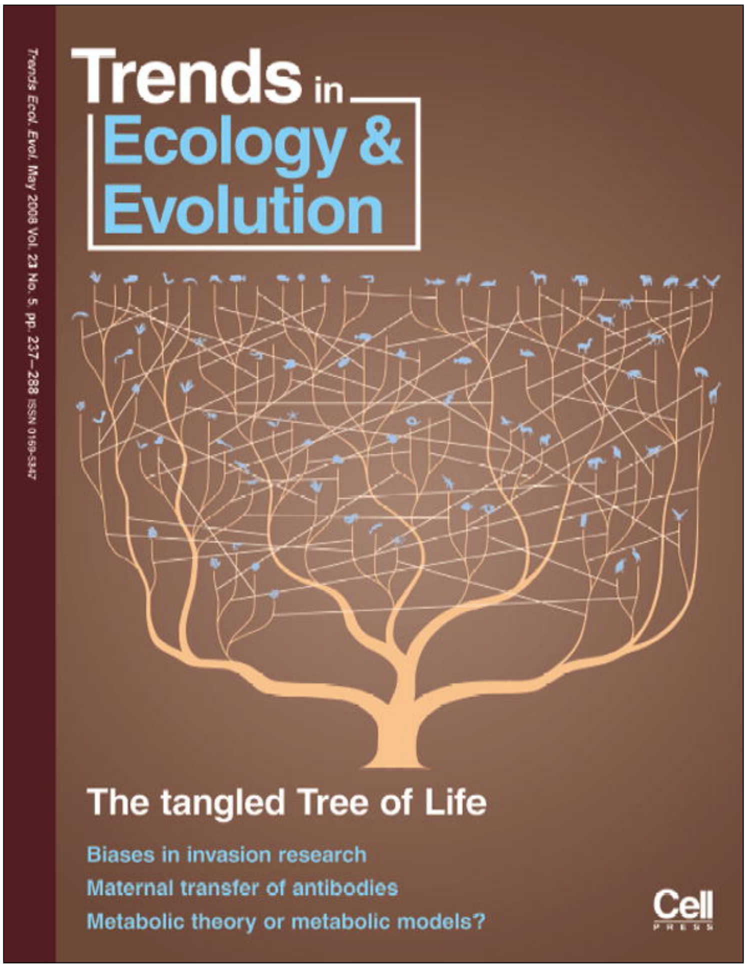
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Geographical and taxonomic biases in invasion ecology

Petr Pyšek[1,2], David M. Richardson[3], Jan Pergl[1], Vojtěch Jarošík[1,2], Zuzana Sixtová[1] and Ewald Weber[4]

[1] Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic
[2] Department of Ecology, Faculty of Science, Charles University, Viničná 2, CZ-128 02 Praha 2, Czech Republic
[3] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[4] Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Invasive alien species come from most taxonomic groups, and invasion biology is searching for robust cross-taxon generalizations and principles. An analysis of 2670 papers dealing with 892 invasive species showed that all major groups of invaders are well studied, but that most information on the mechanisms of invasion has emerged from work on a limited number of the most harmful invaders. A strong geographical bias, with Africa and Asia understudied, inhibits a balanced understanding of invasion, because we might be lacking knowledge of specific invasion mechanisms from poorly studied, regionally specific habitats. International cooperation is required to achieve a more geographically balanced picture of biological invasions. Invasive species with the greatest impact are best studied, but more studies of species that are naturalized but not (yet) invasive are needed to improve understanding of the mechanisms acting during the naturalization phase of invasions and leading to successful invasion.

Need for a synthesis across taxa in invasion biology

Biological invasions are a hot research topic and the impact of species introduced outside their native range by humans is increasing in an era of globalization [1]. Recently, the field has been undergoing an important shift in research priorities. Early research addressed mechanisms and principles of the invasion process for particular taxonomic groups separately [2–4]. Invasion ecology is currently striving for a synthesis by searching for general principles that apply widely across taxonomic groups [5,6]. Nevertheless, a detailed knowledge of the biology and ecology of individual species remains at the core of invasion ecology, and of its practical applications. Case studies of species are thus an important tool in the quest for a better understanding of invasions [7].

This inevitably leads to the questions of which organisms have actually been studied and whether taxonomic and geographical biases undermine our knowledge base. For example, given different amounts of resources available for research in different regions of the world, it might be expected that invasions would be more intensely studied in some regions than would be predicted from the extent to which regions are invaded, and vice versa. Because there are still large taxonomic and geographical gaps in ecological research in general [8], one might ask whether current knowledge in invasion ecology is taxonomically and/or geographically biased. If this is the case, we might need to reassess the allocation of research funding, because although focusing on specific taxonomic groups or regions can provide in-depth knowledge of those species, such a strategy might also constrain our potential for realizing robust generalizations [8].

Which species are studied?

Surprisingly, there has never been a global overview of which invasive species are the subject of detailed case studies. The Web of Science (WoS; http://portal.isiknowledge.com) provides an excellent data source for such an assessment (Figure 1). WoS does not cover gray literature (papers published in regional and local literature and not indexed in international databases), and so the actual number of case studies on invasive species is higher than

Glossary

Alien species (synonyms: exotic, introduced, nonindigenous, nonnative): A species which is not native to a region and which was introduced to that region through human activity.

Casual species: An *alien* species whose continued presence in a region relies on its repeated introduction, for example, by planting and subsequent temporary escapes from cultivation, release into the wild, unintentional introduction of seeds, etc.

Invasion process: A sequence of events and processes during which an introduced species faces, and potentially overcomes, various barriers to its establishment, proliferation and spread in a new region. After overcoming the geographical barrier between native and target region, the species occurs as a *casual* alien. Those species that overcome reproductive barriers are considered *naturalized*. Invasive species are those that overcome barriers to dispersal. The transitions between the three stages (casual, naturalized, invasive) form a continuum; the process has been termed the naturalization–invasion continuum [7].

Invasive species: *Alien* species that reach the final stage of the *invasion process* and have the capacity to spread (a subset of *naturalized* species). To become invasive, a species must overcome dispersal barriers (e.g. lack of spread seeds or restricted distribution of a crucial food plant).

Naturalized species (synonym: established): An *alien* species is considered naturalized if it forms persisting populations and reproduces in the wild without help of humans; it need not be *invasive*. To become naturalized, a species must overcome barriers to reproduction (due to e.g. a lack of pollinators, low population density, absence of individuals of the other sex, climatic and physiological constraints to reproduction, etc.).

See Ref. [10] for detailed definitions.:

Corresponding author: Pyšek, P. (pysek@ibot.cas.cz).

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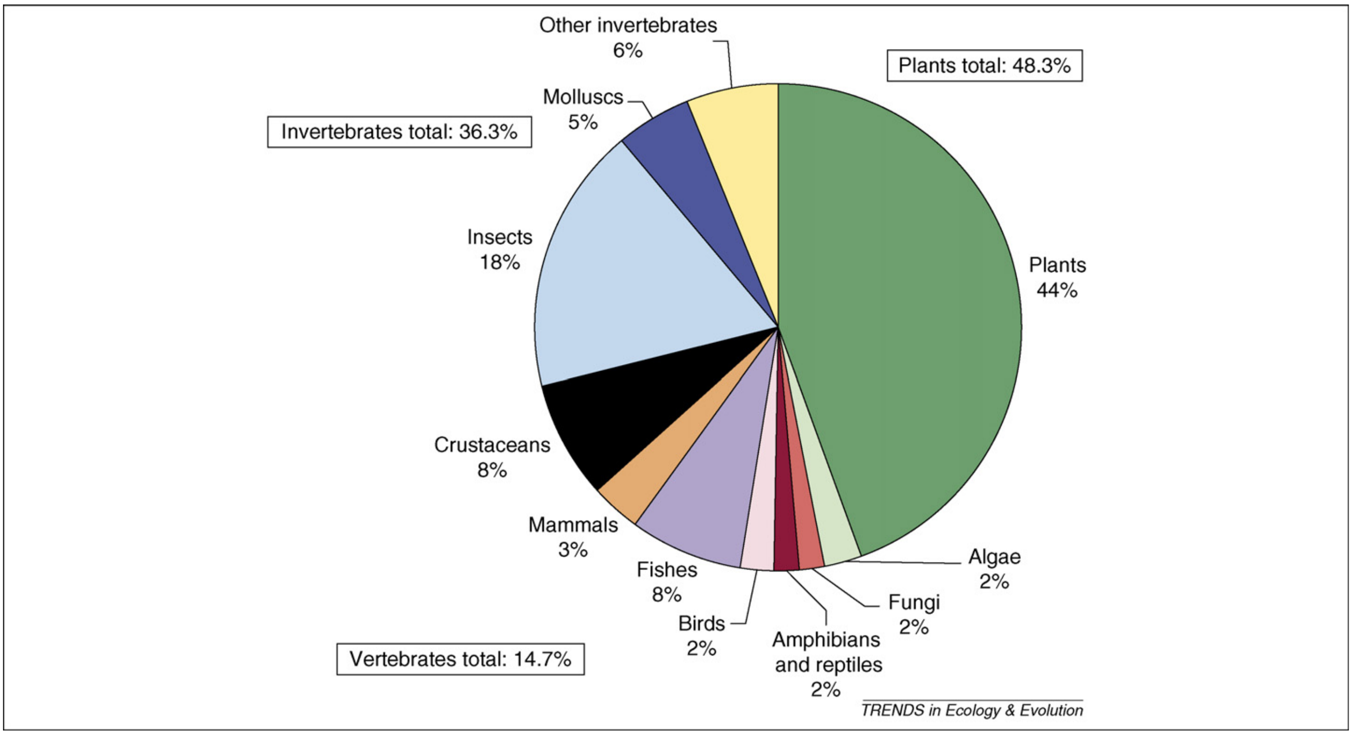

Figure 1. Taxonomic structure of species case studies on biological invasions (892 species from all over the world). Derived from the Web of Science (http://portal.isiknowledge.com, accessed 14 September 2006), searching for the relevant keywords and their derivatives (invasive, exotic, alien, naturalized) in combination with the main taxonomic groups (plant, animal, mammal, bird, insect). The search yielded 4475 papers on various aspects of biological invasions, from which we selected studies focusing on individual species and investigating various aspects of their biology and ecology in detail. This screening yielded 2670 case studies that were classified according to taxonomic group (see online Supplementary Material for details) and geographical region of invasion. Plants and insects together account for two-thirds of the species studied.

reflected in a WoS search. Nonetheless, WoS provides a reasonably representative sample on which to draw conclusions on the structure of studies of invasive biota.

The Web of Science reveals that 892 invasive species were the subject of at least one detailed study between 1980 and 2006, since the first identified paper on the invasion of the honeybee *Apis mellifera* in Hawaii [9]. Plants (395 species) and insects (157) are most represented, together accounting for almost two-thirds of the taxa studied (Figure 1); the only other groups where more than 50 species have been studied are crustaceans and fishes (Table 1).

Only 49 species were the subject of 10 studies or more (see online Supplementary Material for details). The zebra mussel (*Dreissena polymorpha*, mollusc, 64 studies) and the Argentine ant (*Linepithema humile*, insect, 61 studies) are the most intensively researched invasive species. Spotted knapweed (*Centaurea maculosa*, plant), caulerpa (*Caulerpa taxifolia*, alga), red swamp crawfish (*Procambarus clarkii*, crustacean), round goby (*Neogobius melanostomus*, fish), wild boar (*Sus scrofa*, mammal) and cane toad (*Bufo marinus*, amphibian) are the most studied subjects in their respective taxonomic groups (see online Supplementary Material for details). Other evidence that only a minority of species are studied in detail comes from the frequency distribution of the number of studies per species. Only 14 species (1.6% of the total) were subjected to more than 20 studies and 774 (86.8%) to fewer than 6 studies; this type of distribution of research interest is consistent across broad taxonomic groups.

Taxonomic bias: no need to worry?

We suggest that the taxonomic patterns briefly outlined above depict research priorities over the last three decades rather accurately. It does not, however, tell us anything about potential taxonomic biases. Does the taxonomic distribution of research accurately reflect the proportion of invaders in each taxon? Reference data sets providing unbiased estimates of how many invaders there are from individual taxonomic groups are difficult to obtain, because most available databases introduce the danger of circular reasoning (see Box 1). Data from the DAISIE project can be used as such a reference for Europe (Box 1). That DAISIE collates data for a single continent is unlikely to limit the representativeness of results, because Europe is the second most intensively studied region (Table 1).

Figure 2 relates the numbers of alien species in particular taxonomic groups studied in Europe (n = 605) to the total numbers naturalized on the continent, as recorded by DAISIE (n = 3801). The deviation from the slope line indicates that some taxonomic groups (plants, bryophytes, birds, amphibians, reptiles) are less intensively studied than would be expected from the numbers of their alien representatives in Europe, whereas others (crustaceans, molluscs, algae, mammals) are more intensively studied. The position of particular taxa below or above the line of unity depends on the interaction between the numbers of naturalized species and research effort.

Only some naturalized species become the subject of a case study; as we will see, it is the impact of the species that largely determines whether or not it is studied. Further,

Box 1. Reference data set for comparison across taxa: the DAISIE project

Surprisingly, despite a growing number of databases of alien plants and animals [1], reliable and balanced data for unbiased comparison of research effort with levels of invasion are difficult to obtain. To avoid circular reasoning, standard databases (e.g. IUCN; http://www.issg.org/database; see Ref. [1] for an overview) cannot be used for the purpose of such a comparison. Major global databases are selective, because they are not aimed at providing a complete overview of global invaders but rather on documenting those with a serious impact. Moreover, inclusion of species in these databases is largely based on published information, most of which comes from case studies, and thus the databases reflect what has been recorded in the literature rather than the real state of affairs 'out there.' Further, in most databases and checklists, the number of alien species is affected by the sampling effort [42].

The European Alien Species Database, produced by the DAISIE project (http://www.europe-aliens.org), is different and suited to the comparison of research intensity with the extent of invasion. The project aims to provide an inventory of all alien species in all taxonomic groups in all European countries where such information is available, with a primary focus on naturalized plant and animal taxa introduced into Europe after 1500 A.D. Data sources included regional floras, faunas, checklists of alien organisms and unpublished information from numerous collaborators. The project covers documented introduction records of the alien taxa for 71 terrestrial and 9 marine regions of Europe (see Ref. [43] for details on data collation and database structure). There is no danger of circular reasoning because, rather than relying on published case studies of invasions, the project is based on floral and faunal works, and also aims for completeness in terms of taxonomic and geographical coverage. Species numbers yielded by DAISIE are therefore independent of our data. The European Alien Species Database is publicly available on the project portal from 2008 onward (http://www.europe-aliens.org).

The numbers of naturalized plant species in world regions were taken from a Database of Alien Plants of the World based on the global catalogue of invasive plant species published by Ref. [14]. This book includes information on naturalized and invasive plant species, with distribution classified in 32 geographical regions. The database, which served as a basis for the publication in 2003, is continuously updated by the author using the same methods and standards as described in the book [14]. This source, although based on published information, can be used with reasonable confidence as a reference data set, because of its focus on providing as complete a scientific checklist as possible, unlike the standard databases mentioned above which focus on providing practical information for managers and nature conservationists. Further, it uses a large body of gray literature, which makes it essentially independent of our data set derived from the Web of Science.

only some naturalized species become pests, by causing economic impact [10], and particular taxonomic groups differ in proportions of species that become pests. This is why plants seem to be disproportionally understudied; they are most numerous, but a relatively small proportion of naturalized plant species become pests. The situation is different in some other groups, such as mammals, where most naturalized species have clear impacts on invaded ecosystems [11–13].

Bias in selecting species for study: impact is what matters

For insights on which species researchers select as subjects of case studies, we compared our results with data on naturalized and invasive species in the reference Database of Alien Plants of the World based on Ref. [14] (Box 1). There is no global data set that allows a comparison across all taxonomic groups, but the use of plants is justified for this purpose because they represent the most intensively studied group (Table 1).

A regression of the number of case studies performed on those species that were included in our Database of Alien Plants of the World ($n = 232$; see Box 1) on the number of regions where the species is naturalized globally yields a relationship on the border of significance ($F = 3.97$, df 1, 230; $P = 0.047$). The same regression on the number of regions where the species is invasive is highly significant ($F = 6.75$, df 1, 230; $P < 0.01$). This indicates that the more invasive a species is, the more likely it is to become the subject of a scientific study. However, the difference in the significance levels between the two measures used as the explanatory variable (number of regions where naturalized versus where invasive) indicates that naturalized aliens attract much less research attention than invasive aliens (*sensu* Ref. [10]). As the extent of invasiveness is closely associated with the magnitude of impact [15,16], it can thus be assumed that impact is the major aspect enhancing the probability that a species becomes a subject of a case study. Apparently, to be naturalized is not enough; the species needs to be invasive to rank high on research agendas. This is unfortunate, because naturalization is a crucial stage in the invasion process [2,17,18] and, hence, a full understanding of biological invasions demands comprehension of the mechanisms leading to naturalization. Case studies focused on naturalized invaders have proved useful because of their potential to elucidate the determinants of invasion success or failure [19,20], that is, something that a detailed study of an ongoing massive invasion cannot address.

Where are invasive species studied?

America (North, Central and South) and Europe have much higher numbers of both species studied (491 and 247, respectively) and studies published than other regions (Table 1). A more detailed classification of regions (Figure 3) indicates that almost half of all invasive species and more than half of the studies conducted relate to North America.

Evidence for geographical bias: it matters where they invade

To what extent do the geographical patterns of study reflect the real importance of invasive alien taxa globally? For insights on whether the research in invasive species is geographically balanced, we again compared our results to the Database of Alien Plants of the World [14] (Box 1).

Figure 4 relates, for geographical regions at the level of continents, the numbers of plant species studied in a region, as identified by our search of the Web of Science, relative to the numbers of plant species that are naturalized in a region. Naturalized species are those that form persisting populations and reproduce in the wild without the help of humans [10]. The position of America (394 species in the Database of Alien Plants of the World) and Europe (161 species) reflects very high research efforts (Table 1), whereas oceanic islands and Australia have very high numbers of naturalized alien species (358 and 502, respectively), which makes the research effort dispropor-

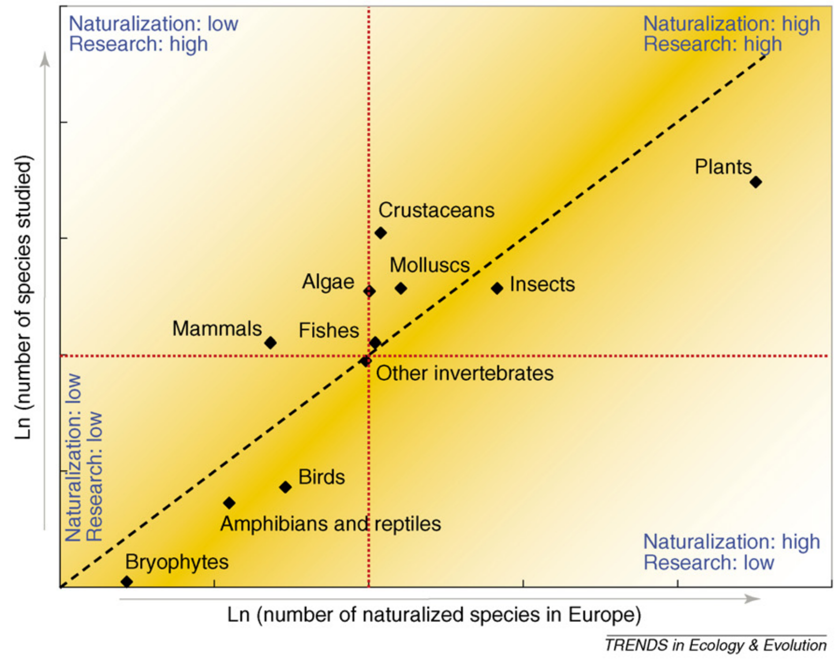

Figure 2. Taxonomic bias in invasion ecology. Numbers of alien species in particular taxonomic groups studied in Europe (n = 605) related to the total numbers naturalized on the continent (n = 3801). The numbers of naturalized species in Europe were taken from the DAISIE database (Box 1). Values are standardized. The line of unity is indicated; red lines indicate average numbers of studied and naturalized species, and separate the plot into quadrants according to levels of research and naturalization. Taxonomic groups below the line are less intensively researched, in terms of species addressed in case studies, than would correspond to their proportional contribution to the total number of naturalized species in Europe, and vice versa.

Table 1. Numbers of invasive species in taxonomic groups studied in different regions of the world

Taxonomic group	Europe	America[a]	Africa	Asia	Australasia	Islands[b]	Total
Vascular plants	80/206[c]	220/795	33/61	28/49	66/104	32/61	395/1274
Bryophytes	2/2	–	–	–	–	–	2/2
Plants: algae	14/58	12/21	–	–	4/7	1/1	22/88
Fungi	1/1	9/12	2/2	–	–	–	14/17
Mammals	12/32	18/46	1/1	–	7/10	8/15	30/102
Birds	5/6	7/13	–	3/3	1/1	3/3	18/25
Reptiles	2/2	2/3	–	1/1	1/1	2/9	6/16
Amphibians	2/3	6/16	–	1/1	1/1	1/1	9/32
Fishes	24/32	33/77	7/6	7/15	13/21	2/2	68/155
Chordata: tunicata	2/2	2/2	–	–	–	–	4/4
Insects	26/60	101/289	9/11	15/24	22/33	13/33	157/454
Crustaceans	37/114	33/103	1/1	2/5	3/5	5/5	69/229
Molluscs	20/60	26/123	3/7	2/4	6/8	1/1	43/201
Annelida	8/10	9/12	–	3/3	1/3	–	21/28
Arthropoda	2/2	4/4	1/1	–	1/1	–	7/8
Bryozoa	2/2	1/1	–	–	2/3	–	5/6
Cnidaria	2/3	4/5	1/1	–	–	1/2	8/11
Echinodermata	–	–	–	–	1/1	–	1/1
Nematoda	2/5	–	–	–	–	–	2/5
Platyhelminthes	3/4	3/3	–	–	–	1/1	7/8
Porifera	1/1	–	–	–	–	2/2	3/3
Rotifera	–	1/1	–	–	–	–	1/1
Plants[d]	97/267	241/828	35/63	28/49	70/111	33/62	433/1381
Vertebrates[e]	47/77	68/157	8/7	12/20	23/44	16/60	135/334
Invertebrates	103/261	182/541	15/21	22/36	36/54	23/44	324/955
Regions totals	247/605	491/1526	58/91	62/105	129/209	72/136	892/2670
Studies per species	2.4	3.1	1.6	1.7	1.6	1.9	3.0

[a]America includes both North and South America.
[b]The numbers in each cell refer to the number of species/number of studies. Note that the totals do not match the sums for regions row-wise, as some species invade in more than one region.
[c]All oceanic islands are treated together regardless of geographical position.
[d]Including fungi.
[e]Including Chordata.

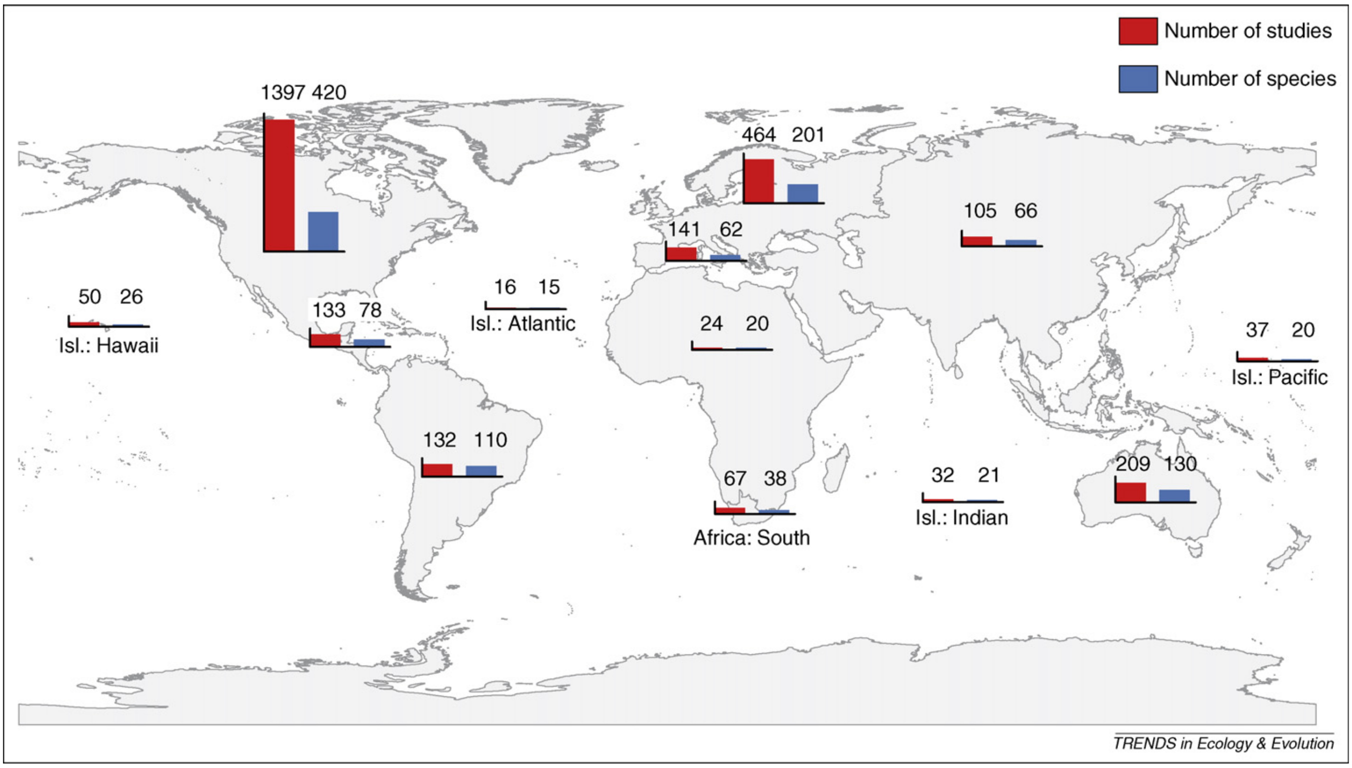

Figure 3. Geographical structure of the invasive biota studied. Sizes of bars indicate proportional contribution of world regions to the total number of invasive species studied (n = 892) and to the total number of studies (n = 2670). The numbers of species/studies are at the tops of the bars. The classification of regions follows Weber [14]. The concentration of research effort in North America and Europe is obvious.

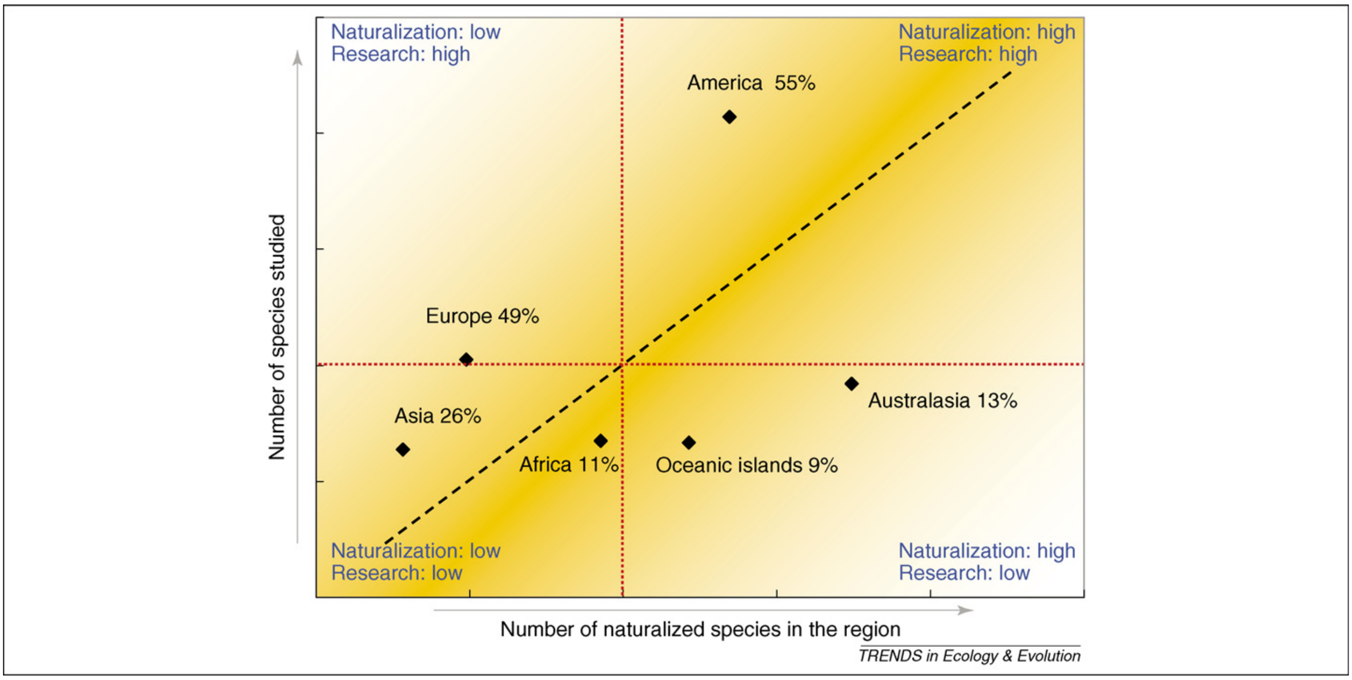

Figure 4. Geographical bias in invasion ecology. The number of plant species studied in regions of the world (n = 395) is related to the total numbers of naturalized species (n = 850). The numbers of naturalized species in regions were taken from a database based on Ref. [14]; see Box 1. Values are standardized. Regions below the line of unity (Australasia, oceanic islands) are less intensively researched, in terms of species addressed in case studies, than would be expected from their proportional contribution to the global pool of naturalized plant species; those above the line (America and Europe) are studied more intensively than expected. Research effort in Africa and Asia is low, but so is the number of naturalized species from these regions. The percentage of studied species among those naturalized is indicated next to the name of the region. Red lines indicate average numbers and separate the plot into quadrants according to levels of research and naturalization; the position in the quadrants indicates whether the deviation from proportional research intensity is a result of high or low research efforts or high or low species numbers.

tionately low (although for Australia it is comparable to Europe). Asia and Africa are the only two continents in the 'low and low' quadrant (Figure 4). The position of Africa (280 naturalized species) is largely determined by South Africa, which alone accounts for two-thirds of research effort on this continent (Figure 3). For Asia it is likely that the continent is under-recorded in terms of the number of naturalized species (105). Thus, the low-studied/naturalized species ratios (Figure 4) are attributable to either extremely high numbers of naturalized species (Australasia, islands) or to poor research intensity (Asia, Africa except South Africa). As far as we know, this is the first quantitative evidence of the serious bias to a geographically balanced knowledge of biological invasions.

Reducing biases in invasion ecology – how important is it?

We have demonstrated geographical and taxonomic biases in the study of biological invasions. What does this say about the foundations of this field of study? Overall, the taxonomic bias in studies on invasive species (Figure 2) is less pronounced than the geographical bias – this is the good news. Major groups of invaders are thoroughly researched and the information accumulated has allowed researchers to formulate general principles that appear valid across taxonomic groups, such as the enemy release hypothesis [21], the biotic resistance hypothesis [22], evolution of invasiveness [23] or the tens rule describing the proportion of alien species reaching the next stage of the invasion process [24]. Other theories remain within the domains of particular taxonomic groups, mostly plants, because of reasons linked with methodology (e.g. evolution of increased competitive ability [25]; fluctuating resources theory of invasibility [26]). It needs to be noted that case studies of particular species or groups of taxa are not the only tool for building theory in invasion ecology. Only a part of invasion ecology, namely the aspects linked to invasiveness (such as genetic and evolutionary aspects, population dynamics, life-history strategies and species traits), rely on detailed knowledge of individual taxa. Nonetheless, detailed studies of species are the core of invasion research – it is individual species and their populations that invade, not floras or faunas. The importance of case studies is emphasized by the fact that 59.7% of the 4475 studies on biological invasions we found address individual invasive species in one way or another. So, attention to reducing the biases identified here is justified.

How could we gain further clarity on the dimensions and magnitude of the taxonomic bias in invasion ecology? This is a nontrivial question. What should form the baseline to which to compare the pattern of research intensity? There are a variety of invasion mechanisms that differ among taxonomic groups and, therefore, if members of a group use the same mechanism, there might be no need to study additional species once the mechanism is identified and understood. This implies that once thorough information on a certain number of species from a taxonomic group has been accumulated, studies of additional species might not add substantial information to the theory. As in the species–area relationship, where simply adding more area beyond a certain level adds few additional species, one can imagine a 'species–information' relationship, where studying more species, beyond some threshold, does not warrant the research effort. Obviously, effective management of any invasive species demands taxon-specific details, suggesting that many more detailed case studies are needed. We suggest that such additional knowledge is, however, unlikely to contribute greatly to robust generalizations and theories.

We suggest that the marked geographical bias (Figure 4) has more significant implications for developments in invasion ecology. This bias can be largely explained by the differing amounts of financial resources available for study in different regions of the world, translated into research intensity [27,28]. For example, if the zebra mussel were a severe problem only in West Africa, far fewer studies would most likely have been published on it. As shown by Wilson *et al.* [8], research agendas are more directly influenced by economic priorities and practical limitations than by geographical and sociopolitical barriers. The economic status of a region affects the research effort not only directly, by more resources being spent on problems of biological invasions in rich states than in poor ones, but also historically, as wealthier states have better-developed systems of science and education. On the other hand, there is a positive feedback between the degree of wealth and invasions, because developed regions with a high gross domestic product and large trade volumes are also those that receive the most alien species as an inescapable byproduct of trade in commodities, and therefore should have the most invasive species [29,30]. Unlike the taxonomic bias, the geographical bias is serious and is probably hampering advances in the overall understanding of biological invasions [31]. The process of invasion depends, to a large extent, on habitat properties [32–35]. Consequently, the lack of information from certain parts of the world with regionally specific habitats exposed to invasions could limit our current knowledge. Unfortunately, this holds for tropical Africa and Asia in particular, which are seriously understudied compared to other parts of the world.

One of the best examples of a paradigm-shifting case study of a single species is that of the fire tree *Myrica faya*, which forms nitrogen-fixing nodules on its roots and invades young, nitrogen-limited volcanic substrates on the Hawaiian Islands. This nitrogen-fixing species has an advantage in primary succession because there are no nitrogen-fixers among native early successional woody species on the islands. The fire tree produces an excess of nitrogen, making the limiting resource available to other plants, many of them alien. Thus, the presence of fire trees adds a novel element to succession, changing its trajectory so as to facilitate invasion by other species [36]. This invasion is specific to the Hawaiian Islands [14], so had this region not been studied in detail, we would have missed a story that contributed substantially to new theory. Perhaps similarly exciting and influential stories are waiting to be discovered in the poorly studied ecosystems of Africa or Asia. Pine (*Pinus)* invasions are another example, providing clear evidence on how sampling a wide range of geographical regions can help to build robust generalizations. Intercontinental contrasts of pine invasions in different parts of both hemispheres have offered insights into the determinants of invasions that could not have emerged from studies at one or a few sites [37]. This example points to another issue linked with a need for sampling in a wide range of regions. Invasions are mediated by the interplay of numerous factors, and such interactions are often too complex to be resolved through formal experiments. Each locality where an invasion is studied under new circumstances is, in effect, a natural experiment; together, such comparisons have huge potential to generate new insights in invasion ecology [38].

The strong bias in choosing which species to study, with impact forming the major selection factor, is understandable with relation to funding availability. A project aimed at an ongoing invasion incurring economic costs is likely to obtain funding more easily than one addressing purely scientific issues. Most researchers therefore work on invasive species with an imminent or realized importance (i.e. impact). Evidence for this comes from global plant data, but there is no reason to expect that the pattern would differ for animals; a brief inspection of the online Supplementary Material shows that the most researched animal taxa are all invaders with a serious impact. Moreover, our data show that only a minority of species are studied intensively (see online Supplementary Material for details). Some of those studies are 'me-too' papers (routine repeats of research already done in another region), which contribute little to fundamental knowledge of the species studied, although they are useful or even essential for managing the species under specific circumstances or in a certain locality. However, a thoroughly studied model species provides information that is practically applicable to a larger group of taxa with similar biologies, invasion pathways and traits that facilitate successful invasion. The question thus arises whether resources spent on repeated studies of the same well-known taxa could be used more efficiently, if the aim is to achieve a robust theory of biological invasions. A more balanced selection of species for study, whereby not only the most successful invaders are included, might also improve our understanding of why some species are never successful, even when introduced repeatedly into a region. Studying failure is just as important as studying success, and invasion ecology generally lacks good information on why some species fail.

That a species is naturalized and not considered invasive in a region is usually a much weaker stimulus than impact for researchers to conduct a study. This is unfortunate because naturalization, that is, the capability to form self-reproducing populations in the wild without the intervention of humans [10], is a critical stage of invasion. Studies on naturalized species can provide valuable information on which external factors and species traits are responsible for the transition of a species from a casual to a naturalized species. Such studies can also shed light on what makes a species invasive and under which circumstances, that is, how a species goes from the naturalized to the invasive stage [39]. More research is thus needed on the naturalization stage of invasion. This brings us back to the close link between globalization and invasion [1]. Highly developed nations contain a disproportionately large proportion of the invasive species of the world, and so as globalization continues and other nations develop further, the stage will be set for more invaders. Addressing naturalized species in developing countries could potentially reduce impacts and costs, but could also prevent introductions elsewhere through trade.

The geographical bias shown in our analysis mirrors differences in human wealth among the regions of the world. What might the implications and recommendations be for policy on invasive species? We suggest that attention should be given to facilitating more research in understudied regions. Perhaps more than any other field of ecology, invasion biology is affected by the fact that plants and animals ignore political boundaries and must be studied across borders. Fortunately, several recent international projects with focus on large regions, such as DAISIE in Europe (Box 1) or BONAP in the United States [40], attest to progress in this area. Such projects help to reduce geographical biases within particular continents. Another example is the ALARM project [41] (http://www.alarmproject.net), which is based on cooperation of invasion biologists from different continents, studying different taxonomic groups and working in different environments. By involving partners from Europe, South Africa and South America, this project systematically addresses determinants and mechanisms of invasions by plants and animals in different stages of the invasion process, over a wide geographical range and various scales. We suggest that, as a further step, resources should be used to support intercontinental cooperation with properly designed research strategies, addressing issues of invasions where current biases can limit our understanding of biological invasions.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2008.02.002.

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