

Global invasive potential of the house crow *Corvus splendens* based on ecological niche modelling

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Summaries of recent rapid range expansions shown by the house crow *Corvus splendens* have provided insights into the global nature of this invasion process, but its long-term potential has not yet been evaluated. To explore the potential dimensions of this geographic expansion, we used ecological niche modeling based on known occurrences of the species on its native distributional area, in the context of GIS data sets describing climatic variables, topographic information, and human presence. Our models provided predictions of areas already invaded that were statistically significantly more coincident than expected under random (null) models. The predicted potential range of the species includes areas already affected, as well as potentially suitable areas in Central America, the Caribbean, equatorial and West Africa, and mainland and insular Southeast Asia, not yet colonized.

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Recent range expansions and the status of new populations of house crow *Corvus splendens* have been documented and summarized in a series of publications by Ryall (1994, 1995, 2002). This species presents great ecological flexibility, as well as an obligate association with human presence, to the extent that no populations are known to live independently of man. The house crow has now established populations along much of the Indian Ocean rim, Arabian Peninsula, eastern and southeastern Africa, some Indian Ocean Islands, and additional sites in southern Asia, Europe (Ryall 2002) and, recently, the United States (Pranty, 2004).

Current reviews of invasive species biology have emphasized the great complexities involved in species' occupancy of new distributional areas (Carlton 1996, NAS 2002). However, advances in the emerging field of ecological niche modeling have opened the possibility of using species' ecological characteristics as evaluated on native distributional areas to predict potential distributional areas in other regions (Panetta and Dodd 1987,

Honig et al. 1992, Richardson and McMahon 1992, Sindel and Michael 1992, Beerling et al. 1995, Martin 1996, Higgins et al. 1999, Skov 2000, Zalba et al. 2000, Hoffmann 2001), given the precept that species' ecological niche characteristics tend to remain fairly constant (Peterson 2003) although some examples of plasticity have been documented (Maron et al. 2004). Herein we applied ecological niche modeling to the question of the global potential for house crow range expansion.

Methods

We obtained detailed native-range occurrence data for *Corvus splendens* via broad query of natural history museums for data associated with specimens and from published records (see Acknowledgements). From both sources, we georeferenced 125 spatially unique localities to the nearest 1' of latitude and longitude using the GEONet Names Server (<http://earth-info.nga.mil/gns/>

html/index.html). Ecological variation was summarized in 9 GIS raster grid data sets ('coverages'), including aspects of topography (digital elevation model: slope, aspect, elevation; from the US Geological Survey Hydro-1K data set, <http://edcdaac.udgs.gov/gtopo30/hydro/>, native resolution 1 × 1 km) and climate (annual means of temperature, frost days, precipitation, maximum, minimum, and mean monthly temperatures; for 1930-1960 from the Intergovernmental Panel on Climate Change, <http://www.ipcc.ch/>, native resolution 50 × 50 km). To minimize scale conflicts between the topographic and climatic data, we conducted analyses at an intermediate resolution (10 × 10 km). We neglect the effects of climate change processes currently occurring, although climate change-driven shifts can be included in such modeling efforts (Roura-Pascual et al. 2004); similarly, we assume that this species is unlikely to be limited geographically by competitor species given its pest status in much of its invaded range.

Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell 1917, 1924). Our approach consisted of 4 steps: (1) model ecological niche requirements of the species based on known occurrences on its native distributional area, (2) project niche models to global scales to identify areas fitting the niche profile, (3) test the accuracy of native and invaded range predictions, and (4) assess potential for the species to invade additional areas worldwide.

The inferential tool used for niche modeling was the Genetic Algorithm for Rule-set Prediction (GARP; Stockwell and Noble 1992, Stockwell and Peters 1999). GARP uses an evolutionary-computing approach to carry out a flexible and powerful search for non-random associations between environmental variables and known occurrences of species. Specifically, available occurrence points are subsampled to create two suites of points: half of the available points are set aside as *extrinsic testing* points; the remaining points are then resampled with replacement to create a population of 1250 presence points; an equivalent number of points is resampled from the population of grid squares ('pixels') from which the species has not been recorded ('pseudoabsence data'). These 2500 points are divided equally into *training* (for creating models) and *intrinsic testing* (for evaluating model quality) data sets.

Models are composed of a set of conditional rules developed through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, range rules etc), and applied to the training data set. Then, rules 'evolve' by a number of means (mimicking DNA evolution: point mutations, deletions, crossing over, etc.) to maximize predictive accuracy. After each modification, rule quality is evaluated based on the intrinsic testing data; change in

predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the final rule-set. The algorithm runs either 1,000 iterations or until addition of new rules has no effect on predictive accuracy. The final rule-set (the ecological niche model) is then projected worldwide to identify a potential geographic distribution.

Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present; Fielding and Bell 1997). Because GARP does not produce unique solutions, we followed recently published best-practices approaches to identifying optimal subsets of resulting replicate models (Anderson et al. 2003). For each analysis, we developed 100 replicate models; of these models, we retained the 20 with lowest omission error (evaluated using the extrinsic testing data). From these 20, we retained the 10 with moderate commission error (i.e., we discarded the 10 models with area predicted present showing greatest deviations from the overall median area predicted present across all models). This 'best subset' of models was summed to produce final predictions of potential distributions. Because our final models consist of composites of 10 best-subsets models (Anderson et al. 2003), they have 11 levels of prediction (0–10), with 10 representing complete model agreement in predictions of presence.

Native-range ecological niche models were projected onto global landscapes to evaluate the species' invasive potential. Given that absence data are not generally available on invaded distributional areas, models of potential spread were validated via chi-square tests (Peterson and Shaw 2003, Peterson et al. 2003) that incorporate dimensions of correct prediction of both presences (based on independent test data) and absences (based on expected frequencies; Stockwell and Peters 1999, Anderson et al. 2003). Random expectations were calculated as the product of the proportional area predicted present and the number of test presence points. Observed and expected frequencies of correct and incorrect predictions of presence were then compared using χ^2 tests (1 df). We used non-native occurrence points (Ryall 1994, 1995, 2002) to test the final prediction, focusing on two areas: Africa and the Middle East (where the crow has managed to sustain impressive populations; Ryall 2002), and Europe (where a few vagrant individuals have survived for a few years in Ireland and the Netherlands, and a small population has become established in the Netherlands; Ryall 2002, Ottens and Ryall 2003).

After obtaining global predicted distributions and carrying out the validations described above based on the topographic and climatic datasets, we included an additional dataset, the Human Footprint Dataset (HFD) to summarize human presence on landscapes.

HFD, produced by the Wildlife Conservation Society and the Columbia University Center for International Earth Science Information Network (2002) was used to account for house crow preferences for urban and other human-altered landscapes. The HFD uses the human influence index (HII), a dataset created from 9 global data layers covering human population pressure (population density population settlements), human land use and infrastructure (built up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers). In ArcView 8.3, we intersected the sum of the 10 best niche models with the HFD layer by applying a threshold of HII >20% to account for areas with high human alteration. The resulting map represents areas most likely to be favorable to house crow establishment, taking into account human presence.

Results

Native-range projections of our ecological niche models (on which all subsequent analyses were based) were highly statistically significantly more predictive than random models (all $P < 10^{-12}$; Fig. 1), based on independent sets of test points. Given this first indication of predictive power of the native-range ecological model, we projected it worldwide to identify areas putatively suitable for house crow populations.

Invaded areas of interest for the purpose of model validation were the Middle East and East Africa, where most reported non-native House crow populations are located (Fig. 2). The coincidence of known records of this species with the area predicted by the projection of the native-range model was excellent, again statistically

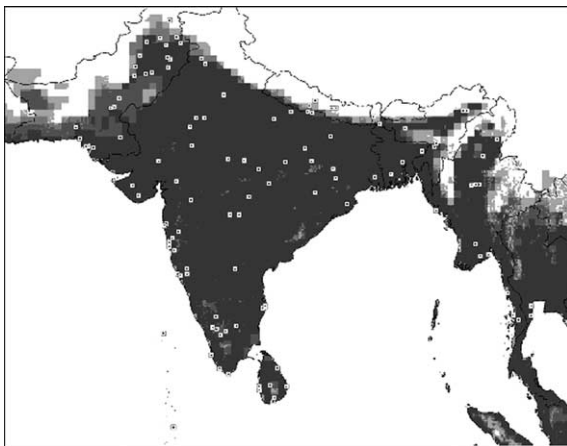


Fig. 1. Native-range prediction of the house crow *Corvus splendens* based on ecological niche models using 125 occurrence points (dotted squares). Darker shades indicate greater model agreement in predicting potential house crow presence.

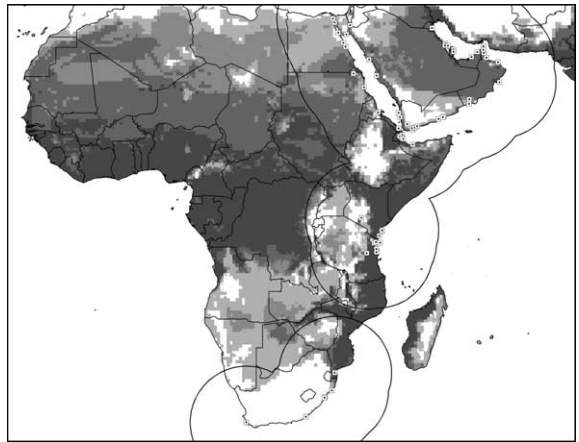


Fig. 2. Predicted potential distribution of house crow based on native-range ecological niche models mapped onto the Middle East and Africa. Dotted squares indicate established populations or sites where the species has been recorded. The 1000 km buffer around known occurrence points indicates area within which model validation was carried out.

significantly more coincident than random models (χ^2 test, all $P < 10^{-5}$).

Another area of known house crow establishment is in northwestern Europe (Ottens and Ryall 2003). A breeding population is established in the Netherlands, and reports of solitary house crows from Ireland, United Kingdom, Denmark, France, Spain, and Poland, some surviving for several years, are suggestive that the species may have broader potential on the European continent. Our native-range model predicted potentially suitable conditions for the species in these areas (at least at low levels of predictive confidence), once again significantly better than random models (χ^2 test, all $P < 10^{-8}$; Fig. 3).



Fig. 3. Predicted potential distribution of house crow based on native-range ecological niche models mapped onto Europe. Known breeding populations from the Netherlands as well as other sightings are marked by dotted squares. The 1000 km buffer around known occurrence points indicates area within which model validation was carried out.

The HII dataset provided a refined estimate of house crow occurrence, focusing on human-altered habitats (Fig. 4). Basically, taking into account the known tie between this species and human presence, areas that are putatively appropriate on climatic grounds but do not have the human presence can be de-emphasized, providing a tighter and more refined prediction of house crow potential distribution. The improvement is particularly notable in considering the distribution of the species in the Arabian Peninsula, where – within its potential distributional area – it occurs only in areas close to human habitations (Fig. 5).

Discussion

Ecological niche modeling provides a means of evaluating ecological factors that participate in delineating a species' geographic distribution. That is to say, species' distributions represent the combined effects of abiotic requirements of species, biotic interactions with other species, and limitations on dispersal (Soberón and Peterson 2005). In the case of invasive species, under the supposition of no evolution of ecological characteristics (Peterson 2003), niche modeling makes possible assessment of the geographic potential of species *were dispersal limitations to be removed*. As such, ecological niche modeling can provide a null hypothesis of geographic potential in absence of evolutionary changes

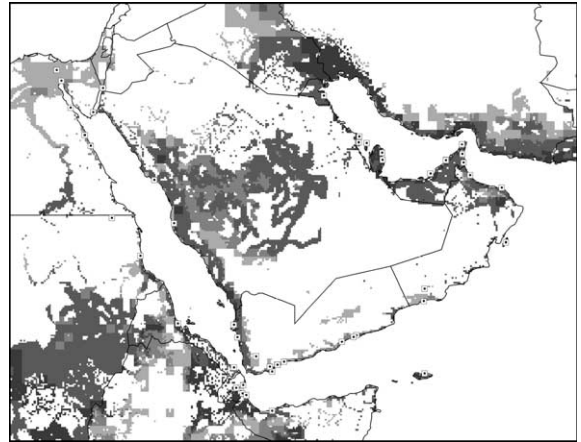


Fig. 5. Enlarged view of the Arabian Peninsula. Potential distribution of the house crow based on native-range ecological niche models and intersected with the Human Footprint Dataset (HFD). Darker shades represent greater model agreement in predicting potential presence. Dotted squares indicate established populations or sites where the species has been recorded.

or shifting effects of biotic interactions on invaded distributional areas.

Although house crows are known to be excellent 'invaders,' reaching pest status in most of their introduced range (e.g. Middle East, Malaysia, Singapore, eastern and southern Africa, some East Asian countries), no analysis of their global invasive potential has yet been undertaken. Our analyses represent an attempt

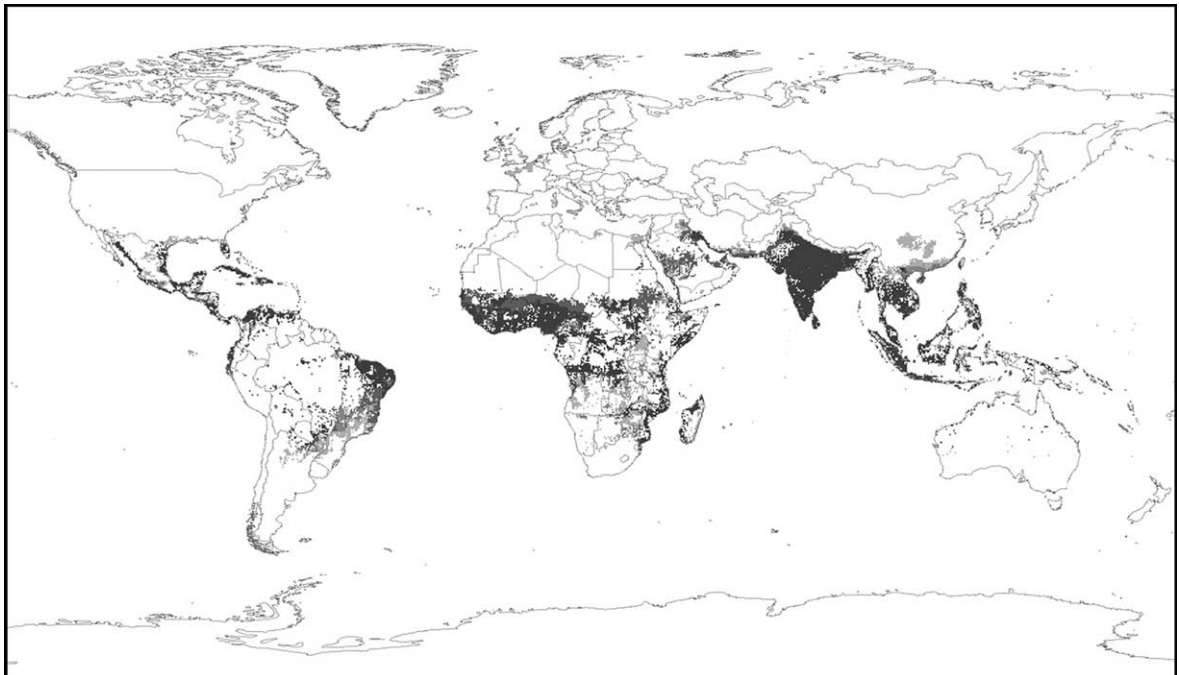


Fig. 4. Global predicted potential distribution of the house crow based on native-range ecological niche models and intersected with the Human Footprint Dataset (HFD). Darker shades represent greater model agreement in predicting potential presence.

to address this question making use of new computational tools to model the ecological niche of the species and predict its worldwide potential distribution. Our tests in three regions (native range, Middle East and East Africa, Europe) suggest that these areas are indeed suitable for House crow populations. Although most European occurrences are of vagrant birds and isolated individual sightings, the growth of the small Hoek van Holland population and establishment of a satellite colony at den Haag in the Netherlands, the first cases of the species breeding in a temperate climatic region, is key in indicating the potentially broad tolerances of this species, at least with human subsidy (Ryall 2002). It is noteworthy that the only known arrivals of pairs of house crows that have *failed* to breed have been in southern Chile, where the pair died during their first boreal winter, and in Australia where they were quickly trapped or shot.

Invaded areas are mainly urban or semiurban, where house crows benefit from improper human food and refuse handling: commercial areas, public housing areas and urban parks are associated with higher abundance (Lim et al. 2003); clearly, this human association broadens the ecological potential of the species into areas that might not otherwise be habitable. House crows spread to adjacent areas for nesting and roosting, often forage in periurban farmland, and can reduce populations of resident bird species markedly (Ryall 1992). House crow populations also have the potential to affect human health, serving as reservoirs of human diarrheal diseases (al-Sallami 1989, 1991) and, like other corvids, of West Nile Virus (Bernard et al. 2001, Eidson et al. 2001a,b, Komar et al. 2003) and, potentially, avian influenza. They are also known to harbor a variety of diseases of livestock (Sulochana et al. 1981, Poon and Chew 1991).

Using the HFD dataset to refine the predicted invasive distribution provided a still-better estimate of areas of possible house crow establishment (Fig. 4). Intersection with the HFD dataset reduced the overall potential area predicted by 38%, emphasizing focal sites that now harbor massive house crow colonies (Ryall 1994, 1995, 2002). In addition, persistence of the small population at Hoek van Holland in the Netherlands is better explained by the inclusion of areas and degree of human development: this population persists, having survived winter temperatures down to -8°C , because of human subsidy and acceptance of the local community towards these birds (Ryall 2002, 2003). This situation contrasts with many "pest status" house crow populations in the Middle East and East Asia (especially Malaysia and Singapore), where our models show high agreement predicting potential presence. The species is likely to expand its range further in this region, having recently arrived in northern Sumatra and northern Borneo (Ryall 2002). An interesting observation is the narrow area of predicted presence after intersection with the HFD layer

around the southern rim of the Arabian Peninsula (Fig. 5), where most human settlements and modified landscapes (and hence sources of food and water), as well as nuisance-level populations of house crows, occur (Ryall 2002). A report of a pair of house crows breeding near Sarasota, Florida, in 2001 (Pranty 2004), also an area of high agreement, could potentially represent the initiation of a North American invasion, as the three or four previous arrivals in the USA have all been of solitary individuals (Ryall 2002), albeit that the bird which arrived at Charleston, South Carolina in 1974 may have survived for several years (Nugent 1984).

Some areas predicted as potentially suitable are novel relative to known house crow occurrences. These areas – West and equatorial Africa, the Caribbean, Mexico, Central America, and parts of South America – represent areas of potential invasion for the species. Given the apparently excellent dispersal capabilities of this species, particularly in light of the large populations now developing in Egypt and South Africa that may act as new nuclei for expansion, these areas should be considered susceptible to invasion by house crows. Madagascar's proximity to the primary source of house crows, the Indian Subcontinent, also puts it at high risk of colonization. Finally, these distributional possibilities may be in the process of shifting, given current global shifts in climates, which would in general act to broaden the species' distributional potential at the poleward limits of its pre-change distribution.

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