

Plant naturalizations are constrained by temperature but released by precipitation

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Abstract

Aim: During naturalization, many species undergo climatic niche expansion, in which they spread into climates with which they have not been associated previously. This suggests that species are absent from some climatically suitable areas in their native range, but the reason for this is unknown. We aimed to evaluate whether the climatic conditions in which expansion occurs provide information about the causes of niche expansion.

Location: Global.

Time period: Contemporary.

Major taxa studied: Terrestrial plants.

Methods: We compiled native and naturalized occurrence data for 606 terrestrial plant species and compared their native and naturalized climatic niches to detect evidence of climatic niche expansion. Where species showed evidence of niche expansion, we used a variety of circular modelling techniques to investigate further whether species were more likely to expand, or expand further, along some climatic axes than others. We also asked, with or without expansion, whether species were more successful at colonizing the hottest, coldest, wettest or driest portions of their potential niche.

Results: We found climatic niche expansion in 45% of naturalizations of 606 terrestrial plants. Species expanded predominantly into wetter climate than their native niche, somewhat less frequently into drier climate, and only in rare instances into hotter or colder climate. Species were least likely to naturalize in the hottest or coldest portions of their native climatic niche.

Main conclusions: Our results could suggest that the wetter margins of native niches are limited by biotic interactions that are relaxed in the naturalized range. Our results could also suggest that evolutionary adaptation to novel precipitation regimes is occurring, and/or there are time lags caused by slow population growth rates in cold and hot conditions. Regardless of the explanation, range margins associated with precipitation might be the least predictable during naturalization or environmental change.

KEYWORDS

biogeography, climate envelope modelling, climatic niche, enemy release, macroecology, niche conservatism, niche expansion, non-native species, plant ecology, range limit

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1 | INTRODUCTION

The increase in human-mediated movement of plant species in recent history has resulted in a huge number of introductions of plant species (Dawson et al., 2017), many of which have impacted native ecosystems, agriculture and human infrastructure (Simberloff et al., 2013). Much research and management of biological invasion has assumed that the climatic niche of a species in its native range could predict its ultimate distribution in the naturalized range (Fournier et al., 2019; Koop et al., 2012; Nishida et al., 2009). However, several studies now demonstrate that species can naturalize in climates different from those occupied in the native range (i.e., they undergo niche “expansion”; Atwater et al., 2018; Early & Sax, 2014; Gallagher et al., 2010; Parravicini et al., 2015). Other work has challenged the assumption that current, native ranges of species are an accurate representation of their climatic tolerances (Bradley et al., 2015; Hill et al., 2017; Li et al., 2014). It is now clear that the native ranges of many species are significantly limited by non-climatic factors. However, it remains unknown whether certain climatic conditions limit native ranges more strongly than others, and the frequency and types of non-climatic range limitation.

Naturalizations of species represent a natural survey that allows us to study non-climatic limits on the native ranges of species globally. If some climatic factors limit ranges more strictly than others, we would expect naturalized species to undergo niche expansion most frequently in the direction where climate plays the weakest role in range limitation. We can then ask what the non-climatic limits on the native range might be. For example, native ranges might be constrained by geographical boundaries such as coastlines or mountain ranges, by the poor dispersal ability of species or by lack of habitat or resources. Such barriers might not exist in the naturalized range; poor dispersal ability can be circumvented by introductions to multiple locations, and necessary resources might abound. None of these limitations should necessarily lead to expansion in a particular climatic direction following naturalization.

Another constraint on native ranges might be biotic interactions with species that are not present in the naturalized range (Gallien et al., 2012). Release from negative biotic interactions could result consistently in niche expansion in a particular climatic direction. It has long been suggested that cold or dry conditions are physiologically stressful and that these climatic conditions limit species ranges directly (Darwin, 1859; Early & Keith, 2019; Louthan et al., 2015). This theory was recently formulated as the “species interactions–abiotic stress hypothesis” (SIASH; Louthan et al., 2015), and there is some evidence that some types of climates pose direct, and therefore stricter, limits on species ranges than others (Vergeer & Kunin, 2013). For example, multiple populations of a given species tend to experience the same cold limits (Alexander et al., 2012; Broennimann et al., 2012; Pellissier et al., 2013), and many species are very sensitive to decreasing precipitation (McCain & Colwell, 2011). On the contrary, highly productive, wet conditions might not be stressful but are correlated with an increase in negative biotic interactions, and it is the interactions that limit species ranges

(Darwin, 1859; Early & Keith, 2019; Louthan et al., 2015). Therefore, release from interactions might permit species to naturalize in wetter conditions than the native range.

Understanding the limitations on range edges, hence how ranges might change in novel circumstances, is important for several reasons. First, predictions of the potential geographical ranges of problematic invasive species frequently use the native climatic niche (Fournier et al., 2019; Koop et al., 2012; Nishida et al., 2009). However, models built with climate alone might underestimate the potential range of naturalized species (Early & Sax, 2014; Wisz et al., 2013). Second, how species respond to environmental change depends greatly on what biotic or abiotic factors structure their range, and how these factors change in the future. Third, in order to understand the fundamental processes driving biodiversity patterns we need to understand the evolutionary pressures imposed by abiotic and biotic factors, which can be informed by range limits. The putative non-climatic limits on species ranges therefore need to be studied in more detail, and to do this we need to know where to focus our efforts.

Previous evaluations of the direction of niche shift have compared the centroid of the native and naturalized niche (Atwater et al., 2018; Perret et al., 2019). Although this is informative in some ways, it does not provide information about the drivers of native range limits. For example, Atwater et al. (2018) found that species niche centroids often shift towards wetter, more productive climate following naturalization, but these shifts were frequently caused by species failing to naturalize in drier parts of their native climatic niche. The potential for species to expand their niches in particular climatic directions, hence the strength of different climatic limits on the native range, is as yet unknown.

Following SIASH (Louthan et al., 2015), we hypothesize that species will be more likely to undergo niche expansion into wetter conditions than they occupied in the native range rather than into colder and drier conditions. Initially, we investigate the frequency of niche expansion by comparing native and naturalized climatic niches in 606 terrestrial plant species across every continent except Antarctica. We then ask whether species are more likely to expand, or to expand further, along some climatic axes than others. Finally, we ask whether species are more successful in colonizing the hottest, coldest, wettest or driest portions of their potential niche.

2 | MATERIALS AND METHODS

2.1 | Collating data and distribution of non-native species

We identified terrestrial plant species that have established on a mainland landmass outside their native continent following introduction by people, using established lists of naturalized species (Randall, 2017). We excluded species that were introduced pre-Columbus (i.e., before 1492), because there is little consensus on whether species that established before this time are truly “native”

or “naturalized”. Species that have not been confirmed to reproduce in their naturalized range were also excluded. Species identities were drawn primarily from Randall (2017). All species that were listed as permanently established non-native species were used (i.e., all species that were not listed as “Casual Alien”, “Unconfirmed naturalization”, “Contaminant” or “Native Weed”). Species listed in the Global Invasive Species Information Network (GISIN, 2015) were also added. For a full species list, see the Supporting Information (Appendix Table S1.1). We used the GBIF backbone taxonomy (GBIF Secretariat, 2021). We consulted the Encyclopaedia of Life (Parr et al., 2014) if species names did not match between GBIF and our species list, and we discarded any that remained ambiguous. Harmonization of taxonomy was carried out using the “taxize” package in R (Chamberlain & Szöcs, 2013).

For all species, we obtained occurrence data from GBIF (downloaded 31 August 2017) using the *dismo* package in R (Hijmans et al., 2015). Locations of occurrence were classified as either “native” or “naturalized” using international and national checklists, in that order of preference (Supporting Information Appendix Table S1.2). Most checklists were published by a national or academic institution or were peer-reviewed floras or databases. In some cases, other sources were used if they provided citations to support the native/naturalized status of the species. The following filters were applied to clean raw GBIF distributional data: Each point was a presence; each point had a valid latitude and longitude, with a coordinate precision > 0.01 and uncertainty $< 10,000$ m; the basis of record was a living specimen; the year of occurrence was after 1970; the coordinates were not 0,0 or at the exact centre of countries or capital cities; the coordinates were not in registered herbaria or museum locations; and the occurrence was on land. This procedure was carried out using the “CoordinateCleaner” package in R (Zizka et al., 2019). Finally, any species that occupied fewer than five 10 arc-min grid cells in either their native or naturalized range were discarded.

For each species, we examined niche expansion in each biogeographical realm in which the species has naturalized (1,852 naturalization events in total). We used biogeographical realms from the multi-taxonomic consensus map of Holt et al. (2013), with an additional distinction between western and eastern Palearctic along the Ural mountains (see Supporting Information Appendix Figure S1.1). The Ural line was added because species that inhabit both Western Europe and eastern Asia are almost always native to one and naturalized in the other. Species that were found to be native and naturalized in the same biogeographical realm were removed from analysis, owing to the difficulty in defining native and naturalized ranges exactly. The biogeographical realms of Holt et al. (2013) were based on the consensus of phylogenetic and distributional data for birds, amphibians and mammals. The diverse life histories and dispersal abilities of the taxa included suggests that results should capture the major biogeographical disjuncts for plants. The realm boundaries largely coincide with major geographical features, which would be very likely to form barriers to the dispersal of plants. By using fairly large biogeographical realms that coincide with major geographical

barriers, we minimized the risk that part of the native range of a species was considered to be its naturalized range, although we might have excluded a few species that are native and naturalized within one of the realms of Holt et al. (2013). After splitting the data into individual realms, we again filtered out any species with fewer than five native or naturalized occurrences in a given realm. After all the filtering steps were completed, the database contained information on the ranges of 606 plant species. Sample sizes were still fair overall: the median number of native occurrences was 593, the maximum 4,633; and the median number of naturalized occurrences was 39, the maximum 2,748.

2.2 | Climatic data

We used the most universal parsimonious variables that influence species ranges (Early & Sax, 2014): mean temperature of the coldest month (TMin), mean temperature of the warmest month (TMax) and total annual precipitation (Precip). Inclusion of a larger number of variables results in less transferability between native and naturalized range, greater niche expansion and less parity between species than the parsimonious set of variables (Early & Sax, 2014). Gridded average climatic variables from 1970–2000 were downloaded from WorldClim at 10 arc-min resolution (Fick & Hijmans, 2017).

2.3 | Restriction of analysis to analogue climate

An apparent niche expansion might occur because species naturalize in climate that does not exist in the native realm (i.e., non-analogue climate; Petitpierre et al., 2012), which species therefore do not have the opportunity to occupy. We did not want this type of niche expansion to be confounded with niche expansion into climate that exists in the native region, because only the latter would indicate non-climatic limitations. To remove naturalizations in non-analogue climate for each species, we first selected the 10 arc-min WorldClim grid cells from the native and naturalized realms. We applied principal components analysis (PCA; *ade4* package; Thioulouse et al., 2018) to produce a gridded climate space of 100×100 cells on two axes (Broennimann et al., 2012). Analogue climate was defined as any climate that was present in both the native and naturalized realms, and any occurrences in non-analogue climate were removed from further analysis. Note that this approach will underestimate niche expansion in comparison to the full native range.

2.4 | Modelling niche expansion

We measured niche expansion using a “global climate space” (i.e., all terrestrial 10 arc-min grid cells were used to produce a gridded 100×100 cell PCA climate space on two axes; Figure 1a). This allows us to compare directions of niche expansion amongst species. An alternative would be to use the biogeographical realms to which

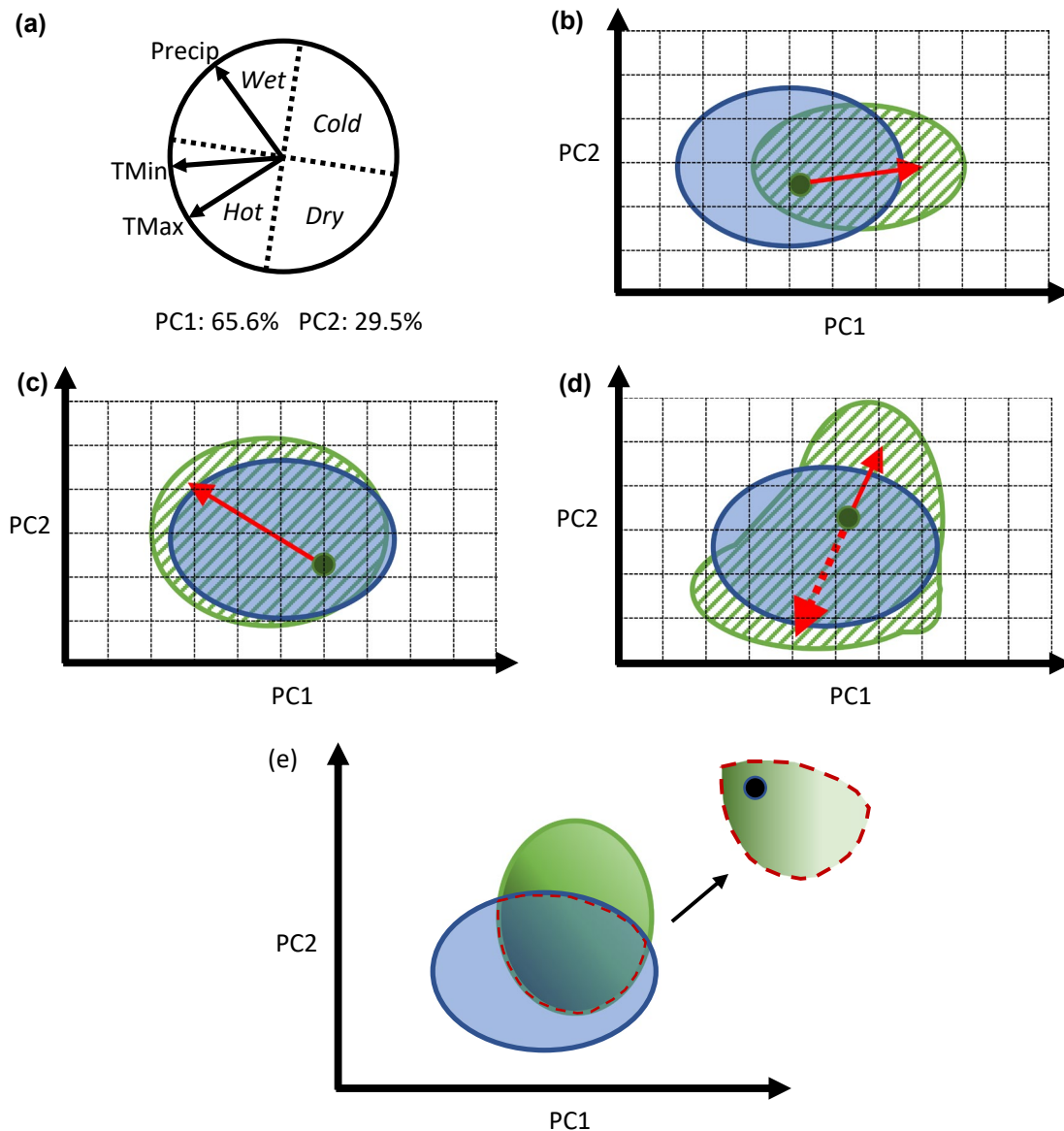


FIGURE 1 Illustration of calculations of the direction and distance of niche expansion. (a) Global climate principal components analysis (PCA) correlation circle. Continuous arrows are directions in PCA space of increasing precipitation (Precip), maximum temperature (TMax) and minimum temperature (TMin). Dotted lines are quarters around climate vectors, used to identify the hottest, wettest, coldest and driest quarters (labelled in italics). Principal component (PC) values are variance explained by each of the two PCA axes. (b–d) Types of niche expansion. Green is the occupied naturalized niche; blue is the occupied native niche. Any green areas that do not overlap with blue are areas of niche expansion. Dark green points are the centre of the expected naturalized niche, and red arrows are the measured direction of niche expansion. (b) The species has expanded in one specific direction in PCA space, which results in a large median distance of expansion and low variance. (c) The species has expanded in one direction but with a high degree of variance, which results in a large median distance and a high variance. (d) The species has expanded in multiple directions by a large amount. This results in a large distance moved in both directions, with high variance in one direction (dotted arrow) and low variance in the second direction (continuous arrow). (e) Illustration of the method used to determine the centre of the expected naturalized niche. The green area represents the naturalized niche, and the green shading represents the density of suitable climate. The expected naturalized niche is the area that overlaps with the native niche (red-dashed outline), and the centre of the expected naturalized niche is the central point of climate density in this region

species are native or naturalized. However, different PCA climate spaces have different orientations, meaning that niche expansion could not be compared between species.

We calculated species occurrence densities in their native and naturalized realms in each PCA grid cell using a kernel smoothed density function (Broennimann et al., 2012). We corrected the

naturalized occurrence density of each species to account for the availability of climate by dividing the naturalized occurrence density in each PCA grid cell by its climate density. All analyses were carried out using the corrected occurrence density.

We rescaled naturalized occurrence densities between zero and one to make them comparable across species. For each species, we

measured niche expansion as the sum of naturalized occurrence density that displayed niche expansion divided by the sum of the total naturalized occurrence density. Species that had an expansion proportion of $> 10\%$ were deemed to show significant expansion (Petitpierre et al., 2012).

Although species that occupied fewer than five grid cells were removed, patterns of niche expansion could potentially be biased by species with low numbers of records, because such species might have poorly characterized niches. To check this, we carried out a beta regression between the number of grid cells and niche expansion (see Supporting Information Appendix Table S1.3).

2.5 | Measurement of direction and distance of niche expansion for each species

We measured the direction of niche expansion from the central point of the “expected naturalized niche” for each species. This central point was defined as the centre of density of climatic conditions present in the naturalized realm that were within the native climatic niche of the species (Figure 1e). The central point thus represents the centre of the naturalized niche of the species if the species were to occupy all grid cells in the naturalized realm that fall within its native climatic niche. We then measured the distance (on PCA axes) between the centre of the expected naturalized niche and each PCA grid cell in which a species underwent expansion (Figure 1). We weighted the distance by the naturalized occurrence density in each cell where expansion had occurred. We note that the PCA approach means that distances moved along temperature and precipitation axes are comparable.

We used circular models to investigate whether species expanded in one, two or multiple directions, and how much circular variance was associated with these expansions (Figure 1). We compared multiple models of circular orientation for each species, including a null uniform model (i.e., expansion is equal in all directions) with nine alternative parametric models (Fitak & Johnsen, 2017; Schnute & Groot, 1992). Alternative models included information on the circular mean, which describes the mean direction of expansion, and the circular variance, which describes the tightness of focus of the direction of expansion. For a full description of all alternative models, see the Supporting Information (Appendix Table S1.4). The best-fitting model subset was defined as the model with the lowest Akaike information criterion (AIC) and any additional models where the relative difference in AIC between a given model and the best model (ΔAIC) was < 7 (Fitak & Johnsen, 2017).

For species for which the null model was rejected in the previous step, we measured the distance of niche expansion. We calculated the median distance from the expected naturalized niche centre to each grid cell in which the species had undergone niche expansion in the mean direction (i.e., grid cells within 45° of the mean direction).

2.6 | Cross-species trends in direction and distance of niche expansion

We tested for trends in the direction of expansion using parametric models of circular orientation. The null model was that expansion is equally likely in any direction in PCA space, and alternative circular models were those listed in the Supporting Information (Appendix Table S1.4). The best-fitting model subset was again defined as those with the lowest AIC and $\Delta\text{AIC} < 7$.

We also tested whether the distance that species expanded corresponded to the climatic conditions. For this, we conducted a nonparametric circular regression between direction in PCA space and the distance of each expansion point from the central point. We used a Nadaraya–Watson estimator and the local linear estimator for circular linear data, taking the von Mises distribution as its kernel, choosing a smoothing parameter with a least squares cross-validation approach (Di Marzio et al., 2013; Oliveira et al., 2014). The degree to which the distance of expansion corresponded to the climatic direction was calculated using a pseudo- R^2 : The proportional reduction in the sum of squared residuals between the null model and the fitted model.

Globally, information on naturalized species is not distributed evenly, and we have more information on naturalization events in some realms than in others. We wanted to detect whether global patterns of niche expansion are truly global or driven by the effect of one or a few realms. Therefore, we reperformed analyses to look for cross-species trends in each biogeographical realm individually.

2.7 | Interpreting niche expansion

In order to estimate the climatic conditions into which each expansion occurred, we measured which quarter of climate space (Figure 1a) mean direction of expansion of a species was associated with. We then measured how closely the expansion of each species was associated with that climatic direction. To do so, we compared the mean direction of expansion with the PCA vector of increasing or decreasing precipitation (whether the mean direction of expansion was in the wet or dry quarter, respectively), or the vector of increasing or decreasing temperature (whether the mean direction of expansion was in the hot or cold quarter, respectively). A value of zero indicates that species expanded on average in the climatic direction tested, with no expansion towards other covarying climatic directions. To determine whether the direction of most frequent expansion corresponded to the direction along which the farthest distances were moved, we compared the vector of greatest distance with the vector of each climatic variable. The hottest and wettest quarters were defined as the quarters of PCA space around the vectors of TMax and Precip, respectively, which were nearly 90° apart, and the coldest and driest as the quarters of PCA space around vectors opposite to those of Precip and TMax, respectively (Figure 1a).

Finally, we investigated whether species were able to naturalize more successfully in some parts of their native climatic niche than in others. For each species, we summed its naturalized occurrence density in each PCA quarter (Figure 1) and divided this by the total naturalized occurrence density of the species. A value of zero indicates that the species did not naturalize at all in that quarter, and a value of one indicates that the species had naturalized only in that quarter.

2.8 | Additional tests of robustness

Our results could potentially be biased by the selection of naturalized species and by the choice of climatic variables. We therefore carried out several additional analyses to test the robustness of our results.

Our dataset of naturalization events contains pseudo-replication because species often naturalized in more than one realm. The median number of realms in which a species was naturalized (i.e., replicates per species) was two; 166 species naturalized in only one realm, and the maximum for any one species was 11 realms. We investigated whether this biased our results in two ways. First, we generated three smaller datasets that restricted each species to a single randomly selected naturalization event, and we re-ran all analyses on each dataset. Second, we ran a Bayesian circular mixed-effects model to investigate whether the random effect of species explains a significant proportion of the direction of expansion. If the proportion of variance explained is high, it would suggest that the direction of niche expansion is driven strongly by species identity. The mixed-effects analysis was carried out using the “bpnreg” package in R (Cremers, 2020). We used a simple model, with circular direction as the response variable and with the intercept and the species identity (as a random effect) as the predictor variables.

The direction of niche expansion could also be biased by the selection of climate variables. We therefore re-ran our niche expansion analyses with two alternative sets of climate variables. First, we re-ran it with just two variables, TMax and Precip. Second, we re-ran it with four variables: TMax, TMin, Precip and precipitation seasonality (PrecipSeas). All data were taken from WorldClim data (Fick & Hijmans, 2017). For both sets of variables, we re-ran our analyses and looked for differences in patterns of niche expansion.

We ran two analyses to test whether expansion into a particular type of climate is an artefact of increased availability of that climate type. First, we asked whether species with more “freedom” to move along a certain climatic direction were indeed more likely to move in that direction (e.g., if a species originated in a very dry climate, was it more likely to move into a wet climate?). To do so, we tested for relationships between the temperature and precipitation at the centre of the native niche and the likelihood or direction of expansion using a generalized linear model with a beta distribution, a circular fixed effects model and a nonparametric circular model with kernel smoothing. Second, the nature of the data means that we cannot calculate the availability of climate in each climatic direction across

a naturalized realm outside the native climatic niche of a species. However, we can calculate the availability of climate in the naturalized realm inside the native climatic niche of a species, and we can ask how much naturalization within the native climatic niche corresponds to climate availability.

3 | RESULTS

In total, there were 1,883 naturalization events, composed of 606 individual species, some of which were introduced to more than one realm. Native and naturalized species' ranges were included from every continent, though the largest number of species were found in Europe, North America and Australia (Figure 2a,b). Niche expansion (> 10% of naturalized density was beyond native climate) occurred in 852 naturalization events (45% of all events; Figure 2d). In total, 404 species showed expansion in at least one of their naturalized realms. Expansions occurred in every continent studied (Figure 2c). Fifty-nine percent of expansions occurred in a single direction from the native niche (unidirectional models M2A, B and C represented 506 of 852 expansions; Supporting Information Appendix Table S1.4). Forty-one percent expanded in multiple directions (multi-directional models M4A, M4B, M5A and M5B represented 346 of 852 expansions; Supporting Information Appendix Table S1.4), although visual examination indicated that in many cases this involved an overwhelming expansion in one direction and a minor expansion in a secondary direction. No species expanded uniformly in every direction (no models were described by model M1; Supporting Information Appendix Table S1.4). The number of naturalized occurrences (measured as the number of grid cells with occurrences in them) was not correlated with the proportion of the naturalized range outside native climate (Supporting Information Appendix Figure S1.2).

Niche expansions were most common towards climate that was wetter than the native range, and secondarily towards drier climate (Table 1; Figure 3a; Supporting Information Appendix Table S1.5). Niche expansion was least common towards colder or hotter climates. Species that expanded towards wetter climate also expanded further than average in that direction (Figure 3b; Table 2). In all other directions, the direction and magnitude of expansion were not correlated with each other.

Species were most successful at naturalizing in the wettest parts of their native niche (Figure 4), even if all species that expanded their niche were removed from the analysis (Supporting Information Appendix Figure S1.3). The median proportion of naturalized occurrences of all species that fell within the wettest quarter was .42, .04 in the hottest, .02 in the driest and .16 in the coldest.

Pseudo-replication did not appear to affect our results. When re-running our analysis with restricted datasets, we found that the patterns of the direction and distance of niche expansion remained the same, with the same overall direction and magnitude (Supporting Information Appendix Figure S1.4). Bayesian circular mixed-effects models found that species identity explained between 0 and 5% of the variance in the direction of expansion (mean of 1%; full details

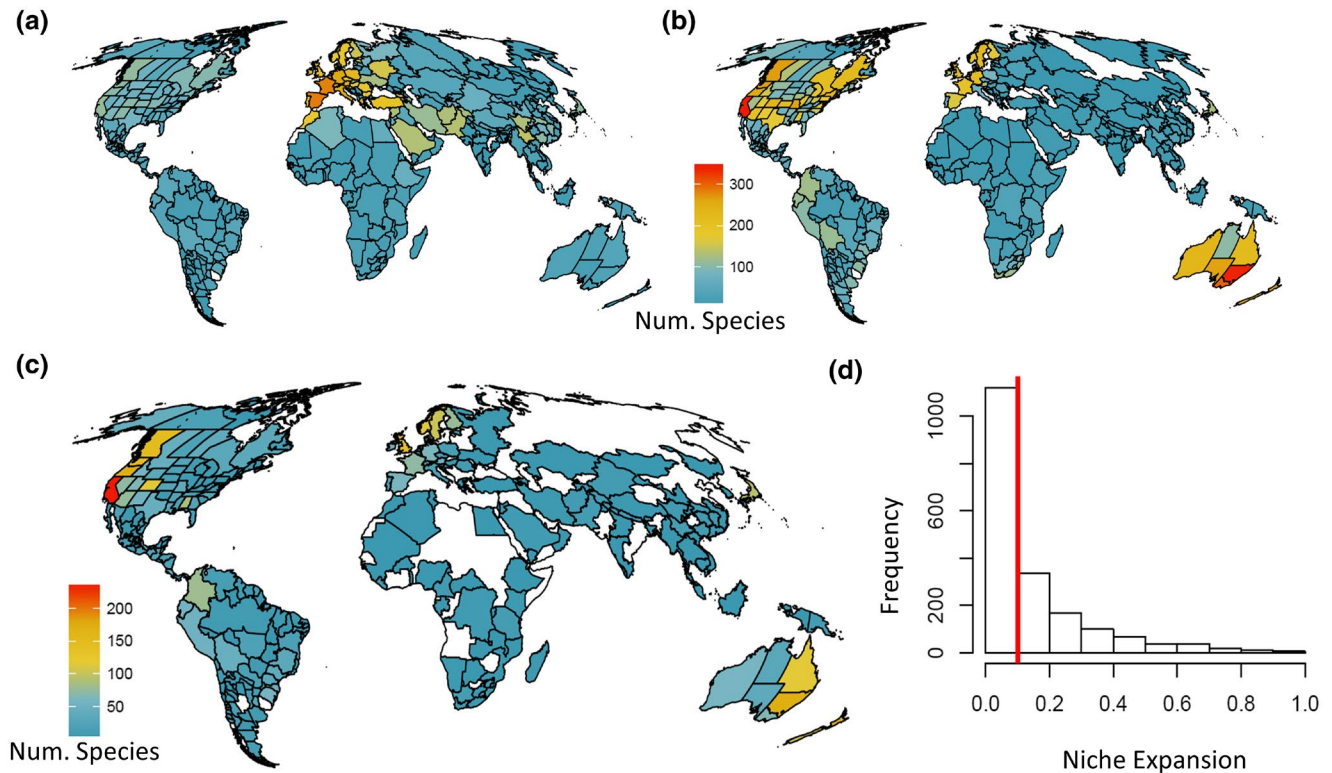


FIGURE 2 (a) Number (Num.) of native species that occur in each administrative area. (b) Number of naturalized species that occur each administrative area. (c) Number of species that undergo climatic niche expansion in each administrative area. (d) Niche expansion for all naturalization events, measured as the summed naturalized occurrence density in principal components analysis (PCA) climate space that was not inhabited in the native realm divided by total naturalized occurrence density. Any species that underwent > 10% expansion (red vertical line) was classified as expanding

of the model can be found in Supporting Information Appendix Table S1.6), which is far lower than the pseudo- R^2 extracted from our fixed-effect analysis of 28% (Supporting Information Appendix Table S1.5).

When only TMax and Precip were included in the PCA, the pattern of increased expansion towards wet climate remained. Expansion towards drier climate was also observed but was weaker than when TMin was included in the PCA (Supporting Information Appendix Figure S1.5). When PrecipSeas was included in the PCA, the PCA correlation circle could no longer be divided up neatly into hot, cold, wet and dry quarters (Supporting Information Appendix Figure S1.6). Nevertheless, visual inspection of the results showed that expansion occurred more frequently towards wetter environments with more seasonal precipitation, and not towards warmer environments (Supporting Information Appendix Figure S1.6).

4 | DISCUSSION

Niche expansions occurred in 45% of observed naturalization events and could occur in any climatic direction outside the native niche. Globally, however, niche expansions were most frequent towards wetter climates and secondarily towards drier climates, rather than towards hotter or colder climates. Naturalized plants expanded

further in the direction of wetter climate than in any other direction (i.e., climates within which species naturalized were wetter, relative to the native ranges of species, than they were drier, hotter or colder). This emphasizes the low conservatism of range margins associated with precipitation and demonstrates that this phenomenon is not attributable to many species moving a relatively small distance into wetter climate. Species were also more successful at naturalizing in the wettest portions of their potential range than in any other climatic axis. The direction and distance of niche expansions observed in most individual biogeographical realms follow the same general pattern as niche expansions at a global scale (Table 1; Supporting Information Appendix Figures S1.7 and S1.8). Naturalizations in the Palaearctic-East and Saharo-Arabian realms differed from the global trends but had a very small sample size (12 and 21 naturalization events, respectively; Figure 4; Supporting Information Appendix Figure S1.9).

There are two broad ecological mechanisms that could underlie the observed trends in the direction and distance of expansion. The first mechanism is that the conditions that species occupy in their native range might not represent true climatic tolerances of the species. This could be: (1) because the climate the species could tolerate is not available in the native realm; (2) because the native ranges are limited by climatic variables other than the variables we used; or (3) because of dispersal or other non-climatic limitations on the native

TABLE 1 Summary of global and regional cross-species trends in direction of niche expansion

Realm	n	Direction of expansion			Climatic direction(s)
		Dir	Mean direction(s)	CV	
Global	852	2	1.95	7.46	Wetter (0.27)
			5.09	0.46	Drier (0.27)
Afro	17	1	1.78	12.12	Wetter (0.43)
Aus	123	1	1.8	51.75	Wetter (0.42)
Mad	3	1	2.05	227	Wetter (0.17)
Nea	201	2	4.39	1.16	Warmer (0.71)
			2.14	17.83	Wetter (0.08)
Neo	135	2	5.56	0.98	Wetter (0.20)
			2.02	6.15	Drier (0.20)
Oce	14	1	0.52	0.77	Colder (0.03)
Ori	49	1	1.65	33.38	Wetter (0.56)
PalE	12	1	2.72	87.65	Warmer (0.48)
PalW	116	2	6.28	0.47	Drier (0.92)
			1.56	11.98	Wetter (0.65)
Pan	66	2	1.85	15.94	Wetter (0.37)
			3.52	0.96	Warmer (0.17)
Sah	21	1	0.45	45.19	Colder (0.10)
Sin	95	1	2.25	22.36	Wetter (0.03)

Note: Global models are shown in bold and, unless stated otherwise, are the primary models referred to throughout the main text and figures. *n* indicates the number of naturalization events either globally or within each biogeographical realm. Dir describes the number of directions of expansion in the selected model for each realm. Mean direction is the mean direction(s) of expansion across all naturalization events (in radians). If the best-fitting parametric model included more than one mean direction, directions are listed in separate rows. The circular variance (CV) for each global or regional mean direction is also included. Climatic direction(s) was calculated as the difference between the mean direction(s) of expansion and the nearest climatic vector in principal components analysis space (Figure 1a). For further model results, see the Supporting Information (Appendix Table S1.5). Afro, Afrotropical; Aus, Australian; Mad, Madagascar; Nea, Nearctic; Neo, Neotropical; Oce, Oceanian; Ori, Oriental; PalE, Palearctic-East; PalW, Palearctic-West; Pan, Panamanian; Sah, Saharo-Arabian; Sin, Sino-Japanese.

range. We can rule out limited climate availability in the native realm (1) because we consider only analogue climate.

It is possible that the native ranges of species are limited by climatic variables other than the variables we analysed (2). For example, the exact timing of rainfall in the life cycles of species can be important (Franks et al., 2007; Miranda et al., 2011). Thus, species might naturalize in areas that have lower annual precipitation than the native range but that experience sufficient precipitation at a particular time of the growth cycle. Indeed, in our analysis drier areas could be more seasonal, particularly if they were hotter (Supporting Information Appendix Figure S1.6). However, expansion into drier conditions happens for hundreds of species, which are from all biogeographical realms and introduced into all biogeographical realms.

It is extremely unlikely that in all these naturalization events species encounter areas with lower annual precipitation than the native range but sufficient precipitation at crucial stages of the growth cycle. Likewise, it seems unlikely that species naturalize in areas with higher annual precipitation than the native range but in which precipitation is not too high at crucial stages of the growth cycle. Moreover, wetter areas tended to be less seasonal (Supporting Information Appendix Figure S1.6), suggesting that plants expanding into wetter areas experience wetter conditions year-round. Although we could have explored this issue further by choosing climatic variables more specific to each species, selection of these variables requires species-specific information on physiology and ecology, which is not available for large numbers of species. Using more specific climatic variables would therefore increase inaccuracy for many species, and we note that it would increase estimates of expansion (Early & Sax, 2014).

Covariance between temperature and precipitation can mean that the native climatic niches of species are not constrained by precipitation per se, but arise because those precipitation conditions always co-occur with the thermal limit of their niche. Examples of the reverse have been documented in many species, where the apparent thermal limit of a species was, in fact, set by precipitation (Crimmins et al., 2011; Lenoir et al., 2010). The interaction between temperature and precipitation could be decoupled in the naturalized range. If this happens, then species could encounter novel combinations of temperature and precipitation and display apparent niche expansion along precipitation axes, while in fact staying within the limits of the climatic variables that limit their native range (i.e., temperature). However, we used PCA axes that largely decoupled the correlation between temperature and precipitation and considered only climate that was analogous to native and naturalized realms. Therefore, similar combinations of temperature and precipitation are available in both the native and naturalized realms, but species do not occupy them in the native realm. Moreover, expansion into wetter and/or drier areas happened for species from and introduced to almost all biogeographical realms. Therefore, although this explanation cannot be ruled out, it seems unlikely to drive the global patterns of niche expansion observed here.

The climate variables we included are long-term means but could be associated with extreme events. For example, wet areas might be prone to flooding, and dry areas might be prone to fires. These disturbances can open the gate for naturalized species to establish and spread at the expense of native plants (Diez et al., 2012). Therefore, it is possible that extreme events could facilitate niche expansion in wet or dry conditions. However, this does not explain why expansion is restricted largely to conditions that are wetter or drier but not hotter than the native range, when fires are more likely in areas that are both dry and hot.

Non-climatic barriers that could prevent species from occupying all areas of suitable climate in the native range (3) could include physical barriers (Holt et al., 2013) or dispersal limitations (Munguía et al., 2008; Svenning et al., 2008). However, it seems unlikely that barriers would exclude the native ranges of species from wetter

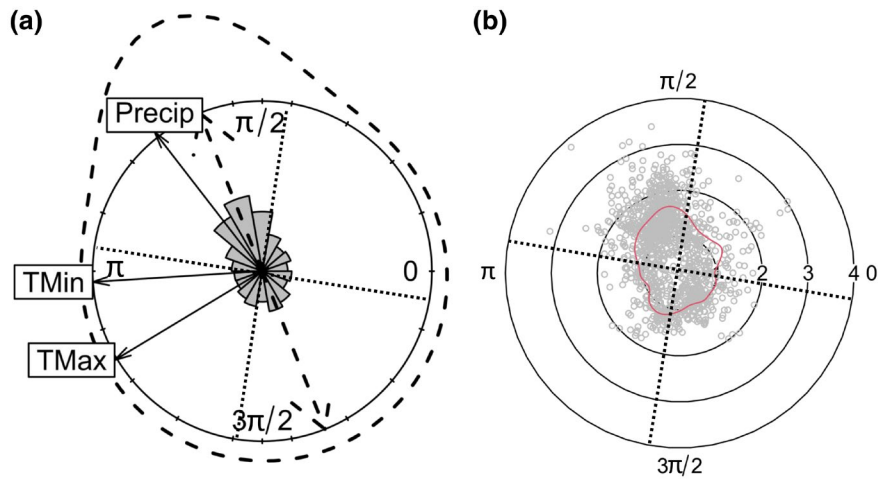


FIGURE 3 (a) Circular histogram of the frequency with which niche expansions happen in each climatic direction (globally), overlaid with the best-fitting parametric circular model (Table 1). The fitted model is a symmetrical bimodal model. Dashed arrows are the mean direction of expansion of all naturalized events, and the dashed outline describes the circular variance around the two mean directions. Continuous arrows represent directions in principal components analysis (PCA) space of increasing minimum temperature (TMin), increasing maximum temperature (TMax) and increasing precipitation (Precip). Dotted lines inside the circle delineate the four quarters of climate space (see Figure 1a). (b) Circular scatterplot of the direction of expansion versus the median distance of niche expansion (distance from the centre). Climate axes are the same as in (a). The outline is the result of the nonparametric regression model and describes the smoothed circular regression estimate between the direction and distance of expansion (Oliveira et al., 2014)

TABLE 2 Summary of global and regional cross-species trends in distance of niche expansion

Realm	n	Distance of expansion			Climatic direction
		Median distance	Maximum distance	Direction of maximum distance	
Global	852	1.26	1.68	1.77	Wetter (0.45)
Afro	17	1.19	1.90	2.12	Wetter (0.10)
Aus	123	1.17	1.76	1.61	Wetter (0.6)
Mad	3	1.24	1.94	3.41	Warmer (0.21)
Nea	201	1.19	1.56	2.20	Wetter (0.02)
Neo	135	1.39	1.66	1.79	Wetter (0.43)
Oce	14	1.31	2.72	2.17	Wetter (0.05)
Ori	49	2.12	2.26	1.74	Wetter (0.48)
PalE	12	1.20	2.16	2.47	Wetter (0.25)
PalW	116	0.90	1.58	1.92	Wetter (0.30)
Pan	66	1.36	1.77	2.14	Wetter (0.07)
Sah	21	0.87	2.29	0.73	Colder (1.47)
Sin	95	1.36	1.68	5.90	Drier (0.54)

Note: Results from the nonparametric circular model, which describe the correlation between direction and distance of expansion in principal components analysis space. The median and maximum distances are for the expansions of all species from the centre of their naturalized potential niche and are unitless. The direction of maximum expansion (in radians) is also included, in addition to the nearest climatic vector in principal components analysis space (as shown in Figure 1a) to the direction along which maximum expansion occurred. The difference between the direction of maximum expansion distance and the nearest climatic vector is included in parentheses. For further model results, see the Supporting Information (Appendix Table S1.5). Afro, Afrotropical; Aus, Australian; Mad, Madagascan; Nea, Nearctic; Neo, Neotropical; Oce, Oceanian; Ori, Oriental; PalE, Palearctic-East; PalW, Palearctic-West; Pan, Panamanian; Sah, Saharo-Arabian; Sin, Sino-Japanese.

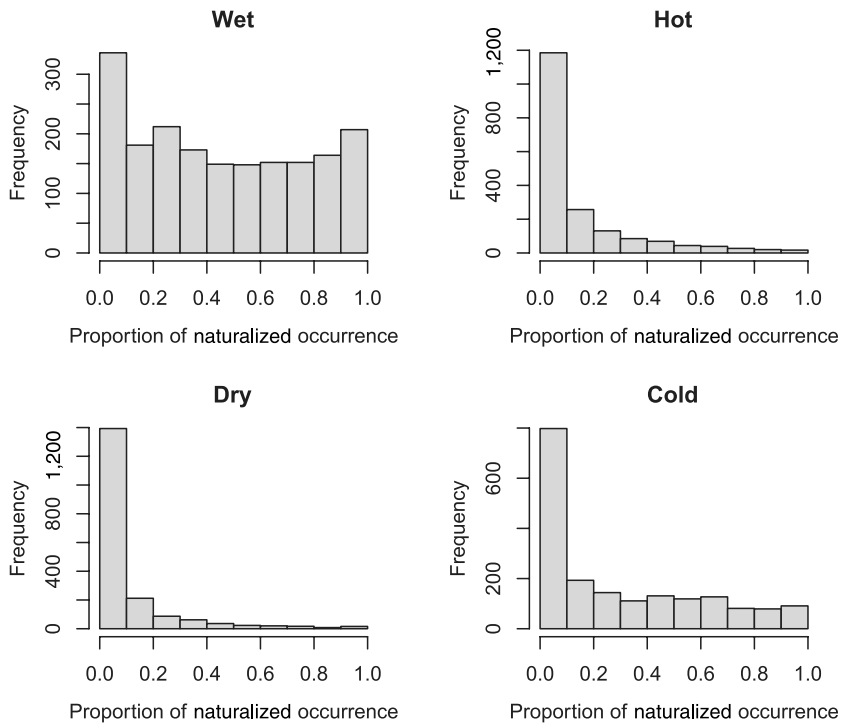


FIGURE 4 The proportion of naturalized occurrences of each species that fall within the wettest, hottest, driest and coldest climatic quarters of their expected naturalized range (for quarters, see Figure 1a). A proportion of zero means that a species did not occupy any climate in the named quarters. A proportion of one means that all naturalized occurrences are in the named quarter

climates in all biogeographical realms. Likewise, native range restriction attributable to dispersal limitation seems unlikely to be a general explanation, because there is no obvious reason why a species in its native range would be unable to disperse to locations with the hottest and coldest conditions that they can tolerate but not the wettest or driest locations.

Another potential non-climatic limit on the native ranges of species is biotic interactions, such as competition or consumption. It has been suggested that species ranges are constrained by physiologically stressful climates, including hot, cold and dry conditions, and by biotic interactions when climate is more productive (for a review, see Early & Keith, 2019; Louthan et al., 2015). Primary productivity and precipitation are strongly correlated in the compiled climate data (Pearson's correlation between global logged precipitation and logged net primary productivity was .72), hence niche expansions into wetter areas are also into more productive areas. Rates of herbivory and infections and abundances of herbivores and pathogens often increase as productivity increases (Early & Keith, 2019; Foster et al., 1992; Hersh et al., 2012; Pennings et al., 2009; Salazar & Marquis, 2012). Indeed, LaManna et al. (2017) found stronger signals of host-specific enemies on plants in high-productivity regions. The effects of competition on plants is also theorized to increase with productivity, although data are somewhat equivocal (Soliveres et al., 2015), and the results of the study by LaManna et al. (2017) might suggest the opposite trend. Enemy release is common during naturalizations and can contribute to species success (Heger & Jeschke, 2014; Liu & Stiling, 2006). It may therefore be that biotic interactions, particularly herbivores or pathogens, prevent plant species from occupying wet, productive conditions in their native region, but that these interactions are released in the naturalised region, resulting in a niche expansion.

The secondary peak in niche expansions towards drier climate is less well explained by enemy or competitor release. Typically, dry climate is physiologically stressful to plants, and standard theory would suggest that the dry edge of a species niche is set by abiotic factors (Louthan et al., 2015). Therefore, niche expansions attributable to enemy release from predators or competitors should be uncommon in relatively dry climate. Despite this apparent contradiction, we would argue that it does not rule out the role of biotic interactions on the driest edge of the species range. Biotic interactions can exacerbate the effects of abiotic stress (Early & Keith, 2019; Silliman & He, 2018), and drought stress, in particular, has been shown to increase vulnerability to predators (Silliman et al., 2005) or disease (Carnicer et al., 2011). Therefore, release from negative biotic interactors in the naturalized range might contribute to niche expansions into dry areas. If this is the case, it suggests that biotic and climatic factors often interact to set wet and dry niche edges of species but are less likely to interact to set hot and cold niche edges.

Our finding that plants are most likely to naturalize and expand in wet conditions contradicts the expected effect of biotic resistance, which is usually expected to increase with precipitation (Stotz et al., 2016). We therefore suggest that the effects of enemy release and biotic resistance need to be studied in conjunction.

For taxa other than plants, it is an open question which niche margins, if any, are particularly limited by biotic interactions. Liu et al. (2016) found that many species of herpetofauna showed little expansion towards hot conditions. However, their results differ from ours in that expansion happened more frequently towards cold conditions than towards wet or dry conditions, and most frequently beyond native limits of temperature seasonality, isothermality and annual range. It is difficult to interpret whether the results of Liu et al. (2016) suggest that biotic interactions limit the native range,

because it is not clear how temperature variability might correspond to the intensity of negative biotic interactions.

An alternative mechanism underlying niche expansion could be that species have undergone evolutionary adaptation to novel climatic conditions in the naturalized realm (Clements & Dittomaso, 2011; Urban et al., 2007; Whitney & Gabler, 2008). If evolution is a primary driver behind niche expansions, our results would suggest that evolutionary adaptation to novel precipitation regimes is much more common than adaptation to novel thermal regimes. There is some evidence that the physiological thermal tolerances of species exhibit relatively strong conservatism (Broennimann et al., 2014; Pellissier et al., 2013; Sunday et al., 2012), and it has been suggested that adaptations that extend the cold niche limit of species are rare owing to the complex genetic and physiological changes involved (Broennimann et al., 2014; Surville et al., 2009). Examples of adaptations to novel precipitation regimes exist (Leger & Rice, 2007; Molina-Montenegro et al., 2011) but, to our knowledge, there has been no research into whether there is a trend for species to adapt to new precipitation regimes more frequently than to new temperature regimes. Many species studied here expand into climate that is very different from their native niche (Figure 3). This suggests that, if adaptation were to be taking place, species are adapting to drastically different precipitation levels and, in many cases, rapidly following naturalization. Of the species studied here, all have naturalized within the last 250 years, and more than half within the last 150 years. If evolutionary adaptation to novel precipitation regimes following naturalization is indeed widespread, why has such adaptation not occurred previously in the native ranges of species? This might suggest that evolutionary adaptation is unlikely to be a major driver of our results or that a fascinating phenomenon is under-appreciated and under-studied.

In addition to ecological mechanisms, it could be asked whether niche expansions are opportunistic and whether observed expansions occur only because climatic conditions in the naturalized realm are predominantly wetter than the native environment. We corrected for this possible bias in several ways. First, we considered only species occurrences in analogue climate space. Second, occurrence densities were corrected for the prevalence of climatic conditions in the native and naturalized regions, hence we accounted for any differences in precipitation regimes between native and naturalized ranges. Indeed, without this correction for climate availability, we found expansions of species into drier climate to be much more prevalent. Third, this analysis is global, and we have introductions from every continent and to every continent except Antarctica. With the exception of realms with very little data on introduced species, patterns of niche expansion are largely similar, regardless of the realms in which species are native or naturalized (Table 1; i.e., plants from realms with relatively dry conditions introduced to wet realms show the same pattern of expansion into wetter climate as plants from wet realms introduced to dry realms). Fourth, we found no relationships between the temperature and precipitation of the native niche and the likelihood or direction of expansion (Supporting Information Appendix Figure S1.10). Fifth, we found no difference in the

availability of different climatic conditions (Supporting Information Appendix Figure S1.11a). Sixth, although occupancy did correspond to the availability of climate, there was no difference in that relationship between different types of climates, hence availability of wet climate affects occupancy no differently than the availability of other types of climates (Supporting Information Appendix Figure 1.11b). Therefore, our results do not seem to be caused by wider availability of wet climates in naturalized realms than in native realms.

Another mechanism underlying our results might be that niche expansions into novel temperature regimes are slower than those into novel precipitation regimes. Plant population growth might be most rapid in the wetter, more productive portion of the climatic niches of species (Del Grosso et al., 2008; Michaletz et al., 2014). Species were also more successful at establishing naturalized populations in wetter quarters of their native climatic niche, as opposed to the hottest, coldest or driest quarters (Figure 4). Rapid establishment in wet, productive parts of the climatic niche might have facilitated expansion at wet niche margins, and it might be only a matter of time until naturalized species fill out or expand beyond other niche margins. More rapid population growth does not seem to be a factor in niche expansion towards dry climates, given that species were least successful at establishing naturalized populations in the driest quarters of their native climatic niche (Figure 4).

In conclusion, plant species more frequently naturalize into wetter and drier climates than those they occupy in their native ranges but naturalize much less into hotter or colder climates. The very large geographical and taxonomic scope of this analysis shows that this is a global phenomenon in plants. The most plausible underlying explanations include time lags, that biotic interactions limit the wet and dry margins of species niches more than the hot or cold margins and, possibly, evolutionary adaptation. Regardless of the cause, our results suggest that annual precipitation limits plant species ranges less frequently than minimum or maximum temperature. Prediction of the effects of precipitation on the ranges of invasive species, or on range shifts in response to climate change, is likely to be more difficult than the effects of temperature. Attention needs to be focused on gaining a better understanding of the relationship between precipitation data and population dynamics of species, in addition to development of methods for incorporating biotic interactions into projections of the potential ranges of species following climate change or naturalization.

AUTHOR CONTRIBUTIONS

H.H. and R.E. conceived the study and developed the concept. H.H. collated the datasets, analysed the data and wrote the first draft of the manuscript. Further developments to the concept and drafts were contributed by D.H. and R.E. All authors contributed revisions.

DATA AVAILABILITY STATEMENT

The underlying code and data can be accessed at: <https://doi.org/10.5281/zenodo.5710327> (<https://doi.org/10.5281/zenodo.5710327>). Links and details to acquire any additional data required are also included.

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BIOSKETCHES

Regan Early aims to disentangle the effects of abiotic and biotic drivers of species distributions, asking how this information can be used to improve biodiversity models and forecasts of climate change, biological invasions and crop pests. She works with a multitude of ecosystems, taxa and geographical regions, using field and computational studies. Her research group can be found at: www.fabiogeography.com.

Dave Hodgson is a quantitative ecologist, with key interests in demography, life-history evolution, conservation, wildlife disease, and the interplay between ecological and evolutionary dynamics. He models the dynamics of structured populations, with a specific interest in how populations respond to disturbances. He uses global databases of life history, extinction risk and invasiveness to try to predict the endangered and invasive species of the future.

Henry Häkkinen works on the effects of climate change and non-native species on native ecosystems. He has worked on species and taxa around the world but focuses on European plants and birds and uses a combination of computational, field and laboratory studies. The aim of his work is not only to build better predictions of how species might spread and shift in the future, but also to devise conservation strategies to cope with such changes.

SUPPORTING INFORMATION

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