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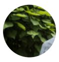

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ORIGINAL PAPER

# Invasive trees and shrubs: where do they come from and what we should expect in the future?

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**Abstract** The global database of invasive trees and shrubs has been updated, resulting in a total of 751 species (434 trees and 317 shrubs) from 90 families (Rejmánek and Richardson 2013 Divers Distrib 19:1093–1094). This database is used to assess major trends in human-assisted exchanges of dendrofloras among 15 major geographical regions. Areas most invaded by non-native trees are Pacific Islands (136 species), Southern Africa (118), Australia (116), and North America (114). Areas most invaded by non-native shrubs are North America (98), Australia (87), Pacific Islands (71), and Europe (61). The most important sources of invasive trees are Asia (122–146 species, depending on how many Eurasian species are considered to have been introduced only from Europe), Australia (81), and South America (81). The most important sources of invasive shrubs are Asia (103–118), Europe (68), and South America (54). Mean number of native geographical regions for invasive trees is 1.64, while the mean number of invaded regions by trees is 2.51. The difference is smaller for shrubs: 1.60 versus 2.11. Asia is the major source of invasive Rosaceae shrubs, as well as invasive Arecaceae and Oleaceae species. South America and Australia are major sources of invasive Fabaceae trees. North America and Europe are major sources of invasive Pinaceae. Most of the invasive Salicaceae are of Eurasian origin. The identified trends will very likely continue in this century. Because of increasing interactions with many states in Asia, even more invasive woody species will be introduced from this part of the world.

**Keywords** Biological invasions · Exchange of dendrofloras · Global database · Homogenization · Invasion debt · Regions of origin · Shrub invasion · Tree invasions

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## Introduction

All seed-producing (and even some sterile) trees and shrubs have ability to spread. For example, the colonization of deglaciated areas and new volcanic substrata have been documented in many studies (Bialozyt et al. 2012; Huntley and Birks 1983; MacDonald 1993; Petit et al. 2004; Rejmánek et al. 1982). Rates of natural migration of European trees were found to depend on competition, habitat connectivity, climate, seed dispersal patterns, and species' traits (Meier et al. 2012). Currently, however, the rate of human-assisted migrations (i.e., invasions sensu Pyšek et al. 2004) of woody species is several orders of magnitude faster. People have been moving plant species around for centuries, but currently, due to intensification of international trade, the human-assisted plant migrations are accelerating (Rejmánek et al. 2013). Woody species with excessive water use, those associated with nitrogen-fixing bacteria, and all invasive woody species taller than native vegetation are of particular interest because, in many situations, adding an extra biogeochemical function or a new vegetation layer may cause drastic changes of whole ecosystems (Dzikiti et al. 2013; Ens and French 2008; Fang and Wang 2011; Jäger et al. 2009; Saure et al. 2013; Tye and Drake 2012; Vitousek 2004). Hybridization of exotic trees and shrubs with native congeners is another serious concern (Barbour et al. 2010; Meirmans et al. 2010; Mercure and Bruneau 2008; Randall et al. 2004). Therefore, an assessment of major patterns in human-assisted exchanges of dendrofloras among geographical regions is long time overdue.

Recently, the global database of invasive trees and shrubs (Richardson and Rejmánek 2011) has been updated, resulting in a total of 751 species (434 trees and 317 shrubs) from 90 families (Rejmánek and Richardson 2013). Here I use this database to answer the following questions:

1. Which geographical regions are invaded by largest numbers of tree or shrub species?
2. Which geographical regions are most often donors of invasive trees or shrubs?
3. Is the mean number of invaded regions already larger than the mean number of native regions for invasive tree or shrub species?
4. Are numbers of invaded (acceptor) regions positively correlated with numbers of native (donor) regions?
5. How much do tree or shrub invasions contribute to the homogenization of the world dendrofloras?
6. How similar are major geographical regions to each other in terms of woody species composition before and after human-assisted migration of trees and shrubs?
7. Are families with many invasive species originating in particular regions?
8. Are there any families invading primarily in particular regions?

Additionally, I discuss what trends we should expect in the future.

## Methods

Methods used to create the world database of invasive trees and shrubs were described by Richardson and Rejmánek (2011). *Species that are included should be not only naturalized (consistently reproducing), but invasive (spreading) in one or more of the 15 recognized geographical regions:* Africa (north of 20°S), Atlantic islands, Asia, Australia, Central America, Caribbean islands, Europe, Indonesia, Indian Ocean islands, Middle East (from Turkey to Iran and Yemen, includes also Cyprus), North America, New Zealand, Pacific Islands, Southern Africa, and South America. Admittedly, the regions recognized in the current database and used in the following analyses are very heterogeneous in terms of their areas and climatic diversity. Obviously, it would be desirable to divide at least Asia, Africa and South America into smaller units. However, in that case we would get highly uneven datasets because still very incomplete reports from Siberia, China, tropical Africa, and tropical South America. Because invasive species are defined as *spreading non-native species* (Pyšek et al. 2004), cases of encroachment by native woody species (e.g., Eldridge et al. 2012; Laborde and Thompson 2013; Leithead et al. 2010; Rejmánek and Rosén 1992; Van Auken and Bush 2013) are not included in the database.

While updating the original database to its present form used in the following analyzes (Rejmánek and Richardson 2013, Supplement S1), the major goal, besides inclusion of all new records, was the delineation of native ranges of all included species. Since accurate distribution maps (e.g., Critchfield and Little 1966; Little 1971) are not available for most species, major floras (e.g., *Flora of Australia, Flora of China, Flora Europaea, Flora of North America, Flora of Tropical East Africa, Flora Malesiana, Flora Neotropica*), recent checklists (e.g., Acevedo-Rodriguez and Strong 2012; Funk et al. 2007; Klopper et al 2006; Zuloaga et al. 2008), and specific monographs (e.g., Adams 2011; Large and Braggins 2004; Prance and Sothers 2003) were consulted for this purpose. There are an increasing number of detailed studies on the human-assisted spread of introduced woody species from their native areas that are based on molecular or, at least, morphometrical data (Gunn et al. 2011; Petersen et al. 2012; Skou et al. 2012; Terral et al. 2012). Unfortunately, however, such studies are available only for a minor proportion of species included in this analysis. Assessing source (donor) geographical regions was simple when the species was native in only one of 15 recognized regions. However, when species were native in two or more geographical areas, some arbitrary decisions had to be made. For example, if a species introduced to North America is native in Asia and Europe, it is more likely that such species was introduced just from Europe. Similarly, if a species introduced to Europe is native in North America and on some Pacific islands, it is more likely that such species was introduced from North America. On the other hand, if there were no a priori reasons for a more likely introduction from one of the potential sources (for example, species introduced to Europe and native in Australia and Asia), numbers of such species were divided equally among their possible sources. Because quite a few invasive woody species are native not only in South America, but also in Central America and Caribbean, these three regions were treated as only one (the Neotropics) in some analyses.

Numerical classification of donor and donor + acceptor geographical regions was conducted using the agglomerative average linkage option in the program HIERCLUS (SynTax 5.1; Podani 2000). Mean similarity (homogeneity) of geographical areas was analyzed using the program DISIMILARITY 2.0 (Microsoft BASIC program written by M. Rejmánek). Similarity of any two regions was expressed either as the Jaccard index of similarity ($J = a/(a + b + c)$ where $a$ is the total number of species occurring in both regions, $b$ is the number of species occurring in the first region but not in the second and $c$ is the number of species occurring only in the second region but not in the first), or as its complement ($1 - J$, therefore dissimilarity). Obviously, the Jaccard index of similarity is equal to zero when no species are shared between two areas and is equal to one when none of the two areas has any extra species. Separate analyses were performed representing with and without human-assisted exchange of dendroflora using data of both native and invaded regions and data of native regions only, respectively. All other numerical analyses were performed in StatView 5.0.1.

## Results

### Which geographical regions are invaded by largest numbers of tree or shrub species?

Areas most invaded by non-native trees are Pacific Islands (136 species), Southern Africa (118), Australia (116), and North America (114) (Table 1). Numbers of introduced invasive trees are highly positively correlated with numbers of donor regions ($r = 0.84$, $p < 0.0001$). Areas most invaded by non-native shrubs are North America (98), Australia (87), Pacific Islands (71), and Europe (61) (Table 1). Again, numbers of introduced invasive shrubs are highly positively correlated with numbers of donor regions ($r = 0.75$, $p = 0.001$). There are disproportionally more shrubs introduced to North America and New Zealand and disproportionally fewer shrubs introduced to South and Central America. Numbers of introduced invasive trees and shrubs in 15 geographical regions are highly positively correlated ($r = 0.78$, $p = 0.0006$).

**Table 1** Total numbers of invasive tree and shrub species in acceptor regions and numbers of donor regions for individual acceptor regions

| Acceptor regions | Trees | Donor regions | Shrubs | Donor regions |
|---|---|---|---|---|
| North America | 114 | 10 | 98 | 9 |
| Europe | 76 | 8 | 61 | 4 |
| Middle East | 39 | 7 | 8 | 5 |
| Asia | 52 | 8 | 36 | 7 |
| Indonesia | 20 | 4 | 21 | 3 |
| Pacific Islands | 136 | 12 | 71 | 9 |
| New Zealand | 55 | 6 | 59 | 9 |
| Australia | 116 | 9 | 87 | 10 |
| Indian Ocean Islands | 90 | 10 | 37 | 6 |
| Africa (southern) | 118 | 13 | 60 | 8 |
| Africa (rest) | 53 | 6 | 34 | 5 |
| Atlantic Ocean Islands | 33 | 8 | 27 | 7 |
| South America | 86 | 7 | 25 | 5 |
| Caribbean Islands | 64 | 6 | 27 | 7 |
| Central America | 43 | 6 | 7 | 4 |

### Which geographical regions are the most important as donors of invasive trees or shrubs?

The most important sources of invasive trees are Asia (122–146 species, depending how many Eurasian species were introduced only from Europe), Australia (81), and South America (81) (Tables 2, 3). The most important sources of invasive shrubs are Asia (103–118), Europe (68), and South America (54) (Tables 2, 4). Australia provided disproportionally more trees, while Europe provided disproportionally

**Table 2** Total numbers of invasive tree and shrub species native in donor geographical regions

| Region | Trees | Shrubs | Trees and shrubs |
|---|---|---|---|
| North America | 55 | 36 | 91 |
| Europe | 56 | **68** | 124 |
| Middle East | 37 | 18 | 55 |
| Asia | **146** | **118** | **264** |
| Indonesia | 23 | 4 | 27 |
| Pacific Islands | 52 | 41 | 93 |
| New Zealand | 3 | 3 | 6 |
| Australia | **81** | 28 | 109 |
| Indian Ocean Islands | 20 | 14 | 34 |
| Africa (southern) | 9 | 16 | 25 |
| Africa (rest) | 46 | 34 | 80 |
| Atlantic Ocean Islands | 6 | 7 | 13 |
| South America | **81** | 54 | **135** |
| Caribbean Islands | 30 | 22 | 52 |
| Central America | 71 | 41 | 112 |

The first two highest numbers in each column are in bold

larger number of shrubs (Tables 2, 4). Numbers of invasive trees and shrubs provided by donor geographical regions are highly positively correlated (r = 0.90, $p < 0.0001$).

Is the mean number of invaded regions already larger than the mean number of native regions for invasive tree or shrub species?

Mean number of native geographical regions for invasive trees is 1.64, while the mean number of invaded regions by trees is 2.51 (Fig. 1). The difference is smaller for shrubs (1.60 vs. 2.11) (Fig. 2). In both cases, there are significant differences between frequencies of species numbers, with respect to numbers of regions occupied, between native (donor) and invaded (acceptor) regions: $X^2 = 60.9$ (DF = 10, $p < 0.0001$) and $X^2 = 23.9$ (DF = 10, $p < 0.008$), respectively. In other words, there are significantly more species of trees and shrubs occupying larger number of invaded regions compared with numbers of regions that they occupy as native species (Figs. 1, 2). Still, it is important to realize that 200 (46.1 %) of tree species are, so far, in only one invaded region and 174 (54.9 %) of shrub species are currently in only one invaded region. Only 39 (8.9 %) of trees are in six or more invaded regions and 18 (5.8 %) of shrubs are in six or more invaded regions.

Are numbers of invaded (acceptor) regions positively correlated with numbers of native (donor) regions?

There is slightly positive but not significant relationship between the number of invaded and native regions for trees ($p = 0.31$; Fig. 3) and significant positive correlation for the same variables for shrubs ($p = 0.0003$; however $R^2$ is very low, 0.041; Fig. 4). Therefore, given the data we currently have, it does not look that the number of native regions could serve as a predictor of invasiveness. It should be stressed that the distribution of data points presented in Figs. 3 and 4 may suggest rather negative relationships, but we have to realize that the majority of the data is concentrated as multiple overlaps in the left hand lower corners of both figures.

How much do tree or shrub invasions contribute to the homogenization of the world floras?

Because about half of the invasive tree and shrub species are known from only one out of 15 invaded regions (46.1 and 54.9 %, respectively), their contribution to the homogenization of the world floras is, so far, relatively low. Still, considering just the woody species included in the present analysis, mean similarity (based on the Jaccard coefficient) of tree floras of 15 recognized geographical areas increased from 0.041 (no human-assisted exchange) to 0.165 (including human-assisted exchange) and mean similarity of shrub floras increased from 0.040 to 0.152. How representative these numbers are for total floras, one may only guess because proper data will be not available for some time.

How similar are major geographical regions to each other in terms of woody species composition before and after human-assisted migration of trees and shrubs?

To get a flavour of what may be the answer to this question, I compared the 15 distinguished geographical regions using agglomerative cluster analysis and 751 invasive woody species included in this study. Before the reported exchanges of dendrofloras, two somewhat distinct clusters of the regions were formed, similar for both trees and shrubs (Fig. 5a, b): 1—

**Table 3** Numbers of invasive tree species provided to acceptor regions by individual donor regions

| Acceptors | North America (Donors) | Europe | Middle East | Asia | Indonesia | Pacific Islands | New Zealand | Australia | Indian Ocean islands | Africa (southern) | Africa (rest) | Atlantic islands | South America | Caribbean islands | Central America |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| North Amer. | 13 | ***28*** | 1 | ***32*** | 0 | 6 | 1 | 16 | 0 | 1 | 0 | 1 | | 17 | |
| Europe | ***23*** | ***25*** | 1 | 9 | 0 | 2 | 0 | 12 | 0 | 0 | 1 | 0 | | 3 | |
| Middle East | 4 | 5 | 1 | ***9*** | 0 | 0 | 0 | ***10*** | 0 | 0 | 2 | 0 | | 8 | |
| Asia | 2 | 1 | 0 | ***17*** | 2 | 2 | 0 | 5 | 0 | 0 | 6 | 0 | | ***17*** | |
| Indonesia | 0 | 0 | 0 | ***4*** | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | | ***12*** | |
| Pacific Isl. | 11 | 3 | 1 | ***28*** | 2 | 13 | 1 | 19 | 4 | 0 | 4 | 2 | | ***48*** | |
| New Zealand | 8 | ***14*** | 0 | 5 | 0 | 1 | 0 | ***21*** | 0 | 0 | 0 | 0 | | 5 | |
| Australia | 17 | 17 | 2 | 19 | 0 | 0 | 0 | ***22*** | 1 | 1 | 8 | 0 | | ***29*** | |
| Indian Ocean | 4 | 1 | 0 | ***29*** | 2 | 2 | 0 | 12 | 2 | 1 | 10 | 0 | | ***27*** | |
| S. Africa | 14 | 13 | 1 | ***21*** | 1 | 2 | 1 | ***44*** | 1 | 1 | 3 | 1 | | 16 | |
| Africa (rest) | 3 | 0 | 0 | ***15*** | 0 | 0 | 0 | 8 | 1 | 0 | 5 | 0 | | ***21*** | |
| Atlantic Isl. | 3 | 5 | 0 | 4 | 0 | 1 | 1 | ***10*** | 0 | 0 | 0 | 1 | | ***8*** | |
| South Amer. | 10 | 12 | 0 | ***26*** | 0 | 0 | 0 | ***18*** | 0 | 0 | 3 | 0 | 12 | 0 | 4 |
| Caribbean | 0 | 0 | 0 | ***19*** | 0 | 0 | 0 | 9 | 0 | 0 | 7 | 0 | ***10*** | 8 | ***10*** |
| Centr. Amer. | 0 | 5 | 0 | ***12*** | 0 | 0 | 0 | ***8*** | 0 | 0 | 3 | 0 | 7 | 0 | 7 |

The first two highest donors for each acceptor are in bold and italics. If a species is native in part of the region and invasive in other part, the region is treated as a donor and acceptor at the same time. Because quite a few invasive woody species are native not only in South America, but also in Central America and Caribbean, these three regions were treated as only one in some analyses

**Table 4** Numbers of invasive shrub species provided to acceptor regions by individual donor regions

| Acceptors | North America<br>Donors | Europe | Middle East | Asia | Indonesia | Pacific Islands | New Zealand | Australia | Indian Ocean islands | Africa (southern) | Africa (rest) | Atlantic islands | South America | Caribbean islands | Central America |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| North Amer. | 7 | ***23*** | 0 | ***41*** | 0 | 1 | 0 | 7 | 0 | 2 | 4 | 2 | | 11 | |
| Europe | 15 | ***18*** | 0 | ***21*** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 6 | |
| Middle East | 1 | 0 | ***3*** | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | | ***2*** | |
| Asia | 5 | 2 | 1 | ***7*** | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 0 | | ***15*** | |
| Indonesia | 0 | 0 | 0 | ***6*** | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | | ***14*** | |
| Pacific Isl. | 7 | 4 | 0 | ***19*** | 0 | 4 | 0 | 5 | 2 | 3 | 3 | 0 | | ***25*** | |
| New Zealand | 5 | ***21*** | 0 | ***16*** | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 2 | | 6 | |
| Australia | 3 | ***27*** | 0 | ***23*** | 0 | 0 | 2 | 3 | 1 | 8 | 1 | 2 | | 17 | |
| Indian Ocean | 0 | 1 | 0 | ***12*** | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 0 | | ***18*** | |
| S. Africa | 3 | 12 | 0 | ***17*** | 0 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | | ***22*** | |
| Africa (rest) | 0 | 0 | 0 | ***6*** | 0 | 0 | 0 | 1 | 0 | 1 | 5 | 0 | | **21** | |
| Atlantic Isl. | 2 | 2 | 0 | 4 | 0 | 0 | 0 | 2 | 0 | 3 | ***5*** | 0 | | ***8*** | |
| South Amer. | 2 | ***11*** | 0 | ***7*** | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 |
| Caribbean | 0 | 2 | 0 | ***6*** | 0 | 0 | 0 | 1 | 0 | 0 | ***5*** | 0 | ***5*** | ***5*** | 4 |
| Centr. Amer. | 0 | 0 | 0 | ***2*** | 0 | 0 | 0 | 0 | 0 | 0 | ***3*** | 0 | 1 | 0 | 1 |

The first two highest donors for each acceptor are in bold and italics. If a species is native in part of the region and invasive in other part, the region is treated as a donor and acceptor at the same time. Because quite a few invasive woody species are native not only in South America, but also in Central America and Caribbean, these three regions were treated as only one in some analyses

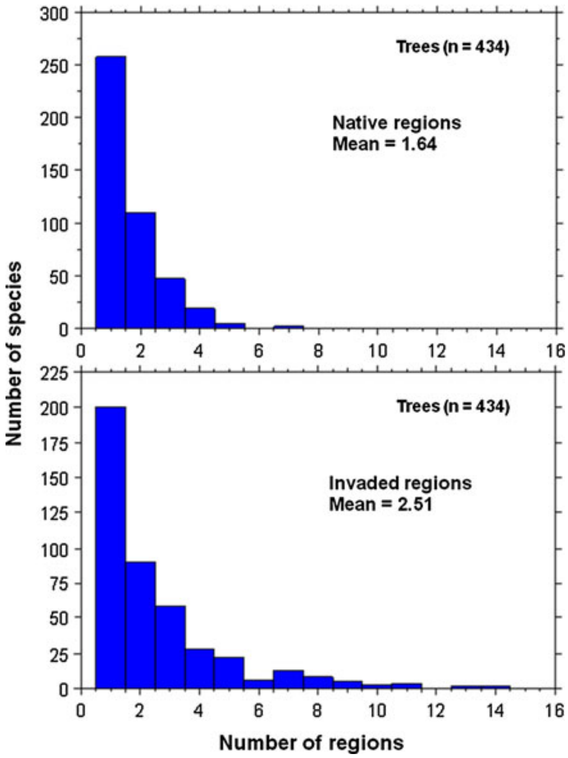


**Fig. 1** Frequencies of numbers of tree species in one or more regions, native or invaded

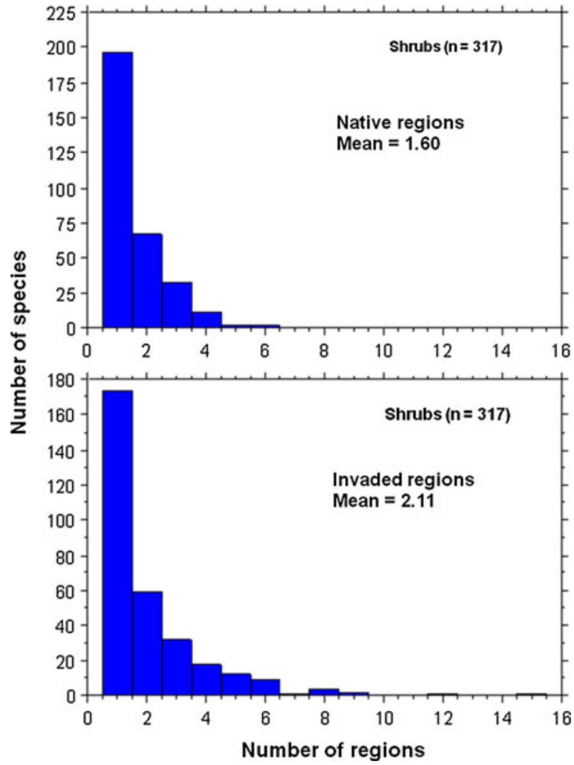


**Fig. 2** Frequencies of numbers of shrub species in one or more regions, native or invaded

Americas and Caribbean; 2—Europe, Middle East, and Africa (rest). As expected, Southern Africa and islands exhibited only a remote similarity with the rest of the regions. Obviously, this pattern is dictated mainly by connectivity and geographical distances among individual regions. On the other hand, agglomerative classifications of the same regions after the exchange of invasive dendrofloras exhibits quite different patterns, probably reflecting introduction efforts and environmental similarities among 15 geographical regions rather than geographical distance (Fig. 5c, d). For example, Australia joins Southern Africa, Europe joins North America, and Africa (rest) joints the Neotropics rather than Europe and Middle East.

## Are families with many invasive species originating in particular regions?

Asia is the major source of invasive Rosaceae shrubs, and invasive Arecaceae and Oleaceae species. It is also very important provider of Fabaceae trees and shrubs (Table 5). South America and Australia are major

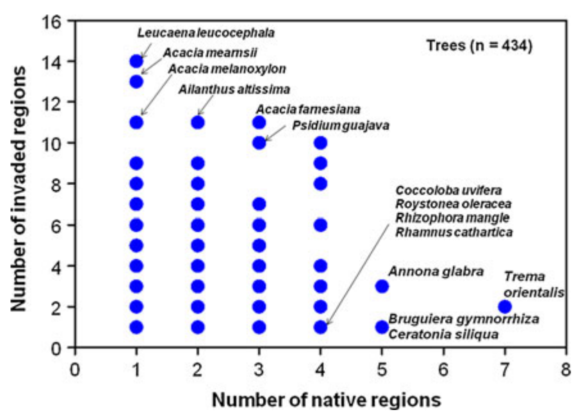


**Fig. 3** Numbers of invaded regions plotted against numbers of native regions for trees. Examples of species with extreme combinations of these two variables are provided

sources of invasive Fabaceae trees. Australia is the major source of invasive dry-fruited Myrtaceae. North America and Europe are major sources of invasive Pinaceae. South America is the major source of invasive woody Solanaceae. Most of the invasive Salicaceae are of Eurasian origin.

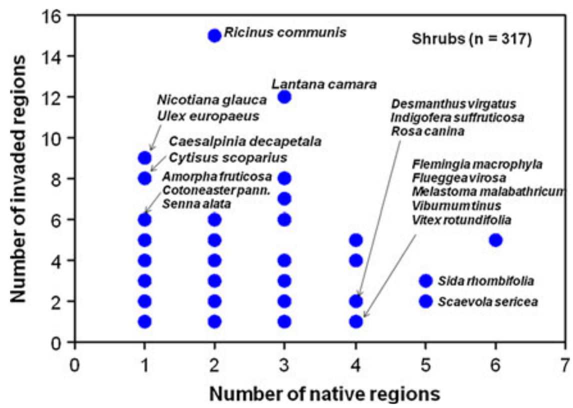


**Fig. 4** Numbers of invaded regions plotted against numbers of native regions for shrubs. Examples of species with extreme combinations of these two variables are provided

## Are there any families invading primarily in particular regions?

The major acceptors of invasive Fabaceae trees are Australia, Southern Africa and Caribbean Islands, while the major acceptors of Fabaceae shrubs are North America, Pacific Islands, and Australia (Table 6). The major acceptors of woody Rosaceae are Europe, North America and Australia. Tropical Africa is the major acceptor of woody Solanaceae. The major acceptors of Pinaceae species are New Zealand and South America. Arecaceae are invasive primarily on Pacific Islands and in South America. The major acceptors for Salicaceae, in terms of numbers of species, are Australia, North America, New Zealand, and Southern Africa.

## Discussion

The fact that some regions are invaded by larger numbers of trees (Pacific Islands, Southern Africa, Australia, North America) or shrubs (North America, Australia, Pacific Islands, Europe) probably does not point to any inherent invasibility features of such regions. Differences in numbers of invasive trees and shrubs in individual regions (Table 1) are more likely

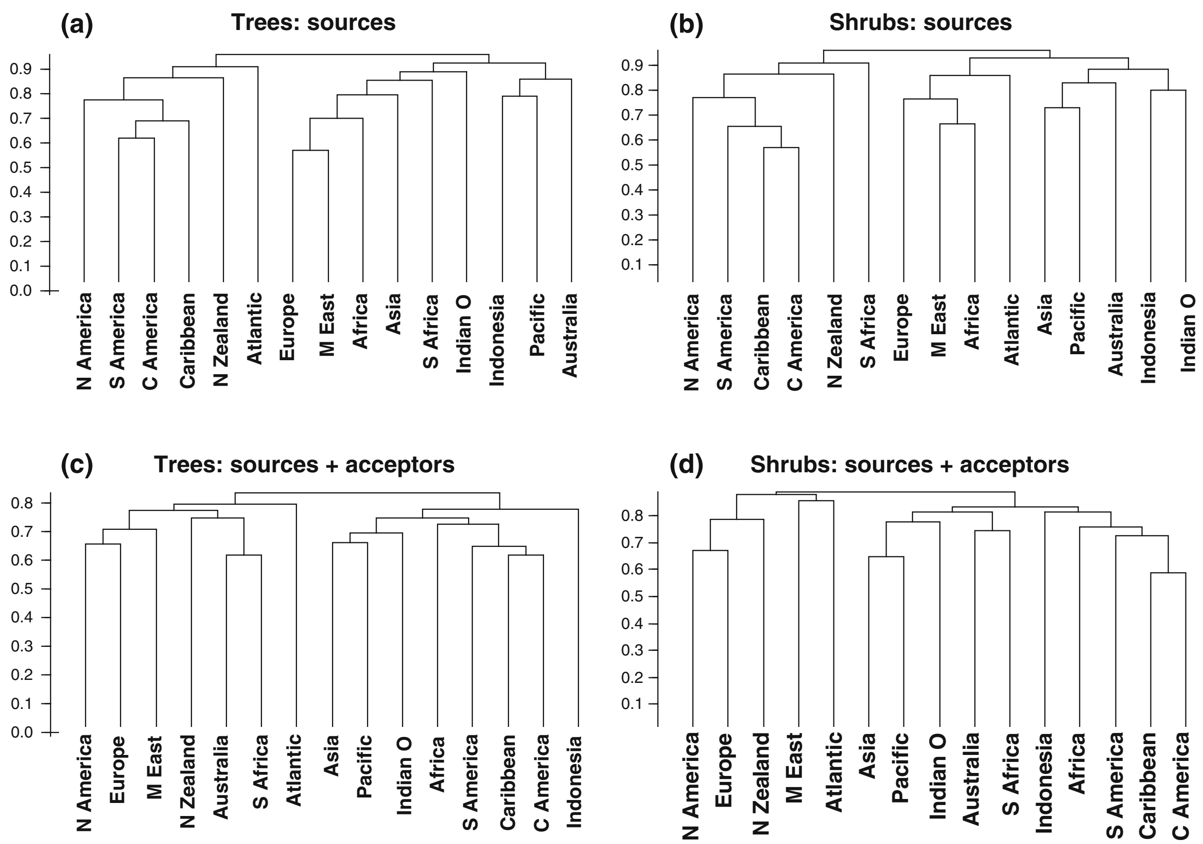


**Fig. 5** Agglomerative classification of source invasive tree (**a**) and shrub (**b**) floras (before human-mediated exchange) and current invasive tree (**c**) and shrub (**d**) floras (in native and invaded regions) based on the complement to Jaccard coefficient of similarity

**Table 5** Major donors of large families (with > 20 invasive species)

| Family | North America Donors | Europe | Middle East | Asia | Pacific Islands | Australia | Africa (southern) | South America | Caribbean islands | Central America |
|---|---|---|---|---|---|---|---|---|---|---|
| Fabaceae trees | | | | 22 | | 27 | | 27 | | 19 |
| Fabaceae shrubs | | 12 | | 13 | | | | 14 | | |
| Rosaceae trees | 3 | 7 | | 6 | | | | | | |
| Rosaceae shrubs | 14 | 29 | | 43 | | | | | | |
| Myrtaceae trees | | | | 3 | | 21 | | 5 | 3 | |
| Myrtaceae shrubs | | | | 1 | | 2 | | 1 | | |
| Solanaceae trees | 1 | | | | | | | 3 | | |
| Solanaceae shrubs | | | | | | | 3 | 11 | | 6 |
| Pinaceae | 16 | 9 | | 5 | | | | | | |
| Arecaceae | | | | 8 | 5 | | | 4 | | 5 |
| Salicaceae trees | 2 | 8 | | 7 | | | | | | |
| Salicaceae shrubs | | 5 | | 4 | | | | | | |
| Oleaceae trees | | 3 | 3 | 7 | | | | | | |
| Oleaceae shrubs | | 2 | | 3 | | | | | | |

The first three donors (in terms of numbers of species) are listed for each category

due to the differences in introduction effort and, to some extent, due to our incomplete knowledge about some regions. Positive correlation between numbers of invasive trees and shrubs and numbers of donor regions is suggestive. It is possible that introductions from multiple regions promotes establishment of more species. However, it is even more likely that the total number of established invasive species and the number of donor regions are both just results of introduction effort in individual acceptor regions. There are remarkable differences in numbers of invasive tree species accepted and provided by some regions. One of the most striking inequalities is represented by southern Africa with 118 invasive tree species introduced from elsewhere while providing only 9 invasive tree species to other regions. The shortage of fast growing trees suitable for construction timber, namely in the Cape province, is undoubtedly one of the most important reasons why so many tree species were introduced and so few donated. Very likely, something similar happened on Pacific Islands (136 vs. 52 tree species). There is a strong correlation between numbers of introduced invasive trees and shrubs, however, relative overrepresentation of shrubs in North America and New Zealand and their underrepresentation in Central and South America (compared to trees) may reflect different priorities in introduction of non-native woody species: ornamental shrubs in the first case and timber producing trees in the second.

We are in a somewhat similar situation with explanations of differences in contributions of individual donor regions. Asia seems to be the major source of both invasive trees and shrubs (Tables 2, 3, and 4). In this case, however, one may argue that, besides that this continent provides the largest species pool (because of its size and environmental heterogeneity), there are also some attributes of Asian (and Eurasian) woody species that make them more invasive. Is there "a general continuum of competitive ability among organisms that extends from the smallest, most remote islands to the largest continental mass" as suggested by Huston (1994, p. 323)? Surprisingly, Reichard and Hamilton (1997) concluded that their continent-wide model of woody plant invasions "associated species native to temperate Asia with a lack of invasiveness." Nevertheless, they admitted that "in some regions (e.g., the southeastern United States) large numbers of the invasive species are from temperate Asia." This trend was later persuasively quantified by Fridley (2008). One of the attributes that makes woody species from Asia more successful, at least in the eastern U.S., is their extended autumn leaf phenology (Fridley 2012, 2013). In comparative studies of native North American and Eurasian (mostly species from temperate East Asia)

**Table 6** Major acceptors of large families (with > 20 invasive species)

| Families | North America Acceptors | Europe | Pacific Islands | New Zealand | Australia | Indian Ocean islands | Africa (southern) | Africa (rest) | South America | Caribbean islands |
|---|---|---|---|---|---|---|---|---|---|---|
| Fabaceae trees | | | 26 | | 35 | | 32 | | | 30 |
| Fabaceae shrubs | 20 | | 19 | | 18 | | 13 | | | |
| Rosaceae trees | 6 | 7 | | | 5 | | 3 | | | |
| Rosaceae shrubs | 25 | 27 | | 19 | 25 | | 17 | | | |
| Myrtaceae trees | 7 | | 10 | | 8 | 8 | 20 | | 7 | |
| Myrtaceae shrubs | 1 | | 3 | 2 | | | 1 | | | |
| Solanaceae trees | 1 | | 1 | 1 | 2 | 1 | 1 | 3 | | |
| Solanaceae shrubs | 7 | | 8 | 5 | | | | 9 | | |
| Pinaceae | | 11 | | 15 | 9 | | 8 | | 12 | |
| Arecaceae | 6 | | 11 | | 3 | | | | 8 | 3 |
| Salicaceae trees | 6 | 5 | | 6 | 7 | | 6 | | | |
| Salicaceae shrubs | 2 | | | | 3 | | | | 2 | |
| Oleaceae trees | 6 | 4 | 4 | 3 | 3 | 3 | 5 | | 4 | |
| Oleaceae shrubs | 5 | 1 | | 1 | 1 | | 2 | | 1 | |

The first four acceptors (in terms of numbers of species) are listed for each category

invasive woody species, invasive species exhibited greater instantaneous photosynthetic energy-use efficiency and marginally greater photosynthetic nitrogen-use efficiency (Heberling and Fridley 2013). Also, data on the proportional range areas of introduced plants as a function of residence time point to the fact that species from eastern Asia are more successful in North America than species introduced from North America to eastern Asia (Guo et al. 2006). When we look the other direction, to Asia as an acceptor, most of the invasive trees and shrubs have been introduced from the Neotropics (Tables 3, 4). This is in agreement with general trends known for all plant species naturalized in Asia (Khuroo et al. 2012; Wu et al. 2010). The largest proportion of invasive trees in Southern Africa is from Australia (37 % from Australia vs. 18 % from Asia; Table 3). This is in agreement with one previously published analysis (Wels et al. 1986). It seems that fire-adapted trees from nutrient poor habitats in Australia are uniquely preadapted to environmental conditions in comparable climates of Southern Africa (Macdonald 1985). Interestingly, also Pacific Islands did not get maximum proportion of invasive dendroflora from Asia. Only 21 % of trees and 27 % of shrubs are from Asia, while 35 % of both trees and shrubs are from the Neotropics (Tables 3, 4).

Mean number of native geographical regions for invasive trees and shrubs is 1.64 and 1.60, respectively, while the mean number of invaded regions by trees and shrubs is 2.51 and 2.11, respectively. The difference between trees and shrubs points to the difference in introduction regimes: many trees have been introduced by foresters in more systematic fashion than shrubs which have been introduced more spontaneously as ornamental species. The frequency distributions are markedly skewed for both trees and shrubs (Figs. 1, 2). Clearly, for those species occupying multiple regions, there are significantly more species of trees and shrubs occupying larger number of invaded regions compared with numbers of regions that they occupy as native species (Figs. 1, 2). However, 46.1 % of tree species and 54.9 % of shrub species are, so far, in only one invaded region. Only 8.9 % of trees and 5.8 % of shrubs are in six or more invaded regions. Such numbers point out to a substantial "invasion debt," i.e., many of those species that are currently reported as invasive in only one or a few regions are potentially invasive in more regions. A similar kind of "invasion debt" was also identified in the recent global comparison of plant invasions on oceanic islands (Kueffer et al. 2010; Fig. 1). Particularly short-distance-dispersing species may be recognized as invasive only after longer times (Bennet et al. 2013).

Several studies showed that sizes of native ranges can serve as predictors of species invasiveness (Boucharová and van Kleunen 2009; Lavoie et al. 2013; Rejmánek 1995; Shah et al. 2012). Also, some recent analyses showed that large native range areas of trees are positively associated with their niche breadth (Kockemann et al. 2009; Morin and Lechowicz 2013). Therefore one should expect strong positive correlation between numbers of native and numbers of invaded regions for trees and shrubs. Yes, the relationship between the number of invaded regions and number of native regions for invasive trees and shrubs is positive, but very weak (non-significant for trees, and only because of large n, it is significant for shrubs) (Figs. 3, 4). Therefore, currently, it does not look that number of native ranges has any predictive value. The weak correlation may results partly from highly uneven areas of recognized regions and partly from the fact that many species are still reported as invasive in only one or in a very few regions and points to the prevailing existence of invasion debt.

In both Figs. (3, 4), extreme values deserve a special attention. First are species native only in very few regions but are successfully invasive in many regions. Obviously, for example, *Leucaena leucocephala, Acacia mearnsii, A. melanoxylon, A. farnesiana, Ailanthus altissima, Psidium guajava, Ricinus communis, Lantana camara, Ulex europaeus*, and *Cytisus scoparius* are notorious invaders in many countries but their native ranges are relatively limited. On the other hand, the following species are native in many regions and, so far, have invaded only a few regions: for example, *Coccoloba uvifera, Bruguiera gymnorrhiza, Ceratonia siliqua, Fluegea virosa, Rhamnus cathartica, Viburnum tinus, Vitex rotundifolia, Rosa canina*, *Desmanthus virgatus, Sida rhombifolia,* and *Trema orientalis* (the last species, however, is very likely polyphyletic, consisting of two different species—Yesson et al. 2004). What makes these two groups of species different? Is it their inherent biological properties? Legumes and bird dispersed species are in both groups. A phylogenetically corrected detail analysis of their biological properties (Grotkopp et al. 2002, 2004) could reveal some differences. However, at this time, I am inclined to believe that differences in introduction effort and therefore in propagule pressure likely overwhelm any differences in biological traits that could promote invasiveness. Besides, some tropical species in the second group already filled most of the suitable regions as natives (*Annona glabra, Cocoloba uvifera*). Still, some of the species in the second group may be major indicators of the invasion depth and should be treated as potentially important invaders.

As expected, numerical classification of 15 regions based on current distribution of 751 woody species included in this study produced different clusters than the same classification based on their native distribution only (Fig. 5). These differences give us an idea how similarities of the world floras can be changed through successful introductions of invasive species. Homogenization of the world floras is in progress. Considering just woody species included in the present analysis, mean similarity (based on the Jaccard coefficient) of tree floras of 15 recognized geographical areas increased from 0.041 to 0.165 and mean similarity of shrub floras increased from 0.040 to 0.152. How far can homogenization go? Considering potentials for temperate versus tropical species, the mean similarities based on our subset of woody species could reach 0.6–0.7. It is still a long way to go, but we are heading in that direction.

Asia is not only the major source of invasive trees and shrubs in general, but it is primary major source of Rosaceae shrubs, invasive Arecaceae, and Oleaceae species. It is also very important provider of Fabaceae trees and shrubs (Table 5). South America and Australia are major sources of invasive Fabaceae trees. Not surprisingly, Australia is the major source of invasive dry-fruited Myrtaceae (traditionally recognized as a mainly Australian complex Leptospermoideae). North America and Europe are major sources of invasive Pinaceae, as has been clearly recognized in many studies earlier (Richardson and Higgins 1998; Richardson 2011). South America is the major source of invasive woody Solanaceae, likely resulting from the fact that this family is most diverse in the Neotropics (Judd et al. 2008). Most of the invasive Salicaceae are of Eurasian origin. In general, it seems that these trends are determined by sizes of available species pools in individual regions. Unfortunately, at this point, we do not have complete lists of native woody species for most of the regions treated in this study.

The major acceptors of Fabaceae trees are Australia, Southern Africa and Caribbean Islands, while the major acceptors of Fabaceae shrubs are North America, Pacific Islands, and Australia (Table 6). The major acceptors of woody Rosaceae are Europe, North America and Australia. Tropical Africa is the major acceptor of woody Solanaceae. The major acceptors of Pinaceae species are New Zealand and South America. Arecaceae are invasive prevailingly on Pacific Islands and in South America. This family emerges as one of the most important sources of invasive trees in the tropics (Hariyadi et al. 2012; Keppel and Watling 2011; Mengardo et al. 2012; Meyer et al. 2008; Svenning 2002). Because species in about 80 out of 183 genera in the palm family have been reported as bird-dispersed in their native areas, invasion potential of fleshy-fruiting palms is enormous (Dransfield et al. 2008; Zoa and Henderson 1989; Zoa 2006). The major acceptors for Salicaceae are Australia, North America, New Zealand, and Southern Africa. However, we should not forget that here we deal only with species presence/absence data. Salicaceae infestations are spatially very limited in North America and much more extensive in the regions of the Southern Hemisphere (Giljohann et al. 2011; Henderson 1991; Holland-Clift et al. 2011; Stokes 2008; Thomas et al. 2012). Based not only on the numbers of introduced species but on the sizes of their infestations, we may speculate that temperate regions of the Southern Hemisphere represent "open niches" for Pinaceae and Salicaceae.

Recognized trends will very likely continue in this century. Horticulture and forestry will continue to be major pathways of woody plant invasions. However, some new alternatives, like biofuels, are also emerging (Gordon et al. 2011). Because of increasing interactions with China and other states in Asia, even more invasive woody species will be introduced from this part of the world. In particular, it will be tempting to introduce many beautiful ornamental woody species (Shulkina 2004; Wharton et al. 2005; Zhang et al. 2003). As for trees, a simple insight of what we should expect is provided by a recent monograph "New Trees—Recent Introductions to Cultivation" (Grimshaw and Bayton 2009). Out of ca 830 tree species recently introduced into cultivation, 46.8 % are from China or Sino-Himalayan region in general. Tree species from Australia and Central America are in second (11.1 %) and third (10.8) places, respectively. Similarly, among 319 plant species available in 22 nurseries in Kentucky, 139 (43.4 %) have been introduced from Asia (Harris et al. 2009). Also, Asia is the major donor of woody species planted in Europe (Kriváneck and Pyšek 2008) and Hogan (2008) recommends for cultivation many more evergreen trees from Asia than from any other region. Even in Fortaleza (NE Brazil), 45 % of exotic street trees are from Asia and only 32 % from the Neotropics (Moro and Westerkamp 2011). However, only 29 % of 719 cultivated species of trees and shrubs in the Hawaiian Islands are from Asia, practically the same proportion (27 %) is from the Neotropics (Staples and Herbst 2005). This may partly explain the larger proportion of Neotropical invasive trees and shrubs on Pacific Islands mentioned above.

Expanding trade with China will be a major factor influencing introduction and naturalization of species from Asia (Normile 2004). However, it is not only China. Recent political developments in Myanmar (Burma) will very likely allow more introductions from this, so far, tightly closed country. If plant woody species from Asia are indeed more invasive as I discussed earlier, than there is a great potential for their invasions and expansions in many acceptor regions. Also, Australian woody species are very popular in cultivation (Elliot and Jones 1980–1997) and their introductions to other regions will continue. Undoubtedly, a few more Australian Fabaceae and Myrtaceae will be recognized as invasive in this century. We may also expect that more attractive trees will be introduced from Brazil and Chile (Hogan 2008; Lorenzi 1992–2009) and some of them become invasive in acceptor regions.

Many non-native plant species are currently profiting from the decreasing number of frost days and longer growing seasons (Osland et al. 2013; Walther et al. 2002; Willis et al. 2010). Invasion of subtropical Asian palm, *Trachycarpus fortunei*, at the southern foot of the Alps is one of the best examples of this process (Walther et al. 2007). It is even possible that recently recognized northward shift of the USDA plant hardiness zones in the U.S. is just another symptom of global warming (http://planthardiness.ars.usda.gov/PHZMWeb/AboutWhatsNew.aspx). Consequently, we may expect more subtropical woody species invading warmer temperate areas, and more temperate species invading warmer boreal zones (Bradley et al. 2011). Detailed climate matching studies for potentially invasive woody species are very important, but may be valid just for a few decades. Predictions that take into account climate change, including elevated $CO_2$, should be incorporated into management planes (Jalili et al. 2010; Kleibauer et al. 2010; van Klinken et al. 2009; Way et al. 2010).

There are many priorities for further research to improve our understanding of the ecology of woody plant invasions and our ability to manage them (Aslan and Rejmánek 2012; Dehmen-Schmutz 2011; Kapler et al. 2012; Richardson and Rejmánek 2011; Vining et al. 2012). In conclusion, it is important to stress that not all species included in this analysis are equally harmful (transformers and/or pests). Evaluations of their economic or environmental impacts have to be done at local scales. Also, without human help, due to dispersal limitations, filling of potential ranges can take enormous time intervals (Nathan et al. 2011; Svenning and Skov 2004; Svenning et al. 2006). Nevertheless, the fact that a non-native woody species considered for cultivation is known to be invasive somewhere else provides a red flag. Prevention is usually cheaper than control (Finnoff et al. 2007; Moran and Hoffmann 2012). Finally, it is important to realize that woody plant invasions in the future may come from altogether novel phenotypes produced through modern genetic and genomic techniques (Flachowsky et al. 2009; Kueffer 2010; Kutsokon 2011; Harfouche et al. 2012).

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