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A worldwide, bio-geographical analysis

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Abstract

The introduction of harmful non-indigenous species is generally acknowledged to depend both on the propagule pressure imposed by openness to international trade and on the health of the receiving ecosystem. Bio-geographical factors however play a crucial role in determining the level of risk associated with trade. We develop an analytical treatment of bio-geographical similarity between trade partners, within a model that links the incidence of invasive species to resource extraction, pollution and to import volumes disaggregated by country and region of origin. The model, estimated with data on invasive species of all taxa in 123 countries, shows that considering the geographical structure of trade flows and the bio-geographical similarity between sources and destinations substantially improves our understanding of the drivers of biological invasions. The results allow us to identify, in a worldwide perspective, the relative risk of biological invasions (by habitat and organism type) entailed by different commercial partners.

Keywords: Invasive species, alien species, non-indigenous species, trade, driving forces, propagule pressure, disturbance, bio-geographical similarity.

JEL Classification: Q01, Q27, Q56, Q57

1.   Introduction

Due to their increasing severity, unintended introductions of non-indigenous species (NIS) and the resulting ecological and economic damage have received growing attention in recent years. If there is a long history of studies on biological invasions in the natural sciences, with classical works dating back to the 1950s (e.g. Elton 1958), economics has begun devoting attention to the issue in the last decade, after international scientific and policy-oriented initiatives (such as the Global Invasive Species Programme, sponsored by the United Nations and major international environmental organizations) called for the inclusion of an economic perspective on the driving forces and on the policy options. The corpus of economic analyses is now relatively rich, comprising studies on the valuation of economic costs (e.g. Turpie and Heydenrych 2000, Pimentel *et al.* 2005, Born *et al.* 2005, McIntosh *et al.* 2007, Adams and Lee 2007, Horsch and Lewis 2009), on the economic determinants (Costello *et al.* 2007, Westphal *et al.* 2008, Hlasny and Livingston 2008, Pyšek *et al.* 2010, Essl *et al.* 2011), on policy strategies (Shogren 2000, Eiswerth and Johnson 2002, Perrings 2005, Leung *et al.* 2005, Finnoff *et al.* 2005, Horan and Lupi 2005, Margolis *et al.* 2005, Costello *et al.* 2007, Batabyal 2006, Mehta *et al.* 2007, Mérel and Carter 2008, Olson and Roy 2010, Liu *et al.* 2011, Rout *et al.* 2011, Margolis and Shogren 2012, among others), and on bioeconomic models that examine the influence of specific traits of invading species on their chances of establishing and on the optimal prevention and management options (Finnoff and Tschirhart 2005, Gutierrez and Regev 2005, Haight and Polasky 2010, Rauscher and Barbier 2010, Finnoff *et al.* 2010, Marten and Moore 2011).

A complete survey of the economic literature on biological invasions – a hint on its dimensions being offered by the about 140 Econlit entries between 2000 and today – is beyond the scope of this paper. This work places itself among the studies that seek to deepen our understanding of the economic determinants of the phenomenon – the human pressures that, by creating pathways of introduction and by altering the conditions of receiving ecosystems, facilitate biological invasions. As to the pathways, the main object of inquiry is international trade. There obviously are NIS intentionally introduced for agriculture, forestry, aquaculture or as pets and ornaments, but there appears to be consensus on the predominant role, in recent decades, of unintentional introductions. The latter also are those posing the most challenging policy issues. The role of trade flows has been examined in several recent studies: Hlasny and Livingston (2008) examine the relation between imports, immigration and international travel and introduction of non-indigenous insects in the United States. Westphal *et al.* (2008) conduct the first worldwide study of the impact of international trade (merchandise imports) on biological invasions, refereed to all species, using a regression tree analysis. Costello *et al.* (2007) investigate how the risk of invasions carried by imports varies by trading partner: they use data on shipping, disaggregated by country of origin, and consider marine species discoveries in the San Francisco Bay between 1853 and 1994. They distinguish imports arriving from the Atlantic/Mediterranean region, West Pacific, Indian Ocean. Essl *et al.* (2011) show the existence of a legacy of past economic activities on biological invasions, using alien species introductions recorded in European countries for different taxa before 1900, between 1900 and 1950, and after 1950 and the historical levels of trade and GDP. Pyšek *et al.* (2010), again using a regression tree approach, find that national wealth and human population density, analyzed

jointly with climate, geography, and land cover, are statistically significant predictors of the numbers of non-indigenous plants, fungi, and animals in European countries.

Until now the availability of data has forced empirical research either to consider very broad variables (such as aggregate imports reaching a country, regardless of their origin) in order to include a large number of countries, or to aim at a deeper analysis at the cost of confining it to one country or site and/or to a restricted set of organism types. As a result, little consensus has emerged as yet on the relative importance of anthropogenic drivers of invasions.

We develop an analytical model taking into account a few further elements that crucially characterize biological invasions dynamics, and then we test it on data pertaining all taxa on a global geographical scale. Specifically, we try to answer the following questions: (i) What is the relative importance of openness to trade and ecosystem health in determining invasibility? (ii) How does the spatial pattern of trade flows (infra-regional *versus* inter-regional flows, i.e. the distance between source and destination) affect the risk of invasion associated with trade? (iii) How does bio-geographical similarity affect the relative risk (for different habitats and by different organism types) entailed by different trading partners?

We develop a conceptual framework based on three prior hypotheses: First, international trade (and merchandise imports in particular) is a crucial pathway of invasions. Second, invasions are more likely to occur where ecosystems are relatively more disturbed by economic activities. Third, the process of introduction and establishment of NIS has a spatially differentiated structure in which key roles are played by the similarity between bioclimatic conditions of the origin and destination site and by the extent to which the two ecosystems have

evolved in separation. The first notion is generally accepted in previous analyses of the economic determinants of invasions (Perrings *et al.* 2002; Levine and D'Antonio 2003; Hlasny and Livingston 2008, among others). The second, known as the disturbance hypothesis, has been dealt with mainly by biologists (e.g. Cohen and Carlton 1998, Enserink 1999, Cumming 2002, Tilman 2004, Pyšek *et al.* 2010), with few exceptions (e.g. Dalmazzone 2000), through empirical studies. The third one, although recognized as a crucial factor by biologists (e.g. Williamson 1996) and by some previous economic studies (e.g. Costello *et al.* 2007), has never been object of specific theoretical or empirical enquiry within the economic theory of biological invasions, and represents the major departure of this paper from the existing literature.

2. Modelling biological invasions

Biological invasion theory generally identifies at least three nested stages leading to NIS-related ecological damage: the transport and introduction of non-indigenous species in a new environment, their establishment in the destination habitat, and their spread to become pests and generate harmful effects for native species and human activities. Transport and introduction are mostly due to the international movement of commodities. Establishment and spread depend on local conditions – the health of the receiving ecosystems, its supply of resources – and on the capacity of the non-native organism to adapt to the new environment. The latter in turn depends on the bio-geographical similarity between the origin and destination sites as well as on the species-specific susceptibility to environmental and climatic conditions.

Biological invasions are a complex phenomenon. To disentangle causalities and relationships within such complexity, studies by natural scientists tend to concentrate on specific taxa and/or receptor sites. Economic analyses, in the attempt to identify general relationships, tend to design more aggregate models in which, however, phenomena affecting different species and different habitats may cancel out or blur the picture. The challenge we take with this research is to design an economic analysis of the determinants of biological invasions characterized by a high generality (worldwide rather than single receptor country or site, and considering all taxa), and at the same time taking into account the specificity of different habitats and of the bioclimatic conditions of the countries of origin and destination of NIS.

We analyze the phenomenon of biological invasions in a multi-scale perspective. Natural scientists tend to consider, through empirical *ad hoc* observations, a restricted range of species at a locally determined geographical scale – generally a specific ecosystem. Economic studies usually investigate the dynamics of one or more species within, to and from one country. We retain countries as the economic unit of analysis, but develop a model that considers economies and ecosystems at a country level as nested in regions of supranational dimension, geographically determined according to the World Bank classification [South Asia (SA), North America (NA), Middle-East and North Africa (MENA), Latin America and Caribbean (LAC), Europe and Central Asia (ECA), Sub-Saharan Africa (SSA), East Asia and Pacific (EAP), Oceania (O)].

The number of species introduced, established and recognized as pests in a single country i (NIS_i) is used as a proxy of the intensity of damage at the national level.[1] Trade within the same macro-region can act as a pathway for species that are more likely to have had a certain degree of co-evolution due to past interaction. This reduces the probability that introductions lead to a pest outbreak, since the functional relationships operating in the new habitat will have some similarity to those of the source habitat. Evolutionary separation between the origin and destination region, conversely, increases the chances that the receiving environment does not possess the biological checks and balances to control the spread of the alien organism. We therefore distinguish between long distance (inter-regional) trade flows and short distance (infra-regional) flows, depending on the fact that country j where imports originate belongs to same region of the destination country i.

Moreover, import flows work as a pathway according to the level of bio-geographical similarity among country i and j. Bio-geographical similarity increases the chances an alien organism has to get established in the new environment. Within the framework of economic evidence-based studies, Costello *et al.* (2007) is the only previous work, to our knowledge, to explicitly deal with this factor. They implement bio-geographical similarity as an unknown parameter, to be estimated via maximum likelihood, reflecting the intrinsic infectiousness of the source region to the destination. Such parameter, however, does not necessarily

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[1] We are aware that this is a simplifying assumption. As Molnar *et al.* (2008:486) put it, "the number of alien species in a habitat does not indicate the level of threat posed to native biota or the damage already done. Many species establish in a new habitat with few disruptions, whereas others alter entire ecosystems or put native species at risk of extinction." It does however convey an indication of the exposure to invasive species – and is the best indicator for which worldwide data exist. More refined analyses, including threat scoring systems based on documented adverse impacts of each NIS, will be due as soon as more detailed databases become available.

disentangle the climate matching effect, since it is likely to capture also a possible range of latent endogenous variables not related to bioclimatic proximity such as evolutionary separation between origin and destination country, shipping technology, policy variables, and so on.

We propose, instead, to explicitly measure the impact of bio-geographical proximity on the invasion risk carried by trade by introducing an index (π_{ij}) measuring the similarity between biomes of the country of origin and destination of the trade flow. The indices π_{ij} are used to weight the amount of imports from j to i. The structure of weights is designed by revisiting the Jaffe index, an index of technological proximity commonly used in the literature of innovation and knowledge economics and based on compositional properties expressed in shares (Jaffe 1986). Our index of bio-geographical similarity can be written as

$$\pi_{ij} = \frac{\sum_{k=1}^{K} f_{ik} f_{jk}}{\sqrt{\sum_{k=1}^{K} f_{ik}^2 \sum_{k=1}^{K} f_{jk}^2}}$$

[1]

where f represent shares of land surface covered by different biomes according to the maps and classification of ecosystem typologies by Olson *et al.* (2001). Through GIS processing we overlaid and intersected political boundaries and ecosystem typologies so as to calculate the shares of land area of the following 14 ecoregions within each country:

1. Tropical and subtropical moist broadleaf forests;

2. Tropical and subtropical dry broadleaf forests;

3. Tropical and subtropical coniferous forest;

4. Temperate coniferous forest;

5. Temperate broadleaf and mixed forests;

6. Boreal forests/taiga;

7. Tropical and subtropical grasslands, savannahs and shrublands;

8. Flooded grasslands and savannahs;

9. Montane grasslands and shrublands;

10. Tundra;

11. Mediterranean forests, woodlands and scrub;

12. Desert and shrublands;

13. Mangroves;

14. Water bodies.

Imports from any given country may also entail a different invasion risk for different habitats in the destination country. Considering NIS suited to different habitats (marine ecosystems, forests, range and grasslands, inland waters, urban areas, agricultural areas) separately allows us to bring to light significant relationships that do not emerge in the aggregate model, and estimate the relative riskiness of imports by region and country of origin for each receiving habitat. This conveys precious information for real world conservation policies.

Disturbances are expected to have a pro invasive effect as they create open space that may allow alien species to get established. Intermediate levels of disturbance, particularly, offer invaders an edge against the better adapted and therefore usually competitively stronger native species (Connell 1978; Rejmánek 1989; Lodge 1993; Etter and Caswell 1994; Pišek *et al.* 1998; Shigesada and Kawasaki 1997 and references therein). Being ours a worldwide analysis, the choice of variables that can be used to estimate this effect is affected by data coverage. We use emissions of PM_{10} and of SO_2 as proxies of local pollution levels, and the extraction of wood biomass as an indicator of the level of pressure on natural resources. In addition, we use per capita GDP (in 2005 US $) as a measure of the level of economic activity and hence as an indirect indicator of overall pressure on a country's natural systems.[2]

Finally, we retain insularity, given the generally acknowledged sensitivity to biological invasions of island ecosystems.

3. Econometric strategy

Our dependent variable is the number of NIS causing harmful effects in country *i*. Invasions depend on merchandise imports, which we distinguish between *infra-regional* (Φ) and *inter-regional* ($\mathbf{T}$) flows, obtained by grouping countries of origin within the boundaries of the World Bank regions listed in Section 2. Other determinants are the disturbances generated by anthropic pressures that may

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[2] We are aware of the limits of using flow variables (such as imports, GDP, emissions) as explanatory of a stock dependent variable (cumulative number of NIS). This is an issue also affecting several previous studies (e.g. Vilà and Pujadas 2001, Westapal *et al.* 2008, Pišek *et al.* 2010). However, information on new additions of NIS is not yet available on a worldwide scale, nor are available cumulative economic data on long time scales.

affect local ecosystems' vulnerability to invasions $(\mathbf{D})$, and insularity (I). A general form of the model can be written as:

$$NIS_i = f(\Phi, \mathbf{T}, \mathbf{D}, I) \qquad [2]$$

Given the non-negative and integer nature of the number of alien species, for the empirical analysis we adopt a count data approach. Negative binomial or Poisson models are standard suitable options. However, when the assumption of equivalence between mean and variance of the dependent variable is violated the estimates of a Poisson model are inefficient, with biased standard errors. For every estimated model a likelihood ratio test allows us to measure the probability of overdispersion. In the absence of overdispersion the Poisson standard model is the preferable option. For those regressions where the dependent variable exhibits overdispersion, we report results of a negative binomial estimation.

Denoting with λ the expected number of NIS, we can express the general model [2] in log-linear form, including inter-regional and infra-regional effects, according to the Poisson and negative binomial approach:

$$\ln \lambda_i = \theta_{sa} \sum_{j_{sa}=1}^{J_{sa}} \pi_{ij_{sa}} x_{ij_{sa}} + \theta_{na} \sum_{j_{na}=1}^{J_{na}} \pi_{ij_{na}} x_{ij_{na}} + \theta_{mena} \sum_{j_{mena}=1}^{J_{mena}} \pi_{ij_{mena}} x_{ij_{mena}} + \theta_{lac} \sum_{j_{lac}=1}^{J_{lac}} \pi_{ij_{lac}} x_{ij_{lac}} +$$

$$+ \theta_{euc} \sum_{j_{eca}=1}^{J_{euc}} \pi_{ij_{eca}} x_{ij_{eca}} + \theta_{ssa} \sum_{j_{ssa}=1}^{J_{ssa}} \pi_{ij_{ssa}} x_{ij_{ssa}} + \theta_{eap} \sum_{j_{eap}=1}^{J_{eap}} \pi_{ij_{eap}} x_{ij_{eap}} + \theta_o \sum_{j=1}^{J_{aus}} \pi_{ij_o} x_{ij_o} + \theta_{sa} \sum_{j_{sa}=1}^{J_{sa}} \pi_{ij_{sa}} x_{ij_{sa}} +$$

$$+ \theta_{na} \sum_{j_{na}=1}^{J_{na}} \pi_{ij_{na}} x_{ij_{na}} + \theta_{mena} \sum_{j_{mena}=1}^{J_{mena}} \pi_{ij_{mena}} x_{ij_{mena}} + \theta_{lac} \sum_{j_{lac}=1}^{J_{lac}} \pi_{ij_{lac}} x_{ij_{lac}} + \theta_{euc} \sum_{j_{eca}=1}^{J_{euc}} \pi_{ij_{eca}} x_{ij_{eca}} + \theta_{ssa} \sum_{j_{ssa}=1}^{J_{ssa}} \pi_{ij_{ssa}} x_{ij_{ssa}} +$$

$$+ \theta_{eap} \sum_{j_{eap}=1}^{J_{eap}} \pi_{ij_{eap}} x_{ij_{eap}} + \theta_o \sum_{j=1}^{J_{aus}} \pi_{ij_o} x_{ij_o} + \alpha_{island} I_i + \delta_{pm10} pm10_i + \delta_{so2} so2_i + \delta_{wood} wood_i + \delta_{gdp} pcgdp_i$$

$$[3]$$

where x_{ij} is the value of trade flows from country j to i, and π_{ij} is the level of bio-geographic similarity between origin and destination measured by the index [1]. Among the unknown parameters to be estimated, θ captures the contribution to invasions of inter-regional imports, while ϕ the invasive potential of infra-regional imports.

We do not consider the issue of the variation of marginal invasion risk as a function of time and of cumulative volume of imports by region, that in Costello *et al.* (2007) introduces a valuable element of realism. Our cross-sectional analysis globalizes the geographic coverage of previous analyses in order to investigate the spatial patterns governing invasion dynamics. The lack of availability of worldwide time series does not allow us to integrate also the time dimension (with current data, a panel analysis would be feasible only on the 28 countries included in the DAISIE European database).

4. Data

The dataset employed for the estimation of model [3] merges various sources of economic and ecological data, all considered at a country level, for 123 units of observation. The number of NIS derives from the IUCN Global Invasive Species Database, listing invasive species across all taxa recorded until August 2012 in 227 geographic areas. This source also supplies the geographical distribution of the native and alien range of each species, identifying the preferred typology of habitat of each invader, and a classification by organism type. This additional biological information allows us to test model [3] on different subsamples of invaders, as discussed in Sections 2 and 5.

The source of merchandise import data is the IMF Direction of Trade Statistics, considered at the year 2005 in order to avoid possible effects of reverse causality on the dependent variable. Data on PM_{10} and SO_2 are from the Emission Database for Global Atmospheric Research (EDGAR) released by the European Commission (2012) and are referred to the total volume of emissions by country in 2005. The World Development Indicators is the source for GDP and area of each country, while the extraction of wood biomass is taken from Kraussmann *et al.* (2008a, 2008b). Synthetic descriptive analyses for these explanatory variables are reported in Table 1. In model [3] all the explanatory variables except dummies are expressed on a log-scale. This allows us to interpret the raw coefficients estimated by negative binomial regressions as elasticities (Cameron and Trivedi 2001).

[Table 1 about here]

5. Results

Models estimations are presented in Table 2. The overall model explains the total number of invasive species by country. The same model is also estimated for subsamples of species classified according to their preferred habitat in their native range.[3] Trade flows (infra-regional and inter-regional imports) are weighted by the matrix of indexes of bio-geographic similarity. We also run our regressions on the corresponding non-weighted models in order to compare the results. Raw coefficients of the import variables can be read as forces that increase (or reduce) the expected stock of NIS in a generic country.

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[3] Identification of these subcategories is possible thanks to the detailed and uniform GISD classification.

[Table 2 about here]

For all the presented models insularity is always significant (at a 99% level) and increasing, as expected, the (count) probability of invasions. Accounting for bioclimatic matching increases the weight of insularity in explaining invasions. In the analysis by habitat type, insularity is suggested to imply a higher risk factor for invasions affecting forests and urban areas, and lower for invasions in agricultural and marine areas. Insularity increases the number of invasive species in a country by a value in the range from $e^{0.3}$ (agricultural areas) to $e^{0.6}$ (forests). This confirms both the biological literature, that focuses on the vulnerability of endemic species evolved in relative isolation on island ecosystems, and previous studies focusing more on socio-economic factors (among which Dalmazzone 2000 and Pišek *et al.* 2010). It appears instead to refuse Westphal *et al.* (2008)'s results that do not find any overall island effect. An economic perspective highlights that island states are also, on average, small open economies, and their higher than average level of imports (as a share of GDP, or per unit of area) adds to their ecological features in explaining their susceptibility to invasions.

The distinction introduced in our model between infra-regional and inter-regional trade flows, which was meant to capture the distance and hence the evolutionary isolation between source and destination, does not provide a clear-cut answer on how the scale of international trade affects the risk of biological invasions. Intercontinental trade flows appear to convey higher risk of invasions in some cases (e.g. imports originating in the East Asia and Pacific region), whereas in other instances it is at the infra-regional scale that we detect the strongest link between commercial exchanges and NIS levels. Countries within Oceania are the most evident illustration of the latter. Most likely, distance acts on the risk of invasion

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success in combination with other factors (among which insularity and bio-geographical similarity). Belonging to the same World Bank region has not impeded species in Australia and New Zealand to evolve in separation and to become (combined with bio-geographical similarity) the most dangerous NIS in the other country. Similarly, trade within Latin America (a region characterized by a very large latitudinal extension and very differentiated ecosystems) if weighted by bio-geographic similarity appears to convey more invasions than intercontinental trade.

Much more definite appears to be the role of bio-geographic variables. The introduction of weights for bioclimatic similarity slightly but systematically improves the goodness of fit of the models.[4] Particularly, it improves the explicative capacity of the inter-regional trade regressors.[5]

Our analysis allows us to derive specific information also on the relative invasion risk linked with imports distinct by habitat of election of invaders. For instance, imports from South Asia convey a significant (at the 90% significance level) risk of invasions, mainly due to marine habitats invaders. Imports from North America, that in the overall model do not appear to affect the conditional average of the NIS number in receiving countries, reveal however to convey a relatively high risk of invasions for forest, agricultural, and urban areas. Similarly, Middle East and North African countries (that in the overall model appear to be harmless) reveal to be, in

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[4] Our modeling framework is based on maximum likelihood. Model selections are based on Pseudo R-squared values. Information criteria such as BIC and AIC do not convey additional insights for the comparison between weighted and non-weighted models, as the number of parameters, the estimation technique and the sample composition remain unchanged.

[5] This could suggest that the bio-geographic similarity weights are helpful in explaining spatial heterogeneity only on long distance trade relationships. If so, a model where weights for bioclimatic similarity are applied only to inter-regional flows should perform even better. We checked: the best overall goodness of fit remains that of the model where weights are applied to all trade flows.

the analysis disaggregated by habitat, trading partners conveying significant invasions risks for marine, urban, and agricultural areas (but not for forests).

Marginal effects of the estimated negative binomial models may be employed to compute values of the marginal risk of invasions across regions, as in Costello *et al.* (2007). This marginal invasion risk (MIR) can be written as

$$MIR_j = \beta_j \exp(\boldsymbol{\beta}'\mathbf{x}_i) \qquad [4]$$

It quantifies the expected increase in the number of invasions generated by a marginal variation of imports from a specific region, and conditional to the point values of other covariates (the vector $\mathbf{x}_i$). This generalizes the results in Costello *et al.* (2007) who compare the time variation of MIR among three wide geographical regions of origin relatively to one destination site (San Francisco Bay). Using regional averages of MIR computed with numerical values of parameters of the overall model in Table 2, we can use [4] to compute for example that a unit increase in imports from South Asia is linked to 3.13 additional NIS for Oceania, 2.06 for North America, 1.35 for European and Central Asian countries, 0.19 for Sub-Saharan Africa, 1.28 for Middle East and North Africa and of 0.33 within countries of the Latin American and Caribbean region. Conversely, one can compute the risk for any country (or region) associated with different trading partners. For example, for the United States the highest expected marginal invasion risk is associated with trade inflows from Oceania (37.02). A marginal increase of US imports from South Asia is expected to generate 17.2 additional invasions, whereas from European and Central Asian countries only 1.70.

Bio-geographic similarity does matter in explaining the relationship between trade and invasions. This notwithstanding, in several cases trading partners that do not emerge as significantly risky in the weighted models do convey a statistically significant risk in the non-weighted models. In the interpretation of the analysis attention should be given to the fact that so far we consider NIS from all taxa grouped together. In the real world the sensitiveness of organisms to bioclimatic matching is far from uniform across taxonomic groups. To address this, we look at the impact of our regressors on different organism types (Table 3). Insects and fungi turn out to be the least sensitive organisms to climate: for them the weighted model does not improve the explicative capacity. This confirms findings in Pišek *et al.* (2010). In other words, the weighted model design based on the Jaffe index risks to overemphasize the importance of bioclimatic similarity in those cases where the prevalent risk of invasions pertains insects or fungi. Asian long-horned beetle *(Anoplophora chinensis)* and other insect infestations in North American forests, for example, may help explain anomalies in the performance of weighted vs. non-weighted models.

[Table 3 about here]

In the weighted model, all indicators of disturbance have a significant, positive correlation with the number of NIS (with the only exception of SO_2 emissions on the number of marine invaders). Among the physical indicators, wood extraction has a higher impact than pollution. This supports the hypothesis that the removal of biomass from ecosystems creates open physical and ecological space for invaders (for example Rejmánek 1989, Williamson 1996, Shigesada and Kawasaki 1997). In both weighted and non-weighted models, per capita GDP appears to be a highly significant determinant of the NIS level in a country. Its coefficient is the highest

among the disturbance variables, consistently with the fact that it subsumes the effect of many different factors.

For all the regressions with the exception of the weighted and non-weighted model for insects, a likelihood ratio test allowed us to reject the null hypothesis of equivalence between mean and variance. The presence of overdispersion induced us to adopt in these cases a negative binomial estimation, as standard Poisson estimates would result in biased standard errors. We implement a second set of χ_2-based LR tests in order to check the equivalence of all the region-specific parameters θ. We also test the null of equivalence of all the parameters ϕ for each regression. These tests are all confirming (at a 95% level) the hypothesis of differentiated magnitudes of risk invasion not only for long distance trade flows, but also for infra-regional exchanges.

Our regression includes a high number of variables relative to sample size. As a robustness check we perform a regression on simplified models of the impact of total exports on the number of NIS exported to other countries and of the impact of total imports on the number of NIS registered in each receiving country. These regressions confirm the contribution of propagule pressure trough international trade on invasives, in both directions (impact of one country on the rest of the world and impact on one country from the rest of the world)

Conclusions

Previous literature has recognized the role of international trade as a driver of biological invasions. It has also been acknowledged that imports from different regions convey heterogeneous risks. This work gives analytical treatment to the

weight of bio-geographical similarity between sources and destinations in determining the risk associated with trade flows, and it includes it in a model taking into account distance between trading partners, sources of anthropic disturbance to ecosystems, affected habitats, organism types.

Our theoretical model is tested through an empirical analysis covering all taxonomic groups of potential invaders, with a geographical coverage of 123 countries in all continents. This expands on many of the studies currently available, which focus on one class of organisms or on one environmental medium, and often focus on one country or site as the object of empirical analysis or as an example for estimating the parameters of a theoretical model.

Using some specific indicators of local pressure on ecosystems (emissions of PM_{10} and of SO_2, extraction of wood biomass) this work also refines previous analyses on socio-economic drivers of invasions based only on more generic proxies of anthropogenic disturbance such as GDP or population density.

Insularity is confirmed to represent an important predictor of invasibility. We estimate it to be a higher risk factor for invasions affecting forests and urban areas, and lower for invasions in agricultural and marine areas. Anthropic disturbance to ecosystems, both measured through physical indicators of emissions and biomass extraction and by broad proxies of economic activity such as per capita GDP, turns out to be significantly associated with NIS numbers.

The empirical analysis confirms the theoretical hypothesis that climate and ecological similarity affect invasion success, showing the superiority of the models accounting for the bio-geographical location of trading partners over those treating all trade flows as involving an identical potential of bioinvasions. The invasions risk

associated with imports from South Asia, from example, varies with the bio-geographical features of the destination, and turns out to be twice as high for trading partners in Oceania than for European and Central Asian countries, and low for Sub-Saharan Africa and Latin America. For the United States imports from Oceania have a potential invasive risk that is the double of that implied by imports from South Asia, and about twenty times the marginal invasion risk of imports from Europe and Central Asia. Our model thus provides an information tool that can be used to compute values of the marginal risk of invasions across regions – the risk of conveying invasions that each country or region represents for others, and the risk for any country or region associated with different trading partners.

The model also allows analysts to estimate the relative invasion risk linked with imports from specified countries and/or world regions distinct by habitat of election of invaders, and hence to identify risky trading partners for marine habitats, urban and agricultural areas, forests. Our analysis shows, for example, that imports from North America convey a relatively high risk of invasions for agricultural, urban and forest areas, whereas imports from Middle East and North African countries are dangerous sources of NIS affecting agricultural, urban and marine systems.

Considering scale and bio-geographical features within a parsimonious analytical framework compatible with currently available datasets can help us better understand the relationship between trade flows and risks of biological invasions. On the one hand, it provides an overall interpretive key of patterns governing biological invasions at a global scale. On the other, it enables country-specific valuations of the risk associated with different trading partners and of the relative

control policies – both generally and with reference to the protection of specific habitats.

A growing awareness of the ecological and economic damages associated with biological invasions and the evolution of monitoring techniques are driving a fast evolving availability of data. This is likely to enable in the near future several desirable refinements of the analysis, with respect to (i) the treatment of endogeneity or spatial dependence between NIS levels in neighboring countries, which could be addressed through spatial econometric techniques; (ii) the use of rates of NIS introductions rather than cumulative stocks as a dependent variable; (iii) consideration of trade flows disaggregated by agricultural, manufactured, fuel imports. The development of analyses based on gravity models would be an ideal extension, which will have to await the availability of large coverage, compatible data on NIS distinct by source country.

Finally, the issue of whether and how the scale of international trade affects the risk of biological invasions needs further research. A separate assessment of the role of intercontinental, regional and local dispersal of NIS requires more complex information than separating infra-regional and inter-regional trade flows, and the development of an *ad hoc* analytical framework. Because global, regional and local dispersal are controlled by different mechanisms and the ecological effects of invasions are scale-dependent, insights on the scale dimension of the invasion processes would contribute to establishing priorities in designing control policies. This is one further interesting direction for future research.

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Table 1   Description of variables

Variable description	Unit	Mean	St.Dev.	Min-Max		Source
Number of NIS		32.32117	49.54498	1-447	2012	GISD
Island		0.116788	0.322347	0-1		Our elaboration
Disturbance variables						
Density of wood biomass extraction	10^9g/km^2	.0305506	.0355877	4.47 e+08- 0.001957	2000	Kraussmann *et al.*, 2008
PM$_{10}$ emissions	10^9g	1.43e+08	4.05e+08	429646.2- 2.56e+09	2005	EDGAR v4.2
SO$_2$ emissions	10^9g	1585.788	5803.417	3.35 - 59505.2	2005	EDGAR v4.2
Per capita GDP	US$	9090.574	14297.15	115 – 66638	2005	WDI
Inter-regional trade variables						
South Asia	10^9US$	1.292427	3.866935	0 - 34.8548	2005	
North America	10^9US$	6.587797	18.74274	0 - 162.7011	2005	
Latin America & Caribbean	10^9US$	4.273188	26.85536	0 - 308.4394	2005	
Middle East North Africa	10^9US$	3.135383	11.20066	0 - 101.1286	2005	IMF Direction of Trade Statistics
Europe Central Asia	10^9US$	9.661675	39.37521	0 - 417.9432	2005	
Sub Saharan Africa	10^9US$	1.187386	5.511928	0 - 57.1656	2005	
East Asia & Pacific	10^9US$	14.45527	55.73803	0 - 586.3042	2005	
Oceania	10^9US$	.990514	3.926123	0 - 33.74123	2005	
Infra-regional trade variables						
South Asia (infra-regional)	10^9US$	.0802044	.4272821	0 - 2.872	2005	
North America (infra-regional)	10^9US$	3.970912	33.20768	0 - 317.604	2005	
Latin America & Caribbean (infraregional)	10^9US$	.8621584	3.22792	0 - 22.61345	2005	
Middle East North Africa (infra-regional)	10^9US$	.2117569	.860327	0 - 6.64211	2005	IMF Direction of Trade Statistics
Europe Central Asia (infra-regional)	10^9US$	33.59502	101.1365	0 -798.8963	2005	
Sub Saharan Africa (infra-regional)	10^9US$	.1376644	.5588395	0 - 5.7537	2005	
East Asia & Pacific (infra-regional)	10^9US$	2.324238	18.37133	0 - 205.6871	2005	
Oceania (infra-regional)	10^9US$	.0886204	.7316118	0 - 6.361	2005	

Table 2   Estimation results, for the overall models and for urban, agricultural areas, marine habitats and forests

	Overall		Urban areas		Agricultural areas		Marine habitats		Forests	
	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted
Island	0.568***	0.535***	0.579***	0.566***	0.382***	0.363***	0.484***	0.336**	0.600***	0.573***
	(4.985)	(4.200)	(5.302)	(4.350)	(3.744)	(3.050)	(3.130)	(2.091)	(5.012)	(4.226)
θ South Asia	0.0697*	1.25e-05	0.0492	1.15e-05	0.0549	1.06e-05	0.110**	1.11e-05	0.0514	8.84e-06
	(1.787)	(1.001)	(1.235)	(0.974)	(1.494)	(1.020)	(2.148)	(1.279)	(1.206)	(0.789)
θ North America	-0.0486	-1.42e-06	-0.0630*	-1.10e-06	-0.0582*	-7.09e-07	0.00619	2.96e-06	-0.0669*	-9.41e-07
	(-1.426)	(-0.711)	(-1.847)	(-0.556)	(-1.853)	(-0.404)	(0.141)	(1.514)	(-1.835)	(-0.475)
θ Middle East North Africa	0.0167	0.0520	0.0467**	0.0779**	0.0419**	0.0741**	0.0585**	0.0984**	0.0433**	0.0311
	(0.901)	(1.443)	(2.553)	(1.997)	(2.443)	(2.121)	(2.477)	(2.008)	(2.206)	(0.781)
θ Latin America Caribbean	-0.0184	-0.00825	-0.00716	0.0428	-0.00416	0.0518	0.0471	0.117**	-0.00432	0.0349
	(-0.750)	(-0.218)	(-0.294)	(1.065)	(-0.186)	(1.425)	(1.390)	(2.148)	(-0.164)	(0.824)
θ Europe Central Asia	0.00691	-0.134*	-0.0388	-0.307***	-0.0516**	-0.324***	0.0235	-0.136	0.000221	-0.262***
	(0.266)	(-1.805)	(-1.486)	(-3.705)	(-2.151)	(-4.325)	(0.670)	(-1.234)	(0.00782)	(-2.999)
θ Sub-Saharan Africa	-0.101***	-0.0557**	-0.107***	-0.0191	-0.111***	-0.0234	-0.119***	-0.0149	-0.0848***	0.0262
	(-4.081)	(-1.969)	(-4.479)	(-0.645)	(-4.982)	(-0.874)	(-3.725)	(-0.375)	(-3.294)	(0.851)
θ East Asia Pacific	-0.00457	0.121**	0.0116	0.197***	0.0150	0.171***	-0.0752	-0.0181	0.0351	0.225***
	(-0.139)	(2.072)	(0.323)	(2.969)	(0.451)	(2.876)	(-1.557)	(-0.191)	(0.897)	(3.268)
θ Oceania	0.133***	0.139***	0.183***	0.0972**	0.153***	0.0977**	0.0890*	0.0719	0.135***	0.0693
	(3.696)	(3.270)	(5.115)	(2.189)	(4.589)	(2.436)	(1.782)	(1.144)	(3.491)	(1.507)
ϕ South Asia	0.0836	-0.0167	0.0556	0.00827	0.0618	0.00693	0.112	0.0575	0.0597	0.0227
	(1.574)	(-0.472)	(1.030)	(0.227)	(1.234)	(0.216)	(1.399)	(1.308)	(1.039)	(0.628)
ϕ North America	0.0723	0.0768**	0.0536	0.0634**	0.0454	0.0525*	0.0736	0.0803***	0.0394	0.0629**
	(1.545)	(2.421)	(1.180)	(2.048)	(1.086)	(1.926)	(1.225)	(2.769)	(0.809)	(2.098)
ϕ Middle East North Africa	0.0384	0.0977**	0.0437	0.120***	0.00695	0.0819**	0.0619	0.184***	0.0101	0.0536
	(0.797)	(2.336)	(0.863)	(2.616)	(0.150)	(2.003)	(0.904)	(3.255)	(0.179)	(1.104)
ϕ Latin America Caribbean	0.0813**	0.0487	0.106***	0.112***	0.0793**	0.0966***	0.103*	0.167***	0.0771*	0.0733**
	(2.219)	(1.469)	(2.842)	(3.220)	(2.272)	(3.133)	(1.887)	(3.595)	(1.855)	(2.025)
ϕ Europe Central Asia	0.00531	-0.104	-0.0443	-0.269***	-0.0744**	-0.302***	0.00270	-0.0891	-0.0229	-0.236***
	(0.172)	(-1.631)	(-1.398)	(-3.714)	(-2.545)	(-4.625)	(0.0613)	(-0.921)	(-0.658)	(-3.095)
ϕ Sub-Saharan Africa	-0.00657	0.00833	-0.000510	0.0812**	-0.0242	0.0548*	-0.0488	0.0749*	0.0260	0.114***
	(-0.150)	(0.255)	(-0.0115)	(2.348)	(-0.582)	(1.770)	(-0.721)	(1.702)	(0.527)	(3.240)
ϕ East Asia Pacific	0.0185	0.0808	0.0178	0.159**	0.0315	0.151**	-0.0990*	-0.0552	0.0376	0.193***
	(0.443)	(1.391)	(0.409)	(2.440)	(0.786)	(2.573)	(-1.651)	(-0.589)	(0.780)	(2.868)
ϕ Oceania	0.316***	0.260***	0.353***	0.222***	0.321***	0.214***	0.195**	0.238***	0.283***	0.187***
	(5.126)	(4.490)	(5.972)	(3.696)	(5.825)	(3.986)	(2.490)	(3.128)	(4.426)	(3.045)
PM10 emissions	0.0903**	0.0654	0.0852**	0.0593	0.0558	0.0390	0.114**	0.0624	0.0830**	0.0492
	(2.412)	(1.585)	(2.266)	(1.330)	(1.629)	(0.989)	(2.224)	(1.122)	(2.035)	(1.063)
SO2 emissions	0.132***	0.106**	0.0802*	0.0745	0.130***	0.120***	0.0587	0.0807	0.0807*	0.0822*
	(3.141)	(2.353)	(1.905)	(1.568)	(3.328)	(2.812)	(0.962)	(1.382)	(1.746)	(1.691)
Wood biomass extraction	0.167***	0.150***	0.193***	0.155***	0.140***	0.102***	0.139***	0.0838*	0.180***	0.139***
	(5.837)	(5.200)	(6.166)	(4.641)	(5.008)	(3.529)	(3.124)	(1.938)	(5.305)	(3.995)
Per capita GDP	0.188***	0.159***	0.237***	0.230***	0.235***	0.224***	0.214***	0.193**	0.191***	0.187***
	(4.068)	(2.790)	(4.854)	(3.538)	(5.265)	(3.925)	(3.178)	(2.283)	(3.645)	(2.795)
Constant	0.300	0.754	-0.0755	0.258	0.0540	0.546	-2.073*	-1.745	-0.235	-0.0188
	(0.371)	(0.875)	(-0.0938)	(0.281)	(0.0729)	(0.671)	(-1.904)	(-1.614)	(-0.271)	(-0.0199)
Overdispersion	-2.639***	-2.424***	-3.179***	-2.646***	-3.351***	-2.929***	-16.84	-16.17	-3.297***	-2.869***
	(-11.56)	(-11.87)	(-8.999)	(-9.970)	(-9.034)	(-10.05)	(-0.0425)	(-0.0478)	(-7.301)	(-8.386)
Observations	123	123	123	123	123	123	123	123	123	123
Pseudo R-squared	0.239	0.231	0.281	0.261	0.274	0.262	0.313	0.291	0.282	0.273

z-statistics in parentheses, *** p<0.01, ** p<0.05, * p<0.1

Table 3 Estimation results, by organism type

	Tree (no)		Shrub (no)		Mammals (yes)		Fungi (no)		Fish (yes)		Bryozoan (yes)		Birds (no)		Grass (-)		Insects (no)	
	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted	not weighted	weighted
Island	0.940***	0.960***	1.103***	1.118***	1.007***	1.011***	-0.475	-0.445	0.319**	0.342***	0.656*	0.671*	0.425***	0.473***	0.223	0.219	0.471***	0.515***
	(4.804)	(4.373)	(5.318)	(5.084)	(3.645)	(3.729)	(-1.488)	(-1.395)	(2.525)	(2.698)	(1.750)	(1.832)	(2.596)	(2.756)	(1.069)	(1.051)	(3.204)	(3.342)
θ Imports	0.354***	0.112**	0.249***	0.0653	0.107	0.166**	0.165	0.0291	0.0935**	0.0829**	0.831***	0.661***	0.245***	0.144**	0.0972	0.0425	0.217***	0.0942**
	(4.722)	(1.971)	(3.013)	(1.104)	(1.055)	(2.169)	(1.248)	(0.294)	(2.006)	(2.387)	(3.213)	(3.371)	(3.227)	(2.489)	(1.222)	(0.698)	(3.827)	(2.189)
ϕ Imports	-0.230***	-0.215***	-0.118*	-0.109*	0.0328	-0.0169	0.112	0.119	0.0272	0.00604	-0.0994	-0.0811	-0.130***	-0.123***	-0.00398	-0.0357	-0.0137	-0.0335
	(-4.121)	(-3.822)	(-1.945)	(-1.934)	(0.425)	(-0.251)	(1.234)	(1.421)	(0.800)	(0.196)	(-0.771)	(-0.812)	(-2.689)	(-2.966)	(-0.0667)	(-0.706)	(-0.333)	(-0.913)
Pm10	0.217***	0.262***	0.169**	0.195**	0.114	0.115	-0.122	-0.0732	-0.00403	0.00889	0.0426	0.146	0.0266	0.0516	0.152**	0.165**	0.146***	0.177***
	(3.234)	(3.620)	(2.255)	(2.510)	(1.264)	(1.316)	(-0.879)	(-0.544)	(-0.0916)	(0.204)	(0.218)	(0.783)	(0.406)	(0.776)	(2.092)	(2.327)	(2.849)	(3.398)
SO2	0.0124	0.109	0.131	0.231**	0.0484	0.0255	0.139	0.211	0.194***	0.198***	-0.125	-0.166	0.125	0.158*	0.123	0.162*	0.00952	0.0691
	(0.147)	(1.247)	(1.348)	(2.415)	(0.436)	(0.245)	(0.847)	(1.350)	(3.455)	(3.658)	(-0.436)	(-0.631)	(1.476)	(1.901)	(1.318)	(1.811)	(0.148)	(1.078)
Wood biomass extraction	0.177***	0.192***	0.184***	0.202***	0.0165	0.0377	0.00512	-0.00974	0.0859**	0.0956***	-0.00444	-0.0416	0.0846	0.0878	0.130**	0.151**	0.0884**	0.108**
	(2.937)	(3.022)	(2.810)	(3.009)	(0.222)	(0.506)	(0.0473)	(-0.0886)	(2.500)	(2.758)	(-0.0226)	(-0.252)	(1.397)	(1.516)	(2.085)	(2.453)	(2.045)	(2.460)
Per capita GDP	0.179*	0.258***	0.161	0.218**	0.346***	0.329***	0.477***	0.557***	0.0138	0.0258	0.294	0.294	0.378***	0.393***	0.205**	0.249***	0.143**	0.208***
	(1.936)	(2.742)	(1.611)	(2.271)	(2.658)	(2.804)	(3.083)	(4.073)	(0.246)	(0.490)	(1.320)	(1.554)	(4.589)	(5.075)	(2.227)	(2.910)	(2.130)	(3.223)
Overdispersion	-1.108***	-0.831***	-0.978***	-0.842***	-0.478*	-0.532**	-16.82	-15.93	-2.341***	-2.336***	-2.497	-14.66	-4.571	-3.488**	-1.319***	-1.343***	-2.084***	-1.894***
	(-4.693)	(-3.853)	(-4.216)	(-3.827)	(-1.823)	(-1.982)	(-0.0146)	(-0.0249)	(-6.091)	(-6.227)	(-0.765)	(-0.0166)	(-1.157)	(-2.371)	(-4.646)	(-4.638)	(-5.884)	(-5.921)
Constant	-3.710**	-3.331**	-3.518**	-3.183*	-5.481***	-4.854**	-5.891**	-6.646**	0.394	0.575	-11.30***	-10.60***	-4.236***	-3.901***	-3.800**	-3.585**	-3.304***	-3.097***
	(-2.574)	(-2.078)	(-2.182)	(-1.861)	(-2.747)	(-2.431)	(-2.081)	(-2.341)	(0.407)	(0.589)	(-2.806)	(-2.747)	(-3.084)	(-2.733)	(-2.462)	(-2.318)	(-2.982)	(-2.678)
Observations	123	123	123	123	123	123	123	123	123	123	123	123	123	123	123	123	123	123
Pseudo R-squared	0.170	0.140	0.180	0.167	0.134	0.141	0.332	0.330	0.142	0.144	0.365	0.369	0.255	0.248	0.164	0.163	0.180	0.167

z-statistics in parentheses

*** p<0.01, ** p<0.05, * p<0.1

Appendix 1. Number of NIS by habitat type

Marine habitats	80
Estuarie habitatas	120
Lake habitats	138
Water courses	178
Wetlands	219
Riparian zones	244
Coastland	171
Urban areas	277
Agricultural areas	297
Ruderal/disturbed	407
Planted forests	241
Natural forests	357
Scrub/shrublads	207
Range/grasslands	215
Tundra	15
Desert	28
Ice	1
Host	34
Vector	11
Riverine forest/freshwater	1

Appendix 2. Number of NIS by organism type

Bryozoan (phylum)	5
Fungus (kingdom)	20
Millipede (class)	1
MiCro-orgaism (domain)	20
Arachnid (class)	4
Insects (class)	86
Centipede)ordine)	1
Flatworm (phylum)	1
Nematoda (phylum)	1
Mollusc (phylum)	32
Algae (polyphiletic)	12
Annelide (phylum)	9
Tunicate	5
Sponge	2
Coral	2
Comb jelly	1
Jellyfish	1
Crustacean	19
Sea star	2
Fish	57
Amphibian	11
Reptile	33
Bird	31