



Latitudinal patterns of alien plant invasions

Abstract

Latitudinal patterns of biodiversity have long been a central topic in ecology and evolutionary biology. However, while most previous studies have focused on native species, little effort has been devoted to latitudinal patterns of plant invasions (with a few exceptions based on data from sparse locations). Using the most up-to-date worldwide native and alien plant distribution data from 801 regions (including islands), we compared invasion levels (i.e. alien richness/total richness) in the Northern and Southern Hemispheres and across continental regions and islands around the globe. Results from quantile regressions using B-splines to model nonlinearity showed (1) declining richness with increasing latitude, although the highest alien richness occurs at around 40 degrees in both hemispheres, (2) decreasing invasion levels towards higher latitudes on islands but a unimodal pattern in invasion level in continental regions in each hemisphere, (3) significantly higher invasion levels on islands than in continental regions and (4) a greater variability in invasion levels on islands at low latitudes than on high-latitude islands. In continental regions, only the mid-latitudes had high variability with both low and high invasion levels. Our findings identified latitudes with invasion hotspots where management is urgently needed, and latitudes with many areas of low invasions but high conservation potential where prevention of future invasions should be the priority.

1 | INTRODUCTION

Latitudinal patterns have been widely recognized in both natural (Rosenzweig, 1992) and other fields of science such as economic and social sciences. Novel latitudinal patterns are now emerging as a result of human activities, and one such pattern under debate involves a latitudinal gradient in species invasions (Dyer, Redding, Cassey, Collen, & Blackburn, 2020; Fine, 2002; Rejmánek, 1996). Biological invasions are the result of human agency (species introductions and

habitat modifications) and are further modulated by natural factors (e.g. dispersal, geographic barriers and environmental conditions). In recent decades, the number of alien species has increased rapidly (Seebens et al., 2017), and the available data have become more easily accessible (e.g. Dyer, Redding, & Blackburn, 2017; van Kleunen et al., 2019). Consequently, previous patterns in invasion levels may have changed, and should be revisited.

For instance, it has long been argued that regions rich in native species are more difficult to invade than species-poor regions (Elton, 1958). While such biotic resistance may exist at small spatial scales, large-scale studies have often observed positive correlations between native and alien species richness due to similar factors affecting both native and alien species richness (e.g. Stohlgren et al., 1999; but see Beaury, Finn, Corbin, Barr, & Bradley, 2019; Fridley et al., 2007). About two decades ago, using the still rather limited data available at that time, Rejmánek (1996), Sax (2001) and Fine (2002) showed that tropical continental regions were less invaded than higher latitude regions, both relative to the number of native species (i.e. invasion level) and in absolute terms (i.e. alien species richness). Greater resistance to biological invasion, faster recovery after disturbance due to higher diversity, lack of life history traits that confer shade tolerance and lower colonization and propagule pressures have been proposed as the major causes of the lower alien richness in tropical continental regions (Fine, 2002; Isbell et al., 2015; Rejmánek, 1996). For islands, however, the pattern was found to be very different, with tropical islands harbouring many naturalized alien species (Rejmánek, 1996).

There are several reasons for the lack of convincing evidence for biotic resistance effects at large spatial scales (Beaury et al., 2019; Pyšek et al., 2017; Stohlgren et al., 1999). One of them is time as most alien species have not yet reached their full potential ranges and abundances (e.g. Bebber, 2015; Byers et al., 2015). However, a key reason also lies in the differences in invasion success metrics such as alien species richness (i.e. the absolute number of naturalized alien species in a region) versus. "invasion level" (calculated as the fraction of alien richness in a region's flora: "alien/[alien + native]", ranging from 0 to 1) (Chytrý, Maskell, et al., 2008; Hierro, Maron, & Callaway, 2005). The former correlates with physical (e.g. area, climate) and biotic features (e.g. facilitation) operating across scales (Kolar & Lodge 2002, Fridley et al. 2007), while the latter reflects how much resources and space are shared between native and alien species. Thus, invasion level measured as the fraction of alien species among the total flora better reflects the degree to which a habitat or a region has been invaded. This metric also relates to the potential for future invasions and is as

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such more informative for management than alien species richness (Essl et al., 2019). Another important advantage of using invasion level, unlike alien species richness, is that it facilitates comparisons across regions of varying sizes or communities with different species richness. Fortunately, recent efforts in invasion biology have generated large amounts of data that allow us to test previously debated hypotheses with greater rigour. Here, we use the recently published GloNAF database (Pyšek et al., 2017; van Kleunen, 2015, 2019) (see Appendix I) to re-examine the previously reported latitudinal patterns of plant invasions across the globe. Particularly, we examine whether plant invasions exhibit similar latitudinal patterns between continental regions and islands around the globe, and whether the patterns and potential causal mechanisms differ between hemispheres.

2 | UPDATED LATITUDINAL PATTERNS OF PLANT INVASIONS

The GloNAF database (van Kleunen et al., 2019) is the most comprehensive global database available on alien plant species distributions; it includes data on the numbers of naturalized plant species (i.e. forming self-sustaining populations in the given regions; see Richardson et al. 2000, Blackburn et al. 2011 for definition) from 801 regions (both continental regions and islands) around the globe (Essl et al., 2019; van Kleunen et al., 2019; Pyšek et al., 2017). The data used for this analysis are from the GloNAF dataset version used by Essl et al. (2019), which included the number of all recorded naturalized alien plant species as well as the subset of all invasive plants in each regional flora (such as countries, states or provinces) along a full latitudinal gradient from tropical to polar regions across continents.

Because different habitats support plant communities with different species richness (Chytrý, Maskell, et al., 2008) and biomass, many studies have used the fraction of alien species (in terms of richness, cover and/or biomass) in the community as a standardized measure of invasion level (Chytrý, Jarošík, et al., 2008; Essl et al., 2019; Guo & Symstad, 2008). However, since large-scale (e.g. continental, regional) biomass data for individual species are usually not available, the majority of large-scale studies could only use the richness and/or fractions of naturalized aliens as a measure of invasion level or invasibility (Elton, 1958; Rejmánek, 1996, Lonsdale 1999).

Here, we depict the observed alien plant richness and invasion levels reported for individual regions across both continental regions ($n = 474$) and islands ($n = 327$) and between regions in the Northern ($n = 408$) and Southern ($n = 393$) Hemispheres. Since the species richness was recorded for regions (incl. islands) of different sizes, we used area-corrected richness estimates to describe latitudinal patterns (for details, see Fridley, Qian, White, & Palmer, 2006). We used a logarithmic transformation of area-corrected richness in a linear quantile regression model (Cade & Noon, 2003) with latitude as the predictor variable. To model nonlinear changes in species richness with latitudinal changes in the Southern and Northern Hemispheres simultaneously, we used a cubic B-spline with a single knot (break-point) at 0 degrees on the predictor latitude (Hastie, 1992). This

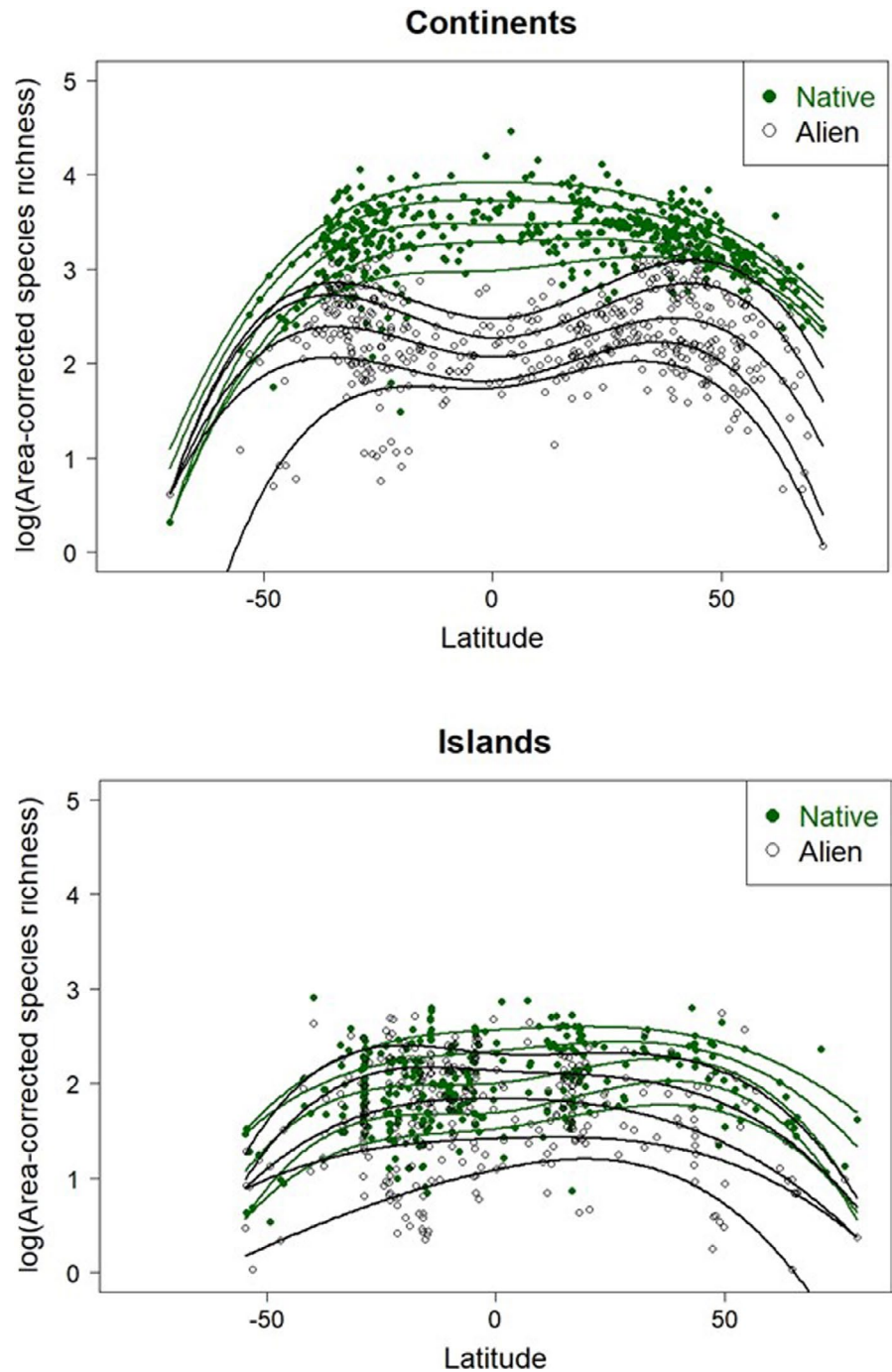
allows the cubic polynomial to have different shapes in the Northern and Southern Hemispheres, thus testing whether the two hemispheres showed similar latitudinal invasion patterns (e.g. Chown, Sinclair, Leinaas, & Gaston, 2004; Hillebrand, 2004; Rejmánek, 1996; van Kleunen et al., 2015). We obtained estimates for the 0.10, 0.25, 0.50, 0.75 and 0.90 quantiles (here denoted as 10th, 25th, 50th, 75th and 90th percentiles) to provide a concise depiction of how the range of values of species richness changes with latitude, and we tested null hypotheses of zero effects using bootstrapped (10,000 resamples) standard errors. We found that the latitudinal patterns were roughly symmetrical between the two hemispheres with declining richness towards higher latitudes, except that alien richness in continental regions exhibited a bimodal pattern with the highest richness at about 40 degrees in both hemispheres (Figure 1).

Our initial observation showed that the variation in invasion levels around the world can be described as a “bounded distribution” (i.e. a distribution with set upper and lower limits; Johnson, 1949), for which a simple regression would not be valid. Therefore, we used quantile regression as it can directly estimate the heterogeneous changes in level of invasion associated with the “bounded distributions”. To describe the latitudinal patterns for invasion level and possible human effects, we used a logistic quantile regression model (Bottai, Cai, & McKeown, 2010) to estimate changes in the bounded distribution in invasion levels (a proportion on the interval [0, 1]) between continents and islands, with changes in latitude and with changes in latitude and human population density (people per km²). This approach uses a logit transformation of invasion level in a linear quantile regression model (Cade & Noon, 2003). We used cubic B-splines with a single knot at 0 degrees on the predictor latitude similar to our models for species richness. To plot the partial effect of latitude in the model that included the natural logarithm of human population density, we selected representative values of population density ($0 = \ln(1)$ person km² and $6 = \ln(403)$ persons per km²) where there were many observations to depict the estimated effect of latitude while fixing the effect of population density. We also examined the partial effect of the logarithm of human population density at two representative values of latitude (0 and 30 degrees). We used the R packages ‘quantreg’ (Koenker, 2018) and ‘splines’ for quantile and splines analyses in the statistical software environment R version 3.5.2 (R Development Core Team, 2018).

The logistic quantile regression estimates indicated that higher invasion levels for islands compared to the continents were heterogeneous, with differences increasing from lower to higher quantiles; 0.052 for 10th, 0.116 for 25th, 0.260 for 50th, 0.332 for 75th and 0.369 for 90th percentiles ($p < 0.0001$ for all quantiles). A Mann–Whitney test showed that islands on average had a significantly higher invasion level (0.348) than continental regions (0.118) ($U = 26,732.50$, $p < 0.001$). A Mann–Whitney test also revealed that regions in the Northern Hemisphere were less invaded (invasion level = 0.158) than regions located at the same latitude in the Southern Hemisphere (invasion level = 0.267) ($U = 54,846.50$, $p < 0.001$). An examination of the patterns of quantile estimates by latitude indicated that most of this difference was attributed to higher invasion levels on islands in the Southern Hemisphere



FIGURE 1 Logarithm of area-corrected species richness for alien plants by latitude (degrees) for 474 regions on continents (top panel) and 327 regions on islands (bottom panel) around the globe. Lines are quantile regression estimates for 10th, 25th, 50th, 75th and 90th percentiles (ascending from lowest to highest) of log (area-corrected species richness) in a linear quantile regression model using cubic polynomials of latitude with a single knot at 0 degrees latitude (B-spline function). The B-spline effects of latitude were statistically non-zero for continents ($p < 0.0001$ for all quantiles for natives and aliens) and for islands ($p < 0.002$ for 10th, 50th, 75th and 90th and $p = 0.168$ for 25th for aliens, and $p < 0.002$ for all quantiles of natives) [Colour figure can be viewed at wileyonlinelibrary.com]



(Figure 2b) because there was less difference in invasion level on continents between the two hemispheres (Figure 2a). When both islands and continental regions were combined (Fig. S1), at low latitudes (i.e. in tropical regions), invasion levels of different regions were high and low, whereas they were consistently low at high latitudes especially in the Northern Hemisphere.

The observed invasion levels across the globe form a pattern that could be described by a “constraint envelope” (Brown, 1995; Hao, Yu, Wu, Guo, & Liu, 2016) with respect to latitude that differs between continental regions (Figure 2a) and islands (Figure 2b). For islands, there was a decrease in invasion level with increasing latitude that was more pronounced in the Northern than in the Southern

Hemisphere. Islands at higher latitudes had low invasion levels but those at lower latitudes, especially the tropical ones, varied greatly in invasion level. While many tropical islands have been heavily invaded, many others still have low invasion levels. For continents, temperate regions (e.g. latitudes around 40°) showed both high and low invasion levels, while most regions in tropical and at very high latitudes (e.g. > 55°) had lower invasion levels than temperate regions.

When we included effects of human population density in the model, it had a positive, statistically non-zero effects on the invasion level distribution after adjusting for the nonlinear effects of latitude (Fig. S2). The partial effects of human population density demonstrate that this factor significantly affects the invasion levels on the

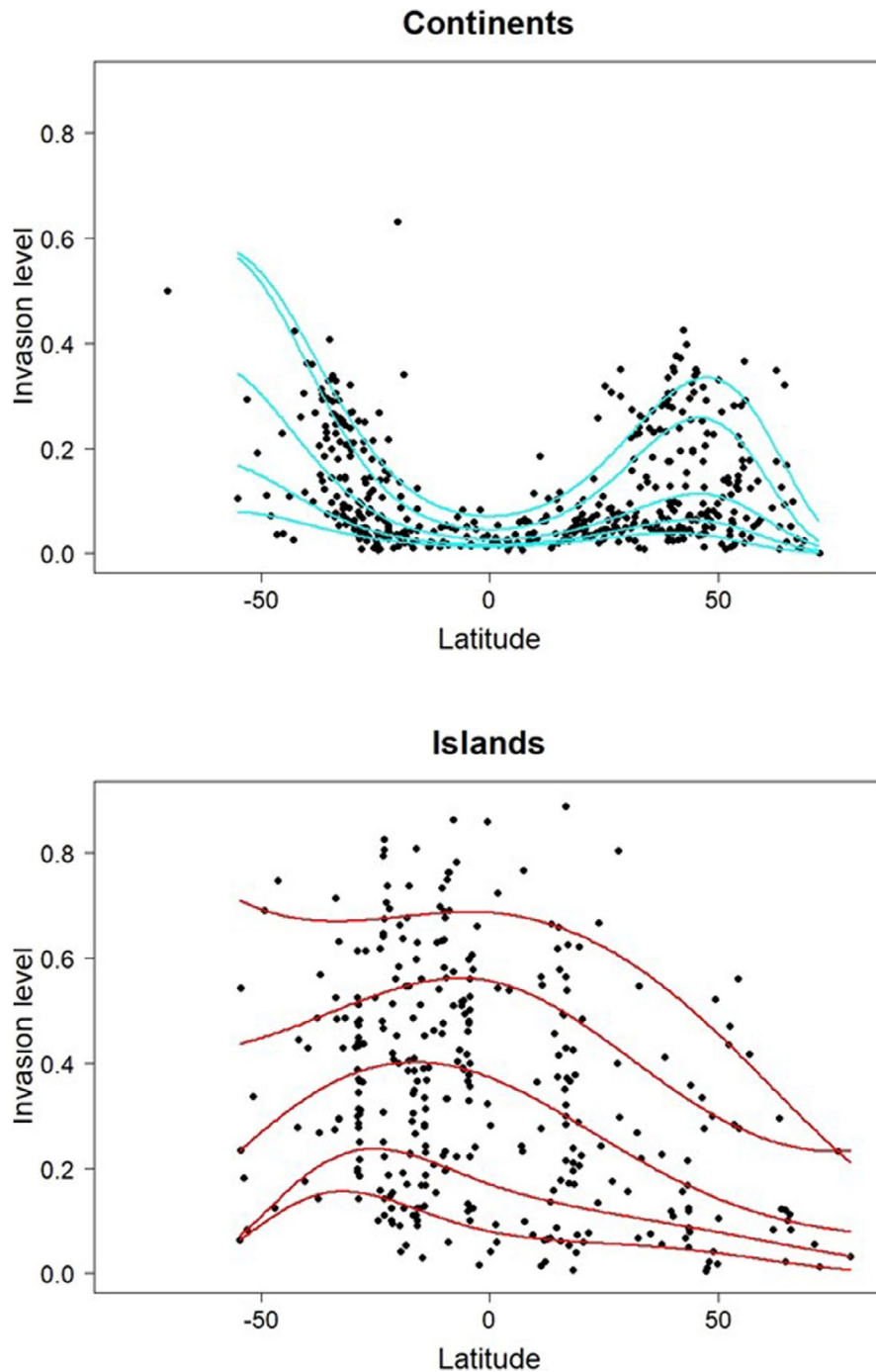


FIGURE 2 Invasion level (alien richness/overall species richness) for plants by latitude (degrees) for 474 regions on continents (top panel) and 327 regions on islands (bottom panel) around the globe. Lines are quantile regression estimates for 10th, 25th, 50th, 75th and 90th percentiles (ascending from lowest to highest) of invasion levels from a logistic model form using cubic polynomials of latitude with a single knot at 0 degrees latitude (B-spline function). The model was estimated in its linear form by making a logit transformation of invasion level (which is a proportion), $\text{logit}(\text{invasion level}) = \log((\text{invasion level} - 0.0 + \eta)/(1.0 - \text{invasion level} + \eta))$, where $\eta = 0.001$ is used to handle any values equal to 0 or 1. Estimates were then back-transformed to the nonlinear logistic model form (Bottai et al., 2010). The B-spline effects of latitude were statistically non-zero for continents ($p < 0.0001$ for all quantiles) and for islands ($p < 0.010$ for 10th, 25th, 50th and 75th and $p = 0.012$ for 90th) [Colour figure can be viewed at wileyonlinelibrary.com]

continents and on the islands even after accounting for the collinearity between human population density and latitude. Furthermore, the partial effects of latitude indicate that there are effects of latitude on invasion levels that are not directly related to human population density (Figure 3).

3 | POSSIBLE CAUSES FOR THE LATITUDINAL PATTERNS

The results based on the most comprehensive naturalization data set available to date ($n = 801$ islands/regions) show patterns similar

to previous analyses based on smaller numbers of regions (e.g. $n = 115$ in Rejmánek, 1996) (see also Sax, 2001 and Fine, 2002), and indicate that these findings are robust. A common notion that tropical regions are more resistant to invasion has existed in the literature for some time (e.g. Dobzhansky 1950). However, the true processes behind the observed patterns may be more complex than biotic resistance alone. We outline some of the possible causes below.

1. Propagule and colonization pressure: First, previous research showed that propagule and colonization pressures are strongly linked to human population density, land use, agriculture and

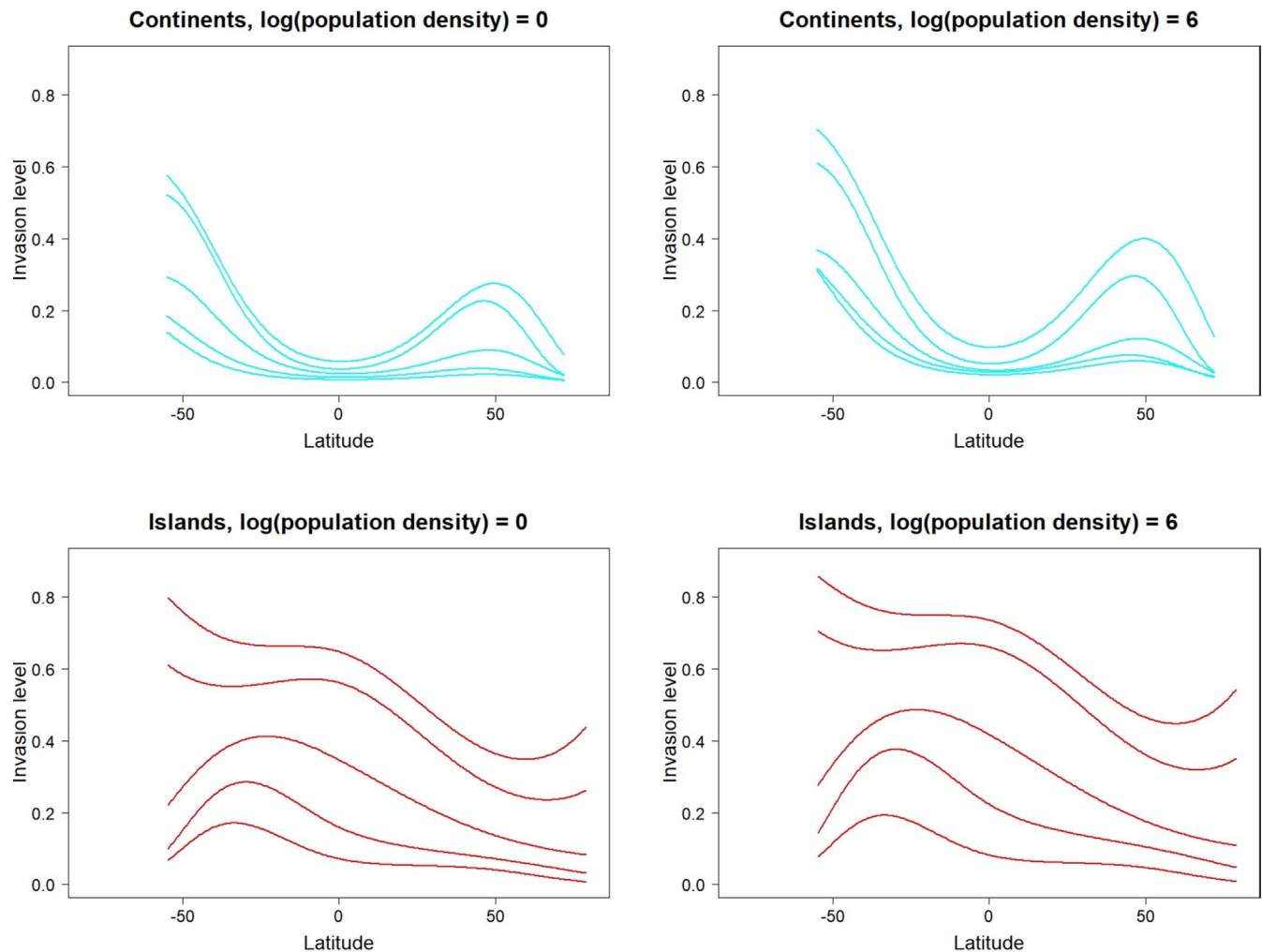


FIGURE 3 Partial quantile regression estimates for plant invasion levels (alien richness/overall species richness) by latitude (degrees) at logarithms of population density equal to 0 (1.0 per km²) and 6 (403.4 per km²) for 474 regions on continents (top panels) and 327 regions on islands (bottom panels) around the globe. Lines are quantile regression estimates for 10th, 25th, 50th, 75th and 90th percentiles (ascending from lowest to highest) of invasion level from a logistic model form using cubic polynomials of latitude with a single knot at 0 degrees latitude (B-spline function) and a linear function of log(population density, number per km²). Note, when a region had 0.0 people per km² this was converted to 0.005 to be able to take logarithms. The model was estimated in its linear form by making a logit transformation of invasion level (which is a proportion), $\text{logit}(\text{invasion level}) = \log((\text{invasion level} - 0.0 + \eta)/(1.0 - \text{invasion level} + \eta))$, where $\eta = 0.001$. Estimates were then back-transformed to the nonlinear logistic model form (Bottai et al., 2010) [Colour figure can be viewed at wileyonlinelibrary.com]

disturbance (Lockwood, Cassey, & Blackburn, 2009; Pyšek et al., 2010). The higher invasion levels on tropical islands than in tropical continental areas could in part be due to differences in human population density and tourism (Moser et al., 2018; Rejmánek, 1996). Particularly, across tropical zones, humans seem to prefer tropical islands for travel and even residency over tropical continental areas (Figs. S2–S3)(Gössling, 2003; McElroy, 2003). Second, propagule and colonization pressure are also closely related to patterns of global trade and travel. There was, and still is, a much stronger trade between temperate regions (e.g. between Europe, North America and Asia) than between tropical regions (Seebens et al., 2015). Temperate continental regions also experienced greater land use changes coupled with higher colonization and propagule pressures in the past than the tropical continental regions.

2. Latitudinal distribution of native species and land area: Although land mass in the Southern Hemisphere is largest in the tropics, in the Northern Hemisphere, it is largest in the temperate zone between 30 and 60° (Fig. S4). Nevertheless, tropical regions have larger native species pools than regions at higher latitudes for both hemispheres (Rosenzweig, 1992). Hence, the impact of native species distribution and land area may further explain the observed latitudinal invasion patterns. Even though the number of alien species per unit area remains the same, invasion level is lower in tropical regions than in temperate regions because tropical regions have higher native species richness per unit area.
3. Biotic resistance: The tropics have higher overall species richness, which implies that there are more competitors (plants) and enemies such as herbivores and pests (Freestone, Ruiz, & Torchin, 2013). It is also possible that the larger species pool in

the tropics compared to temperate zones results in higher species density (the number of species per unit area) and more complete occupancy of the ecological niche space. This might result in a higher resistance against invasions of species from both non-tropical and other tropical regions. This is the case at smaller scales when high native richness is coupled with relatively low human population density and thus less human-induced disturbance (Levine & D'Antonio, 1999). Nevertheless, whether and how small-scale invasion (and resistance) phenomena can be translated to regional- and global-scale patterns remains to be explored.

Among the three major possible mechanisms behind the observed latitudinal patterns described above, the biotic resistance hypothesis lacks the most direct and solid evidence. Indirect evidence for biotic resistance may be inferred from comparisons of geographic range boundaries in species' native and naturalized ranges. The upper latitudes of alien species distributions can be higher or lower than those in their native ranges, but their distributions in lower latitudes are unlikely to be lower than those in their native ranges (Sax, 2001). This observation seems consistent with the hypothesis that continental regions in the tropics are more difficult to invade than those at higher latitudes and supports the notion that biotic resistance may play a role in limiting species invasions.

Species interactions may be more important towards the equator (e.g. Roslin et al., 2017), whereas physical factors may be more important in determining species distribution at higher latitudes (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). This has important implications for species invasiveness and habitat invasibility. Furthermore, work at large spatial scales suggests that biotic interactions in the tropics that ultimately inhibit species invasions (i.e. those determining biotic resistance) may be mediated primarily through the actions of predators and pathogens rather than competitors (Freestone et al., 2013). This is potentially a critical insight for ecological research because current efforts to document biotic resistance to invasion in plant communities have been dominated by research on competition (Levine, Adler, & Yelenik 2004).

Relative to the Northern Hemisphere, the Southern Hemisphere has less land mass (Fig. S4) but higher invasion levels, at least partly suggesting that a large number of alien species might have been introduced from the Northern Hemisphere. This is consistent with the observation by Darwin (1859) and a recent finding by van Kleunen et al. (2015) based on the GloNAF database. This might partly be because plants from the Northern Hemisphere are disproportionately over-represented among plants that are cultivated for their economic uses (van Kleunen et al., 2020).

Global warming could be another contributing factor to our observed patterns as it has been demonstrated that many species have shifted their ranges poleward (Thomas, 2010). Warming climates coupled with increased human introductions could increase the likelihood that many tropical species will invade temperate regions (although few species from temperate regions might become established at higher elevations in the tropics) (Guo, Sax, Qian, & Early, 2012; Pyšek et al., 2010; Thuiller et al., 2005).

An important finding of this study is that, despite the general trends in Figure 2, many tropical islands and temperate regions have very low invasion levels. The main reason could be that they are under much lower human influence, but the true causes need to be examined for each region or island individually (Figure 2, Figures S2, S3). In contrast, higher invasion levels on some tropical islands could be due to their lower native richness (lower resistance) and disharmonic species composition which are both related to their remoteness and/or isolation (König et al., 2019; Moser et al., 2018). Another point is that the higher variation in invasion level may be mostly due to difference in latitudinal patterns between native and alien species. That is, while native richness clearly declines with latitude (Rosenzweig, 1992), the pattern for alien richness is much more variable (i.e. when plotting richness against latitude, natives have smaller residuals and stronger coefficients than alien species; Figure 1).

At the current pace of species invasions associated with climate change and other human disturbances (Guo et al., 2012), it is likely that the increased invasion levels across latitudes and regions may lead to increased extinction of locally native species and biotic homogenization (Winter et al., 2009). While it is true that around the globe high latitudes and tropical continents consistently have lower invasion levels, it is critical to investigate in the future why temperate continents and tropical-temperate islands show such drastic variations in their invasion levels (i.e. range from close to 0 to close to 1; Figure 2).

Finally, as is the case with many ecological studies, inference from our study may be limited by sampling bias and/or incompleteness of available data (Yang, Ma, & Kreft, 2013). For example, sampling is more intense and extensive in temperate regions than in tropical regions (van Kleunen et al., 2019; Pyšek et al., 2008) (Figure 1). However, given the overall large sample size, we believe that the general conclusions are robust.

4 | LINKS TO OTHER GLOBAL AND REGIONAL PATTERNS

Although the latitudinal differences in invasion level are evident, regions in the same latitudinal zone also show very different invasion levels (Fig. S5). Despite socioeconomic factors, including human population density, which is regarded as a major driver of large-scale invasion patterns (Essl et al., 2011, 2019; Pyšek et al., 2010), anthropogenic effects are not consistent across all regions. For example, eastern Asia and North America have similar latitudes and areas, but the former has a higher native species diversity and as a consequence a lower invasion level (0.066) than the latter (0.192). Furthermore, some regions with very high human population densities, especially those in tropical zones, such as southern and south-eastern Asia, show moderate invasion levels (e.g. tropical Asia's = 0.145) (Pyšek et al., 2017).

Such differences in invasions among continents have been poorly studied so far (Fig. S5) (Heberling, Jo, Kozhevnikov, Lee, & Fridley, 2017; Rejmánek, 2003). However, it would be insightful if, when discussing latitudinal patterns, we also make comparisons of species invasions across continents. According to climate



matching, it is expected that most alien species in each latitudinal zone might have come from the same latitudinal zone. Thus, we would expect introduced species from tropical regions to have a greater chance of naturalization in other tropical regions, than non-tropical species. Further work should explore how plant invasion is modulated by biotic interactions, biotic resistance and enemy release (Liu & Stiling, 2006). Comparisons of invasion success among environmentally similar regions would be informative to detect biotic interactions particularly biotic resistance (Guo, Qian, Ricklefs, & Xi, 2006; Heberling et al., 2017; Pauchard, Cavieres, & Bustamante, 2004).

Using the most comprehensive database available, we have examined the latitudinal patterns of plant invasions. The great differences between islands and continents and between tropical and temperate continental regions that we found have important implications for invasion biology and biogeography. For example, due to species niche conservatism (Wiens et al., 2010), everything else (e.g. propagule pressure) being equal, one might expect greater homogenization across longitudes than across latitudes. If the velocity of climate change accelerates, species might show more frequent shifts across latitudes. Such changes could affect speciation (e.g. through hybridization between natives and aliens) and extinctions at different latitudes and on different continents (Abbott, 2017; Bebber, 2015; Todesco et al., 2016). Finally, management should pay more attention to latitudes in which invasions occur, as invasion levels vary with geography and may require different approaches. For example, in habitats with low invasion level but high invasion potential, early prevention and detection of high-risk species may be more effective. To better understand latitudinal patterns of invasion, large-scale experiments and further elaboration of theoretical framework is needed. Also, it would be very useful to compare both the latitudinal and longitudinal (among continents) invasion patterns between plants and other taxonomic groups such as birds, mammals and fishes particularly because of their different dispersal capacity, introduction history and sensitivity to climate/land use changes (e.g. Dyer et al., 2020; Sax, 2001).

5 | CONCLUSIONS

Our results show clear latitudinal patterns of plant invasions, which differ between islands and continents. Humans are a dominant factor explaining the observed patterns in invasion levels after latitude, but species pool size, climate warming and biotic resistance likely also play a role (Karger et al., 2016). Although the latitudinal patterns in species invasions between the Northern and Southern Hemispheres are somewhat similar, there are significant differences in the invasion levels. More importantly, while the patterns are similar across both hemispheres for continental regions, they differ between hemispheres for islands. The latitudinal invasion pattern suggests that, while invasion levels on islands decrease with latitude towards polar regions more strongly in the Northern Hemisphere and those on continental regions peak

at mid-latitudes in both hemispheres, invasion levels could occur anywhere below the upper bounds of the distribution. The general trends – modulated by substantial variation in invasion levels – imply that there are still many regions or islands that currently are not heavily invaded. Such large differences in invasion levels may have important implications for decisions on management and conservation priorities. Future work should closely monitor species invasions across latitudes and major geographic regions and focus on the local–regional–global links with long-term perspectives (Dawson et al., 2013).

KEYWORDS

biogeography, biotic homogenization, globalization, human population, invasion level, macroscale, propagule pressure

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DATA AVAILABILITY STATEMENT

Data analysed in this study and the code for analyses in R can be download from Dryad repository. Dataset <https://doi.org/10.5061/dryad.qnk98sfd8>.

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**BIOSKETCH**

The authors are broadly interested in community ecology, invasion biology and biogeography.

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Author contributions: QG initiated the research, BC and QG analysed the data, WD, FE, HK, JP, PP, MvK, PW and MW collected data and all authors contributed to developing and writing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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