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Integrating invasion and disease in the risk assessment of live bird trade

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ABSTRACT

Aim International trade in plants and animals generates significant economic benefits. It also leads to substantial unintended impacts when introduced species become invasive, causing environmental disturbance or transmitting diseases that affect people, livestock, other wildlife or the environment. Policy responses are usually only implemented after these species become established and damages are already incurred. International agreements to control trade are likewise usually based on selection of species with known impacts. We aim to further develop quantitative invasive species risk assessment for bird imports and extend the tool to explicitly address disease threats.

Location United States of America.

Methods We use a two-step approach for rapid risk assessment based on the expected biological risks due to both the environmental and health impact of a potentially invasive wildlife species in trade. We assess establishment probability based on a model informed by historical observations and then construct a model of emerging infectious disease threat based on economic and ecological characteristics of the exporting country.

Results We illustrate how our rapid assessment tool can be used to identify high-priority species for regulation based on a combination of the threat they pose for becoming established and vectoring emerging infectious diseases.

Main conclusions Our approach can be executed for a species in a matter of days and is nested in an economic decision-making framework for determining whether the biological risk is justified by trade benefits.

Keywords
Bioeconomic, biological invasions, birds, ecological-economic decision model, emerging infectious disease, import policy.

INTRODUCTION

Live plant and animal imports provide economic benefits but also pose serious biological invasion and disease risks (Karesh *et al.*, 2005; Smith *et al.*, 2009). Species that escape and become invasive disrupt economic and ecological systems, reduce agricultural productivity, lower biodiversity and/or act as vectors for diseases of humans and wildlife (Pimentel *et al.*, 2005). Over recent decades, the size of the international trade in non-native species has increased rapidly, leading to greater numbers of recorded invasions (Dehnen-Schmutz *et al.* 2007, Keller and Drake, 2009). Some notable examples are the Burmese python, which is linked to severe declines in native mammal populations in Florida

(Dorcas *et al.*, 2012) and water hyacinth, a plant that has disrupted recreation, navigation and aquatic ecosystems across many regions (Adebayo *et al.*, 2011). Additionally, the import of live animals, for example through the pet trade, has contributed to the spread of a host of diseases affecting humans, livestock, and native plants and animals. For example, monkeypox was introduced to the United States in 2003 in imported African rodents and caused 72 human cases (Reed *et al.*, 2004). Trade in wildlife has also been implicated in the spread of highly pathogenic avian influenza (H5N1) (Van Borm *et al.*, 2005) and amphibian chytridiomycosis (Schloegel *et al.*, 2010, 2012; Fisher *et al.*, 2012), the latter of which has caused extirpation and extinction of some native amphibians.

Efforts to prevent the arrival of harmful species from trade can be guided by risk assessment tools that discriminate (with varying levels of accuracy) between species likely to cause harm and those likely to be benign (Keller & Springborn, 2014). These tools allow the majority of benign species, which are beneficial to trade, to be imported, and allow agencies to ban the import of species predicted to be invasive (Keller & Drake, 2009). While the threat of pathogen spread by live animal importation is widely acknowledged, only limited attempts have been made to formalize and integrate this concern quantitatively in risk assessment tools. Instead, tools focus almost exclusively on either the probability that a species will become established and/or invasive, or on pathogen transmission risk from importing livestock (Murray *et al.*, 2004; Bomford, 2008).

In this study, we develop a rapid risk assessment tool for estimating the likelihood that a bird species in trade will cause negative environmental and health impacts if imported to the United States. Birds are well studied ecologically and taxonomically, and abundant data are available to investigate the factors that make them likely to establish (or not), become invasive and transmit diseases. Thousands of non-native bird species have been transported and introduced across the globe by humans (Bomford *et al.*, 2003; Blackburn *et al.*, 2009a). At least 2760 release events are known, of which 1292 have led to established populations (Sol *et al.*, 2012). These established populations cause negative impacts including reduced agricultural yields, loss of native biodiversity and damage to infrastructure (Pimentel *et al.*, 2005; Brochier *et al.*, 2010; Kumschick & Nentwig, 2010; Newson *et al.*, 2011; Kumschick *et al.*, 2013). In addition, non-native birds are reservoirs of introduced zoonotic pathogens (e.g. West Nile virus (WNV) and avian influenza virus), as well as pathogens that threaten livestock (e.g. Newcastle disease virus) and wildlife (e.g. WNV, *Mycoplasma gallisepticum* and *Trichomonas gallinae*) (Fischer *et al.*, 1997; Falcon, 2004; Hosseini *et al.*, 2006; Kilpatrick *et al.*, 2006; LaDeau *et al.*, 2007; Boyce *et al.*, 2009; Kilpatrick, 2011; Lawson *et al.*, 2012). The potential for future invasions and disease spread by birds is large, as international trade continues to grow (Smith *et al.*, 2008, 2009) and birds are reservoirs for just over 10% (82/800) of all known zoonoses (Cleaveland *et al.*, 2001).

Despite risks from movement and potential establishment of non-native birds, there are few international agreements that restrict the trade of harmful species, and these focus on just a small number of diseases that could be carried (Keller & Perrings, 2011). At a national level, some countries (e.g. Australia, New Zealand) routinely conduct risk assessment for newly imported species, and the European Union has imposed a total ban on imported wild birds to protect against introduction of avian influenza (Van den Berg, 2009). The United States does not routinely assess imported bird species for invasion risk, but the US Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) has banned the import of all birds from the 46 countries in which highly pathogenic avian influenza is considered to be present (USDA-APHIS 2013).

Although few countries use risk assessment tools, there is a growing academic literature describing how they can be created. Models relating invasiveness of bird species to their traits, environmental tolerances and invasion history, have been created for New Zealand (Veltman *et al.*, 1996), Australia (Duncan *et al.*, 2001; Bomford, 2008), North America and Europe (Jeschke & Strayer, 2005), and globally (Blackburn *et al.*, 2009b; Sol *et al.*, 2012). To the best of our knowledge, only the Bomford (2008) model has been implemented in a national biosecurity programme. Each of the models listed above focus on the risk of bird establishment and invasion, but none incorporate the risks of new diseases, nor do they integrate risk assessment with an economic decision model. We are not aware of an avian risk assessment model that has previously been developed specifically for the United States, one of the largest players in global bird trade.

Because sufficient data are not available to delineate between low and high impact establishers, we consider establishment as the undesirable end-point of bird introductions. All established non-native bird species in the United States incur some costs from population monitoring, and all established species present a risk of vectoring diseases. A subset of these also cause economic and/or ecological impacts by, for example, reducing crop yields, competing with native species, or vectoring diseases. In our two-step risk assessment approach, we first assess establishment probability by constructing a model based on historical observations of the outcomes from bird introductions to the United States. Economic criteria are then used to establish a threshold for determining whether a given species poses an establishment risk greater than its projected benefits and should thus be barred from trade. Second, we construct a model of emerging infectious disease threat based on economic and ecological characteristics of the exporting country. This step effectively extends the current USDA-APHIS program for avian influenza to include a wider range of disease risks. We illustrate how the establishment and disease models can be combined to identify high-priority species for exclusion and/or extended risk assessment.

METHODS AND RESULTS

In this section, we develop the model and discuss intermediate results for each subcomponent of the tool before illustrating the integrated model. First, we summarize information on live bird imports to the United States and describe its use in characterizing the baseline rate of bird establishments and the welfare value of trade. Next, we combine this value of trade with damages from species establishment in an economic decision rule that identifies how high the probability of establishment for a species can be before it warrants exclusion. Estimating this probability of establishment is the objective of the next section, in which we show how biological data on established and non-established species

are leveraged to parameterize a predictive model. Finally, we describe our model of avian infectious disease risk and its integration with the establishment model.

Trade in live birds

We obtained data on the quantity and customs value of bird imports to the United States by species from 1999 to 2010 from the US Fish and Wildlife Service (USFWS) Law Enforcement Management Information System (LEMIS) database. These data originate from the USFWS declaration form for the import or export of wildlife and their products (Form 3–177) and were obtained by Freedom of Information Act requests (Romagosa et al. 2009). These data were updated to current taxonomy following Clements et al. (2012) and used to analyze patterns of avian importation and parameterize the models below. These records indicate that over 2.6 million individuals from 947 species were imported. To assess the rate of establishment of previously imported birds, we obtained similar data from USFWS for imports from 1968 to 1972 (Romagosa, In press). We do not address the illicit trade in non-native birds in this study – the importance of smuggling and limitations in data for assessing this pathway is discussed by Ferrier (2009).

Economic rule for excluding a species

To capture gains from trade, let $V_T > 0$ represents the expected present value of the long-term benefits from importing a bird species. To specify potential damages, let $V_E > 0$ represents the expected present value of long-term losses due to the establishment of a non-native species. The net benefit of excluding a species when the species is an establisher (i.e. is able to establish) is given by $V_E - V_T$. Alternatively, when a species is excluded but not an establisher, net benefits are simply the lost value of trade: $-V_T$. Let p represent the probability that a species is an establisher. Following Springborn et al. (2011), taking as a baseline the payoffs when species are accepted for importation, it is optimal to reject a species for importation when doing so leads to an expected net gain in social welfare, that is when

$$p(V_E - V_T) + (1 - p)(-V_T) > 0. \qquad (1)$$

Rearranging and simplifying reveals a simple threshold decision rule: reject a species for importation when

$$p > \frac{V_T}{V_E}.$$

We estimated the welfare loss from rejecting a live species for import (V_T = $79.3K) as the compensation required to achieve the level of utility enjoyed when imports are not restricted, an economic measure known as compensating surplus, CPS (Just et al., 2004). Details are given in Appendix S1 in Supporting Information and Springborn et al. (2011).

A systematic estimate for damages from bird establishments is currently lacking. Instead of estimating V_E directly, we assess various levels of V_E as determined in proportion to the better understood parameter V_T. To begin, let the population proportion of establishers be given by π, that is, the unconditional probability that a randomly chosen proposed species for import will be an establisher. We examine a set of alternative ratios of V_T to πV_E, where the latter term reflects the expected damage of a species before the true status of the species is known. This ratio is given by the proportion $\alpha = \frac{V_T}{\pi V_E}$. This approach enables easy illustration of various cases in relation to a benchmark scenario where $\alpha_{BM} = 1$. Under the benchmark case, $V_T = \pi V_E$; the expected costs and benefits of importing a proposed species are equal. Under this scenario, a decision-maker would be indifferent between banning all imports and accepting all imports (in the absence of an informed screening system). We also consider alternative scenarios, ranging from establishment damages that are 50% smaller ($\alpha = 1.5$) to 50% bigger ($\alpha = 0.5$).

The population proportion of establishers, π, is an input to both the decision threshold and the statistical model for estimating p. We used a dataset of bird imports to the United States between 1968 and 1972 from USFWS reports. The base rate π is estimated as the proportion of species that are now established. This early subset was selected to minimize downward bias in the estimate that could be driven by either a lag in establishment or a delay in recording establishment. This estimated baseline rate of establishment for a randomly chosen imported bird species is $\pi = 0.026$. At $\pi = 0.026$ and our benchmark scenario of $\alpha = 1$, the ratio of V_E to V_T is approximately 38.

Establishment probability model

We developed and parameterized a trait-based statistical model of establishment probability (p) using the dataset of introduction events and life history characteristics for bird species assembled by Sol et al. (2012). Species were considered introduced if they have ever been found beyond captivity in the United States, regardless of how they were released. Established species are those that developed self-sustaining populations that persisted for at least 20 years. Let S_N represent the available training dataset for N species, including the observed outcome of binary variable y—which specifies species as either established ($y = 1$) or not established ($y = 0$)—and a set of variables given by x that are predictive of y. These data are given by $S_N = [(y_1, x_1),...(y_N, x_N)]$ for species $n = 1,...,N$. Let $p(x_n; \theta)$ represent the probability that a given species n is an establisher conditional on x_n and a vector of model parameters, θ: $p(x_n; \theta) = \Pr(y_n = 1|x_n; \theta)$. We model the probability of establishment using logistic regression, $\mathrm{logit}(p(x_n; \theta)) = \theta x_n$, based on 12 variables from the Sol et al. (2012) dataset. These regressors (x) fall into the categories of taxonomy (*order, family*), morphology (*relative brain size, body mass*), reproduction (*broods per year, brood size, offspring per year, egg mass, days of incubation*) and

biology/ecology (*habitat generalism, development strategy, life span*). We added *established elsewhere*, a binary indicator of whether the species had a history of non-native establishment prior to its introduction to the United States. See Appendix S2 for details.

The dataset includes $N = 165$ bird species that are non-native to the United States but have been recorded beyond captivity, 34% of which have established. The dataset S_N is a non-random sample – the proportion of establishments (0.34) is 13 times greater than our estimate of the establishment rate for birds imported to the US ($\pi = 0.026$). We correct for this endogenously stratified sample (details in Appendix S3) to ensure that fitted estimates based on the model are interpretable as probabilities.

Incomplete observations are another common problem in trait-based risk assessment. In our training, dataset several variables were incomplete: *clutch size* (18% of data missing)*, body mass* (25%), *egg mass* (26%), *incubation* (27%), *life span* (39%), *broods per year* (49%) and *fecundity* (49%). If a large number of observations were simply dropped, the correction procedure for the endogenously stratified sample could become unstable. To address missing data, we used multiple imputation (MI) (Rubin, 1987; Schafer, 1999), a Monte Carlo technique for simulating missing values while accounting for the uncertainty of the missing data process (see Appendix S4). We also evaluated a complete case model that eschewed MI and report results below confirming that MI improved performance.

To identify the best performing set of predictive variables, we first excluded variables with particularly weak explanatory power ($P > 0.5$). The three variables with clear predictive power ($P < 0.1$) were *established elsewhere, habitat generalism* and *days of incubation*. To determine whether any of the five remaining variables with questionable predictive power (*P*-values between 0.1 and 0.32) should be included, we relied on two other metrics of model performance that go beyond hypothesis testing (see Appendix S2). The first metric is the area under the receiver operating characteristic (ROC) curve or AUC. While the *AUC* metric characterizes model performance across the entire range of possible probability cut-offs at which the decision-maker might want to set the threshold, we are particularly concerned with performance at the optimal cut-off of $p = V_T/V_E$ from Equation 1. Thus, our second performance metric is the per species expected net benefits (ENB) of applying risk assessment, given the true positive rate (TPR) and false positive rate (FPR) that result at that optimal cut-off:

where $\hat{y}$ indicates a prediction of 'establisher' (=1) or 'non-establisher' (=0). This expression for ENB is appropriate if the status quo is an 'open door' where, in the absence of risk assessment, species are allowed for import. This generally reflects the current approach in the United States.

We are also concerned with how model performance will generalize to species beyond those in the current dataset. In the absence of additional data, we use leave-one-out cross-validation, in which the fitted probability for each species is calculated using model parameter estimates generated by withholding that observation from the regression (Arlot & Celisse, 2010).

After implementing the endogenously stratified sample correction and MI, we found that the same set of predictive variables generate the highest AUC as well as the highest ENB (averaged across the range for α). This best performing model includes the regressors *established elsewhere, habitat generalism, incubation days, relative brain size, broods per year, clutch size, fecundity* and *life span*. All subsequent results are based on this model.

In Fig. 1, we present the ROC curve illustrating predictive performance in terms of the TPR as a function of the FPR. The stringency of the threshold cut-off for acceptable risk ranges from an open door approach (bottom left) to a closed door (top right). At the bottom left, the cut-off is at its maximum ($P = 1.0$), and everything is accepted. No establishers are excluded (TPR = 0), but there is also no mistaken rejection of non-establisher species (FPR = 0). At the closed door extreme (top right), the cut-off is at its minimum ($P = 0$) such that all establishers (TPR = 1) and non-establishers (FPR = 1) are excluded. Overall, the AUC is 0.82. We also evaluated a complete case model to test the usefulness of MI. In this case, the number of usable observations in the training dataset falls from 165 to 108. Evaluating the complete case model with and without the endogenously stratified sample correction results in lower AUC scores of 0.77 and 0.66, respectively. These comparative, leave-one-out cross-validation results show that MI is a promising approach for addressing incomplete data.

The optimal threshold cut-off under our benchmark scenario ($V_E = \$3.0M$) is given by $V_T/V_E = 0.026$. This benchmark case is plotted in Fig. 1 at the point given by FPR = 0.40 and TPR = 0.86. To convey sensitivity of the optimal cut-off with respect to losses from established species, further cases are plotted for alternative values of establishment damages (V_E) in Fig. 1 (see also Table 1).

$$\text{ENB} = \underbrace{\Pr(y=1)}_{\substack{\text{Probability that a} \\ \text{random species} \\ \text{is an establisher}}} \underbrace{\Pr(\hat{y}=1|y=1)}_{\text{TPR}} \underbrace{[V_E - V_T]}_{\substack{\text{Net benefit} \\ \text{of excluding} \\ \text{an establisher}}} + \underbrace{\Pr(y=0)}_{\substack{\text{Probability that a} \\ \text{random species} \\ \text{is a non}-\text{establisher}}} \underbrace{\Pr(\hat{y}=1|y=0)}_{\text{FPR}} \underbrace{[-V_T]}_{\substack{\text{Net benefit} \\ \text{of excluding} \\ \text{a non}-\text{establisher}}} \quad (2)$$

$$= \pi \cdot \text{TPR} \cdot [V_E - V_T] + [1 - \pi] \cdot \text{FPR} \cdot [-V_T].$$
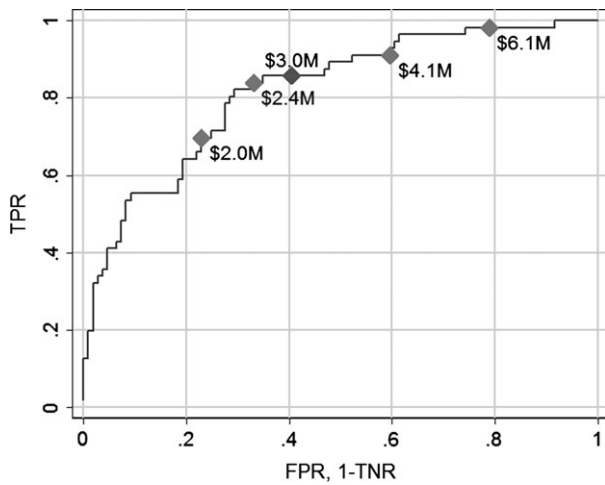
Figure 1 ROC curve presenting the true positive rate (TPR) as a function of the false positive rate (FPR = 1 – true negative rate). Optimal thresholds (diamonds) are indicated for the different levels of V_E.

Table 1 Establishment risk assessment model performance

V_T ($K)	α	V_E ($K)	cut-off	TPR	TNR	ENB ($K)	AUC
	0.50	6077	0.013	0.98	0.21	92	
	0.75	4051	0.020	0.91	0.40	48	
79	1.00	3038	0.026	0.86	0.60	35	0.82
	1.25	2431	0.033	0.84	0.67	26	
	1.50	2026	0.039	0.70	0.77	18	

Implied V_E, optimal cut-off, true positive rate (TPR, 'sensitivity'), true negative rate (TNR, 'specificity'), expected net benefits (ENB) of risk analysis per species (2010$) and area under the ROC curve (AUC) for different levels of α.

While the predictive model is imperfect—identifying 86% of the establishers and falsely rejecting 40% of the non-establishers in the benchmark case – the expected payoffs are substantial. The expected net benefit per species assessed is ENB = $35K for the benchmark scenario ($\alpha = 1$). Table 1 illustrates that as average establishment damages (V_E) vary from low ($2M) to high ($6M) the optimal cut-off becomes more stringent and the rate at which establishers are excluded (TPR) approaches one. While the rate of mistaken exclusion of safe species (1-TNR) also grows over this range, the expected net benefit of screening increases with V_E.

Disease risk assessment

Reliable outbreak-level data are available for human and livestock diseases, but information on the origin (alternate hosts) of livestock pathogens is much sparser than for human diseases. We therefore developed an infectious disease threat index using a 13-year record of World Health Organization (WHO)-reported, country-level avian infectious disease outbreaks (Chan *et al.*, 2010; Bogich *et al.*, 2012),

proxies for the capacity of countries to identify and report outbreaks (Hosseini *et al.*, 2010), and socio-economic and ecological variables known to facilitate or augment outbreaks (Jones *et al.*, 2008; Bogich *et al.*, 2012). We modelled the cumulative number of outbreaks in each country as a Poisson process with a mean given by the log of a linear combination of explanatory variables.

The number of avian infectious disease outbreaks per country served as the dependent variable with socio-economic and ecological data as explanatory variables. Data for the dependent variable were assembled from a WHO database of infectious disease outbreaks between 1996 and 2009 (Chan *et al.*, 2010; Bogich *et al.*, 2012). Potential explanatory variables consisted of a series of socio-economic and ecological variables shown previously to facilitate or augment outbreaks (Jones *et al.*, 2008; Bogich *et al.*, 2012). Socio-economic data included human population size (United Nations, 2011), gross domestic product and health expenditures (World Bank, 2013). Each potential explanatory variable was considered for inclusion in the model at its 2010 level and in the form of percentage change over the period 1996–2010. As a measure of governance, we used the Kraay *et al.* (2005) Control of Corruption index. Ecological variables included an indicator of poultry production (Wint & Robinson, 2007) and avian diversity (number of bird species per country) (Birdlife International, 2004). All socio-economic data were obtained for the years 1996 and 2010, which bookend the outbreak data. After records from a small number of countries as well as all islands and territories (e.g. overseas territories) were removed due to lack of data, our dataset included 145 countries.

We identified the preferred model by iteratively selecting variables from the full set to create a model with the lowest Akaike information criterion (AIC) (Burnham & Anderson, 2002). Model structure, variable selection and regression results for alternative and preferred models are presented in Appendix S5.

Integration of disease and establishment risk

In Fig. 2a, we plot each species in the sample by the fitted probability of establishment versus the EID threat index given by the most likely exporting country (highest historical export share of the species). The EID threat index on the horizontal axis is a fitted, country-specific, estimate of the number of expected avian EID outbreaks observed between 1996 and 2010. Species above the cut-off in the establishment probability rejection region (non-shaded) warrant exclusion based on establishment probability alone, irrespective of disease risk. Remaining species in the shaded region below the cut-off can then be prioritized for further assessment based on both (1) vertical proximity to the cut-off, and (2) EID threat. In Fig. 2b, we magnify the region of interest, at and below the establishment probability cut-off (Pr(Establishment) = 0.026). In addition to the EID threat index of the likeliest exporting country (dot), we include a bar extending

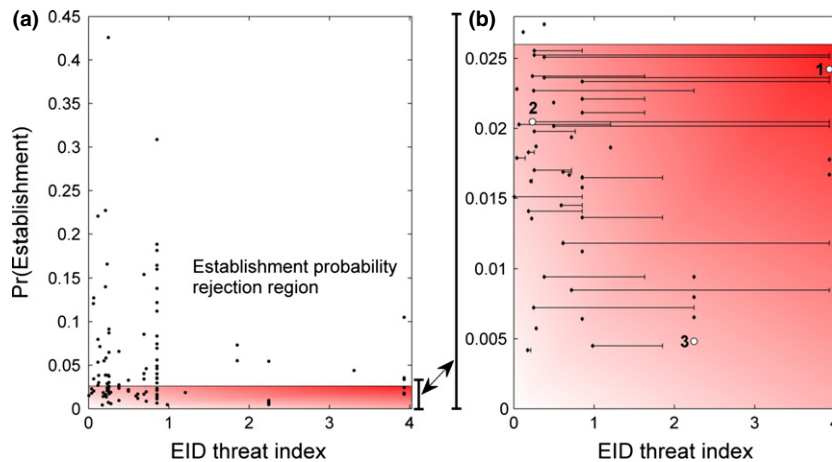**Figure 2** Species plotted by EID threat index versus probability of establishment, Pr(Establishment). The non-shaded area represents the rejection region based on establishment probability for (a) the full sample of 165 species and (b) The subsample of species below the establishment probability cut-off at Pr(Establishment) = 0.026. The EID threat index for each species is given by the most likely exporting country (dot) and a bar extending rightward to the highest index across all exporters of the species. The gradient in the shaded region from light to dark indicates increasing EID threat and Pr(Establishment). Numbered species examples (white dots) are (1) *Anser cygnoides*, (2) *Carduelis carduelis* and (3) *Erithacus rubecula*.

rightward from each dot to the highest index across all exporters of the species.

DISCUSSION

Our risk assessment framework is, to our knowledge, the first to quantitatively assess the expected biological risks due to both the environmental and health impacts of a potentially invasive, traded wildlife species. As more information is available for assessing establishment outcomes (relative to disease threats), the first step involves excluding a subset of species based on establishment risk alone. Further assessment for disease threat from these species is unnecessary. For species below the cut-off (Fig. 2b), estimates of disease threat can be combined with estimates of establishment probability to prioritize them for further assessment—priority should increase as species approach the north-east corner of the shaded area. A final benefit of the framework is use of the EID threat index as an input to prioritizing border inspections to monitor remaining incoming trade.

To illustrate interpretation of the results in Fig. 2 and how the framework can be used to prioritize species, we discuss three species selected from different regions of Fig. 2b. First, the swan goose [*Anser cygnoides,* species (1) in Fig. 2b] is imported to the United States primarily from China, which has a high EID risk of 3.9. This species has an establishment probability of 0.024, just below the exclusion threshold of 0.026. It has been reported as a carrier of WNV, and at the genus level, five other pathogens have been reported, including an unnamed Coronavirus. This combined establishment and disease threat indicates that it may be rational to restrict this species from trade until a more detailed risk assessment is conducted, or until quarantine programmes could be

established to determine whether imported individuals are carriers of concern for EIDs.

Second, the European Goldfinch [*Carduelis carduelis,* species (2) in Fig. 2b] has a relatively high establishment probability of 0.020 and is imported in highest numbers (~75,000 year^{-1}) from Australia, which has a low disease threat index of 0.23. It is also imported in high numbers (~69,000 year^{-1}) from the Russian Federation, which has a relatively high disease threat index of 2.25. If an extended risk assessment confirms that the benefits outweigh the establishment risks, it may still be rational to only allow imports from countries with low disease risks.

Third, the European Robin [*Erithacus rubecula,* species (3) in Fig. 2b] has a very low establishment probability (0.005) but is imported from some high risk countries, including the Russian Federation. Several attributes of the European Robin are associated with a lower probability of establishment: the species is not established elsewhere and – relative to training dataset averages–the European Robin has a lower level of habitat generalism, many fewer days of incubation and a higher level of fecundity (Sol *et al.*, 2012). Among other diseases, it is a carrier of WNV and Usutu virus (USUV), the latter being a novel disease with the potential to emerge in humans. This pathogen has become established in Europe (Weissenböck *et al.*, 2013), causing several episodes of wild bird deaths in Italy (Mani *et al.*, 1998; Manarolla *et al.*, 2010), Austria (Weissenbock *et al.*, 2002; Chvala *et al.*, 2007), Hungary (Bakonyi *et al.*, 2007), Switzerland (Steinmetz *et al.*, 2011), Germany (Becker *et al.*, 2012) and Spain (Höfle *et al.*, 2013). In humans, USUV can impair neurological function. At least five non-lethal human cases have been reported in Europe since 2009 (Vazquez *et al.*, 2011), but USUV has not yet been recorded in the New World. USUV

presents all the eco-epidemiological (e.g. mosquito-borne) and virological characteristics (e.g. RNA virus) to invade and become an established pathogen in naive wild bird populations of the United States and other countries in the region.

The work detailed here advances risk assessment methodology by quantitatively considering the well-known risks that imported organisms will act as reservoirs for damaging diseases and integrating this with a model of species establishment. The value of this framework for policy is heightened by the fact that, once in place, it can be executed for new species in a matter of days because many of the species-level data required to assess new species are readily available.

In building the framework, we develop novel models for the stepwise assessment of both establishment and EID threat. Our approach can also be applied to other taxonomic groups and regions, although building the model for a particular taxa involves investing in obtaining, analyzing and updating key ecological and economic datasets. Periodic updates to the disease threat index would be particularly useful as more outbreaks are reported. The problem of balancing biological risks from species imports against the gains from trade is complex, and perfect prediction of outcomes is unobtainable. However, the framework developed here provides an approach for organizing many sources of information in support of transparent decisions.

There are several ways in which the framework could be improved. The establishment probability model currently supports species-specific, trait-based estimates of establishment likelihood. In contrast, estimates of establishment damages are made only for species on average. These damages could be further refined to the species level if even coarse data on establishment damages for a large number of species became available. Our establishment probability model may also be improved by extending the set of explanatory life history variables to include factors like trophic status or climate match.

The disease threat model only considers the number of avian infectious disease outbreaks in the country of origin for the species and not disease transmission risk of the particular bird species. Additionally, the analysis does not account for either the timeframe of outbreak non-detection or the conditions in which the birds are bred, captured and transported. The model would benefit from inclusion of these factors if they become available in the future. The data could also suffer from reporting bias, as not all countries report avian infectious disease outbreaks with the same regularity.

The risk assessment tool presented here provides a rigorous and transparent economic basis for determining which species should be allowed for trade. We address the significant invasion and disease risks posed by bird imports to the United States with a framework that could readily be expanded to other taxa. If implemented as a management tool, this approach would explicitly recognize that importation of non-native species carries risks for both invasion and spread of EIDs and that estimates of the combined threats from these factors should drive decisions about which species are acceptable for trade.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Calculating compensating surplus to estimate trade benefits.

Appendix S2 Establishment probability model.

Appendix S3 Endogenously stratified sample correction.

Appendix S4 Multiple imputation methodology for missing data.

Appendix S5 Estimation of the disease threat index.

Table S1 Variables used to construct establishment probability model.

Table S2 Regression results from the disease threat index model selection process.

BIOSKETCH

The aim of this research team is to integrate disease and invasion ecology with economic risk assessment to support empirically informed risk assessment of live species trade.

Author contributions: M.S., R.K. and P.D. conceived the framework; C.R. and R.K. collated and processed the species establishment data; M.S. estimated the establishment probability model; S.E. and C.Z. developed and estimated the disease threat index; M.S. analysed the integrated disease and establishment probability model. All authors contributed to the writing.

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