



HAL
open science

Predicting the potential distribution of the invasive Common Waxbill (Passeriformes: Estrildidae)

Darius Stiels, Kathrin Schidelko, Jan O. Engler, Renate Elzen, Dennis Rödder

► **To cite this version:**

Darius Stiels, Kathrin Schidelko, Jan O. Engler, Renate Elzen, Dennis Rödder. Predicting the potential distribution of the invasive Common Waxbill (Passeriformes: Estrildidae). *Journal für Ornithologie = Journal of Ornithology*, 2011, 152 (3), pp.769-780. 10.1007/s10336-011-0662-9 . hal-00669207

HAL Id: hal-00669207

<https://hal.science/hal-00669207>

Submitted on 12 Feb 2012

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Predicting the potential distribution of the invasive Common Waxbill *Estrilda astrild* (Passeriformes: Estrildidae)

Darius Stiels^{1,*}, Kathrin Schidelko¹, Jan O. Engler², Renate van den Elzen¹, Dennis Rödder²

¹ Zoological Research Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany

² Biogeography Department, Trier University, D-54286 Trier, Germany

* Author for correspondence, e-mail: d.stiels.zfmk@uni-bonn.de, Tel.: +49-228-9122 230

Abstract

Human transport and commerce have led to an increased spread of non-indigenous species. Alien invasive species can have major impacts on many aspects of ecological systems. Therefore, the ability to predict regions potentially suitable for alien species, which are hence at high risk, has become a core task for successful management. The common waxbill *Estrilda astrild* is a widespread African species, which has been successfully introduced to many parts of the world. Herein, we used MAXENT software, a machine learning algorithm, to assess its current potential distribution based on species records compiled from various sources. Models were trained separately with records from the species' native range and from both invaded and native ranges. Subsequently, the models were projected onto different future climate change scenarios. They successfully identified the species known range as well as some regions that seem climatically well suited, where the common waxbill is not recorded yet. Assuming future conditions, the models suggest pole ward range shifts. However, its potential distribution within its tropical native and invasive ranges appears to be more complex. Although the results of both separate analyses showed general similarities, many differences have become obvious. Niche overlap analysis shows that the invasive range includes only a small fraction of the ecological space that can be found in the native range. Thus, we tentatively prefer the model based on

native locations only, but in particular we highlight the importance of the selection process of species records for modelling invasive species.

Key Words

ecological niche modelling, species distribution model, niche overlap, MAXENT, climate change, invasive species

Zusammenfassung

Vorhersagen zur möglichen zukünftigen Verbreitung des invasiven Wellenastrilds *Estrilda astrild* (Passeriformes: Estrildidae)

Weltweiter Handel und Mobilität haben zu einer zunehmenden Ausbreitung nicht-heimischer Arten geführt. Invasive Arten können großen Einfluss auf zahlreiche Aspekte ökosystemarer Zusammenhänge haben. Deshalb ist die Fähigkeit, Regionen vorherzusagen, die für solche Arten potentiell geeignet und daher möglicherweise bedroht sind, eine Kernaufgabe erfolgreichen Managements. Der Wellenastrild *Estrilda astrild* ist eine weit verbreitete afrikanische Art, die erfolgreich in viele Gebiete der Welt eingeführt wurde. Mit Hilfe der Software MAXENT, einem Algorithmus, der auf maschinellem Lernen basiert, haben wir seine gegenwärtige, potentielle Verbreitung basierend auf Fundpunkten aus verschiedenen Quellen modelliert. Die Modelle wurden sowohl mit Nachweisen aus dem heimischen als auch dem invasiven und heimischen Verbreitungsgebiet gemeinsam trainiert. Nachfolgend wurden beide auf unterschiedliche zukünftige Klimawandelszenarien projiziert. Die Modelle identifizierten erfolgreich sowohl das bekannte Verbreitungsgebiet der Art, als auch Gebiete, die klimatisch gut geeignet erscheinen, in denen der Wellenastrild aber noch nicht nachgewiesen wurde. Unter zukünftigen Bedingungen legen die Modelle eine polwärts gerichtete Verschiebung der Verbreitungsgebiete nahe, obwohl die potentielle Verbreitung innerhalb der Tropen des heimischen und invasiven Areal komplexer erscheint. Trotz allgemeiner Übereinstimmung zwischen beiden Analysen wurden einige Unterschiede auffällig. Eine Analyse des Überlappungsbereiches der Nischen ergab, dass invasive Fundpunkte innerhalb des ökologischen Raumes liegen, der durch die Fundpunkte aus dem natürlichen Verbreitungsgebiet aufgespannt wird. Wir tendieren daher

vorsichtig zu dem Modell basierend auf der natürlichen Verbreitung, unterstreichen aber vor allem die Bedeutung des Auswahlprozesses der Fundorte für Modellierungen invasiver Arten.

Introduction

Human transport and commerce has led to an increased spread of non-indigenous species (Mack et al. 2000), which can have major impacts on ecological systems by altering mutualistic and competitive interactions among species, ecosystem functions, and resource distributions (Mooney and Cleland 2001). Among exotic species, birds are particularly ubiquitous. Although in general, impacts on native species are suggested to be rather weak, also substantial impacts are observed at times including competition, predation, disease transmission but also mutualisms (Blackburn et al. 2009, chapter 7.5 and references therein). Herein, we aim to predict the recent and future potential distribution of the granivorous common waxbill, one of the most successful invaders among estrildid finches and a species that might even belong to the most successful among all tropical birds (see Lever 2005). Although studies on interactions with native species are largely lacking, granivorous passerines (“finches”) can be substantial predators on plant seeds (Cueto et al. 2006) and are thus likely to influence ecosystems extensively. Food seems to be one of the most important factors determining finch densities and thus making food competition among these birds very likely (Schluter and Repasky 1991). Competition largely affects assemblages of invasive avian finch communities (Lockwood and Moulton 1994). Thus, identification of potential risk areas for a finch like the common waxbill is especially appealing.

Estrilda astrild is a widespread African species (Clement et al. 1993), originally endemic to mainland areas south of the Sahara and some islands (Fig. 1), including Bioko and Mafia. Distributional gaps exist in the rainforest areas of the Congo basin, and more arid parts of Western Africa and the northern Sahel zone, where it seems to be partly replaced by *Estrilda troglodytes*, with which it may form a superspecies (together with *Estrilda nigriloris* and *Estrilda rufibarba*; Fry 2004). It is a polytypic species with currently 15 (Fry 2004) to 17 (Dickinson 2003) recognized subspecies, although these taxa intergrade and most are only slightly differentiated in colour and size (e.g. Goodwin 1982). *Estrilda astrild* favours open habitats such as savannas as well as areas characterized by tall grasses, and it can be common around human settlements (Fry 2004, Goodwin 1982). Like most estrildid finches, common waxbills depend on at least some small puddles for drinking and bathing (Goodwin 1982). Experiences from birds in captivity show that common waxbills are sensitive to low temperatures (below 15° C) and seem to suffer from cold-wet weather conditions in

particular (Steinbacher and Wolters 1965, Nicolai and Steinbacher 2002). They sometimes roost in nests (Fry 2004), which might maintain a favourable microclimate under harsher weather conditions (compare Ricklefs 1974). Otherwise, common waxbills are highly gregarious and, although in most parts of their range are resident birds, local movements and nomadism seems to be not uncommon (Fry 2004).

Common waxbills have been introduced, with and without intent, as a result of the pet trade to many parts of the world (Fig. 1). These introductions often date back to the 19th century, and for some cases the introduction event is well known (Lever 2005). Although not all introductions have resulted in successfully established populations, some occur e.g. in the Iberian Peninsula, where it was introduced in 1964 (Reino and Silva 1998 and references therein), in South America and on several tropical islands around the globe. The latter include Oahu (Hawaii), Society Islands (Tahiti), New Caledonia, Amirantes, parts of the Seychelles archipelago, Mauritius, Réunion, Rodrigues, Ascension, St Helena, São Tomé and Príncipe, Bermuda, Trinidad, Cape Verde and Canary Islands (e.g. Fry 2004, Lever 2005). Other parts of the world might offer also environmentally suitable conditions for the species, and further spreads are likely. During the last decades the species increased its invaded range at least within the Iberian Peninsula (Silva et al 2002). Based on data presented by Reino et al. (2009), the species might further expand its invaded range in south-western Europe making future predictions on a global scale especially appealing.

Species distribution models (SDMs) are tools to assess the potential distribution of species (Guisan and Thuiller 2005, Jeschke and Strayer 2008, but see Elith and Leathwick 2009 for discussion on terminology) including birds (Peterson 2001, Martinez-Meyer et al. 2004, Walther et al. 2004, Strubbe and Matthysen 2009, Echarri et al. 2009). A special case of SDMs are climate envelope models, which rely on the climatic niche of the organism only (Guisan and Thuiller 2005, Elith et al. 2006). SDMs are widely used to predict possible further spreads of invasive species (Menke et al. 2009, Peterson and Vieglais 2001, Rödder and Lötters 2010). In particular, SDMs offer the possibility to project models derived from current conditions into the past or the future using palaeo climate layers or climate change scenarios of forthcoming decades (Peterson et al. 2002, Peterson and Nyári 2007, Rödder and Dambach 2010, Waltari et al. 2007).

Commonly, SDMs are derived from information of the spatial distribution of the target species and environmental, often climatic, variables at these locations. Subsequently, the model is projected into geographic space using a geographic information system (GIS). Preferably, predictor variables should be proximal factors limiting the niche of the species (e.g. Austin 2002, Elith and Leathwick 2009, Rödder et al. 2009a). Models base upon the ecological niche concept, which assumes that the ecological niche of a species is the range of biotic and abiotic conditions in a multidimensional space, which allows the species to persist without immigration (Hutchinson 1957, Soberón 2007, Soberón and Peterson 2005). One needs to keep in mind that SDMs postulate three key assumptions that are mostly not strictly met in nature (Jeschke and Strayer 2008). First, climatic tolerances of the species should be the main determinants of their distribution, neglecting dispersal limitations and biotic factors (e.g. competition, predation), which can only seldomly be incorporated in SDMs (e.g. Rödder et al. 2008a,b). Therefore the realized niche, i.e. environmental conditions present within the geographical space occupied by the species, is under natural circumstances only a subset of the fundamental niche (Hutchinson 1957, Soberón and Peterson 2005). In addition, SDMs assume that the range of the species under study is in equilibrium with environmental parameters (Pearson and Dawson 2003, Araújo and Pearson 2005) and the niche is conservative over time and space (Peterson et al 1999, Wiens and Graham 2005). Finally, SDMs cannot easily cope with dispersal limitations and thus claim that species occur at all locations where environmental conditions are favourable and nowhere else (Jeschke and Strayer 2008). Note that these assumptions are not undisputed (e.g. Beale et al. 2008, Losos 2008, Rödder and Lötters 2009, Warren et al. 2008).

When modelling the potential distribution of an exotic species, the question arises how to treat observations from the native and the invaded range, respectively. Upon recently, SDMs were commonly derived from either species records obtained from the native range (e.g. Peterson and Viglais 2001, Thuiller et al. 2005) or the invaded range (e.g. Mau-Crimmins et al. 2006). As recent findings highlighted a failure of models trained with native records to predict invasive ones (Fitzpatrick et al. 2007, Rödder and Lötters 2009, Beaumont et al. 2009), Broennimann and Guisan (2008) recommend using occurrence data from the whole range of the species. Herein, we approach this issue using a split dataset from the (1) native as well as (2)

from the native and invaded range of *Estrilda astrild* and describe its consequences for (a) current and (b) future predictions of the potential range of this species.

Methods

Common waxbill records

Species records were obtained from the “Global Biodiversity Information Facility” (GBIF, <http://www.gbif.org>), from the “Invasives Information Network” (I3N, http://i3n.institutohorus.org.br/filt_especies.asp) of the Inter-American Biodiversity Information Network, from labels of museum specimens held in the Zoological Research Museum Alexander Koenig, and from additional literature references (Fry 2004, Gatter 1998, Leonard 2005). All records were mapped using DIVA-GIS 5.4 (Hijmans et al. 2001, available through <http://www.diva-gis.org>) for visual inspection, and coordinates were checked to spot possible errors, i.e. if coordinates were not sufficiently accurate (possible spatial error decisively larger than selected spatial resolution of grid size of environmental data, see below) or otherwise unreasonable (e.g. coordinates of the museum instead of the location of the bird), locations were excluded from the analysis. Localities without coordinates were georeferenced by consulting online gazetteers, i.e. the Biogeomancer (<http://bg.berkeley.edu/latest>, last access 18.05.2009) and Falling Rain (<http://www.fallingrain.com/world>, last access 18.05.2009). Furthermore, specimens collected before 1950 were not included in this study to be in concordance with the temporal resolution of the environmental predictors (see below). For each grid cell only one record was permitted in any analysis, resulting in 135 species records from the native and 341 species records from the introduced part of the range.

Spatially unbalanced sampling designs may cause artificial regional clusters of species records (Dormann et al. 2007). To minimize such effects, a cluster analysis based on Euclidean distances in feature space was conducted with XLSTAT 2009 (Addinsoft, <http://www.xlstat.com>). The resulting dendrogram was blunted leaving each 118 native and invasive classes, and only one randomly chosen record per class was used for further processing. This method has been used to reduce effects of spatial autocorrelation (e.g. Rödder et al. 2009b), and simulations suggest a superior performance compared to simple distance buffers (Schmidtlein, Rödder and Feilhauer, unpubl. data). As AUC scores are affected by prevalence, and although

native and invasive data did not contribute equally within the NAT+INV model, this procedure allows a better comparability between the NAT and the NAT+INV models.

Environmental data

We used climate data taken from WorldClim, v. 1.4 (Hijmans et al. 2005, <http://www.worldclim.org>), which cover the period from 1950-2000. Data from a global network of weather stations were interpolated for the whole land surface of the globe with latitude, longitude and elevation as independent variables (Hijmans et al. 2005). Monthly temperature and precipitation data were summarized into 19 so called Bioclim variables (Busby 1991). We used only eight of them as predictor variables in our ecological niche models to reduce effects of overfitting and multi-collinearity of predictors (Heikkinnen et al. 2006). Given the changing seasonal aspect of grasslands and the need for open water for the species, we selected variables covering annual parameters (BIO1, annual mean temperature; BIO12, annual precipitation), quaternary aspects (BIO10, mean temperature of warmest quarter; BIO11, mean temperature of coldest quarter; BIO16, precipitation of wettest quarter; BIO17, precipitation of driest quarter) and seasonal characteristics (BIO4, temperature seasonality; BIO15 precipitation seasonality) of the climate as a biological meaningful combination of predictors. We used a rather coarse resolution of 2.5 arc-minutes (about 4.63 km at the equator) meeting the accuracy of most available occurrence data (see Graham et al. 2008 for a discussion on spatial errors) and at least slightly compensating for the nomadic biology of the species.

For future projections, we obtained climate data of six climate scenarios describing projected conditions for the year 2080 under two different emission scenarios (A2a, B2a) and two different climate models, respectively. The scenarios are described in detail in the “Special Report on Emissions Scenarios” by the Intergovernmental Panel on Climate Change (IPCC, http://www.grida.no/publications/other/ipcc_sr/, last access 10.08.2010). In general, scenarios belonging to the A2 family assume higher CO₂ concentrations as well as higher surface temperatures for the end of the century than assumed under B2 scenarios. In order to deal with uncertainties that are prone to every single climate model, we use two currently available climate model outputs (CSIRO, CCCMA). Final distribution maps are based on average values of both models respectively

representing one family of emission scenario. Original data were downscaled by R. J. Hijmans and can be obtained from <http://www.worldclim.org> (last access 10.08.2010).

Climate envelope modelling

We chose MAXENT v.3.3.3a (Phillips et al. 2004, Phillips et al. 2006, available through <http://www.cs.princeton.edu/~schapire/maxent/>), a machine learning program which uses environmental variables as predictors, for species distribution modelling (SDM). MAXENT has frequently outperformed other competing algorithms (Elith 2006, Heikkinnen 2006), in particular, when the number of data points was limited (Hernandez 2006, Wisz et al. 2008). For model evaluation we use the area under the receiver operation characteristic curve (AUC), which is generated by MAXENT for each run derived from ten random splits of the species records (70% / 30% test). The results were summarized as average of the ten models. We are aware that AUC values have been criticized recently (e.g. by Lobo et al. 2008), but given the general problems with different model evaluation approaches (see examples in Baldwin 2009) and the ongoing wide use of AUC values in ecological studies, we only call for caution if relying on them alone. For common waxbills, descriptions of the current range are broadly available from the literature, and visual inspection of the maps might help interpreting model outputs.

We followed two different modelling approaches: (1) models trained with species records from the native range only (termed NAT in the following), or (2) with records from both native and invaded ranges (termed NAT+INV). All runs were conducted using the default settings of the program.

Ideally, random background points, which are automatically selected by MAXENT, should reflect an area potentially colonisable by the target species (Phillips et al. 2009). Therefore, we restricted the spatial extent of the background records to an area encompassing largely the African continent and thus the complete native range in model (1), and to the transatlantic range including Africa, the Atlantic islands and huge parts of South America east of the Andes in model (2). Subsequently, averages of both models were projected on a global scale onto current climatic conditions and the future climate change scenarios. In order to reduce model uncertainty, we did not extrapolate into climates exceeding those conditions in the background regions. We chose the logistic output format, resulting in values between 0 and 1 for each grid cell, where higher values indicate more suitable climatic

conditions. MAXENT ASCII-outputs were imported into DIVA-GIS, and species presence is presented for two different thresholds: the 10 percentile training presence logistic threshold and the minimum training presence logistic threshold. Both are non-fixed thresholds, as recommended by Liu et al. (2005), which provide minimum requirements for the species climate preferences. Variable response was estimated using the implemented jackknife approach of MAXENT (e.g. Yost et al. 2009). Area calculations of global potential distribution were performed with ArcMap 9.1 (ESRI, Redlands, California).

Comparison of climate niches

In order to illustrate the relative positions of native vs. invasive ranges in ecological space (E-Space) as well as the potential niche available for each of them, we computed principal component analyses (PCA) depending on the environmental variables used for modelling. Only those principal components were selected which had eigenvalues ≥ 1 because these PCs explain more variance than the original data does (here, two PCs were extracted). To assess the niche overlaps in E-space, we subsequently performed linear discriminant analysis (LDA) following Rödder and Engler (in press). This method has the advantage of comparing niche-overlap directly in ecological space instead of geographical space. Hence, it is independent from SDM predictions. In LDA native and invasive ranges were *a priori* defined as groups, each with equal prior probabilities and compared through a set of explanatory variables, representing the E-space spanned by principal components. The discriminant model was constructed with a randomly selected subset of 70% of the dataset and validated with the rest of the data. Total overlaps in E-space were derived by summing all falsely classified values and dividing them by the total of all values resulting in a metric ranged between 0 (no overlap) to 1 (total overlap). Accounting for possible variations caused by data splits, this procedure was repeated 1000 times. Computations were conducted using R 2.11.1 (R Development Core Team, 2010).

Results

Model Performance

We received similar AUC values in both model approaches, i.e. for NAT based on the native range ($AUC_{\text{Test}} = 0.8211$) and NAT+INV including data points from the native

and the introduced range ($AUC_{\text{Test}} = 0.7567$) (Fig. 2). AUC values can be considered at least as “useful” (>0.75) or even good (>0.8) although classification schemes might differ according to the aim of the study (Swets 1988). Analysis of variable contributions revealed high values for mean temperature of the warmest and coldest quarters as well as precipitation variables (Figs. 3a, b). In general, variable contributions were similar in both models, although we detected pronounced differences in the contributions of ‘temperature seasonality’. Response curves for each predictor variable are provided in the online supplementary material. The minimum training logistic threshold was 0.0822 for NAT and 0.0883 for NAT+INV. Values of the more relaxed 10% training presence logistic threshold were also similar in both models (0.2483 for NAT, 0.2820 for NAT+INV, Fig. 4). The spatial extent of the potential distributions derived from the more restrictive 10% training presence logistic threshold was generally smaller (Table 1).

Current potential distribution

Based on both models (Figs. 5a, b) the common waxbill has a huge potential distribution throughout the tropics, subtropics and some temperate regions. The spatial extent of the potential distributions suggested by the models is not consistent over both thresholds (Table 1). Both models show general similarities, although differences in some tropical areas are obvious (e.g. within Australia and Southeast Asia). Unsurprisingly, within Africa the NAT model better reflects the actual distribution when compared with the expert map. The NAT+INV model seems to overpredict some sub-Saharan areas like the Congo basin. According to the NAT+INV model (Fig. 5b) the potential distribution of *E. astrild* is slightly more concentrated in the tropics, and less so in the subtropics. Both models predict suitable areas in some temperate regions including parts of Europe and North America. Although the NAT+INV model includes data points from South America, the NAT (Fig. 5a) model projects larger areas of highly suitable conditions within this continent. However, the native as well as the introduced range of the common waxbill is well covered by both models. Note that large areas that host suitable climatic conditions for the species, e.g. in Australia, South East Asia and the Andes, are currently not populated by the species.

Future potential distribution

Under projected climate conditions for the end of the 21st century, both models predict a general reduction of climatically suitable areas (Table 1). Furthermore, a slight pole ward shift of current northern and southern distribution limits is suggested (Figs. 6a-d). This is mainly a shift of the northern potential distribution limit as even under current climate conditions the southernmost parts of Africa, Australia, and South America show suitable climatic conditions. In western North America, the NAT+INV model predicts only a slightly higher probability of occurrence (Fig. 6c-d) while under the NAT model this change is more obvious (Fig. 6a-b). In Europe, the NAT+INV model predicts a decline of suitable areas in parts of the Mediterranean region while these changes are less clear assuming the NAT model. The situation in the tropics is even more complex. In most parts of the native African range of the common waxbill, the NAT model predicts a strong reduction of occurrence probabilities. However, this pattern is reversed in Southern Africa, where higher suitability values are predicted for the future (Fig. 6a-b). Suitability also decreases according to NAT in parts of its invaded range such as in the Caatinga region of north-eastern Brazil and in areas not populated by common waxbills such as in India and in the south-western part of the Arabian Peninsula. The NAT+INV model also predicts lower likelihoods of occurrence in parts of South America and India (Fig. 6c-d). Inside Africa, these results contradict the outputs of the NAT model as declines in suitability are much less pronounced and are only obvious in central Southern Africa, where the likelihood of occurrence might drop below the chosen thresholds. Decreases in suitability might also occur within the southern Congo basin and along the current northern natural border of the common waxbill's range.

In direct comparison, both emission scenarios closely resemble each other although there are differences in some smaller areas. Assuming the A2a scenario, the NAT model predicts a stronger decrease in suitability than the B2a scenario within parts of tropical Africa and South America (Fig. 6a vs. 6b). This regional trend becomes also evident on a global extent. Here, decreases for the A2a scenario are more severe than for the B2a scenario.

Comparison of climate niches

PCA-LDA resulted in an overlap value of 0.32 (sd \pm 0.057) of climate niches between the records from the native and records from the invasive distribution of the common waxbill. This low overlap is largely due to the fact that invasive locations occupy a

smaller climate space than the native ones and are nested within the native E-space (Fig. 7). This indicates that the NAT+INV model does not incorporate any additional climate space in comparison to the NAT model.

Discussion

Model performance and current potential distribution

Based on our SDMs we were able to predict the current and future global potential distribution of the common waxbill. Compared to the expert map, our prediction reflects current distribution fairly well applying the minimum training presence threshold. This is especially true for the native afrotropical range, which has its northern limit south of the Sahel zone, well reflecting the gap in the Congo Basin applying the NAT model. The high occurrence probabilities in the invaded range of the Iberian Peninsula or in parts of eastern coastal Brazil are in concordance with the realized distribution of the species (Reino and Silva 1998, Ridgely and Tudor 2009). However, the current potential distribution limited by the 10% training presence threshold seems to underestimate its realized distribution, at least within the native African range. Hence, given the threshold dependencies, our global quantifications based on estimated areas should be interpreted with care.

Variable contributions and response curves are well in concordance with the known climatic demands of the species (see introduction). However, seasonality parameters - with the noteworthy exception of temperature seasonality in the NAT+INV model - did not highly contribute to the model. This is possibly due to a high variability in parameters in the overall range, which is quite large.

When interpreting the potential distribution of a species derived from a SDM, it is necessary to consider possible discrepancies between the fundamental climatic niche and the realized niche of the species (Hutchinson 1957, Soberón and Peterson 2005). Besides climatic demands, biological interactions, accessibility of regions and non-climatic habitat parameters need to be considered (Heikkinen et al. 2006, Davis 1998). Thus, unsurprisingly our models predict a potential distribution notably larger than the one actually inhabited by the species (Gioia and Pigot 2000). Huge parts of Central America, Australia as well as South and Southeast Asia harbour climatic conditions well suitable for the common waxbill. High occurrence probabilities are also found in mountainous areas of the Andes and the Himalaya. These areas might have not been colonized yet, maybe due to dispersal limitations, i.e. the species has

not been released there or did not make its way on its own from colonized areas. In any case, finding suitable conditions for a species on a rather coarse scale in climatically diverse areas such as the Andes does not surprise. Competition may play a role and theoretically could explain the absence of the common waxbill on mainland Asia and Australia as these areas are home to a variety of other estrildid finches (Clement et al. 1993, Restall 1996).

Reino (2005) related an expansion of the invaded range of the common waxbill in Portugal mainly to spatial-temporal variables, but in a recent publication, temperature and relative humidity were identified as important predictor variables (Reino et al. 2009). This ongoing range extension might indicate that at least some northern invasive populations are not in environmental equilibrium. Modelling of species with ongoing range extensions is a special challenge (Elith et al. 2010). However, we rest our results upon a large sample of locations from a huge part of the known distribution of the species and hence at least mitigate possible effects. In any case, interpretations of the common waxbill's potential distribution should be done cautiously as the species, although well studied for an estrildid finch, is still little known from the field. Exact temperature requirements rely on experience with pet birds only rather than from scientific experiments. Furthermore, variation in the climatic niche among populations and subspecies is hardly investigated although Nicolai and Steinbacher (2007) suppose considerable geographic differences, again mainly derived from temperature sensitivity of birds kept in captivity (Mau 2002). This would potentially violate one of the basic assumptions for niche models. However, for most areas of the introduced range, subspecific status of the populations is unknown although mainly the subspecies *jagoensis* (e.g. on Cape Verde), *astrild* and *angolensis* (Príncipe, São Tomé) might be involved (Fry 2004).

The large distribution of suitable climate around the globe shown in this study underlines the invasive potential of the species. While many other estrildid finches are invasive on islands only, the common waxbill already has noteworthy populations on continents making these areas also relevant for considerations of invasive species management. Our models predict a larger potential distribution range than actually occupied within South America, where competitive (Peterson and Robins 2003) or mutualistic interactions with ecomorphologically similar species of the genus *Sporophila* (Emberizidae) and other syntopically granivorous species (Manhães and Loures-Ribeiro 2005) are likely. This is of particular concern as many seedeaters of

the genus *Sporophila* are under severe threat, partially due to bird trapping, but also due to habitat destructions (Silva 1999). So these potential interactions are a rewarding field for future research. As long as detailed studies on the impact of common waxbills on native species are lacking, we can only recommend an enhanced monitoring of the species where it is already established. Our potential distribution maps may also indicate areas where pet trade of *Estrilda astrild* should be under particular control.

Future Predictions

Our models predict less climatically suitable area for the common waxbill on a global scale. This trend is consistent over thresholds and models. However, note that we did not extrapolate onto climate conditions exceeding the calibration range of the models. Hence, any novel climate conditions occurring in the future are assumed to be unsuitable for the species. Furthermore, we do not take any evolutionary or behavioural adaptations into account. Besides this global trend, a more regional view is warranted. The suggest pole ward shift in northern temperate areas is a common phenomenon predicted under climate change (Thomas and Lennon 1999, Parmesan 2006 and references therein). However, predicted shifts suggest a reduction of habitat suitability in some areas (e.g. North Africa) and range extensions in others (e.g. Northern Central Europe). Our current models confirm detected and predicted range extensions in the Iberian Peninsula (Reino et al. 2009). However, for central Spain our future projections rather suggested less suitable future conditions underlining the complexity of observed patterns. Interpretation of distributional change in the tropics seems to be even more difficult. While our models predict an increased climate suitability in parts of South Africa, the distributional gap in the Congo Basin may also grow. Suitability inside today's tropical rain forest areas might be reduced in the invaded range (e.g. Amazonia), but results for both models are not without contradiction (see below). Predictions of range changes due to microhabitat availability were not part of this analysis. Dealing with a species living in open areas, ongoing deforestation in tropical areas also needs to be considered explaining range shifts on a smaller scale (Pearson and Dawson 2003).

When predicting the future, many uncertainties arise in addition to the well known biological uncertainties and those related to the SDMs. Climatic uncertainties include the unknown development of greenhouse gas emission, all issues related to

the climate models and the downscaling of data and the resulting future climatic scenario (Beaumont et al. 2005). We dealt with this problem by using two different kinds of climate models and two different emission scenarios. However, given the current state of knowledge, our predictions are necessarily preliminary, and we agree with Beaumont et al. (2005) that repeated analysis with most recent data is warranted.

Comparison of modelling approaches

Both models NAT and NAT+INV were able to predict the current distribution of the common waxbill quite well. However, differences also became evident. AUC values were higher for the NAT model, but balancing up on this statistical measurement alone is certainly unsatisfying as stated above. Additionally, the native range shows fewer commission errors and is thus better reflected by the NAT model. However, this could be caused by a reduced number of records located in the native range used for the NAT+INV model as we use equal total sample sizes in both models. Furthermore, higher commission errors in the NAT+INV model are not unexpected because the species may not have reached all suitable habitat yet making an increased rate of false positives likely. In the South American part of the invasive range the NAT+INV model shows fewer commission errors compared to the expert map. Therefore, rating of both models is not straight forward. Interestingly, differences between both models become more obvious considering the future potential native range (e.g. Fig. 6a and 6c / A2a conditions) further underlining the influence of location selection.

When applying SDMs on invasive species, the fundamental niche is possibly not sufficiently represented within the native range so that the true dimensions of the climatic niche could be hidden due to e.g. dispersal limitations and/or climatic interactions (e.g. Pearson and Dawson 2003). Another possibility within the “realized niche dilemma” (Gallien et al. 2010) is the occurrence of a true evolutionary niche shift of an invasive population (Broennimann et al. 2007, Rödder and Lötters 2009). Evolutionary niche shift in invasive populations compared to native ones have been recently shown between populations of some species (Fitzpatrick et al. 2007, Broennimann et al. 2007). Yet, our PCA-LDA does not suggest any niche shift between native and invasive populations. Instead of that, within the invasive range only a rather small fraction of the climate space present in the native range is represented. This could be caused by the fact that the species is still under

expansion and thus has not covered the whole range yet (Gallien et al. 2010). Alternatively, invasive populations truly have a smaller climate niche than the native ones, possibly based on founder effects or subspecific differences (see above). Both explanations are not mutually exclusive.

In conclusion, even in the absence of niche shifts between invasive and native ranges of a species the choice of occurrences from one or both areas influences the potential present and future distribution. Tentatively, our results indicate that for the common waxbill the SDM developed with data from the native range only provides more reliable predictions than by omitting the potential bias due to incomplete niche filling. Hence, we call for care when selecting species records from native and invaded ranges for modelling purposes of an invasive species and underline the importance of niche positions in ecological space.

Acknowledgements

We thank two anonymous referees for their comments on the manuscript. DR is grateful to the research initiative of the Ministry of Education, Science, Youth and Culture of the Rhineland-Palatinate state of Germany for financial support.

References

- Araujo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecogr* 28: 693-695.
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Model* 157: 101-118.
- Baldwin RA (2009) Use of maximum entropy modeling in wildlife research. *Entropy* 11: 854-866.
- Beale CM, Lennon, JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. *PNAS* 105: 14908-14912.
- Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers Distrib* 15: 409-420.

- Beaumont LJ, Hughes L, Poulsen M (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol Model* 186: 250-269.
- Blackburn TM, Lockwood JL, Cassey P (2009) Avian Invasions. The Ecology & Evolution of Exotic Birds. Oxford Avian Biology Series. Vol. 1.
- Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biol Lett* 4: 585-589.
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecol Lett* 10: 701-709.
- Busby JR (1991) BIOCLIM – A bioclimatic analysis and predictive system. In: Margules CR, Austin MP (eds) *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. 64–68. CSIRO, Canberra.
- Clement P, Harris A, Davis J (1993) *Finches & Sparrows. An Identification Guide*. Christopher Helm, A & C Black, London.
- Cueto VR, Marone L, Lopez de Casenave L (2006) Seed preferences in sparrow species of the Monte desert, Argentina: implications for seed-granivore interactions. *Auk* 123: 358-367.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783-786.
- Dickinson EC (2003) *The Howard & Moore complete checklist of the birds of the world*. 3rd edition. Princeton University Press, Princeton, New Jersey.
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609-628.
- Echarri F, Tambussi C, Hospitaleche CA (2009) Predicting the distribution of the crested tinamous, *Eudromia* spp. (Aves, Tinamiformes). *J Ornithol* 150: 75-84.
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz

- MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151.
- Elith J, Leathwick JR (2009). *Species Distribution Models: Ecological Explanation and Prediction Across Space and Time*. *Annu Rev Ecol Evol Syst* 40: 677-697.
- Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Global Ecol Biogeogr* 16: 24-33.
- Fry CH (2004) *Estrilda astrild*. In: Fry CH, Keith S (eds. *The Birds of Africa Vol. VII*. Christopher Helm, London.
- Gallien L, Münkemüller T, Albert CH, Boulangéat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? *Divers Distrib*. DOI: 10.1111/j.1472-4642.2010.00652.x.
- Gatter W (1998) *Birds of Liberia*. Pica Press, The Banks, Mountfield.
- Gioia P, Pigott (2000) Biodiversity assessment: a case study in predicting richness from the potential distribution of plant species in the forests of south-western Australia. *J Biogeogr* 27: 1065-1078.
- Goodwin D (1982) *Estrildid finches of the world*. British Museum (Natural History) and Oxford University, London, Oxford.
- Graham CH, Elith J, Hijmans RJ, Guisan A, Peterson TA, Loiselle BA, The NCEAS Predicting Species Distributions Working Group (2008). The influence of spatial errors in species occurrence data used in distribution models. *J Appl Ecol* 45: 239-247.
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Let* 8: 993-1009.
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog Phys Geogr* 30: 751-777.
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modelling methods. *Ecogr* 29: 773-785.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International J Clim* 25: 1965-1978.

- Hijmans RJ, Cruz JM, Rojas E, Guarino L (2001) DIVA-GIS, version 1.4. A geographic information system for the management and analysis of genetic resources data. Manual. International Potato Center and International Plant Genetic Resources Institute, Lima, Peru.
- Hutchinson GE (1957) Concluding remarks. Cold Spring Harbour Symposia on Quantitative Biology 22: 415–427.
- Jeschke JM, Strayer DL (2008) Usefulness of bioclimatic models for studying climate change and invasive species. Ann NY Acad Sci 1134: 1-24.
- Leonard P (2005) Important Bird Areas in Zambia. The Zambian Ornithological Society, Lusaka.
- Lever C (2005) Naturalised birds of the world. T & AD Poyser, London.
- Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28: 385-393.
- Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Global Ecol Biogeogr 17: 145-151.
- Lockwood JL, Moulton MP (1994) Ecomorphological pattern in Bermuda birds: the influence of competition and implications for nature preserves. Evol Ecol 8: 53-60.
- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol Lett 11: 995-1007.
- Mack RN, Somberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control. Ecol Appl 10: 689-710.
- Manhães MA, Loures-Ribeiro A (2005) Spatial Distribution and Diversity of Bird Community in an Urban Area of Southeast Brazil. Braz Arch Biol Techn 48: 285-294.
- Martinez-Meyer E, Peterson AT, Navarro-Sigüenza AG (2004) Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). Proc R S Lond B 271: 1151-1157
- Mau KG (2002) Weltbürger Wellenastrild. Gefiederte Welt 126: 258-261.
- Mau-Crimmins TM, Schussman HR, Geiger EL (2006) Can the invaded range of a species be predicted using only native-range data? Lehmann lovegrass

- (*Eragrostis lehmanniana*) in the southwestern United States. *Ecol Model* 193: 736-746.
- Menke SB, Holway DA, Fisher RN, Jetz W (2009) Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. *Global Ecol Biogeogr* 18: 50-63.
- Mooney HA, Cleland, EE (2001) The evolutionary impact of invasive species. *PNAS* 98: 5446-5451.
- Nicolai J, Steinbacher J (eds) (2007) *Handbuch der Vogelpflege. Prachtfinken. Afrika.* 3rd edition. Eugen Ulmer, Stuttgart.
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637-669.
- Pearson RG, Dawson TE (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. *Global Ecol Biogeogr* 12: 361-371.
- Peterson AT, Nyári ÁS (2007) Ecological niche conservatism and pleistocene refugia in the Thrush-like Mourner, *Schiffornis* sp., in the Neotropics. *Evolution* 62: 173-183.
- Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 416: 626-629.
- Peterson AT, Robins CR (2003) Using ecological-niche modeling to predict Barred Owl invasions with implications for Spotted Owl conservation. *Conserv Biol* 17: 1161-1165.
- Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. *Science* 285: 1265-1267.
- Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* 51: 363-371
- Peterson TA (2001) Predicting species' geographic distributions based on ecological niche modeling. *Condor* 103: 599-605.
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190: 231-259.

- Phillips, SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudoabsence data. *Ecol Appl* 19: 181-197.
- Phillips, SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. Proceedings of the 21st International Conference on Machine Learning. Banff, Canada.
- Reino L (2005) Variation partitioning for range expansion of an introduced species: the common waxbill *Estrilda astrild* in Portugal. *J Ornithol* 146: 377-382.
- Reino L and Silva T (1998) The distribution and expansion of the Common Waxbill (*Estrilda astrild*) in the Iberian Peninsula. *Biol Cons Fauna* 102: 163-167.
- Reino L, Moya-Laraño J, Heitor AC (2009) Using survival regression to study patterns of expansion of invasive species: will the common waxbill expand with global warming? *Ecogr* 32: 237-247.
- Restall R (1996) *Munias and Mannikins*. Pica Press, Sussex.
- Ricklefs RE (1974) Energetics of reproduction in birds. In: Paynter R (ed) *Avian Energetics*. Publ Nuttall Ornithol Club 15:152-297.
- Ridgely RS, Tudor G (2009) *Field Guide to the Songbirds of South America: The Passerines* (Mildred Wyatt-Wold Series in Ornithology). Texas University Press, Austin.
- Rödder D, Dambach J (2010) Bioclimatic models as predictive GIS tools for the identification of potential refuges and possible migration pathways. In: Habel JC, Assmann T (eds) *Relict species: phylogeography and conservation biology*, Springer, Berlin, Heidelberg.
- Rödder D, Engler JO. In press. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Glob Ecol Biogeog*.
- Rödder D, Lötters S (2009a) Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob Ecol Biogeogr* 18: 674-687.
- Rödder D, Kielgast J, Bielby J, Schmdtlein S, Bosch J, Garner TWJ, Veith M, Walker S, Fisher MC, Lötters S (2009b) Global amphibian extinctions risk assessment for the panzootic chytrid fungus. *Diversity* 1: 52-66.
- Rödder D, Lötters S (2010) Potential distribution of the alien invasive Brown tree snake, *Boiga irregularis* (Reptilia: Colubridae). *Pac Sci* 64: 11-22.

- Rödger D, Schmidlein S, Veith M, Lotters S. (2009) Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? PLoS ONE 4: e7843.
- Rödger D, Solé M, Böhme W. (2008a) Predicting the potential distribution of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). North-West J Zool 4: 236-246.
- Rödger D, Veith M, Lotters S. (2008b) Environmental gradients explaining prevalence and intensity of infection with the amphibian chytrid fungus: the host's perspective Anim Conserv 11: 513-517.
- Schluter D, Repasky RR (1991) Worldwide limitation of finch densities by food and other factors. Ecology 72: 1763-1774.
- Silva JMC (1999) Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. Stud Avian Biol 19: 272-280.
- Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10: 1115-1123.
- Soberón J , Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiv Inform 2: 1-10.
- Steinbacher J, Wolters HE (eds) (1965) Vögel in Käfig und Voliere. Ein Handbuch für Vogelliebhaber. Prachtfinken. Vol. 1: Astarilde. 2nd edition. Hans Limberg, Aachen.
- Strubbe D, Matthysen E (2009) Establishment success of invasive ring-necked and monk parakeets in Europe . J Biogeogr 36: 2264-2278.
- Swets K (1988) Measuring the accuracy of diagnostic systems. Science 240: 1285-1293.
- Thomas CC, Lennon JJ (1999) Birds extend their ranges northward. Nature 399: 213.
- Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11: 2234-2250.
- Waltari E, Hijmans RJ, Peterson AT, Nyári AS, Perkins SL, Guralnick RP (2007) Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PLoS ONE 2(7) e563. doi:10.1371/journal.pone.0000563
- Walther BA, Wisz MS, Rahbek C (2004) Known and predicted African Winter distributions and habitat use of the endangered Basra reed warbler

- (*Acrocephalus griseldis*) and the near-threatened cinereous bunting (*Emberiza cineracea*). *J Ornithol* 145: 287-299.
- Warren DL, Glor RE, Turelli, REM (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evol* 62, 11: 2868-2883.
- Wiens, JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology and conservation biology. *Annu Rev Ecol Evol Syst* 36: 519-539.
- Wisz MS, Hijmans RJ, Peterson AT, Graham CH, Guisan A, NPSDW Group (2008) Effects of sample size on the performance of species distribution models. *Div Distrib* 14: 763-773.
- Yost AC, Petersen SL, Gregg M, Miller R (2008) Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. *Ecol Inform* 3: 375-386.

Fig. 1 Expert map of the current distribution of *Estrilda astrild* based on published references (e.g. Fry 2004, Lever 2005). Grey areas show the native range, crosshatched areas and arrows mark invasive occurrences

Fig. 2 AUC values of model trained with occurrences from the native range (NAT) and from the native and the invasive range (NAT+INV). Boxplots show range, quartile and median, a cross indicates the mean

Fig. 3 a Variable contribution of models: **a** For model NAT trained with occurrences from the native range. **b** For model NAT+INV trained with occurrences from the native and the invasive range. Boxplots show range, quartile and median, a cross indicates the mean, see text for explanation of variables

Fig. 4 Minimum training presence logistic threshold (Min train) and 10 percentile training presence logistic threshold (10% train) for models based on training points from the native (NAT) and from the native and invasive range (NAT+INV). Boxplots show range, quartile and median, a cross indicates the mean

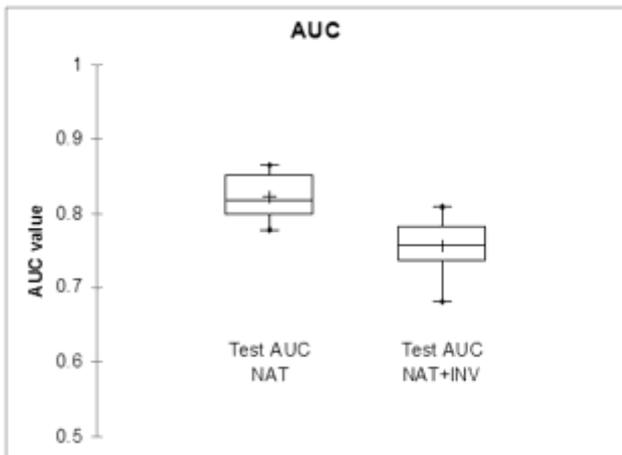
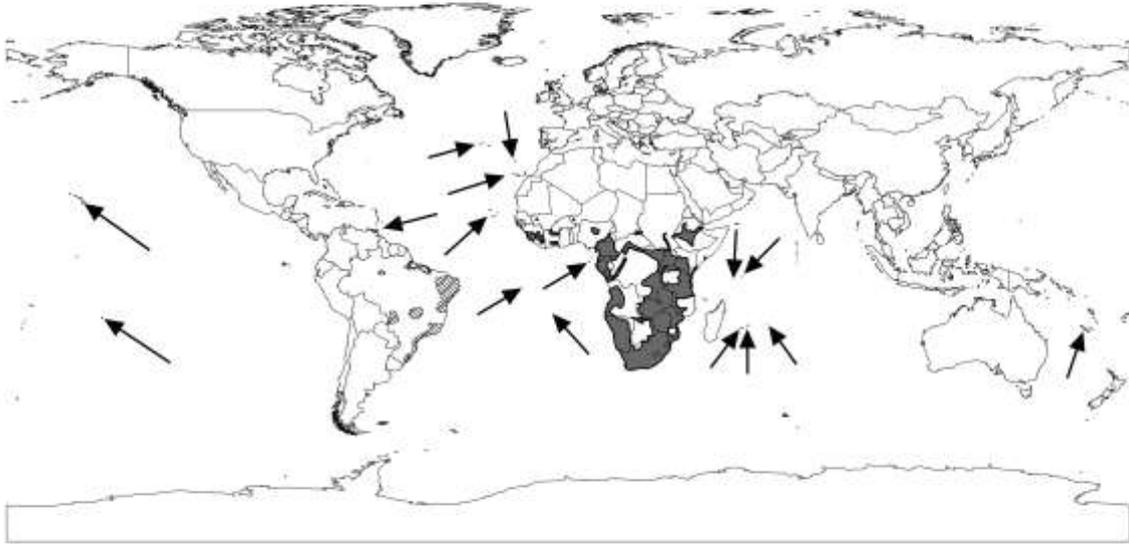
Fig. 5 Current potential range of *Estrilda astrild*. **a** based on model NAT trained with occurrences from the native area only and **b** trained with occurrences from the native and the invasive area. Species records are shown as white circles. Areas characterized by MAXENT values above the minimum training presence logistic threshold are grey, areas having MAXENT values above the 10 percentile training presence logistic threshold are shown in black

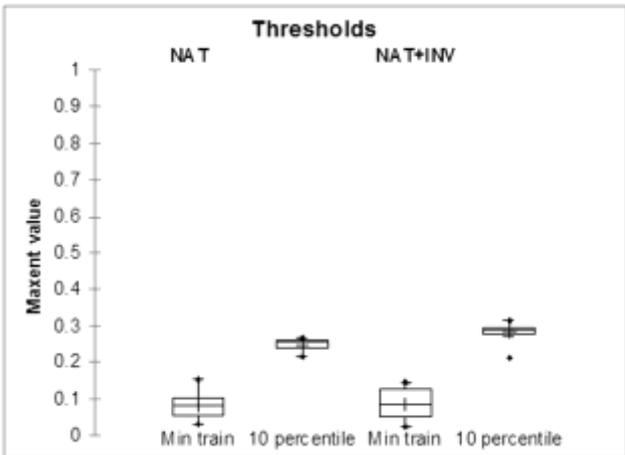
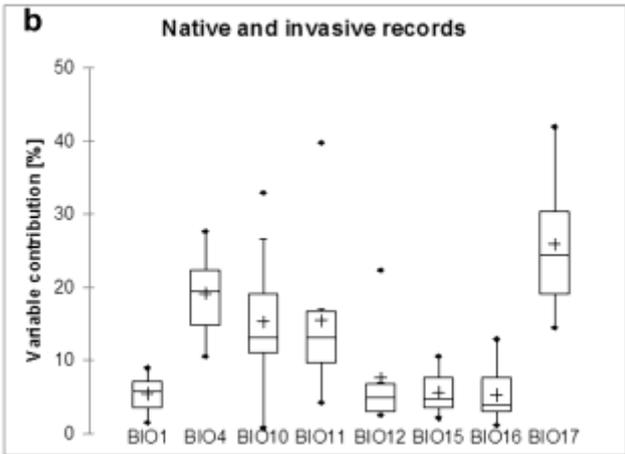
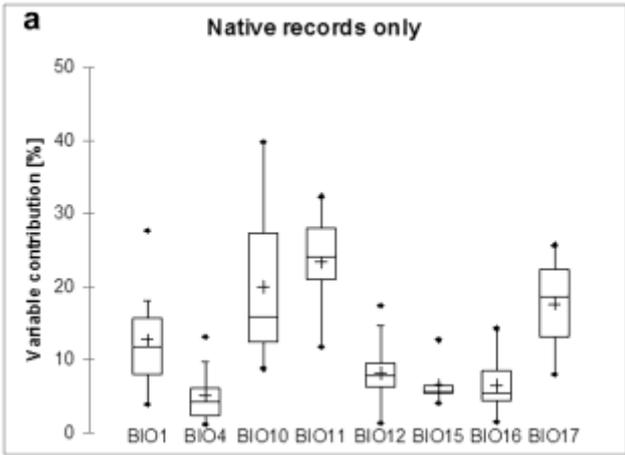
Fig. 6 Future potential range of *Estrilda astrild* under global climate change: **a** based on model NAT trained with occurrences from the native area only for the emission scenario A2a; **b** based on model NAT for the emission scenario B2a; **c** based on model NAT+INV trained with occurrences from the native and the invasive area for the emission scenario A2a; **d** based on model NAT+INV for the emission scenario B2a; shade of grey as in Fig. 5.

Fig. 7 Positions of native (squares) and invasive (triangles) presence locations of *Estrilda astrild* in ecological space represented by two Principal components (PC1 & PC2). Background samples are shown behind the presence locations as semi transparent point cloud for invasive and native ranges respectively (see electronic appendix for a coloured plate).

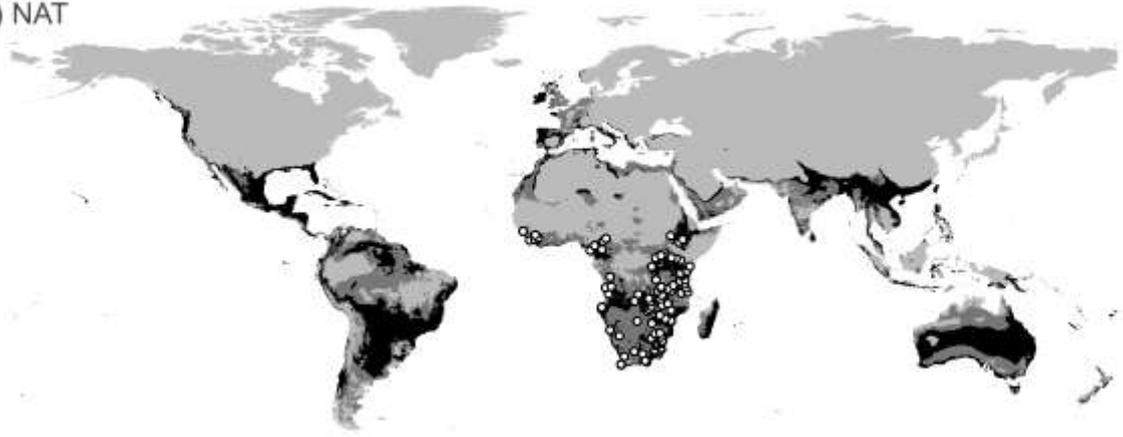
Table 1 Spatial extend of the potential distribution (in Million km²) of *Estrilda astrild* derived from two different modelling approaches (NAT, NAT+INV, see running text for explanation) and applying two different thresholds (MIN = minimum training presence logistic threshold; 10% = 10% training presence logistic threshold, see running text for details) under current and predicted climate for the end of the 21st century (A2a and B2a climate change scenarios, differing in green house gas emission).

	NAT		NAT+INV	
	MIN	10%	MIN	10%
Current Climate	47.73	23.04	51.92	16.70
A2a 2080	34.36	14.47	37.66	8.21
B2a 2080	39.62	16.96	43.38	10.12

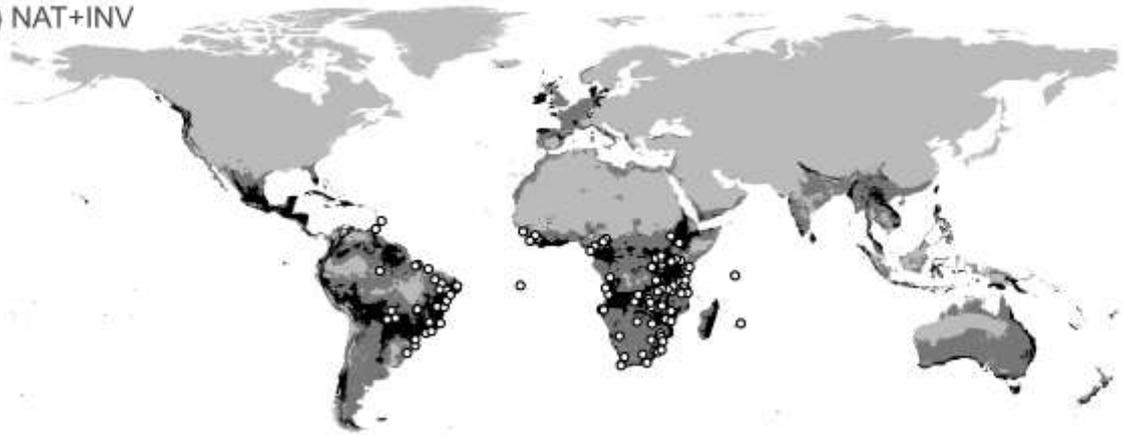




a) NAT



b) NAT+INV



a) NAT - A2a



c) NAT+INV - A2a



b) NAT - B2a



d) NAT+INV - B2a



