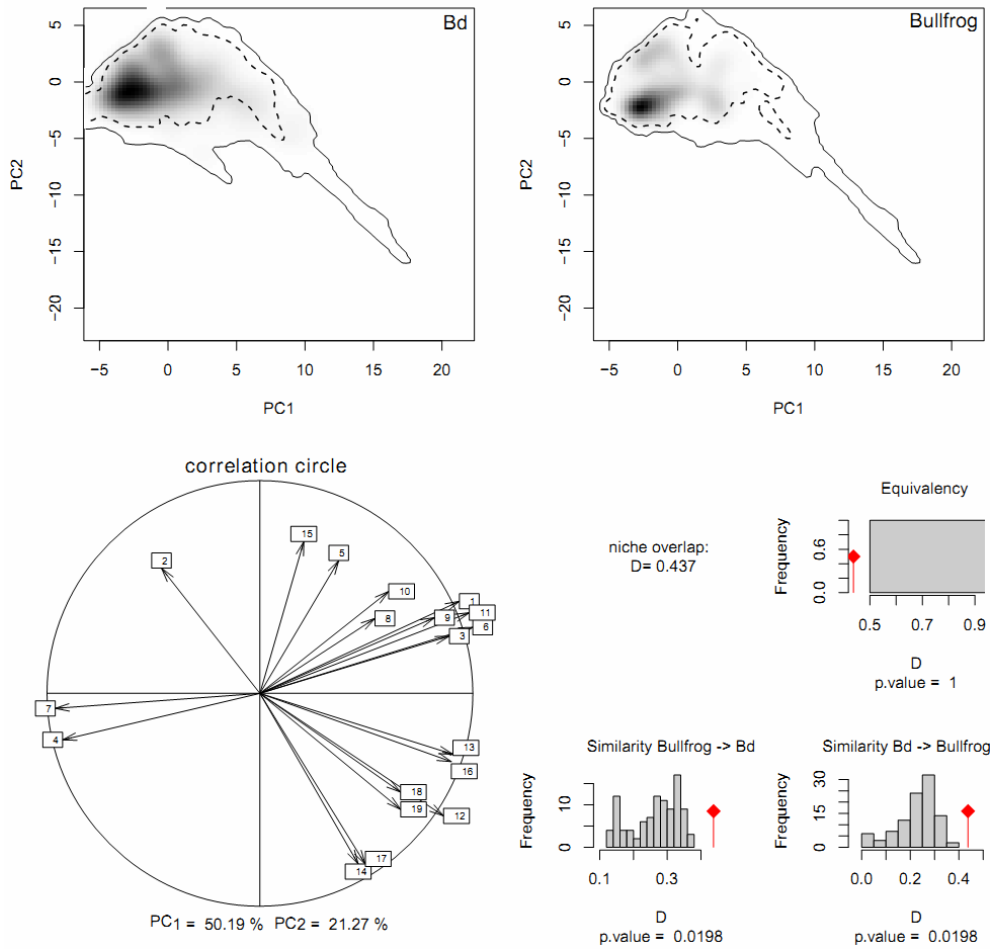


Figure 2. Comparisons of the realized climatic niches of Bd and bullfrogs. Darker areas in the PCA plots indicate a higher density of species records, wherein the available climate spaces within the general area of occurrence are indicated by solid (100%) and dashed lines (50%). The histograms show the results of the null-model of the niche identity and similarity tests calculated from 100 iterations, wherein the red diamonds indicate the actual observed niche overlap. Abbreviations of the bioclimatic variables in the correlation circle are: 1 = annual mean temperature, 2 = mean diurnal range, 3 = isothermality, 4 = temperature seasonality, 5 = max temperature of warmest month, 6 = min temperature of coldest month, 7 = temperature annual range, 8 = mean temperature of wettest quarter, 9 = mean temperature of driest quarter, 10 = mean temperature of warmest quarter, 11 = mean temperature of coldest quarter, 12 = annual precipitation, 13 = precipitation of wettest month, 14 = precipitation of driest month, 15 = precipitation seasonality, 16 = precipitation of wettest quarter, 17 = precipitation of driest quarter, 18 = precipitation of warmest quarter, 19 = precipitation of coldest quarter.

differentiations can be interpreted as preferences of both species for specific environmental conditions over others, which likely reflect physiological optima and tolerance limits.

Laboratory growth experiments of isolates of *B. dendrobatidis* from different amphibian hosts (not bullfrogs) defined a wide range of temperature (4-25 °C) as suitable for the growth and re-

production of the fungus, pronouncing the ability of the pathogen to persist within a variety of different environments (Piotrowski et al. 2004). According to the authors, the optimal temperature range inducing the fastest growth was determined between 17-25 °C, which is congruent with the highest density of Bd records along the mean temperature of the warmest quarter (Fig. 1). Under

laboratory conditions, at 28 °C growing is stopped and zoospores died after two days of incubation. Higher temperatures exceeding 30 °C may kill the fungus within eight days (Piotrowski et al. 2004). In the wild, these temperature dependencies are well reflected in decreasing infection load quantities with increasing temperatures approaching 30 °C (e.g. Kielgast et al. 2010, Kriger et al. 2007). These findings clearly demonstrate that an upper temperature threshold for Bd establishment exists and ambient temperatures above 25 °C apparently not favour epidemics (Berger 1998). This trend is also evident in the density distributions of Bd across analysed bioclimatic parameters, e.g. the annual mean temperature and the mean temperature of the warmest quarter (Fig. 1). Contrarily, even at very low temperatures (e.g. 4 °C) over a long time period (e.g. 6 months) some isolates may still survive under laboratory conditions, raising the question of possible overwintering in host species within icebound water bodies (Piotrowski et al. 2004). Water temperatures may not fall as low as air temperatures, likely explaining why Bd occurs in areas where the minimum temperature of the coldest month may be even lower than -20 °C (Fig. 1).

Considering the physiology of Bd it is thought that the outbreak of chytridiomycosis in Central and South America will be restricted to cooler mountainous areas as shown in Panama (Berger et al. 1998). Although studies on frog species at different altitudes in tropical South America (Gründler et al. 2012) and subtropical Australia (Kriger & Hero 2008) demonstrated that frogs at all altitudes were infected. Kriger & Hero (2008) found that Bd infections persist longer during summer in upland than in lowland habitats. Gründler et al. (2012) found the prevalence and infection intensity of Bd are highest at high elevations, where overall environmental conditions for Bd are most favourable. As a result, montane amphibian populations are threatened by disease outbreaks for longer time periods. Furthermore, the time of metamorphosis in montane frog populations may coincide with optimal temperatures for chytrid growth (Kriger & Hero 2008).

The nested niche of bullfrogs in relation to the niche of Bd contributes to and expands the disease-carrier hypothesis regarding the linkage between spreading of Bd and bullfrogs (e.g., Schloegel et al. 2009, 2010b, 2012). It is possible that bullfrogs carry the disease to sites where they are introduced. Subsequently, the disease, with a

larger niche breadth can spread into adjacent areas and occupy a larger distribution. Assuming this scenario (bullfrogs being one of the major Bd carriers in the Americas) control measures must be applied rapidly. Chytridiomycosis has recently been listed by the World Organization for Animal Health (OIE) as an internationally notifiable disease, which means that it is now subject to OIE's standards (Schloegel et al. 2010a). However, this first legal step should be strengthened by the worldwide prohibition of trade with live bullfrogs. Frozen and skinned frog legs do not transmit chytridiomycosis and could be an efficient trade solution. Europe already prohibited the imports of live bullfrogs (Schloegel et al. 2010b, and references therein) and this measure is highly recommended for the Central and South Americas.

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