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ORIGINAL ARTICLE

Predicting the invasive potential of the cladoceran *Daphnia lumholtzi* Sars, 1885 (Crustacea: Cladocera: Daphniidae) in the Neotropics: are generalists threatened and relicts protected by their life-history traits?

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ABSTRACT

Invasive species are one of the major threats to biodiversity, which is aggravated in poorly known groups, such as cladocerans. *Daphnia lumholtzi* Sars (Cladocera: Anomopoda: Daphniidae) is currently invading the Neotropical region, and there are few records of this process. Our goal was to predict the invasive scenario for *D. lumholtzi* in the Neotropics using species distribution modelling and to assess the climatic overlap of the invader with the native species. We trained our MaxEnt model using occurrence records from native and invaded areas and projected it in the Neotropics. Additionally, we compared the climatic niche of some native species with the invader's niche. Our model showed high environmental suitability in areas connected by the lowland Paraná River Basin (southwestern Brazil, eastern Argentina and Uruguay), in south-central Chile and Atlantic coastal areas. Widely distributed native species showed climatic overlap with the invader, while relict species did not. Daphnia lumholtzi thrives in warm and stable environments (e.g. the Paraná River basin), which of concern because the invader could already be spreading in that area. Native species could suffer due to climatic niche similarity, while natural barriers and local environmental conditions may protect relict species. We urge the need for further studies to understand this invasion process more fully.

Key words: Biodiversity conservation; dispersion; invasive species; reservoirs; Paraná River Basin; species distribution model.

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INTRODUCTION

Invasive species are considered one of the main threats to native ecosystems, because they can cause negative impacts on the stability and evolutionary trends in any community *via* changes in ecological, behavioral and genetic interactions (*e.g.*, hybridization and introgression; Mooney and Cleland, 2001; Cox, 2004; Simberloff, 2010). To make matters worse, the number of anthropogenic-mediated invasions increased in recent years due to globalization (Perrings *et al.*, 2005; Poulin *et al.*, 2011). The process of biological invasion is fairly complex and can be affected by several factors. The first factor is the capacity of the potential invader to transpose environmental filters, which can interact with the number and frequency of invading propagules (Colautti and McIsaac, 2004). The second factor is the species' capacity to establish itself and spread in novel environments. High adaptability to new conditions is a crucial trait at this stage, because if they cannot adapt to local conditions they can neither establish themselves nor invade (Jímenez-Valverde *et al.* 2011; Dobrzycka-Krahel and Graca, 2014; Dobrzycka-Krahel *et al.,* 2015). The third and last factor is the susceptibility of the ecosystem to invasive species (Colautti and McIsaac, 2004; Cox, 2004; Colautti *et al.,* 2006). Due to this inherent complexity, conservation measures employed to mitigate the threat of invasive species need to cover all steps of the invasion process. Consequently, these measures quickly become expensive, highlighting the need for cost-effective measures.

According to Hulme (2006), the most cost-effective measure is preventing the potential invader from establishing itself in the novel environment; these measures are relatively cheap and have a high chance of success, if employed correctly. One tool that can be used to help guide the conservation efforts is species distribution modelling (SDM) (Araujo and Guisan, 2006; Jiménez-Valverde *et al.,* 2008). SDM techniques calculate the environmental space ('climatic niche') of the species based on the environment in which it currently occurs (occurrence records), thus being a portion of the realized niche (Soberón, 2007). This climatic niche can then be projected on to the geographic space, including areas in which the species is not currently found (Jiménez-Valverde *et al.,* 2011). If used in the context of biological invasions, SDM can indicate geographical regions that are suitable for a given species, potentially to establish itself and have a positive growth rate (Jiménez-Valverde *et al.,* 2011). Therefore, it offers a framework for conservation strategies to be drawn up more effectively (Guisan *et al.,* 2013). This type of modelling has been used extensively in recent years and has become a useful tool to study invasion ecology (*e.g.* Peterson, 2003; Nori *et al.,* 2011; Palaoro *et al.,* 2013; Campbell *et al.,* 2015; Marcantonio *et al.,* 2016). Another source of evidence we can use to predict the impact of the invader is to compare the invader's climatic niche with that of a native species. If native and invasive species have similar climatic niches, it is possible that they may compete for resources on a smaller scale, creating further disturbances for native species (Palaoro *et al.,* 2013).

Neotropical biodiversity has been considered vulnerable to invasive species, with many groups of native plants and animals - especially freshwater organisms - threatened by extinction due to the activity of invasive species (Rodríguez, 2001; Clavero and García-Berthou, 2005; Speziale and Lambertucci, 2010). A particularly striking example is the thermophilic cladoceran *Daphnia* (*Ctenodaphnia*) *lumholtzi* Sars, 1885 (Crustacea: Cladocera: Daphniidae). This species complex is native to southern Asia, Australia and Africa (Kotov and Taylor, 2014), but it successively invaded North America in the 1990's (Havel and Hebert, 1993; Havel *et al.,* 2000; Havens *et al.,* 2000). Although Havens *et al.* (2012) indicated no evidence for competitive exclusion of native cladocerans by invasive species in lakes of North America, experimental studies showed that *D. lumholtzi* is able to tolerate a wide range of temperature variation (Brown, 1999; Johnson and Havel 2001; Fey and Cottinghan, 2012) and that, in the presence of predators, *D. lumholtzi* increases its investment in reproduction, becoming a stronger competitor when compared to native species (Dzialowski *et al.*, 2003). In invaded habitats, *D. lumholtzi* might suppress native species at least seasonally (Dobberfuhl and Elser, 2002). So far, there is no consistent information on the influence of *D. lumholtzi* on the provision of ecosystem services in invaded habitats, or of economic impacts of the invasion process.

After the establishment of the first populations in North America (Havel and Hebert, 1993), a rapid colonization proceeded (Dzialowski *et al.*, 2003). Soon after that, *D. lumholtzi* was reported in Mexico (Eliás-Gutierréz *et al.,* 2008; Silva-Briano *et al.,* 2010), Brazil (Zanata *et al.*, 2003; Simões *et al.,* 2009) and, more recently, Argentina (Kotov and Taylor, 2014). A darker scenario emerges when we realize these records are distant from each other, both in space and time - thus not enough sampling has been done, and the situation in the Neotropics may be significantly underestimated. Of all *Daphnia* species with exclusive occurrence in the Neotropics (see Kotov *et al.,* 2013), only *D. gessneri* Herbst, 1967 has a wide distribution range. At least five other *Daphnia* species are endemic to a few water bodies or even a single one (Hann, 1986; Valdivia-Vilar and Burger, 1989; Kotov *et al.,* 2010), thus being considered geographical relicts (*sensu* Grandcolas *et al.,* 2014). This is troubling, since a high level of endemism usually correlates with environmental specificity, which increases the risk of functional and local extinction (Carlton *et al.,* 1999; Sodhi *et al.,* 2009). Therefore, the invasion of *D. lumholtzi* increases the potential risk of extinction for the Neotropical *Daphnia*, which makes understanding the invasive potential of *D. lumholtzi* even more necessary.

In this study, we used SDM to predict the invasion scenario for *D. lumholtzi* in the Neotropics. We used occurrence records of this species (including both native and invaded areas) to build a model and then project it in the Neotropics. In addition, we checked if *D. lumholtzi* and the endemic Neotropical species of *Daphnia* occupy similar, or significantly overlapping, climatic niches.

METHODS

We found 137 occurrence records of *D. lumholtzi* in different locations throughout the world (Fig. 1). These data were obtained from the Global Biodiversity Information Facility (GBIF) (http://www.gbif.org), United States Geological Survey (USGS, 2012) and from different previously published literature sources (Supplementary References). We did not include records from the Caspian region, because it represents a separate species initially described as *Daphnia lumholtzi palaeartica* Behning, 1928. It has obvious morphological differences from *D. lumholtzi* and has a distinct life-history, *i.e.* it is adapted to cooler temperatures than its congeners (Behning, 1941).

To build the SDM, we did not distinguish between records of native and invaded populations, because invasive species may violate two premises of SDMs: i) the invasion process may not be complete; ii) the niche may change in novel habitats (Peterson, 2003; Guisan and Thuiller, 2005; Broennimann *et al.,* 2007; Jiménez-Valverde *et al.,* 2011). The recommended method to overcome these issues is to include both the native and invaded ranges, since these models how better performances than models using only the native range (Broennimann and Guisan, 2008; Beaumont *et al.,* 2009; Capinha *et al.,* 2011). The SDM was performed using eight climatic variables taken from the Wordclim database (Hijmans *et al.,* 2005) (download: http://www.worldclim.org) and one topographic variable (Breakline emphasis GMTED2010) at a spatial resolution of 30 arc-seconds

(Tab. 1). These variables were chosen because they were not highly correlated (Pearson's $r < |0.9|$). According to Jiménez-Valverde *et al.* (2011), it is also necessary to consider the biological relevance of the variables chosen. Thus, all variables used to build the SDM are related with features from the biology or ecology of the cladoceran species (Tab. 1).

Maximum entropy modelling (MaxEnt) is a machine learning method that is considered the most robust method for predicting environmental suitability using presence-only data. The advantages of this method are: i) mathematical functions are concise and the results are easily interpreted (Phillips *et al.,* 2006; De Marco and Siqueira, 2009); and ii) MaxEnt can make accurate predictions using a reduced set of occurrence records (Costa *et al.,* 2010). When compared to other SDM techniques, MaxEnt was among the most effective when using presence-only data, with a performance comparable to techniques that use presence and absence data (Elith *et al.,* 2006; Costa *et al.,* 2010). Thus, we chose MaxEnt to model the environmental suitability of *D. lumholtzi* in the Neotropics. We used occurrence records from both native and invaded areas to calibrate the model, which was then projected to the Neotropical region, following the sugges-

Tab. 1. Variables used to build the species distribution model of *Daphnia lumholtzi* from native and invaded areas, and the relative contribution of each environmental variable to the model.

Variable (data source)	Contribution (%)	Justification
Breakline emphasis (GMTED2010, be30_grd)	4.8	Topographic variable is important for delimitation of rivers, streams, ponds and floodplains
Annual Mean Temperature (Worldclim, bio_1)	20.8	Temperature and precipitation are linked to homeostasis and reproduction
Isothermality (WorldClim, bio_3)	17	
Temperature Seasonality (WorldClim, bio_4)	8.5	
Temperature annual range (WorldClim, bio_7)	5.6	
Mean diurnal range (WorldClim, bio_2)	5	
Mean Temperature of Warmest Quarter (WorldClim, bio_10)	2.7	
Precipitation of driest quarter (WorldClim, bio_17)	2.6	
Precipitation of coldest quarter (WorldClim, bio_19)	2.3	

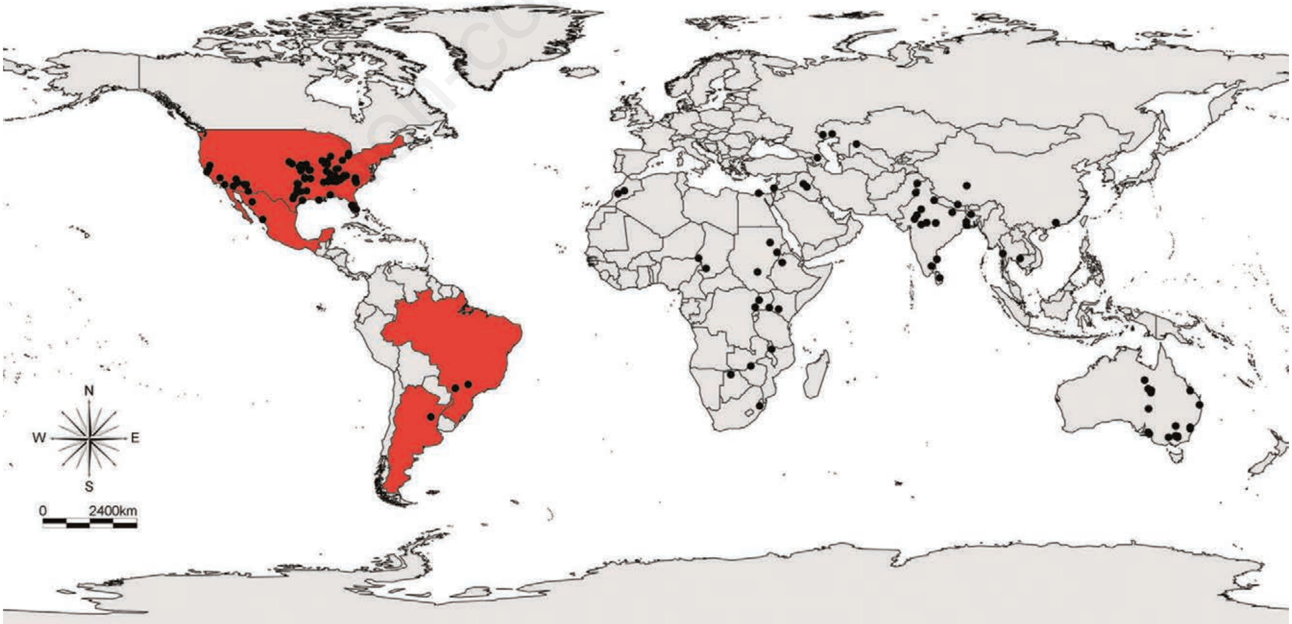

Fig. 1. Records of *Daphnia lumholtzi* used in our species distribution model based on data from both native and invaded areas. Invaded countries in North and South America are presented in red. Data obtained from Global Biodiversity Information Facility (GBIF) (http://www.gbif.org), United State Geological Survey (USGS, 2012) and from published literature (see Supplementary References).

tion of Peterson (2003) and Jimenéz-Valverde *et al.* (2011). A cross-validation with 10 replications was used to estimate errors of adjusted functions and the predictive power of data held for testing (Palaoro *et al.,* 2013). The SDM for *D. lumholtzi* was assessed using the area under the receiver-operating characteristic curve (AUC). The AUC provides a threshold independent measure of model performance compared to null expectations. It has been used to assess SDMs due to the evaluation of specificity (absence of commission errors) and sensitivity (absence of omission errors) (Elith *et al.,* 2006). If AUC values are close to 1, they indicate a good performance of the SDM. To help in the interpretation of results we followed the suggestion of Palaoro *et al.,* (2013), as follows: AUC >0.9=excellent; 0.8 >AUC <0.9=good; 0.7 >AUC <0.8=fair; 0.6 >AUC <0.7=bad; AUC <0.6=failed.

To observe if the climatic niche of *D.* (*Ctenodaphnia*) *lumholtzi* may overlap with that of native species of the genus, we obtained the occurrence records of *D.* (*Daphnia*) *gessneri* Herbst, 1967, *D.* (*D.*) *peruviana* Harding, 1955, *D.* (*D.*) *marcahuasensis* Valdivia-Villar & Burger, 1989, *D.* (*Ctenodaphnia*) *chilensis* (Hann, 1986), *D.* (*C.*) *dadayana* (Paggi, 1999), *D.* (*C.*) *inca* Korinek & Villalobos, 2003, *D.* (*C.*) *menucoensis* Paggi, 1996, *D.* (*C.*) *ornithocephala* Baribén, 1953, *D.* (*C.*) *paggii* Kotov, Sinev & Berrios, 2010, *D.* (*C.*) *spinulata* Baribén, 1917. Due to the uncertainty of several occurrence records in the literature, we checked all native species on the List of Cladocera of the World to ascertain that they are only endemic in the Neotropics (Kotov *et al.,* 2013).

After that, we gathered the environmental variable values for each occurrence record of the native species and *D. lumholtzi* and transformed the data using ranging transformation:

$$[(x\text{-}\min_x)/(\max_x\text{-}\min_x)]$$

Lastly, we performed an ordination analysis (principal components analysis - PCA) using a covariance matrix. Data were analyzed in the Software PAST (Hammer *et al.,* 2001).

RESULTS

The calibrated model had a mean AUC of 0.884±0.03, suggesting a good model (Fig. 2). The projection showed high suitability in the regions connected by the Paraná River Basin between southwestern Brazil, eastern Argentina and Uruguay (Fig. 2). High suitability was also found in South-central Chile, coastal areas of Brazil (Atlantic coast) and Mexico (Fig. 2).

PCA axis 1 (PC1) explained 54.48% of the variance with an eigenvalue of 0.16, while axis 2 (PC2) explained 18.17% of the variance with an eigenvalue of 0.05. The ordination presented a clear gradient related to climatic variables (from the right to the left) with *D. spinulata*, *D. menucoensis*, *D. dadayana*, *D. ornithocephala* and *D. gessneri* showing different degrees of overlap with *D. lumholtzi* (Fig. 3 A,C,D,G,H,K). In contrast, *D. lumholtzi* does not overlap with species that are endemic to mountainous regions, *i.e. D. chilensis, D. inca, D. marcahuasensis, D. paggii* and *D. peruviana* (Fig. 3 A,B,E,F,I,). The most important variables (r >|0.7|) observed were isothermality (r=-0.94), temperature seasonality (r=0.98), temperature annual range (r=0.95) for PC1, and precipitation of the driest quarter (r=-0.73) for PC2.

DISCUSSION

Our results showed that *D. lumholtzi* has the potential to invade large portions of the Neotropics that are not yet colonized (or regarded as not yet colonized due to insufficient sampling). We highlight the high environmental suitability of *D. lumholtzi* in Argentina, Chile and Uruguay, which should increase the probability of invasion in many water bodies in that region (Fig. 2; Sousa *et al.,* 2014). This result is worrying, because *D. lumholtzi* disperses both adults and resting eggs (in the ephippia) *via* lotic systems, and uses stagnant water bodies - such as reservoirs and dams - to establish viable populations (Panov *et al.,* 2004: Havel and Medley, 2006). These lowland man-made reservoirs are more susceptible to invasions when compared to natural water bodies, because they function as stepping stones for the invaders (Havel *et al.,* 2005, 2015; Johnson *et al.,* 2008). The main issue is that the Paraná River basin, the most vulnerable area for the invasion of *D. lumholtzi* according to our model, connects three countries on a large spatial scale by lotic and flood systems with periodic hydrological cycles - also presenting numerous dams and reservoirs. Due to this, the population found in Argentina by Kotov and Taylor (2014) could have come originally from Brazil, since the first reports in South America come from there (Zanata *et al.*, 2003; Simões *et al.,* 2009). Further colonization of the Neotropics could occur by dispersion via water currents (*e.g.* the Argentinian population) or by waterfowl (*i.e.*, carrying the ephippia on their feathers and through midgut passage; Incagnone *et al.,* 2015).

Daphnia lumholtzi shows a considerable climatic niche overlap with some native lowland species (Fig. 3). Havens *et al.* (2012) indicate no evidence of the competitive exclusion of native species by *D. lumholtzi* invaders in lakes of North America. However, some key sources of evidence show why *D. lumholtzi* may negatively affect native *Daphnia* species. *Daphnia lumholtzi* has a relatively higher fitness in warmer waters when compared to other *Daphnia* species (Kolar *et al.,* 1997; Work and Gophen, 1999; Lenon *et al*., 2001; Wittmann *et al.,* 2013). In addition, *D. lumholtzi* increases its reproductive effort when exposed to predators (Dzialowski *et al.,* 2003) and develops a long and strong helmet and tail spine, serving as a mechanism to reduce predation, causing difficulties to invertebrate predators and even fish larvae (Engel and Tollrian, 2009; Engel *et al.,* 2014).

In the Indian subcontinent, Padhye *et al.,* (2016) indicated that the distribution of *D. lumholtzi* was associated with localities that show warm and stable temperatures. Likewise, the relatively higher temperatures and higher stability of lowland Neotropical ecosystems when compared to temperate ecosystems would thus increase any competitive advantage of *D. lumholtzi* over the native species (McMahon, 2002). This was supported by the PCA, where isothermality (related to climatic stability) and temperature seasonality (related to climatic seasonal-

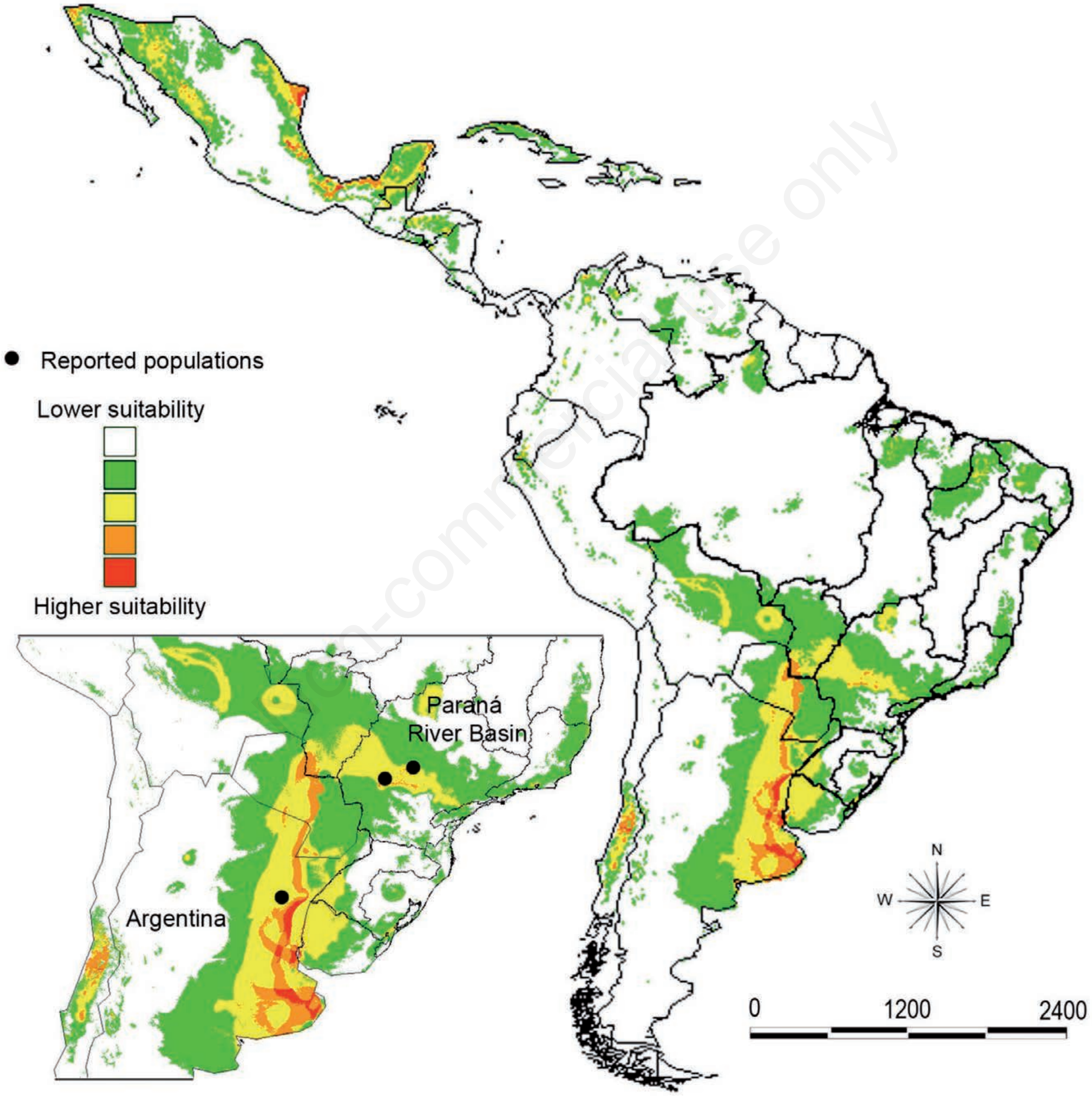

Fig. 2. Environmental suitability of the invader *Daphnia lumholtzi* in the Neotropics. The model was calibrated using native and invaded occurrence records, then projected to the Neotropical region (AUC: 0.884 ± 0.03). Brazil is subdivided in hydrographical regions (Resolution number 32 of the National Council of Hydric Resources). Warmer colors indicate higher environmental suitability.

ity) seem to be responsible for the ordination of *D. lumholtzi* to *D. chilensis, D. inca, D. marcahuasensis, D. paggii, D. peruviana* (Fig. 3 A,B,D,E,F,I,J). These five mountainous endemics do not show a climatic niche overlap with *D. lumholtzi*. However, *D. lumholtzi* may also influence these native species via niche expansions or shifts that may occur during the invasion process (*e.g.*, predator release effect, niche shifts; Capinha *et al.,* 2011; Petitpierre *et al.,* 2012).

If widely distributed lowland species are more vulnerable to the invader, endemic species of *Daphnia* may be protected against such a fate by natural barriers and unusual (extreme) environmental conditions. At least some South American endemic daphniids with very local distribution could be regarded as relicts (Kotov *et al.,* 2010). Relicts, usually occurring in extreme habitats, are extinction-prone due to environmental disturbances caused by human activity (Pitman *et al.,* 2002; Lavergne *et al.,* 2006;

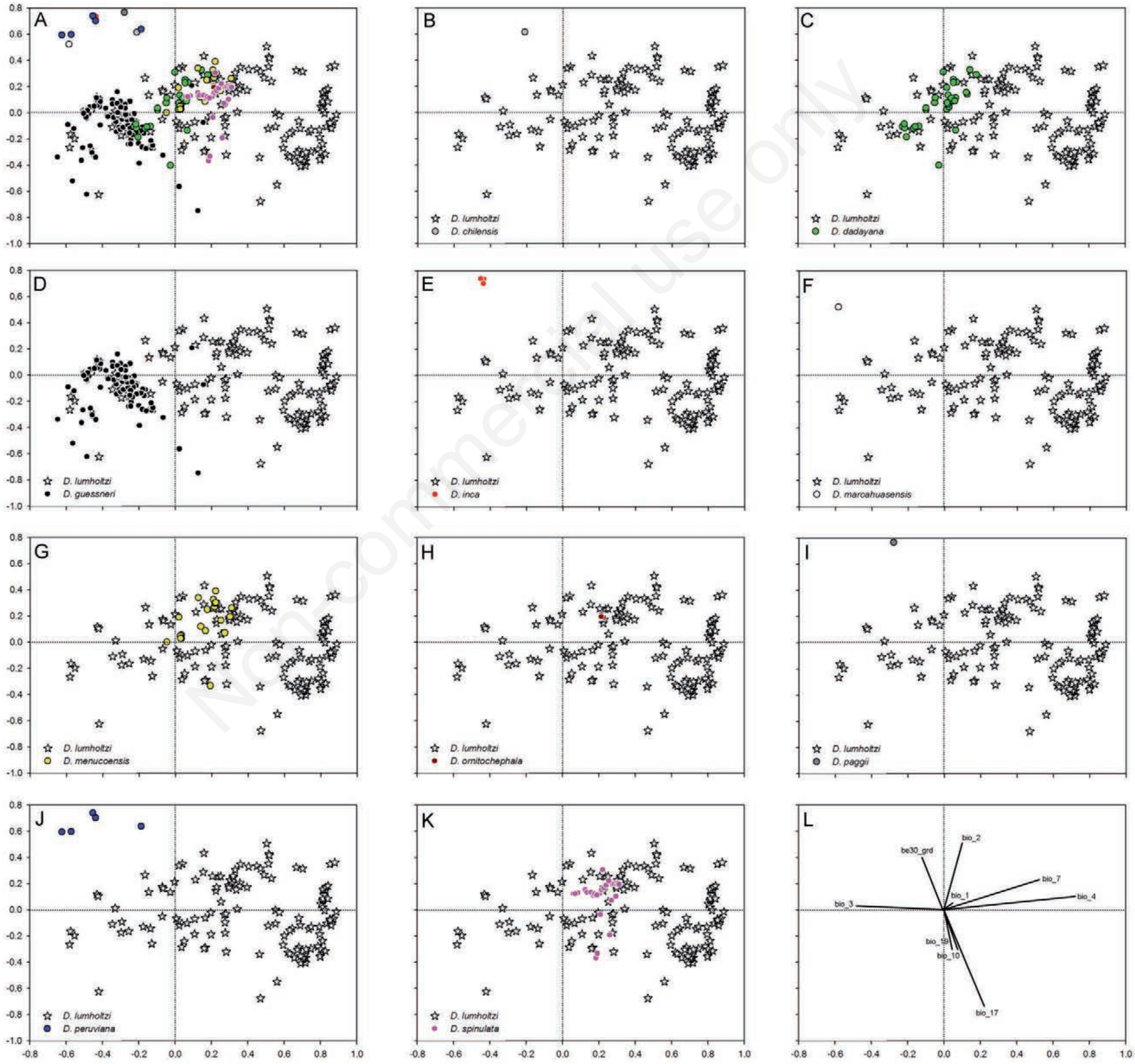

Fig. 3. A) Biplot of principal components analysis, which was made with eight climatic and one topographic variable (see Tab. 1). The first and the second axis explain more than 70% of the observed variance. B-K) Ordination of native versus invasive species. L) Vectors from climatic variables. *Daphnia chilensis* (B), *D. inca* (E), *D. marcahuasensis* (F), *D. paggii* (I) and *D. peruviana* (J). *Daphnia lumholtzi* presents a high climatic niche overlap with most of the native species - except for *D. chilensis* (B), *D. inca* (E), *D. marcahuasensis* (F), *D. paggii* (I) and *D. peruviana* (J).

Chambers *et al.,* 2008). Paradoxically, we found that locally distributed relicts may be better protected against invaders due to the climatic and geographic singularities in which they occur. Zhang *et al.* (2016) showed that geographic isolation was an important predictor of the distribution pattern of relict populations of the plant *Emmenopterys henryi* Oliv. (Rubiaceae). In the case of Neotropical relict *Daphnia* species, current geographic isolation provided by mountains (especially the Andes) can be an important barrier to prevent propagule pressure of *D. lumholtzi* from the lowlands. Indeed, the connections between aquatic systems (especially man-made) and their position in the landscape seems to have a primary and important role in the invasion process of *D. lumholtzi* in North and South American lowlands (Havel and Medley, 2006; Simões *et al.,* 2009). Unfortunately, such barriers are not effective in the case of occasional or deliberate human-mediated dispersion.

Another factor that was not covered in the model is UV radiation, which is very strong in the highlands. Most mountainous endemic species are strongly pigmented (Benzie, 2005; Kotov *et al.,* 2010) to protect themselves against UV radiation. The situation in the Neotropics could be similar to that in water bodies of the African Rift Valley, where 'aggressive' American clones of *D.* cf. *pulex* replaced the native daphniids in many lowland water bodies (Mergeay *et al.*, 2005a, 2005b, 2006) but did not impact the endemic species, *D. izpodvala*, which inhabits the Bale Mountains. *Daphnia izpodvala* Kotov & Taylor, 2010 is strongly pigmented, while *D.* cf. *pulex* is not able to produce such melanin pigmentation (Kotov and Taylor, 2010).

CONCLUSIONS

Our results represent the first approach using modelling distribution of *D. lumholtzi* on a large spatial scale. Landscape features, higher temperatures and climatic stability in lowlands may facilitate the invasion process of *D. lumholtzi* due to the connectivity of lotic systems, presence of man-made water bodies, and higher fitness of the invader in warmer and more stable climates. In the Neotropics, generalist species, such as *D. gessneri*, might be relatively more threatened by the invasion process than other species. *Daphnia lumholtzi* and *D. gessneri* already co-occur in the Paraná River Basin (Zanata *et al.*, 2008; Simões *et al.,* 2009). Meanwhile, the other relict species seem to be protected from the invader due to the geographic isolation and local conditions of their habitats, features that may prevent *D. lumholtzi*'s establishment in the region. Regarding future studies, in vulnerable regions, such as the coastal regions of Brazil and Mexico, we urge for a continuous monitoring of the cladoceran fauna. In the regions already invaded by *D. lumholtzi* we recommend further studies so we can fully understand the extent of the current invasion. More studies on how the invader may affect native species, either via ecological (*e.g.*, the interaction between the species) or evolutionary studies (*e.g.*, behavior, genetic studies), are also needed. The co-occurrence of *D. lumholtzi* and *D. gessneri* in the Paraná River Basin seems particularly interesting for this purpose. It is also necessary to emphasize that the water bodies where the relict species occur are located in areas that have experienced minimal human disturbance. By keeping them preserved, the risk of occasional introduction of *D. lumholtzi* ephippia in those environments decreases, thus protecting the relict taxa.

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