

Contrasting patterns of naturalized plant richness in the Americas: Numbers are higher in the North but expected to rise sharply in the South

Abstract

With increasing availability of plant distribution data, the information about global plant diversity is improving rapidly. Recently, Ulloa et al. (2017) presented the first comprehensive overview of the native vascular flora of the Americas, yielding a total count of 124,993 native species. Of these, 51,241 occur in North America and 82,052 in South America. By combining these data with the information in the Global Naturalized Alien Flora (GloNAF) database of naturalized alien floras, we point out that for a complete picture of the regional and continental plant richness, the naturalized alien species need to be considered. Ignoring this novel component of regional floras can lead to an inaccurate picture of overall change in biodiversity in the Anthropocene. We show that North and South America might face contrasting challenges in terms of potential threats to biodiversity posed by alien plant species, because of the different past and present dynamics of invasions and predictions of future development. In total, there are 7,042 naturalized alien plants occurring in the Americas, with 6,122 recorded in North America and 2,677 in South America; if only introductions from other continents are considered additions to the native continental flora make up 6.9 and 1.4 %, respectively. Nevertheless, predictions of naturalized plant trajectories based on global trade dynamics and climate change suggest that considerable increases in naturalized plant numbers are expected in the next 20 years for emerging South American economies, which could reverse the present state.

KEYWORDS

biodiversity, native species, North America, plant invasion, regional floras, South America

1 INTRODUCTION

With growing awareness of the key role that basic floristic data play in botanical research and in ecological studies at various scales (e.g., Fridley, 2008; Kier et al., 2005; Whittaker et al., 2005) and increasing availability of data, the information about continental (e.g., Kartesz, 2015; Kartesz & Meacham, 1999) and global plant diversity is rapidly improving. Recently, Ulloa et al. (2017) presented the first comprehensive overview of the native vascular flora of the Americas, yielding a total count of 124,993 species. Of these, 51,241 native species occur in North America and 82,052 in South America, with the sum of the two exceeding the total number owing to species that are

native to both continents. In terms of completeness, the authors point to a rate of 744 new species added annually over the past 25 years by means of description of new species and predict that with this factor accounted for, we can expect to reach a total of c. 150,000 species for the Americas. The publication of a checklist for two megadiverse continents by Ulloa et al. (2017) is a great achievement and major milestone that will facilitate future botanical research on these continents. However, we would like to point out that for a complete picture about the regional and continental plant richness, the information on native species needs to be complemented by considering the additions to floras by alien species invasions that nowadays make a significant contribution to species richness in many regions of the world (Pyšek, Pergl et al., 2017; van Kleunen et al., 2015).

In the last few years, global knowledge of naturalized alien plant species has dramatically improved with the launch of the Global Naturalized Alien Flora (GloNAF) database, which provides the most comprehensive naturalized alien species checklists for > 947 non-overlapping regions of the globe to date, covering both mainland and island regions (Pyšek, Pergl et al., 2017; van Kleunen et al., 2015, 2019). At present, there are \geq 12,427 confirmed naturalized alien plant species globally (with infraspecific taxa, the number is 13,083; van Kleunen et al., 2019), that is, those species that have been introduced by humans to areas beyond their native range and, by forming self-reproducing populations, have become persistent components of local floras and ecosystems (Blackburn et al., 2011; Richardson et al., 2000).

The availability of the GloNAF database as a new resource in plant invasion ecology makes it possible to obtain insights into the dynamics of the invasion process. The aim of our paper is therefore to address an important, yet still common, shortcoming of many biodiversity assessments: to consider only native species, without mentioning the addition of alien species, among which the subset of those that are naturalized or invasive (the latter defined as those rapidly spreading over large areas; Richardson et al., 2000) can profoundly change diversity patterns. We support the growing consensus that we need to count those species in order to understand how much humans are changing biodiversity patterns (Bustamante et al., 2018; Pauchard et al., 2018; Vellend et al., 2017). The Americas are particularly relevant to illustrate these issues; as we show, the naturalized alien fraction of the floras reveals different past dynamics with potential consequences; North and South America might face contrasting challenges in terms of potential biodiversity threats posed by alien plants.

2 DIFFERENT PATTERNS OF PLANT INVASIONS IN THE AMERICAS

These new data revealed that in total there are 7,042 naturalized alien plants occurring in the Americas, and this figure is a conservative estimate, because data from some regions are still incomplete or even missing; a previous GloNAF paper referred to 95.9 and 95.8% of North and South America covered, respectively (Pyšek, Pergl et al., 2017; for the most recent complete list of regions with available data, see van Kleunen et al., 2019). Including Central America and Caribbean within the North American continent and excluding the Hawaiian archipelago and other islands (as in the study by Ulloa Ulloa et al., 2017), the numbers for North and South America are, however, strikingly different, with 6,569 naturalized alien plant species recorded for the Northern American continent and 1,961 naturalized species occurring in South America (van Kleunen et al., 2019). When comparing the frequency distribution of regions on the two continents with respect to the proportion that naturalized species contribute to their floras, there is a clear shift towards greater values in North America, indicating that regions with high percentages of naturalized aliens are more likely to occur there (Figure 1). These numbers, however, also include species that are native in some parts of the continents and naturalized in other parts (van Kleunen et al., 2015), and the two components unfortunately cannot be disentangled owing to the insufficient spatial resolution of the information on species' native ranges. At the continental scale, for the Americas together, this holds for 3,349 of the 7,042 naturalized species (i.e., 47.6%); these species are native to some regions of North or South America and naturalized in other parts of the continents.

We therefore argue that to capture the increase in plant diversity attributable to the addition of naturalized aliens, one also needs to look at extracontinental introductions, that is, species that are naturalized in the Americas and have their native ranges outside

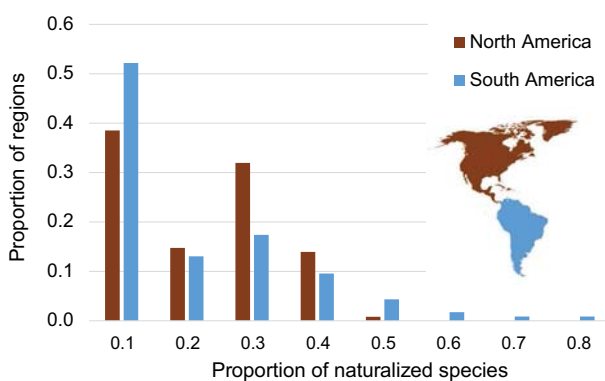


FIGURE 1 Comparison of frequency distributions of the proportion of naturalized alien plant species among all species in regions of North America ($n = 122$, mean 17.8%) and South America ($n = 117$, mean = 16.3%). The differences in the proportions between the two continents are significant (Wilcoxon test, $W = 8,294$, $p = .03$). Central America and the Caribbean are included within North America, as in the study by Ulloa Ulloa et al. (2017). Based on data from Pyšek, Pergl et al. (2017) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

this continent. The Americas currently contain at least 3,693 naturalized alien plant species introduced from other continents; this figure represents an addition of 3.0% of species. North and South America, however, differ again; 3,535 naturalized alien plants in North America add 6.9% to the 51,241 native species reported by Ulloa Ulloa et al. (2017), whereas the 1,134 naturalized species occurring in South America add to the native flora of 82,052 species by only 1.4%.

Although it also needs to be taken into account that the differences in numbers of naturalized plants between North and South America are most probably caused, at least in part, by unequal sampling effort, which is much lower in most parts of South America (Meyer, Weigelt, & Kreft, 2016), we argue that this might not explain the magnitude of the differences by itself and that there are historical reasons for the observed disparity. The greater contribution of naturalized alien species to the flora of North America results from long-lasting and more widespread human-related pressures associated with developed economies, a factor repeatedly reported to facilitate biological invasions (Essl et al., 2011; Pyšek et al., 2010), and from differences in industrialization and the intensity of human emigration from Europe, which was a major donor of alien species to a large part of this continent (van Kleunen et al., 2015; Winter et al., 2010). After the industrial revolution, industrialized economies and trade links have grown in North America, namely the USA, in a way that was not reflected in the South America, and there were greater numbers of Europeans emigrating to North rather than South America in the 1800s. After the end of the Napoleonic Wars in 1815, until 1920 some 60 million Europeans emigrated, of whom 71% went to North America and 21% to South America (Klaumann Cánovas, 2004). These factors might explain the sharper increase in the number of species introduced from other continents after the late 1800s in North America (Figure 2a).

Interestingly, the difference between the two continents shown in Figure 2 is becoming less pronounced in recent decades. Based on the Alien Species First Records Database (Seebens et al., 2017), between 1975 and 2000, North America received 184 and South America 110 new alien plants from other continents that have subsequently become naturalized. This means that the ratio of newly introduced naturalized species between North and South America, which was 3.0 for the period of the last 300 years, decreased to 1.7 in the last quarter of the 20th century (Figure 2b). Although information on the first records is missing for many alien plants and regions, which makes these figures conservative, and the real numbers of newly established species will be substantially higher, it needs to be borne in mind that these introductions represent a large source of species that may become invasive in the future.

3 PREDICTIONS OF FUTURE INVASION DYNAMICS

Nevertheless, predictions of naturalized plant trajectories based on global trade dynamics and climate change suggest that considerable increases in naturalized plant numbers are expected in the

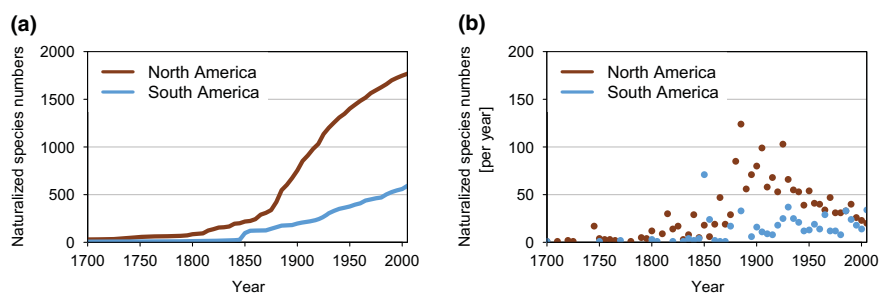


FIGURE 2 Dynamics over time of new species introductions to North and South America. (a) Cumulative numbers of species. (b) Numbers recorded per year. Based on data from the Alien Species First Records database, which includes information on the first reports of species that have later become naturalized (see Seebens et al., 2017, 2018). Note that the plots show species that were introduced from overseas, that is, have their native ranges outside the Americas. The cumulative species numbers are lower than those reported in the text for the two continents, because information on the first records is available for only 1,799 and 599 species (50.9 and 52.8% of the total), respectively [Colour figure can be viewed at wileyonlinelibrary.com]

next 20 years for emerging South American economies, Brazil and Argentina in particular, which are also biologically megadiverse (Seebens et al., 2015). This is expected despite the fact that temperate regions of the Northern Hemisphere are predicted to become progressively more invaded under climate change than countries in the tropics and subtropics of the Southern Hemisphere, because rising temperatures in the former will open ways to invaders from species-rich subtropical regions (Bellard et al., 2013). Another important driver will be rising imports; trade-related increases in naturalized aliens are predicted to generate greater numbers of invasions to South rather than North America (Seebens et al., 2015). These authors arrived at this conclusion by combining data on 60-year trends of bilateral trade, biodiversity and climate that were used to model the global spread and future dynamics of plant species among 147 countries (Seebens et al., 2015). This prediction is supported by recent analyses of newly emerging naturalized species numbers over time, which show that global accumulation of naturalized species is set to continue (Seebens et al., 2017, 2018).

The above issues relate closely to an ongoing debate about how alien species contribute to biodiversity change (Cardinale, Gonzalez, Allington, & Loreau, 2018; Vellend et al., 2017) and disruption of natural biogeographical regions (e.g., Capinha, Essl, Seebens, Moser, & Pereira, 2015). We argue that future assessments and inventories should include and give status information about all species, native and alien. However, rather than lumping them together (as recently proposed by Schlaepfer, 2018), a clear distinction based on broadly accepted definitions and concepts (Blackburn et al., 2011; Richardson et al., 2000) needs to be made between the two groups, and the species origin, ecological context and evolutionary history should be considered carefully (Pauchard et al., 2018). This is essential because some alien species can become invasive and produce major ecosystem disruptions and even declines in native species (Downey & Richardson, 2016; Pyšek, Blackburn, García-Berthou, Perglová, & Rabitsch, 2017; Vilà & Hulme, 2017). Moreover, although native species clearly differentiate ecoregions in the Americas and globally (Capinha et al., 2015; Holt et al., 2013), naturalized species include many generalists

associated with human-disturbed landscapes (Kalusová et al., 2017), and their integration in local floras results in the loss of local uniqueness at different levels of biodiversity (Rejmánek, 2000; Winter et al., 2009).

Our point raised here, using North and South America as an example, illustrates that ignoring naturalized alien species leads to an incomplete picture of the overall change in biodiversity and its consequences in the Anthropocene (for more discussion, see Pauchard et al., 2018). A complete and balanced picture of the biodiversity of continents is necessary not only to allow for further scientific progress in studies of biological invasions but also to assess the conservation implications of invasive species (Bustamante et al., 2018).

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