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RESEARCH ARTICLE

Non-natives are linked to higher plant diversity across spatial scales

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Abstract

Aim: Although non-native and invasive plants often pose a significant threat to biodiversity, global-scale studies have yet to conclusively demonstrate a systematic pattern of reduced native plant diversity in areas affected by these invasions. Here, we aim to explore the association of non-native and invasive plants with the species richness and evenness of plant communities from the local to global scale.

Location: Global.

Methods: We use the world's largest vegetation plot repository—sPlot—to compare species richness and community evenness between invaded (by invasive or non-natives) and native plots of equal size, paired within 32 km^2 grid cells distributed across all continents. Aggregating plots at the cell, biome and global level, we also quantified differences in gamma diversity at different spatial scales.

Results: We found that invaded plots had higher species richness and similar community evenness, a trend largely consistent across biomes. The higher total species richness was not the result of additional invasive or non-native species, as the number of native species was also higher in invaded plots. These patterns persisted at larger spatial scales. Cell, biome and global gamma species richness of invaded plots were consistently higher than of native plots. All these patterns held regardless of whether the non-native species in a plot were invasive or non-invasive.

Main Conclusions: Our study reveals a globally consistent pattern: plant diversity, both total and native, is higher when invasive or non-native plants are present, spanning spatial scales from local to global. Although we cannot infer causal effects, our results challenge the prevailing hypothesis that non-native and invasive species universally depress plant diversity.

KEYWORDS
biological invasions, biosecurity, biotic homogenisation, ecological impacts, global change, sPlot

1 | INTRODUCTION

The spread of non-native plant species is a conservation concern, with impacts on biodiversity and ecosystem functioning (Daru et al., 2021; Mack et al., 2000; Winter et al., 2009; Yang et al., 2021). Such species are implicated in the homogenization of the global flora (Daru et al., 2021; Yang et al., 2021), and their rise coincides with population declines in native species, leading to concerns that escalating plant naturalisations and invasions could imperil plant biodiversity (Blackburn et al., 2019; McKinney & Lockwood, 1999; Pyšek et al., 2020). Amidst this backdrop, the Kunming and Montreal Global Biodiversity Framework has prioritised mitigating biological invasions by 2030 (https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222). However, the latest assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services reveals that just 15.4% of the 218 alien taxa causing local extinctions are plants (Roy et al., 2023). This implies that only 0.24% (34 out of 13,939 species, Van Kleunen et al., 2019) of the world's naturalised flora are identified as extinction drivers. Concurrently, the scientific literature also describes positive impacts of non-native species on biodiversity, and suggests that the disproportionate focus on non-natives' negative impacts may be biasing scientific conclusions (Davis et al., 2011; Guerin et al., 2018; Gurevitch & Padilla, 2004; Maskell et al., 2006; Powell et al., 2013; Sax et al., 2022; Thomas & Palmer, 2015).

Concerns over non-native species' impacts are linked to spatial scale, whether invasive or not (Kindlund & Tyler, 2023; Kortz & Magurran, 2019; Powell et al., 2013; Thomas, 2020; Tomasetto et al., 2019; Vellend et al., 2017). At the plot level, non-native plants are often assumed to play a negative role by decreasing native species abundance, reducing diversity and driving local extinctions (Bacher et al., 2023; Blackburn et al., 2019; Elton, 1958; Wilcove et al., 1998). But various factors may confound the role of invasions in altering plant diversity (Gallardo et al., 2016; Jauni et al., 2015). For instance, invasions may be more common in disturbed, early-successional communities than in late-successional ones (Martin et al., 2009), where early successional plots could be more species-rich simply because plants are smaller than in later-successional stages, where fewer, taller species dominate (Odum, 1969; Staude et al., 2023). Conversely, communities with higher species diversity may be inherently less invasible because more niches are filled, leaving fewer opportunities for invaders (Elton, 1958). While there is little systematic evidence of direct negative impacts of non-native (non-invasive) plants (Andreu & Vilà, 2011; Davis et al., 2011; Gaertner et al., 2009; Jeschke et al., 2014; Sax et al., 2022), synthesis studies on invasive plants do find negative effects (Hejda et al., 2009; Pyšek et al., 2012, 2020; Vilà et al., 2011). However, these are often context-specific, linked to the biome, invasive species' functional traits and their interaction with the invaded community—among other factors (Pyšek et al., 2012). Moreover, the classification of species as invasive can vary and be independent of its impact (Fachinello et al., 2022; Pereyra, 2016; Richardson et al., 2000). For instance, a species deemed invasive in a large, ecologically diverse political unit may not uniformly harm local plant communities across that region (Davis et al., 2011; Tomasetto et al., 2019). Thus, it is likely that even invasives do not universally affect local plant communities negatively.

At the landscape scale, non-natives are typically found to offset losses in native flora (Vellend et al., 2017). Non-native species are mostly occurring at low densities in the landscape and at that scale do not threaten native flora (Kindlund & Tyler, 2023). Even for invasive species, studies shows that their negative impact decreases with increasing spatial scale (Powell et al., 2011; Tomasetto et al., 2019). While some native species may be outcompeted and driven to local extinction, they often still occur in the wider landscape, where other factors tend to play a role in extinctions from larger spatial units (e.g. land-use change or land abandonment; Kindlund & Tyler, 2023). At even larger spatial scales, the most profound effect of non-natives is their contribution to biotic homogenisation, leading to a convergence of flora across different countries (Baiser et al., 2012; Daru et al., 2021; Li et al., 2020; Winter et al., 2009; Yang et al., 2021). Indeed, some authors suggest that although non-native species may increase species richness at local and landscape levels, this trend can obscure the ongoing loss of native species, biotic homogenisation and, in the bigger picture, a global decline in biodiversity (Kortz & Magurran, 2019; Sax et al., 2022). The prevailing hypothesis holds that larger-ranged non-native species, by replacing smaller-ranged native flora, contribute to a decrease in gamma diversity (Kortz & Magurran, 2019; Staude et al., 2020). Alternatively, gamma diversity of invaded plots could be higher if (a) non-native species colonise but do not replace native species (Gilbert & Lechowicz, 2005) and (b) colonising non-native species—despite their larger range—differ across plots (Thomas, 2020). Globally, with over 13,000 naturalising plant species (Seebens et al., 2023; Van Kleunen et al., 2019), this additional species pool could enhance gamma diversity in invaded areas across spatial scales if native species diversity is not lost in that process.

Here, we investigate these scenarios by exploring patterns and associations between the presence of non-invasive non-native (hereafter 'non-native') and invasive non-native plants (hereafter 'invasive') with total as well as native plant diversity across multiple spatial scales. Using sPlot, the most extensive global vegetation plot database to date, we compare local (alpha) diversity between spatially proximate invaded (by non-natives or invasives) and native plots. We go beyond the local scale, aggregating plots within 32 km^2 cells, biomes and globally to quantify the association of non-native/invasive species presence with gamma diversity across spatial scales. We have two alternative hypotheses. (1) Invaded plots may have consistently lower alpha diversity than native plots because a few non-native plants replace many native ones, where this impact is especially pronounced when invasives invade. At larger spatial scales, invaded plots may feature lower gamma diversity than native plots, because invaders have larger range sizes leading to more convergent species compositions across invaded plots. (2) Invaded plots may have equal or greater alpha diversity than native plots due to gains in non-native/invasive species or other factors unrelated to non-native/invasive species presence. At larger spatial scales,

invaded plots may have equal or greater gamma diversity than native plots because invaders vary across plots and native flora is not consistently lost. While this study cannot infer mechanisms and causal effects, it tests whether diversity patterns between invaded and non-invaded communities are consistent with the prevailing hypothesis that non-native/invasive species pose a systematic threat to native flora.

2 | MATERIALS AND METHODS

2.1 | Databases

We differentiated plots with invasive species, plots with non-native species and plots with only native species by combining sPlotOpen (Sabatini et al., 2021), GloNAF (Van Kleunen et al., 2019) and GRIIS (Pagad et al., 2018). sPlotOpen collates vegetation community data for 95,104 plots sampled between 1988 and 2015 ranging from 0.01 to 40,000 m^2 containing the presence and abundance of vascular plant species. We used GloNAF species lists to identify non-native plant species within each plot. We used GRIIS species lists to identify invasive plant species within each plot. GloNAF includes non-native species recorded under two possible statuses: alien and naturalised. An alien species is defined as "a species whose presence in a region is attributable to human activities that have enabled it to overcome the barriers that define its natural range", and naturalised species are "a subset of alien species which have established a viable self-sustaining population" (Roy et al., 2023, p. 9). Here, we do not distinguish between alien and naturalised species and therefore designate both types as non-native. We used the region polygons provided by GloNAF to spatially match the geographic coordinates of each plot from the sPlot database to identify non-native species in sPlot. Using the alpha-3 country codes in both sPlot and GRIIS, we identified invasive species. Aligning with GRIIS's definition of invasive species ("a taxon whose introduction and/or spread threatens biological diversity"; Pagad et al., 2018, p. 2), we consider all invasive species to be non-native. All species in sPlot that did not match with species from GloNAF or GRIIS databases were assumed to be native. A total of 1,780,022 (97.5%) species records were native, 33,903 (1.9%) were non-native, and 11,510 (0.6%) were invasive. Each plot was assigned a plot status: (1) "invasive plot": contains at least one invasive plant (may additionally contain non-natives); (2) "non-native plot": contains at least one non-native plant, but no invasives; (3) "native plot": contains only native plants.

2.2 | Plot selection

To quantify diversity differences between invaded (by invasives or non-natives) plots and native plots, plots had to be spatially proximate. We grouped plots onto a discrete, equal-area global grid with hexagonal grid cells of 32 km^2 (Barnes, 2017). We required that cells had at least three native plots, and either at least three non-native plots or at least three invasive plots. We required all plots within a given cell to have the same size, given the dependence of species richness on plot size. To find the highest number of equal-sized plots within a grid cell, we calculated the mode (i.e. the most frequent) plot size in each cell, discarding all plots of different sizes in the cell. Plot number (minimum three) and grid cell size (32 km^2) was chosen to maximise the number of cells and plots analysed, while ensuring that plots for our comparison were geographically close (maximum 7 km apart, which is the maximum distance in a 32 km^2 hexagon). The total number of plots was 1645 for the invasive vs. native plot comparison, with 694 native plots (42%) and 951 invasive plots (58%), across 109 cells and 9 biomes; median plot size was 78.5 m^2 (min = 0.25, max = 100). The total number of plots was 2117 for the non-native versus native plot comparison, with 739 native plots (35%) and 1378 non-native plots (65%), across 127 cells and 10 biomes; median plot size was 100 m^2 (min = 0.25, max = 1600). Our analysis of invasive vs. native plot diversity covered all biomes in sPlot, except for the polar and subpolar zones; our analysis of non-native vs. native plot diversity spanned all 10 biomes in sPlot (sBiomes classification described by Bruelheide et al., 2019). Certain regions were under- or over-represented. Most data were available for Central Europe, while little or no data were available for Western Asia, the Middle East, North Africa, and Sub-Saharan Africa (Figure 1).

2.3 | Biodiversity metrics

For our comparison of alpha diversity between invaded and native plots, we tested two aspects of biodiversity: species richness and community evenness (measured as Pielou's J). Due to sPlot's taxonomic standardisation, some species were listed more than once in some plots. Their relative cover was summed and richness was computed by counting all distinct species in a plot. Although sPlot contains data on the relative abundance of each species in each plot normalised to 1, data for some plots are computed based on simple presence-absence data and therefore do not accurately inform on the relative coverage. A total of 109 and 34 plots for comparing invasive vs. native plots and non-native vs. native plots, respectively, were originally recorded with presence-absence data and thus removed from the evenness analysis. For our gamma diversity comparison between invaded and native plots across spatial scales, we focused on species richness. We measured richness at three additional spatial scales: cell, biome and global. To calculate richness at these scales, we adopted a sampling procedure. To calculate gamma richness in the invaded/native part of, for example, a cell, we aggregated species across all the invaded/native plots in a given cell, while dealing with the differing number of plots that were invaded/native. To aggregate consistently across the same number of plots in each plot status (i.e. invaded/native), we sampled repeatedly (i.e. 100 times) *n* plots from the plot status with more plots, where *n* is the number of plots from the plot status with fewer plots. For example, if a cell had 28 native plots, but only 5 invaded plots, we sampled 100 times 5 plots from the 28 native plots. For each sampling

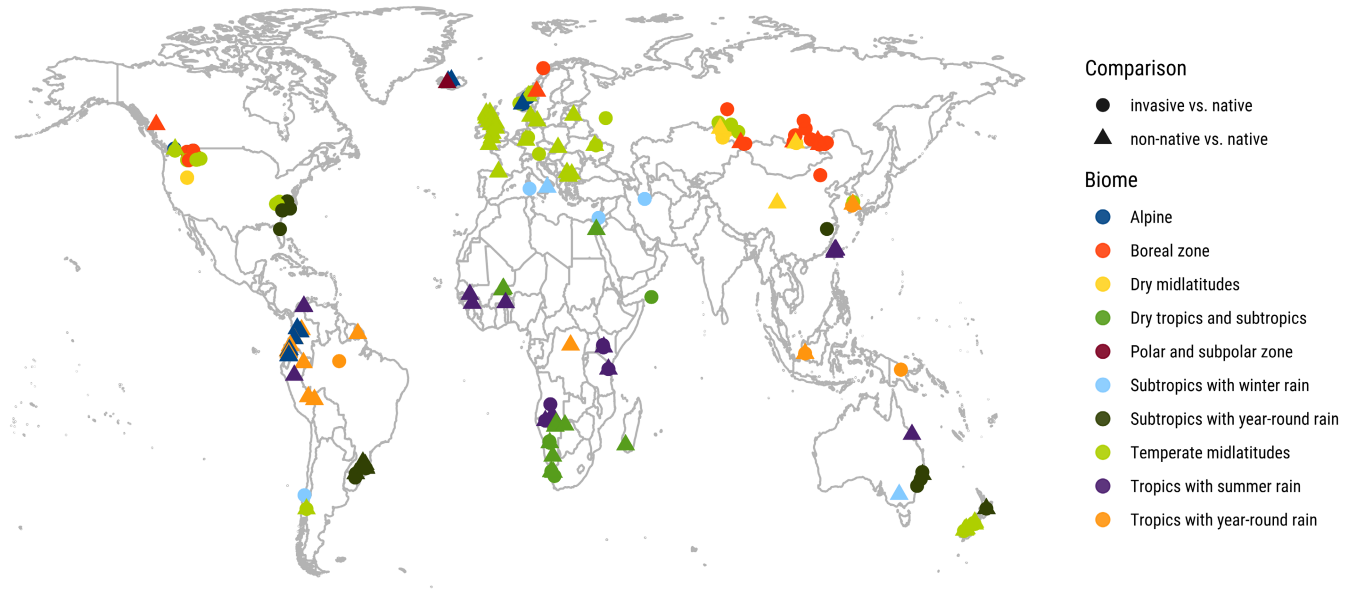

FIGURE 1 Our study comparing alpha and gamma diversity of invaded and native plots spans 10 biomes and 3762 plots. Map shows the plots included in our comparison of diversity between non-native and native plots (circles), and invasive and native plots (triangles). Plots were compared within 32 km^2 grid cells. Grid cells had to comprise at least three native plots, and either at least three non-native or invasive plots, where all plots had to have the same size.

repetition, we calculated gamma richness. We then averaged values across repetitions. We followed the same protocol to calculate biome/global richness: we sampled cells as before, but instead of calculating gamma richness for a cell, we further aggregated species not only across all plots in a cell but across all cells in a biome/on the globe for each sampling repetition.

2.4 | Statistical analysis

Differences in alpha diversity metrics were assessed with generalised linear mixed effect models. We conducted distinct analyses to compare alpha diversity, separately evaluating differences between invasive and native plots, and between non-native and native plots. Models were set up with plot status (indicating either invasive/native plots or non-native/native plots) as fixed effect and cell as random effect to pair plots within cells. We used Poisson mixed effect models for richness as a discrete response variable, and Gaussian mixed effect models for Pielou's J as a continuous response variable. To test for biome-specific variation in the relationship between diversity and plot status, biome was included as a second fixed effect interacting with plot status. We further analysed whether there were any richness differences when *only* the native part of the invaded community was considered. For this, we ran the same models as above but used the species richness of native plants as the response variable. For our comparison of gamma richness across spatial scales, we ran Gaussian linear mixed effect models (i.e. richness was not a discrete variable due to the averaging across sampling repetitions) with gamma richness (log-transformed) as response, plot status as fixed effect, and cell or biome as random effect. Linear models were implemented in R using the lme4 package (Bates et al., 2015). We checked whether assumptions of models were met using residual plots from the DHARMa package (Hartig, 2022). Using the emmeans package (Lenth, 2022), we quantified the mean difference of richness/Pielou's J and its uncertainty between invaded and native plots. All R code for data handling and carpentry, statistical models, and data visualisation are available on github at: https://github.com/istaude/splot-non-native-div.

3 | RESULTS

On average, we found higher plant species richness in plots where invasive and non-native species were present than in plots where they were not (Figure 2a). Richness was on average 25.3 (95% CI [22.6, 28.3]) in plots with invasive species, compared with 22 (95% CI [19.6, 24.6]) in plots with only native species; and 20.5 (95% CI [18.4, 22.7]) in plots with non-native species, compared with 17.1 (95% CI [15.4, 19]) in plots with only native species. There was, on average, 15% more species in plots with invasive species (95% CI [1.13; 1.8]) and 19% more species in plots with non-native species (95% CI [1.17, 1.22]) than in plots with only native species.

We further found that the higher richness in invaded plots was due not only to additional non-native species, but also to higher numbers of native species (Figure 2a). When examining the native part of plant communities in invaded plots, we found that native species richness was 9% (95% CI [1.07; 1.1]) and 13% (95% CI [1.11; 1.16]) higher, respectively, in plots with invasive and non-native species than in plots with only native species. These average richness trends were largely consistent across biomes. With the exception of

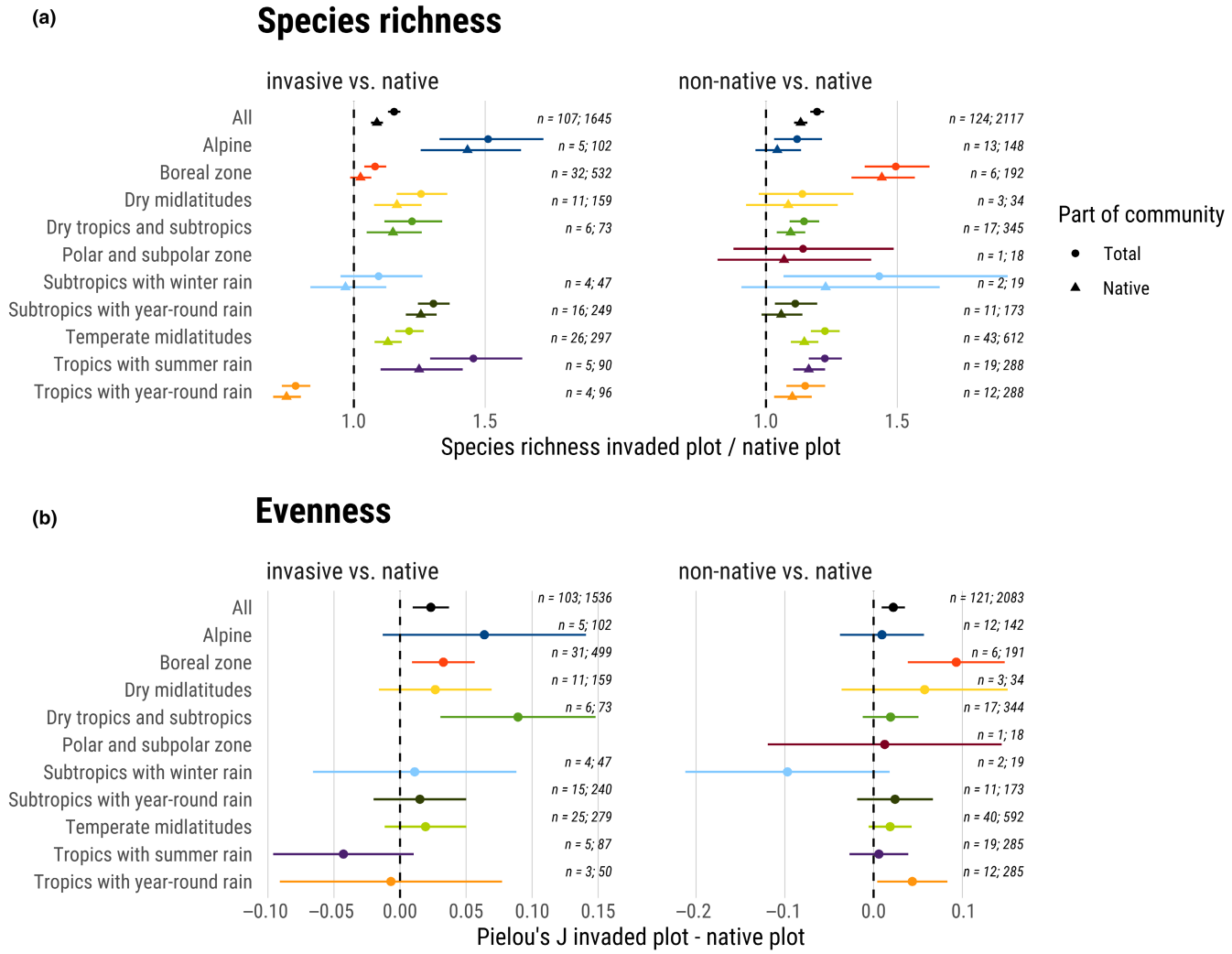

FIGURE 2 Alpha diversity is higher in invaded than native plots overall and across biomes. (a) Comparison of total (circle) and native (triangle) plant species richness between invaded and native plots. (b) Comparison of community evenness (calculated as Pielou's J) between invaded and native plots. Points indicate the estimated mean ratio of species richness or difference in Pielou's J between invaded and native plots. Lines are 95% confidence intervals. Dashed vertical line represents zero difference. Numbers (from left to right) indicate the number of cells and plots included in the analysis. For raw data plots, see Figures S1–S3.

plots with invasives in the tropics with year round rain, invaded plots had consistently higher richness than native plots.

A similar (but weaker) trend was found for community evenness (Figure 2b). Pielou's J averaged 0.71 (95% CI [0.69; 0.71]) in plots with invasive species, compared with 0.69 (95% CI [0.67; 0.71]) in plots with only native species, and 0.73 (95% CI [0.71; 0.76]) in plots with non-native species, compared with 0.71 (95% CI [0.69; 0.74]) in plots with only native species. Pielou's J was, on average, 0.02 (95% CI [0.01; 0.04]) higher in plots with invasives and non-native species than in plots with only native species (Figure 2b). While these overall differences were statistically clear (albeit rather minor), differences varied considerably across biomes and were statistically unclear in most biomes. Only in the boreal zone, invaded plots (both invasive and non-native) had consistently higher evenness than native plots.

The higher species richness in invaded plots was not only a local pattern, but persisted at larger spatial scales (Figure 3). When species were aggregated across plots within cells, we found that, on average, gamma richness of plots with invasives and non-native was 14% (95% CI [1.07; 1.22]) and 13% (95% CI [1.07; 1.2]) higher than gamma richness of plots with only natives (corresponding to mean gamma richness of 58.4 vs. 51.2 and 47.4 vs. 41.8, respectively). Aggregating plots within biomes revealed 16% (95% CI [1.01; 1.34]) and 10% (95% CI [1.03; 1.18]) higher gamma richness of invaded than native plots (corresponding to mean gamma richness of 435 vs. 373 and 269 vs. 244, respectively). At the global scale, gamma richness was 6% (3948 vs. 3737 species) and 7% (3814 vs. 3574) higher in invasive and non-native plots, respectively, compared to native plots.

4 | DISCUSSION

Here, we studied the difference in alpha and gamma diversity between plots containing only native species and plots containing also either non-native or invasive species, using the world's largest

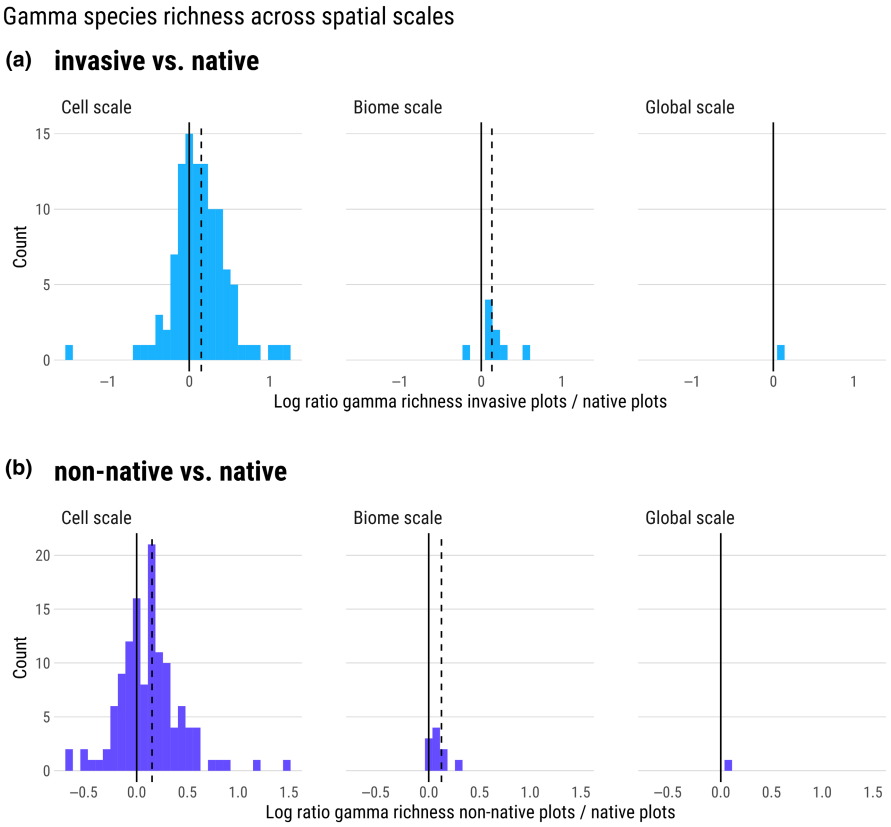

FIGURE 3 From the spatial scale of a 32 km^2 hexagonal grid cell to the globe, gamma species richness of invaded plots is higher, on average, than of native plots. Histograms of effect sizes of richness differences between invasive (a) and non-native (b) to native plots aggregated at different spatial scales (from left to right: grid cell, biome, globe). Effect size is calculated as the log ratio of invaded to native gamma richness. Dashed vertical line represents the estimated mean difference. Black vertical line represents zero difference. For raw data plots, see Figure S4.

vegetation plot repository, sPlot. We found higher average species richness and evenness in plots invaded by invasive or non-native species compared to native plots. Native species richness was also higher in invaded plots, suggesting that differences in richness are not only due to additional invaders. A cross-biome comparison revealed a largely consistent higher alpha richness in invaded plots across biomes; evenness differences showed more variation across biomes, indicating that there may not be a systematic difference in evenness between invaded and native plots. Gamma species richness of invaded plots—aggregated at the spatial scale of a 32 km^2 grid cell, biome and the globe—was consistently higher than of native plots. These results are in stark contrast to the commonly held and prevailing negative perception of non-native (and invasive) species in relation to species diversity.

Our most unexpected finding is that invasive species were not associated with lower alpha diversity, conflicting with findings from previous meta-analyses (Pyšek et al., 2012; Vilà et al., 2011). This may have several reasons. On the one hand, collation of studies aiming to assess the impact of invasive species may be biased towards sites where invasives are already dominant and hence focus on the strongest negative outcome for native flora (Kumschick et al., 2015; Ricciardi et al., 2013). This bias may be less pronounced in global vegetation plot databases, which are not designed per se to study the impact of non-natives (Sabatini et al., 2021). On the other hand, it could indicate that species defined as invasive in a given country may not consistently have detrimental ecological impacts in that country – this may be particularly the case in large political units. Countries may further vary in how they define invasiveness leading to the inclusion of species that have established but are ecologically harmless (Fachinello et al., 2022; Pereyra, 2016). These reasons may all act together to paint a different picture of invasive and non-native species when studying their impact with a global vegetation plot repository. Moreover, the data underlying our analyses tend to neglect the many island ecosystems that show rather consistently negative responses to plant invasions (Pyšek et al., 2012; Simberloff, 1995). In that way, our analyses—albeit covering most biomes—are also not free of bias. Yet, the available data suggest that invasives are not, on average, associated with lower alpha diversity that is typically thought to arise from displacement of native by invasive species.

Not only was native species richness not lower or similar in invasive and non-native plots, it was even higher. We suggest it is unlikely that non-natives or invasives directly increase native plant diversity. Instead, we hypothesise that plant invasions are neither the single cause for modulations in alpha diversity nor always a direct threat, but rather a symptom. It could indicate that communities might already possess a higher species richness prior to invasion, which would contradict the diversity-invasibility hypothesis (Elton, 1958), but be consistent with the idea that disturbance can create conditions that temporarily boost species diversity (Odum, 1969). Previous analyses point to the observation that plant invasions are related to disturbance, where invasions tend to be rarer in mature and undisturbed ecosystems due to a greater biotic resistance of these systems (MJ, 1987; Naeem et al., 2000; Jauni et al., 2015). Disturbed habitats are often early-successional, and at the plot level, plant diversity can often be higher in early than in late succession, given that one species of woody plant may replace several herbaceous species in the

course of succession at this spatial scale (Odum, 1969). Thus, plots with non-natives may be more species-rich, simply because they are more likely to be disturbed. In addition, environments that favour native species richness have also been shown to allow non-native species (Gilbert & Lechowicz, 2005; Meiners et al., 2004). That is, plots with a higher species richness could, stochastically, have a greater likelihood of including non-native species than less species-rich plots (Peng et al., 2019). Thus, we speculate one possible explanation for the higher diversity in invaded plots is that, albeit spatially proximate, native plots differ from invaded plots in relation to factors, such as disturbance, successional stage and habitat quality.

While some local studies similarly show that non-native species are associated with higher local plant diversity (Gilbert & Lechowicz, 2005; Kortz & Magurran, 2019; Maskell et al., 2006; Meiners et al., 2004; Szymura et al., 2018), some report lower diversity at larger spatial scales (Kortz & Magurran, 2019). In our data, we find the reverse pattern. Aggregating plots within cells, biomes and globally, revealed that invaded plots had also higher gamma species richness. Previous analyses focusing on the diversity balance of entire countries reported plant invasions, despite leading to biotic homogenisation, increase a country's plant diversity (Winter et al., 2009). While our results align with these studies, our analysis differs, in that we do not investigate the diversity of entire countries, but aggregate species across multiple plots. At the country level, extinctions are considerably less probable compared to colonisations, as this would require the loss of all individuals of a species. Conversely, at the plot level, the chances of extinction and colonisation tend to be more evenly balanced. That is, invasives, which are typically associated with high vegetation cover, or non-invasive non-natives, which when present also occupy physical space, should be more likely in our analysis to displace native species (Pyšek et al., 2012; Vilà et al., 2011), and cause gamma diversity loss when aggregating plots. But according to our analysis and sPlot data this is not the case: native species richness is also higher in invaded plots. Given that we find no indication of native by non-native displacement in our study, we suggest there is no strong reason to expect gamma diversity to decrease due to non-native species.

While our findings challenge the view that non-native and invasive species universally threaten plant diversity, we emphasise that our work has several limitations. Primarily, we use spatial data as a substitute for temporal analysis, where the assumption that non-invaded plots reflect a pre-invasion condition may not be true. Temporal data would offer much deeper insights into the real and causal effects of plant invasions. Additionally, the observed increase in species richness and evenness in invaded plots could be temporary, a phenomenon potentially explained by invasion debt and extinction debt (González-Moreno et al., 2017; Sax & Gaines, 2008). A critical unknown in our study is the introduction time of non-native plants; if these plants are recent arrivals, their full negative impact may not yet be evident. This may be especially problematic as 'invasion meltdown'—where non-native species trigger a cascade promoting further invasions—can progressively exacerbate impacts on native biodiversity over time (Simberloff & Von Holle, 1999). Additionally, the relationship between non-native species and biodiversity at small spatial scales is influenced by multiple, sometimes interacting, factors, including anthropogenic pressures (Bowler et al., 2020; Pretto et al., 2012), habitat type (Tomasetto et al., 2019), habitat modification (Chytrý, Jarosik, et al., 2008), and landscape histories (Didham et al., 2007; González-Moreno et al., 2017). These factors all vary across spatial and temporal scales, and can act additionally, synergistically or antagonistically, creating complexity that is difficult to capture and impedes the identification of direct impacts of non-native plants in our analysis. Thus, we note that our results are purely correlative, and that confounding variables should always be considered when interpreting such results.

Overall, our findings indicate that non-native and invasive plants are linked with higher total and native plant diversity at scales ranging from local to global. However, this association should not overshadow the potential detrimental effects these species can have. Invasive plants, particularly in fragile island ecosystems and areas with high endemicity, can have dramatic consequences on plant diversity. Yet, our study suggests this trend is not universally observed across all regions and ecosystems. While we cannot establish causality between diversity changes from invasive and non-native plants, our research highlights the need for a more nuanced understanding of these dynamics. It cautions against the blanket assumption that plant naturalisations and invasions universally threaten biodiversity.

AUTHOR CONTRIBUTIONS

SL led the analysis, with support from JS and IRS. SL, JS and IRS wrote the manuscript. IRS devised the study.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in "splot-non-native-div" at https://github.com/istaude/splot-non-native-div.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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