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LETTER

Regional Bans on Wild-Bird Trade Modify Invasion Risks at a Global Scale

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Abstract

Wildlife trade is currently the most important and increasing source of vertebrate invasive species. However, exhaustive analyses of potential side effects of trade regulations on this pathway of introduction are lacking. We addressed this by combining environmental niche models and global trade data on parrots (Psittaciformes), one of the most widely traded and worldwide invasive taxa. We used the wild bird trade bans of United States (1992) and Europe (2005) as case-studies. Results showed that regional bans can generate geographic redirections in trade, with important consequences on worldwide invasion risk. While the amount of parrots traded internationally remained largely constant, changes in trade destination occurred. Consequently, the world surface predicted at risk of parrot invasions increased with successive bans. Of concern, a redirection of trade toward developing countries was observed. Attention should be paid on the mismatch between the global requirements of invasion management and the regional scales governing trade regulations.

Introduction

Wildlife trade poses a major threat to biodiversity conservation worldwide (Broad *et al.* 2003). The Convention on International Trade in Endangered Species (CITES) was established to regulate international trade in wild species and to ensure their survival is not threatened. Over 35,000 species are listed within CITES Appendices, categorized depending on how threatened they are by international trade. Additionally, severe restrictions such as bans on commercial trade of wild species have been established for some taxa in some geographies/economies.

While trade bans may be necessary and valuable tools in specific cases, such as when unsustainable trade of highly attractive pet species is driving them to extinction (Tella & Hiraldo 2014), their usefulness as generic conservation approaches is actively debated. It has been argued that blanket trade bans are difficult to apply, can be counter-productive—by promoting illegal trade or the development of new markets to support demand—and may produce negative impacts on the livelihoods of local human communities from the exporting countries (Cooney & Jepson 2005; Rivalan *et al.* 2007). But trade bans could also have important indirect consequences for importing countries. Wildlife trade mostly involves wild-caught individuals (Carrete & Tella 2008b), which have high invasive potential compared to captive-bred ones––due to changes in behavioral and physiological traits that affect their fitness in the wild (Cabezas *et al.* 2013; Carrete & Tella 2015). Thus, trade on wild birds constitutes a major source of biological invasions (Carrete & Tella 2008a). Despite the goal of trade bans is usually not related to the control of invasive species, changes in trade regulations can affect trade routes and open new ones, thereby changing transport, introduction, and invasion of new alien species in importing countries. Unfortunately, the potential indirect consequence of trade bans on invasion risks has been so far overlooked.

Although some species-specific life history traits and propagule pressure are relevant factors for explaining the establishment of alien species (Sol *et al.* 2012; Blackburn *et al.* 2015), the hospitability of the environment where a species is introduced might greatly affect invasion success (Duncan *et al.* 2014). In this sense, many invasive species conserve their native environmental niche in the invaded areas (Strubbe & Matthysen 2014; but see Early & Sax 2014) and thus, environmental niche models (ENMs) calibrated with occurrence data in native ranges have been proposed as valuable first-screening tools to identify those regions that are less safe in terms of environmental suitability (Thuiller *et al.* 2005).

Here, we combine ENMs with bird trade data to describe how world trade routes of parrots (Psittaciformes) have changed after two major regional trade bans, and to determine whether these changes could be promoting new invasion risks worldwide. Psittaciformes are among the most traded bird taxa (Beissinger 2001). This trade strongly contributed to the decline of many parrot species (Tella & Hiraldo 2014), but also caused parrots to be among the most widespread invasive birds in the world (Cassey *et al.* 2004; Strubbe & Matthysen 2009). Almost all parrot species are listed in CITES Annexes and thus, their trade requires permits which detail the origin and destination of the individuals involved. Therefore, trade in parrots constitutes a unique opportunity to assess how past regional trade bans may have changed worldwide trade routes and how these changes could promote future invasions. Particularly, we focused on the 12 parrot species most traded in the last decade to provide an estimate of major risks likely to happen in the near future. These species also allow us to quantify the accuracy of invasion risk model predictions, since they were also traded in large numbers and established several non-native populations worldwide in past decades. As case studies, we focused on two main bans. The Wild Bird Conservation Act, which was enacted by the United States in 1992, prohibits the importation of wild birds, unless they are collected in accordance with predefined management plans for sustainable use of the species. In Europe, the Wild Bird Declaration also prohibits wild-caught bird importations. It was adopted in 2005, first as a temporal measure to prevent the spread of avian flu and other diseases, and since 2007 as an indefinite measure also focused on conservation and animal welfare.

Methods

Data compilation

Occurrence data of the 12 parrot species representing *c.* 90% of total trade in parrots in the period 2006–2013 (Supporting Table S1) were compiled from the eBird database (Sullivan *et al.* 2009). Occurrence data were classified as pertaining to the native or invasive ranges according to BirdLife International & NatureServe (2014) and revised based on updated distributions provided by Forshaw (2010) for native ranges and Lever (2005) and CABI (2016) for invasive ranges. Occurrence data were aggregated at 0.5° resolution (~50 km), resulting in 1,949 locations for native and 613 for invasive ranges (native species occurrences vary between 21 and 440; for the invasive range, this is 0–315; Supporting Figure S1).

To describe environmental niche, we employed eight 0.5 °-resolution bioclimatic variables from WORLDCLIM (Hijmans *et al.* 2005), which are known to affect bird distributions (e.g., Strubbe *et al.* 2013): annual mean temperature, mean temperature of the warmest month, mean temperature of the coldest month, temperature seasonality, annual precipitation, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality. Land-use and human variables did not improve model accuracy and were not considered in analyses (Supporting Appendix S1).

Propagule pressure was estimated as the total number of live parrots reported by CITES that were imported by each country from 1975 (the first year for which CITES compiled records) to 2013 (www.cites.org). Since captive-bred individuals have a small chance of contributing to invasive populations (Carrete & Tella 2008a, 2015, 2016), we excluded from trade databases registers that explicitly refer to captive-bred origin. We therefore considered wild-caught and birds with unknown origin for analyses. However, none of the species considered are known to be bred in captivity for exporting from native countries and thus "unknown" birds are expected to be wild-caught.

Ecological niche modeling

Species niches were characterized using an ensemble model of four techniques: generalized linear models, MAXENT, gradient boosting machine, and random forest using R library biomod2. We only used occurrence data in native ranges for model calibration, since wild-caught birds were imported from their native range directly. We conducted one ensemble model for each species, except for the ring-necked parakeet *Psittacula krameri*, whose disjointed Asian and African distributions have been shown to have different invasive potentials (Strubbe *et al.* 2015; Cardador *et al.* 2016). Models were run with a single set of 10,000 pseudo-absences randomly drawn from all biomes occupied by each species across its native ranges (Guisan *et al.* 2014) (Supporting Figure S1). Presences and pseudoabsences were weighted as such to ensure neutral (0.5) prevalence (Strubbe *et al.* 2015). To reduce uncertainty caused by sampling artifacts, we conducted 10 replicates for each model by dividing the occurrence data into random training (70%) and test (30%) data sets. However, full models considering total sample size provided highly concordant predictions (Pearson correlation coefficient > 0.90 for all species). For each species, consensus models were generated as averaged means. Averaged models were evaluated using the area under the receiver operating characteristic curve (AUC) (Phillips *et al.* 2006) and the true skill statistic (TSS) values (Allouche *et al.* 2006). Finally, the continuous suitability outputs were transformed into binary suitable/unsuitable maps. To be conservative, all pixels with predicted suitability above the 1% of values of occurrences in the native ranges were considered as suitable. To reduce problems related to model extrapolation, model projections were adjusted using multivariate environmental similarity surfaces (MESSs) (Mateo *et al.* 2014). Environmental suitability in highly dissimilar areas (MESS < -20) (Mateo *et al.* 2014) was considered to be 0 (Supplementary Figure S2).

Model predictions and invasion success

Predicted environmental suitability was compared against species occurrences in non-native countries where the species were traded. We conducted generalized linear mixed models (GLMMs) with mean habitat suitability in each country as a predictor, species as a random factor, and the proportion of surveyed grids occupied as the response variable (numerator: number of occupied grids; denominator: number of surveyed grids according to eBird data; binomial error distribution and logit-link function). We also included propagule pressure and year of first importation as control covariates (Cardador *et al.* 2016). Additionally, since the proportion of occupied grids per country is likely to vary according to its extent, we included the area of each country as offsets in all models (Cardador *et al.* 2016). To reduce the complexity of analysis, for the ring-necked parakeets, we only considered the Asian range, as this seems to be the origin of most of the invasive populations (Strubbe *et al.* 2015; Cardador *et al.* 2016). All predictors were standardized for modeling. Deviance partitioning was used to assess pure and joint contribution of different predictors (Cardador *et al.* 2016).

Changes in trade routes and invasion risks

Trade data were classified into three periods: before U.S. ban (1975–1992), after U.S. ban (1993–2005), and after EU ban (2006–2013). To disentangle the effects of bans on temporal trade patterns from other effects such as unequal socio-economic changes across countries, we compared trade in parrots with trade in live reptiles with commercial purpose according to CITES data. Reptiles were also widely traded for the pet markets but not regulated by trade bans. We conducted a GLMM with number of exports as the response variable and year, region, taxa, and their interaction year × region × taxa as predictors. GLMs were conducted in R software.

To provide an estimate of invasion risk in each period for the considered parrot species, we constructed surfaces of cumulative risks as the sum of binary suitable/unsuitable maps for all species (Thuiller *et al.* 2005). For those analyses, African and Asian ring-necked parakeets were considered separately. To account for trade limitations, invasion risk for each species and each period was set to 0 in pixels included in countries where the species were not traded. Cumulative world surface at risk of parrot invasions was then calculated as the total surface of pixels with cumulative risk >0 in a given period and the previous one/s, using a cylindrical equal area projection.

Results

Niche-model predictions and invasion success

The predicted distributions showed a very high agreement (all AUC > 0.90 and TSS > 0.60) with occurrences in the native ranges (Table 1). In non-native countries, a significant relationship between occurrence rate and predicted habitat suitability was found, while controlling for the significant effects of propagule pressure

Table 1 Predictive performance of the ensemble models of four ENMs used to model the macroclimatic niche of study species in their native ranges

Species	*N*	AUC	TSS
Amazona amazonica	218	0.93	0.70
Amazona ochrocephala	207	0.93	0.73
Ara ararauna	172	0.91	0.62
Ara chloropterus	139	0.93	0.68
Cyanoliseus patagonus	92	0.95	0.77
Myiopsitta monachus	433	0.96	0.76
Poicephalus gulielmi	28	0.99	0.93
Poicephalus senegalus	84	0.94	0.74
Psittacara frontatus	21	0.96	0.85
Psittacara mitratus	54	0.98	0.90
Psittacula krameri (Asia)	373	0.93	0.74
Psittacula krameri (Africa)	67	0.95	0.78
Psittacus erithacus	61	0.97	0.87

For each modeling technique, 10 replicates were computed using as training data 70% random samples of the complete data set. Sample size (*N*) at 0.5° resolution (~50 km) is provided.

Table 2 Results from multivariate generalized linear mixed models (binomial error distribution; logit-link function) relating occurrence rate of parrot species in non-native countries with environmental suitability, propagule pressure, and year of first importation

	Estimate	*Z*	*P*
Intercept	−11.10 ± 0.41	−26.87	<0.001
Habitat suitability	3.64 ± 0.05	69.8	<0.001
Propagule pressure	0.14 ± 0.05	2.87	0.004
Year of first importation	−2.43 ± 0.07	−32.58	<0.001

Country surface was included as an offset in all models and species as a random factor. All predictors were standardized.

and year of first importation (Table 2). Total deviance explained by the model was 50%, with pure contribution of habitat suitability accounting for 51.8% and propagule pressure together with time since first importation (i.e., pure + joint contribution of these two variables) for 41.2% of the explained deviance (Supporting Figure S3).

Global changes in trade routes

Trade data revealed similar numbers in total exports of the 12 species across periods, although countries with the highest contribution as importers changed (Figure 1a). These changes were consistent among species (Supporting Figures S4–S6). Before the U.S. ban, a total of 2.2 million individuals (0.13 million per year) were traded. U.S. (47.3%) and EU countries (45.9%) were the main importers (Figure 1b). After the U.S. ban, a similar number of parrots (2.1 million individuals; 0.16 million per year) were traded worldwide. However, EU countries dominated the international trade (79.6%). Imports also increased in Mexico, South-America, countries of the former Soviet Union, and across Southeast Asia. After the EU ban, imports reached almost zero in EU countries (except for *Psittacus erithacus* in the years 2006–2007, Supporting Figure S6). A total of 0.80 million individuals (0.10 million per year) were traded, most of them with Mexico (75.4%) as main destination (Figure 1b).

Global trade in reptiles (not affected by bans) showed a temporal pattern different from parrots (interaction year × region × taxa: $\chi^2 = 410{,}291$, df = 6, $P < 0.001$), since trade similarly increased with years in all world regions (Figure 1c). Therefore, changes in trade routes for parrots (Figure 1b) are more likely attributable to regional bans rather than to socioeconomic improvements in particular regions.

Global changes in invasion risk

The worldwide potential distribution of the considered species highlighted some areas highly susceptible to invasion according to climatic suitability (Supporting Figures S7 and S8). When taking into account trade destination, changes in invasion risks were observed among periods (Figure 2). Consequently, the cumulative world surface at risk of parrot invasions increased up to 31% after successive trade bans (Figure 3). In the period prior to the U.S. ban, areas most susceptible to invasion were North, Central and South America, Europe, Southern Africa, Arabian Peninsula, Southern Asia, Indonesia, and southern and eastern coasts of Australia. Cumulative risk values ranged between 2 and 3 in most of these areas, although higher values were observed in particular regions. After the U.S. ban, cumulative risk values increased the most in Central and South America and Indonesia, while moderate increases were also observed in Eastern Europe, Southern Asia, Arabian Peninsula, and some parts of Africa (Figure 4). On the contrary, cumulative risk values were mostly the same in the United States, meaning that although trade numbers decreased, potentially invasive species were still imported. After the EU ban, United States, Central and South America, Southern Africa, Southern Asia, and Indonesia are still among the areas most susceptible to invasion. However, cumulative risk values have broadly decreased worldwide (Figure 4), especially in large areas of Western Europe and United States where invasion risks were initially the largest.

Discussion

Our results provide evidence that regional blanket trade bans may reduce invasion risks in previously importing countries, but can also generate redirections in international trade, with important consequences on worldwide

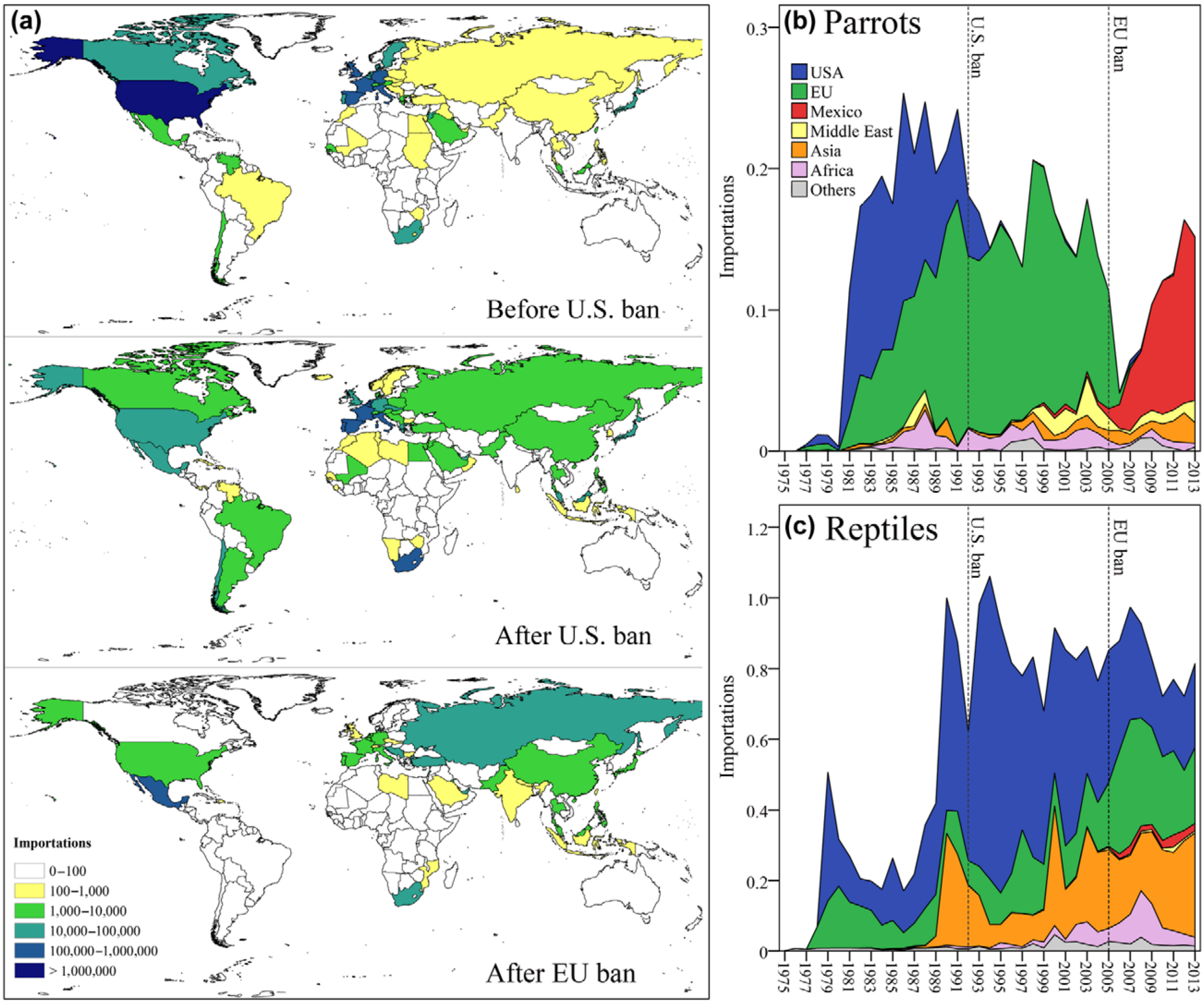

Figure 1 Trade patterns for the 12 considered parrot species (a, b) and reptiles (c) in different geographic areas in three main periods according to CITES (1975–2013). For parrots, spatial (a) and temporal (b) patterns are shown. Imports are based on live individuals from the direct international trade to reduce double counting of reexported specimens. Note that in (b) and (c), importations represent cumulative values across regions and are expressed in million individuals. In (b) and (c), vertical dashed lines represent wild-bird trade bans of United States in 1992 and EU in 2005.

invasion risks. While annual export numbers of the most traded parrot species remained similar after the U.S. and EU bans, important changes in trade final destination were observed. This suggests a redirection of commercial species to new markets following trade prohibitions in the main importer countries, likely favored by a cross-cultural preference for parrots as pets (Tella & Hiraldo 2014). Changes in socioeconomic forces such as gross domestic production in developing countries may have also contributed (Weber & Li 2008). However, differences in temporal trade patterns with other vertebrates not affected by the U.S. and EU bans suggest that the spatiotemporal patterns of trade in parrots were mostly influenced by trade bans.

As a result, increases in cumulative invasion risks have been noticeable, particularly in the period after the U.S. ban and in some areas such as Mexico and Indonesia. In fact, some predicted invasions after redirected commerce have been recently proved, as in the case of the monk parakeet (*Myiopsitta monachus*) in Mexico (Macgregor-fors 2011). Although the number of established non-native species in such predicted areas is still limited by the date of this study, our results suggest that further invasion events are likely in the near future. Areas with high invasion risks where non-native species have not been reported could be sites not yet invaded. In fact, the occurrence of lag phases typical of alien populations—estimated between 10 and 38 years for birds—suggests

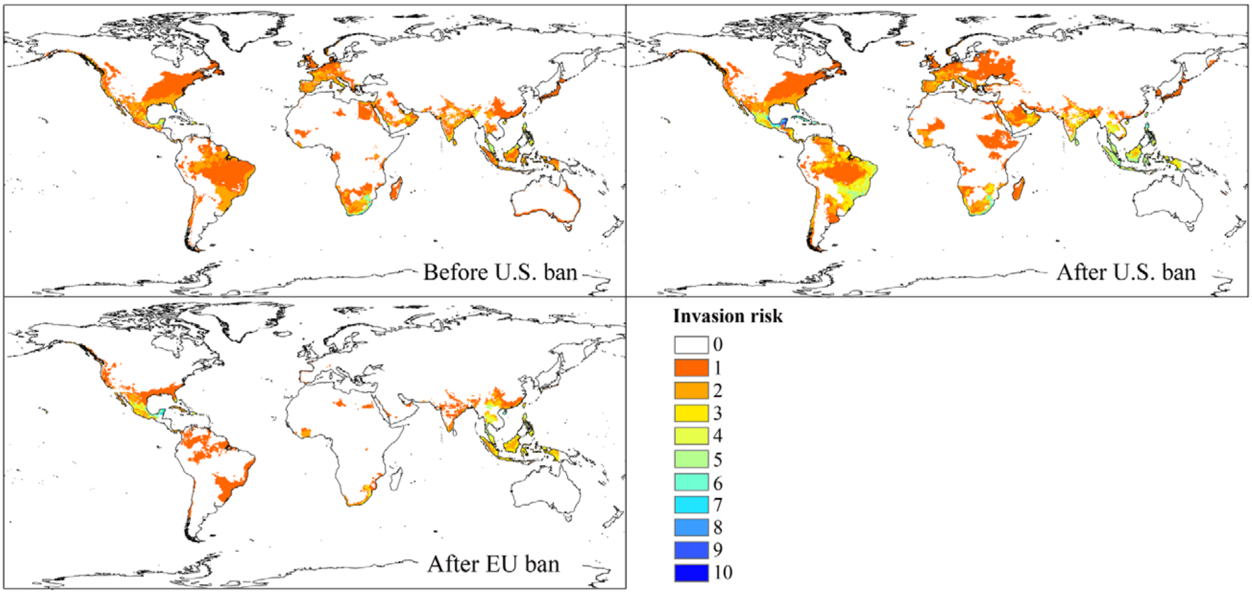

Figure 2 Changes in cumulative risk probabilities for the presence of the 12 considered parrot species as derived from a macroclimatic ensemble model of four ENMs according to temporal variation in trade patterns. Note that African and Asian ring-necked parakeets were considered separately in those analyses, thus cumulative risk can range between 0 and 13.

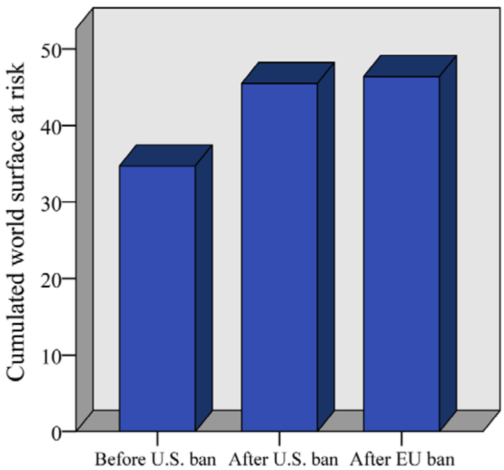

Figure 3 Cumulated world surface at risk of parrot invasions. Cumulated extent (unit: millions of km^2) of areas exposed to at least one potential invasive parrot species according to habitat suitability across periods is shown.

that currently rare alien species may exhibit a strong increase in numbers and geographic extent later (Aagaard & Lockwood 2014). This may explain the major role of the year of first importation in present-day occurrences of studied species. Additionally, increased propagule pressure may also favor invasions by increasing probabilities of birds escaping from cages, thereby helping to overcome environmental and demographic stochasticity (Blackburn *et al.* 2015). It is important to note that our results are conservative, since they assume that imported species can only establish alien population if there is climate matching with native regions. While some birds could also establish alien populations in other areas, their capacity to spread and become invasive is expected to be strongly influenced by climate matching (Duncan *et al.* 2001).

From a conservation-policy perspective, our results highlight that, in the current context of globalization, more attention should be paid to the differences between regional goals of trade regulations and its global implications. The U.S. and EU trade bans were designed for different purposes, including human health and animal welfare, but also with a strong focus on species conservation. Although a reduction of international parrot imports following trade bans was clear in both regions, the amount of parrots traded internationally remained largely constant and thus trade is still contributing to threaten several parrot species (Tella & Hiraldo 2014). Of additional concern, the redirection of trade from developed countries, where knowledge and resources to combat invasive species are available and social awareness is high, to developing countries, which are less well equipped to deal with invasions, may strongly increase invasion risks and impacts in these areas (Nuñez & Pauchard 2010; Early *et al.* 2016).

While it is recognized that wildlife trade is currently the most important and increasing source of vertebrate

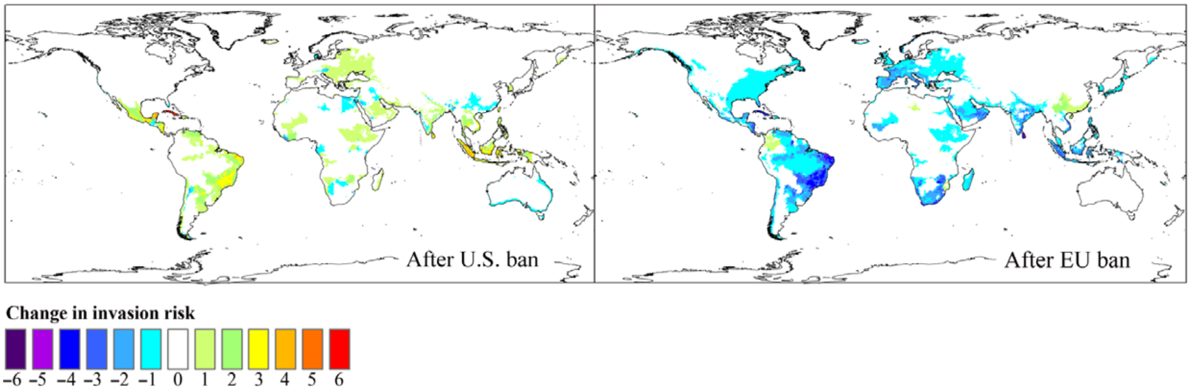

Figure 4 Changes in cumulative risk probabilities from the risk assessment after the U.S. and EU bans. Cumulative probabilities for the presence of the 12 considered parrot species are based on ensemble models of four ENMs used to model the macroclimatic niche of study species in their native range. Note that African and Asian ring-necked parakeets were considered separately in those analyses.

invasive species, trade regulations are usually not concerned about invasion risks. The only blanket ban focused on avoiding invasion risks is the Spanish one (a national ban, Real Decreto 630/2013), which since 2011 prohibited the importation of all wild-caught birds from any species (Abellán *et al.* 2016). This is a good example of how the responsibility for protection against invasive species still lies mostly with national governments, despite biological invasions have become a global issue. Our results highlight the need to proactively develop more holistic and global strategies, aimed to incorporate invasion risk as a priority objective of trade regulations and to promote international cooperation (Perrings *et al.* 2005; Inderjit *et al.* 2006). Prioritization of the more risky species for assessment or establishment of trade bans could be an option. However, the huge amount of traded species may make invasion risk assessments an unaffordable goal, even more for developing countries. Thus, applying the precautionary principle (Carrete & Tella 2016), a worldwide ban on wild-bird trading should be enacted. At the same time, captive breeding and trade of captive-bred individuals—which have low invasive potential (Carrete & Tella 2016)—could be promoted to satisfy the global demand of pets and cage birds (Carrete & Tella 2008a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. List of the parrot species traded from 1975 to 2013 according to CITES data.

Figure S1. Occurrence data in native and invasive ranges for the 12 considered species.

Figure S2. Multivariate similarity surface analyses for the 12 considered species.

Figure S3. Deviance partitioning analysis for the probability of occurrence of the studied species.

Figures S4–S6. Number of individuals of considered parrot species imported per country in the period before the U.S. ban, after the U.S. ban, and after the EU ban, respectively.

Figure S7. Worldwide climatic suitability for the 12 considered parrot species.

Figure S8. Predicted occurrences for the 12 considered parrot species.

Appendix S1. Comparisons of climatic and climatic + habitat models.

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