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Article

# Invading plants remain undetected in a lag phase while they explore suitable climates

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Successful alien species may experience a period of quiescence, known as the lag phase, before becoming invasive and widespread. The existence of lags introduces severe uncertainty in risk analyses of aliens as the present state of species is a poor predictor of future distributions, invasion success and impact. Predicting a species' ability to invade and pose negative impacts requires a quantitative understanding of the commonality and magnitude of lags, environmental factors and mechanisms likely to terminate lag. Using herbarium and climate data, we analysed over 5,700 time series (species × regions) in 3,505 naturalized plant species from nine regions in temperate and tropical climates to quantify lags and test whether there have been shifts in the species' climatic space during the transition from the lag phase to the expansion phase. Lags were identified in 35% of the assessed invasion events. We detected phylogenetic signals for lag phases in temperate climate regions and that annual self-fertilizing species were less likely to experience lags. Where lags existed, they had an average length of 40 years and a maximum of 320 years. Lengthy lags (>100 years) were more likely to occur in perennial plants and less frequent in self-pollinating species. For 98% of the species with a lag phase, the climate spaces sampled during the lag period differed from those in the expansion phase based on the assessment of centroid shifts or degree of climate space overlap. Our results highlight the importance of functional traits for the onset of the expansion phase and suggest that climate discovery may play a role in terminating the lag phase. However, other possibilities, such as sampling issues and climate niche shifts, cannot be ruled out.

Biological invasions constitute a substantial facet of global environmental change with marked environmental and socio-economic impacts[1–4]. Particularly concerning are the numerous alien species that have already been introduced into many regions of the world, for which we do not know whether they will become impactful invaders of the future. Some alien species may remain in a quiescence state, referred to as 'lag phase'[5,6], after their introductions, occupying a small area for several years (or even centuries) before rapidly expanding[5,7,8].

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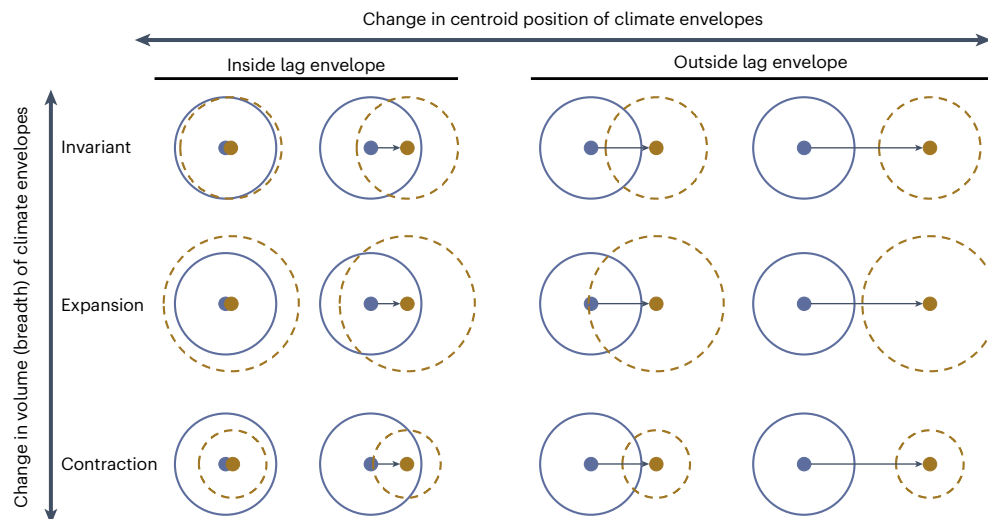
**Fig. 1 | Potential scenarios for differences between the climate envelopes of lag and post-lag phases.** The diameter of a circle and the solid point indicate the volume (breadth) and the centroid of a climate envelope, respectively. Volume change scenarios are shown on the vertical axis and centroid displacement (shown with arrows) on the horizontal axis. When the centroid of the post-lag climate envelope deviates from that of the lag period, it may remain inside the climate envelope of the lag period or entirely fall outside the lag envelope. Lag phase, blue solid-line circles; post-lag phase, brown dashed-line circles.

Failure to consider the lag times of such 'sleeper' species[9] can lead to an underestimation of their potential impact in risk assessments[10]. As some invaders experience a lag phase before they become widespread[11–14], an appreciation of the frequency and magnitude of lags will allow us to understand the temporal dynamics better and proactively manage invasive species.

Several not mutually exclusive mechanisms, including intrinsic eco-evolutionary processes[15–17] and extrinsic environmental conditions[18,19], could lead to a prolonged lag preceding the expansion phase. For example, a lag phase might be due to a long generation time[20] or reflect the time needed for adaptation to enable the species to colonize new environments[21,22]. Alternatively, an alien species might be introduced to a marginally suitable environment, and once some propagules arrive at a more suitable environment, they can significantly increase in abundance[23]. Even without such long-distance dispersal events[24,25], the lag may be terminated by changes in the environment (biotic and abiotic), such as changes in fire frequency[26], land management[27] or climate[5]. Establishing a direct link between a particular mechanism and the lag time of invasions remains challenging because multiple factors can change simultaneously, leading to complex interactions[28–30]. Niche theory[31–33] provides a context to better understand the dynamics of invasions in general and lags in particular, as a niche defines the conditions under which a species can succeed.

The geographic limits of species at large scales are mainly determined by climate. Although soil, land use, dispersal barriers and other abiotic factors play a role, the realized climate niche is frequently used to test niche conservatism versus niche shift[32,34,35]. Niche conservatism in alien species has almost exclusively been tested by comparing the realized climate niche in the native range against that in the entire invaded range, independent from the invader's position on the introduction–naturalization–invasion continuum[36–39]. However, the niche theory can be used to test the role of climate in driving lags within the invaded range. For those species that exhibit biphasic population dynamics (that is, lag and expansion phases), the realized climate space in the invaded range can be partitioned temporally into lag and post-lag envelopes without regard to the native realized climate space. These two post-introduction climatic spaces may constitute a subset of the native climate or its expansion.

Changes in the climate envelope of the post-lag period compared with those of the lag period can occur along two axes (Fig. 1): changes in the size of the climate envelope and shifts in the position of the centroid. The volume (niche breadth) of the post-lag climate envelope, compared with that of the lag climate envelope, may remain unchanged, expand or contract with or without significant shifts in its centroid position. The post-lag centroid may move significantly but remain within or entirely fall outside the lag climate envelope (Fig. 1). In either case, a portion of the post-lag envelope will be novel and outside the lag climate envelope. Finally, the two climate envelopes can be disjunct regardless of their volume differences.

In this study, we calculated the degree of centroid shift and overlap between the lag and post-lag climate envelopes as measures of differences between the climate conditions of the two invasion phases. This allows us to test whether the transition from a lag phase to an expansion phase has been coupled with changes in the climate spaces occupied during the post-lag period. Where the climate sampled during the expansion phase differs from the climate of the lag period, we may suggest that the arrival of the species into suboptimal (marginal) climate conditions has pinned the invasion[40], but has later been alleviated by dispersal to potentially more suitable climates.

## Results and discussion

Here we report the results of a large-scale, systematic evaluation of the lag phase phenomenon linked to the possibility of temporal changes in the realized climate niche within the invaded range. We collated lists of naturalized alien plants for nine regions (that is, Australia, North Island and South Island of New Zealand, Madagascar, South Africa, Japan, Great Britain, Ireland land-mass and the United States). The regions were selected to cover diverse climate zones in both the Northern and Southern hemispheres and have a sizeable invasive flora well represented in biodiversity data. We analysed 5,711 species (Tables 1 and 2, and see Supplementary Fig. 1 for an overview of the procedure). Accounting for temporal variability in sampling efforts[41], we first tested for evidence of a lag and then estimated its length. For species with biphasic population growth (Fig. 2), the differences in climate envelopes between lag and expansion phases were assessed using multivariate analysis[42]. We further hypothesized that species with a detected time lag differ in functional traits from species without a lag phase. Therefore, we investigated the relationship between traits and lag existence and length by collating data on life form, woodiness, lifespan, vegetative reproduction, type of seed production, mating

**Table 1 | The existence and length of lag phases in naturalized plant species from nine regions worldwide and the results of the two-sided Blomberg's K test for detecting phylogenetic signals**

| Region | Total number of naturalized species | Lag phase | | | Blomberg's K test | |
|---|---|---|---|---|---|---|
| | | Number of species analysed | Number of species with a significant lag | Average lag length (years) | K for lag length[e] | P value |
| Australia | 2,416 | 1,682 | 513 (31.6%)[c] | 47.2 (39.7)[d] | 0.02 | 0.67 |
| Ireland[a] | 564 | 318 | 98 (30.8%) | 31.5 (28.3) | 0.05 | 0.04 |
| Japan | 1,311 | 315 | 107 (34.0%) | 25.2 (16.7) | 0.06 | 0.84 |
| Madagascar | 517 | 97 | 36 (37.1%) | 38.9 (24.4) | 0.19 | 0.02 |
| New Zealand (North Island) | 387 | 101 | 24 (24.5%) | 28.4 (12.9) | 0.2 | 0.34 |
| New Zealand (South Island) | 387 | 93 | 29 (33.7%) | 26.8 (16.6) | 0.2 | 0.02 |
| South Africa | 1,020 | 376 | 137 (36.4%) | 42.8 (23.9) | 0.05 | 0.78 |
| United Kingdom[b] | 1,428 | 975 | 351 (36.0%) | 53.9 (51.2) | 0.04 | 0.01 |
| United States | 4,508 | 1,754 | 703 (40.1%) | 43.9 (27.9) | 0.01 | 0.78 |
| All regions | 12,538 | 5,711 | 1,998 (33.3%) | 37.7 (10.1) | 0.01 | 0.25 |

We classify a species as having a significant lag phase if the model chosen has at least one knot and if the slope is positive after the first knot. [a]Including Northern Ireland. [b]Excluding Northern Ireland. [c]Values in parentheses indicate the percentage of species with a significant lag (>5 years). [d]Values in parentheses indicate the standard deviation. [e]The larger the value of K, the stronger the phylogenetic signal; that is, close relatives are more similar than expected under a Brownian motion evolutionary model.

**Table 2 | The key features of species from nine regions worldwide**

| Region | Key features of species with the longest lag period | | | | | |
|---|---|---|---|---|---|---|
| | Species | First year | Lag length (years) | Family | Lifespan | Growth habit |
| Australia | *Nassella trichotoma* | 1770 | 221 | Poaceae | P | G |
| Ireland[a] | *Mercurialis annua* | 1866 | 130 | Euphorbiaceae | A | F, H |
| Japan | *Galium verum* | 1894 | 80 | Rubiaceae | P | F, H |
| Madagascar | *Desmodium incanum* | 1834 | 121 | Fabaceae | P | F, H, Sb |
| New Zealand (North Island) | *Spartina anglica* | 1937 | 48 | Poaceae | P | G |
| New Zealand (South Island) | *Erica lusitanica* | 1930 | 60 | Ericaceae | P | S |
| South Africa | *Spergularia media* | 1883 | 114 | Caryophyllaceae | A, P | F, H |
| United Kingdom[b] | *A. pseudoplatanus* | 1613 | 320 | Aceraceae | P | T |
| United States | *Plantago lanceolata* | 1822 | 177 | Plantaginaceae | A, B, P | F, H |

A, annual; B, biennial; P, perennial; G, graminoid; F, forb; H, herb; S, shrub; Sb, subshrub; T, tree. [a]Including Northern Ireland. [b]Excluding Northern Ireland.

system, pollen vector, dispersal system, Grime's competitor, stress tolerator, ruderal (CSR) strategies and geographical origin as traits previously identified to be associated with invasion success and population growth[43–46].

## Time lags in 35% of all naturalized neophytes

Almost one-third of naturalized plant species in the nine regions showed a lag period (Table 1). The United States had the highest percentage of species with lags (40%), while the North Island of New Zealand had the lowest (24%). Our analysis shows that lag phases are not as frequent and common as stated anecdotally in the invasion literature[5,7,44,47,48]. The use of inappropriate statistical methods, such as fitting models to cumulative time series[47], probably resulted in an overestimation of the frequency of this phenomenon in plant invasions[41].

The median lag length varied from 15 years in Ireland to 37 years in the United Kingdom and the United States. Averaged over all regions, the median length of the lag period was 34 years (Table 1). With a lag length of 320 years, *Acer pseudoplatanus* (sycamore maple), a deciduous, broad-leaved tree first recorded in the United Kingdom in 1613, exhibited the most prolonged lag phase among all species examined. The share of species with very long lag times (>100 years) was highest in the United Kingdom (13%), followed by Australia (9%) and the United States (5%) (see Supplementary Fig. 2 for the frequency distribution of lag lengths).

Through an interregional study, the connection between biogeographical history and human activities can enhance our understanding of the context-dependent nature of invasion events[49,50]. The observed variations in the length of lag among regions can be attributed to biological factors and the history of specimen collection and recording. For instance, it is worth noting that the oldest record in our dataset dates back to 1613 in the United Kingdom, while Australia has records from as early as 1770. These countries have a long history of herbarium collections and extensive transportation of plants, which could influence the availability and documentation of early invasion events. Another factor that could specifically contribute to long lag phases in Australia is the limited human movement and transportation across the land. Given that most major cities in Australia are coastal and there is relatively less transportation infrastructure across the country, opportunities for dispersal by humans have been constrained. This limited human-mediated dispersal could potentially contribute to longer lag phases in Australia than in regions with higher human mobility and transportation networks. By contrast, the shorter lag times observed in South Africa may be explained by the similarity of climate conditions to the native ranges of these species. Many of the introduced plants in South Africa originate from regions with comparable climates[51] and biomes, which could facilitate their successful establishment and rapid spread. Biogeographical factors, including differences in species composition, dispersal capabilities and community interactions, can
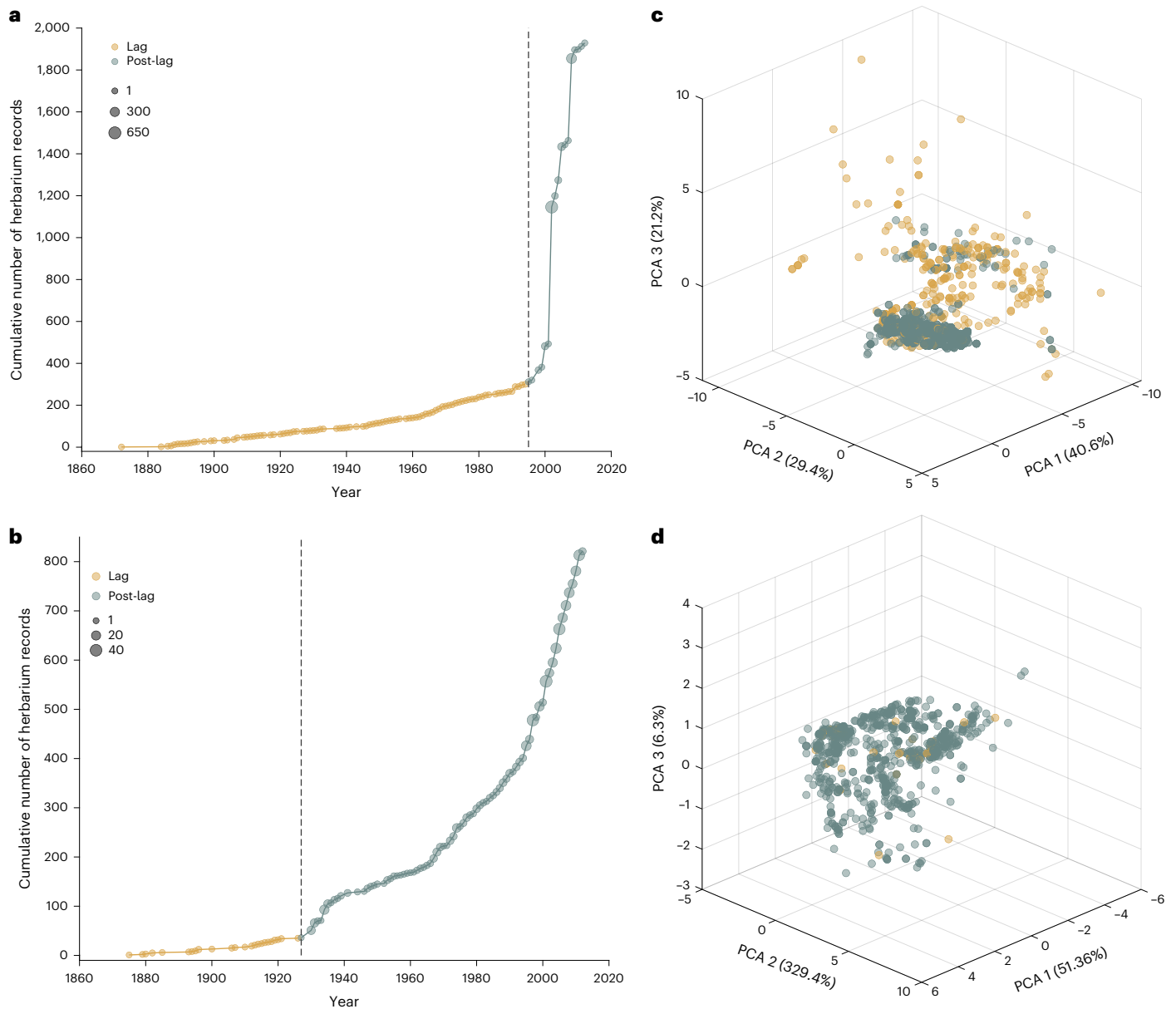
**Fig. 2 | Biphasic temporal trends. a,b,** Examples of biphasic temporal trends are represented by the invasions of *Centaurea calcitrapa* (**a**) and *Chloris virgata* (**b**) in Australia. **c,d,** While dissimilar climate conditions have been sampled during the lag and post-lag periods in *C. calcitrapa* (**c**), *C. virgata* exhibited analogous climate spaces during the two invasion phases (**d**). The vertical dashed lines in **a** and **b** indicate the lag year. Principal component analysis (PCA) plots are based on eight bioclimatic variables. Lag and post-lag records are shown as orange and dark grey circles, respectively.

contribute to variations in invasion patterns. Historical influences, such as colonization history, introduction pathways and human activities, can further shape the spread and establishment of non-indigenous species in different regions. Considering such historical factors alongside biological factors is crucial in interpreting and understanding the observed interregional differences in lag times.

Species introduced to more than one region serve as experimental replicates and provide insights into shared spatio-temporal invasion trajectories. Therefore, we tested for constancy in species' response to lag existence (or absence) using 1,292 species naturalized in more than one study region. This multiregional analysis revealed that the species could be grouped into three categories: 'lag-persistent' species always exhibited lags wherever they invaded (12% of the total species), 'lag-variable' species showed lags at least in one region but not in the other regions (58% of the total species) and 'non-lag-persistent' species never experienced a lag phase during any of their invasions (30% of the total species). These findings suggest that for most species (~60%, lag variable), whether they will experience a lag phase depends on the region they invade rather than their inherent attributes. This observation may help explain why most trait and phylogenetic analyses[49–52], including ours, have found a weak signal for lag and, therefore, low predictive power. However, we might have better success in identifying species that never experience lag (that is, non-lag persistent) as we observed a greater constancy for species with no lags than those with lags.

### Self-fertilizing species are less likely to experience a time lag

Phylogenetic analysis showed (Table 1) some level of clustering for species exhibiting no time lags across regions, again suggesting greater constancy for species without a lag phase. A given species may have been introduced to these regions at different times (variable residence time) and exposed to different environments. Predictions based on
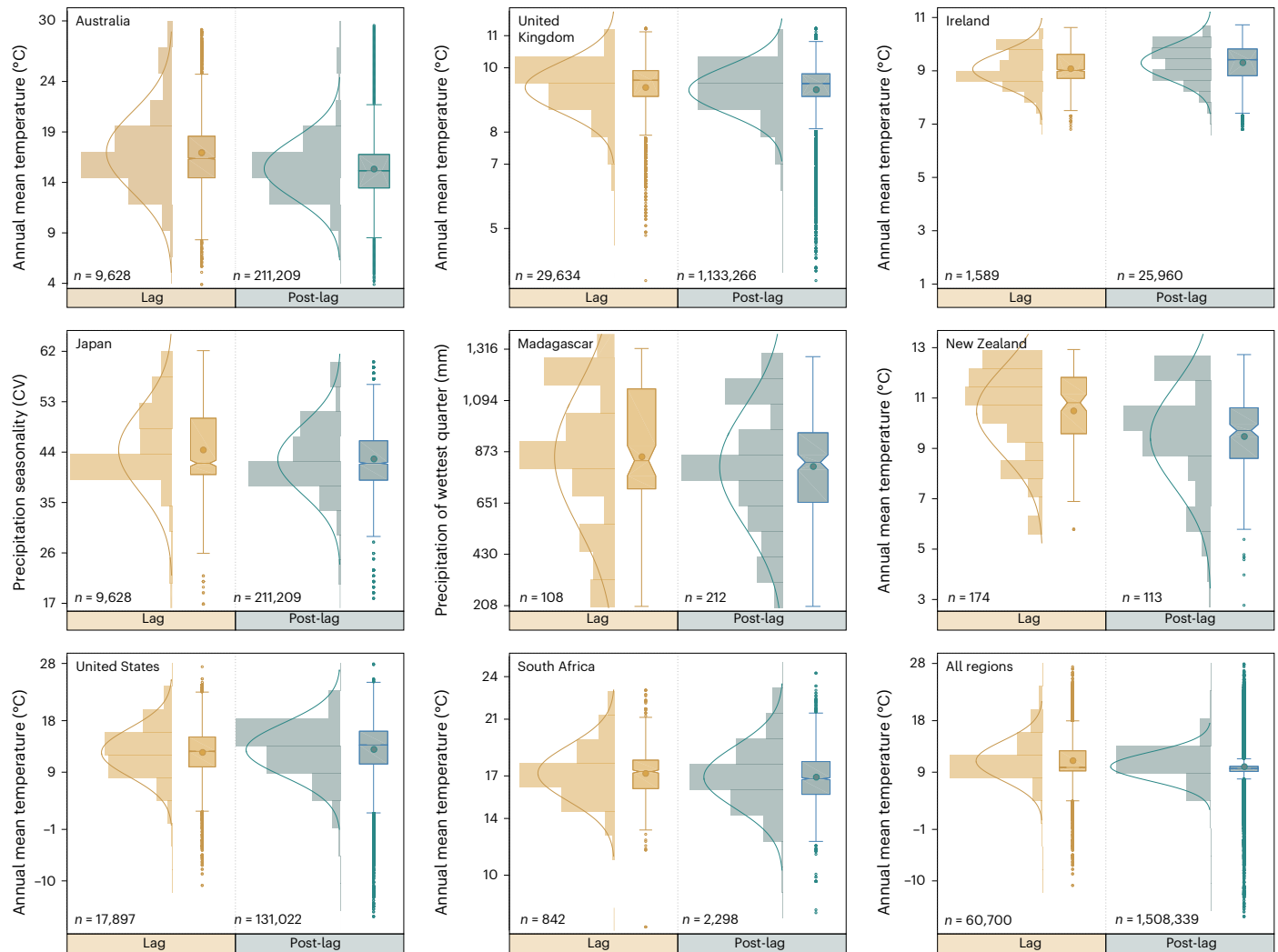
**Fig. 3 | The comparison of lag and post-lag periods for climate variables identified as the most influential in causing a climate niche shift between the two invasion phases based on multivariate analysis.** The horizontal lines in the boxplots indicate the median, while the circles inside the boxes represent the mean. The box limits show the interquartile range (that is, 25th and 75th percentiles), whiskers contain 99% of the data and points occurring above or below the whiskers indicate outliers. The sample sizes are shown in the respective plots. CV: coefficient of variation.

phylogeny would gain more support if the multiregional invasions of a given species follow a consistent trajectory (that is, repeated lags or lack thereof). Phylogenetically corrected, generalized estimating equations were used on 1,731 species to test whether the traits predict lag length or probability. The lag-phase length was not correlated with these traits (Fig. 4). Still, the two traits interacted to affect the probability of the lag phase occurring ($P = 0.024$). In selfing species, annuals were less likely to experience a lag, while in outcrossing species, perennials had a lower probability for a lag than annuals (Fig. 4). For species that showed lags of over 100 years, a perennial life cycle was significantly over-represented (63% perennial and 37% annual, binomial $P = 0.0137$, $n = 88$), while selfing was least frequent (18% selfing, 50% mixed mating and 32% outcrossing; multinomial $P = 0.0013$; $n = 88$). Some plant families accommodate more (for example, Poaceae, 60%) or fewer (for example, Lamiaceae, 25%) alien species with lag phases than expected (Supplementary Fig. 2).

Given that the result of the trait-based approach is sensitive to the selection of traits, we used Blomberg's $K$ [53,54] to test for a phylogenetic signal. We found no evidence of a phylogenetic signal for the lag phase at the global scale (Table 1). However, regional analyses for Ireland, Madagascar, the South Island of New Zealand and the United Kingdom showed that species with a lag phase tend to be more related than

expected under a Brownian motion evolutionary model (Table 1). Furthermore, for all studied regions, no evidence of a phylogenetic signal was found for species with significant climate differences according to Blomberg's $K$ test (Table 1).

**Evidence for climate discovery as realized climate spaces differ between lag and post-lag phases**

To investigate whether the end of the lag phase is associated with climate, we compared the climate envelopes of lag and expansion phases. For this analysis, we excluded species with fewer than 15 records per invasion phase and removed those with a very short lag phase of <5 years ($n = 105$), which appeared ecologically irrelevant [48]. A total of 553 species met the above criteria. Climate difference was measured as a change in the centroid position of the climate envelopes captured during the expansion phase relative to the lag phase. We also quantified the degree of novelty (overlap) between the climate envelopes of the two invasion phases. The climate envelope was described by eight bioclimatic variables [55] and was selected to reflect the average, extreme and variability of hydrothermal conditions, using the climate data from a single period [55] to avoid the confounding effect of climate change. A climate shift was deduced as significant if the Mahalanobis distance between the centroids of the two climate spaces was larger than that expected
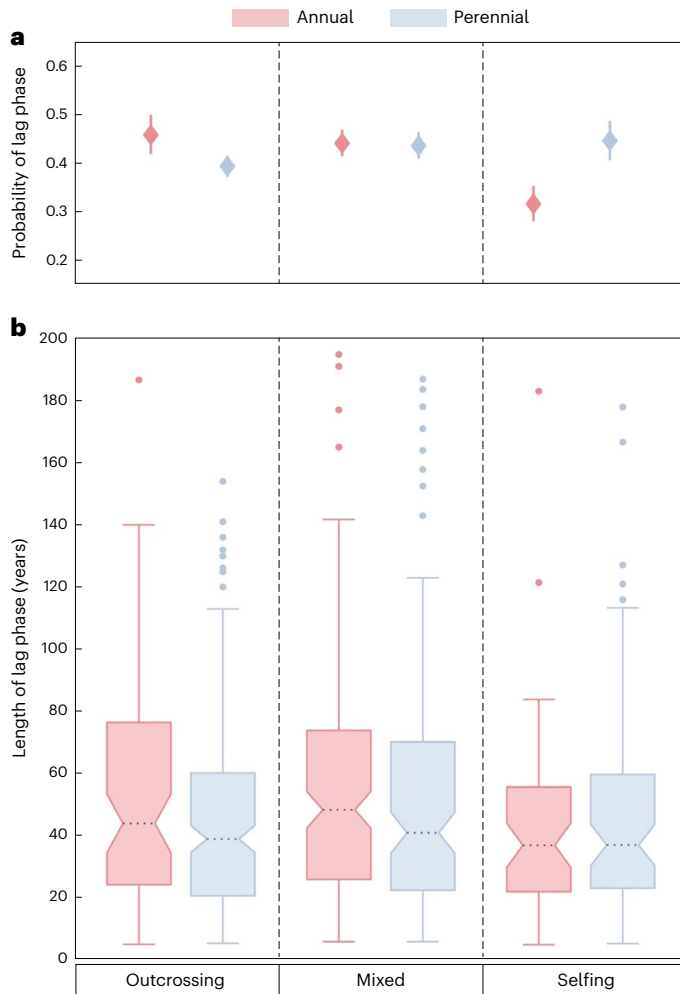
**Fig. 4 | Probability and length of lag phase. a,b,** Probability (**a**) and length (**b**) of the lag phase in relation to the breeding system and lifespan of naturalized plants. Probability values are least-squares means, estimated, along with standard errors (vertical bars), from fitting a generalized linear mixed model. In the boxplots, the dotted horizontal lines indicate the median. In addition, the box limits indicate the interquartile range (that is, 25th and 75th percentiles), whiskers contain 99% of the data and points above the whiskers indicate outliers. Species rely on pollen from other species for seed production as opposed to selfing (or self-compatible) species ($n_{annual}$ = 173, $n_{perennial}$ = 157), which allows for uniparental reproduction. However, a mixed-mating ($n_{annual}$ = 162, $n_{perennial}$ = 528) system can produce seeds through selfing and outcrossing ($n_{annual}$ = 365, $n_{perennial}$ = 346).

at random through a permutation test (see 'Comparison of Climatic Envelopes' in Supplementary Information).

We found evidence of a significant shift of the climate space centroid during the transition from a lag to an expansion phase in 81% (n = 446) of species. We also estimated the degree of climate novelty as the percentage of records from the post-lag phase outside the lag climate envelope. This metric quantifies the expansion into novel climates as the species spreads through geography. The average climate novelty for species with lags was 44%, ranging from 34% in Australia to 61% in Madagascar. An expansion into conditions non-analogous to the lag phase climate was not uncommon, as 37% of species expressed climate novelty values >50%. Assessing shifts in centroids and degree of novelty showed that the transition from a lag to an expansion phase coincides with a climate space expansion (Fig. 3), suggesting climate discovery as a potential factor terminating the lag phase. The climate discovery and occupation of distinct climatic spaces by invasive species can be influenced by a range of biotic factors, such as the emergence

of mutualistic relationships (for example, with mycorrhizal fungi and pollinators) and the absence of antagonists (for example, competitors and herbivores). The interplay of these biotic factors with evolutionary processes, functional trait plasticity and the introduction of different genotypes can shape the success and spread of invasive species across varying climatic conditions[19].

Invaders may experience slow population growth (lags) because they were introduced to habitats with marginally suitable climatic conditions. Once the invaders manage to disperse (or new introductions occur) into regions with climate conditions that they are more adapted to, a rapid increase in their abundance may follow. Changes in the geographical range (that is, dispersal or independent introduction to a new geographical region) and geographical infilling can expose the invader to novel climate conditions leading to a difference between the observed lag and post-lag climates. To test whether the climate dissimilarity is driven by exploring new environments through dispersal, we quantified the degree of geographical expansion as the percentage of post-lag points that occur outside the geographical domain of the lag records. Geographical expansion ranged from the post-lag range being entirely contained within the lag geography (0%) to complete separation (100%), with a mean of 51% of the post-lag records in novel geographies. Furthermore, the geographical expansion was negatively correlated with the climate novelty in the United States ($r = -0.41$, $P \le 0.001$, $n = 229$), Britain ($r = -0.38$, $P \le 0.001$, $n = 119$) and Australia ($r = -0.35$, $P \le 0.001$, $n = 124$). While these regions account for 85% of test species, we observed no significant correlation in other regions. These results suggest that climate differences between the two invasion phases may not simply result from geographical expansion.

To further investigate the hypothesis that the lag phase is related to climate discovery, we compared climate envelopes in non-lag species ($n = 1,849$) by randomly splitting their time series into two subsets while maintaining the chronological order of records, as if their invasions had undergone lag-expansion phases. As we did to species with a real lag phase, we then calculated the Mahalanobis distances between the centroids of the climate envelopes associated with these two subsets. The distances for non-lag species were significantly smaller than those of the lag species (Supplementary Fig. 4), implying that shifts in climate space in lag species cannot be obtained by chance or simply due to sampling issues. The distance between the centroids of the lag and post-lag climate envelopes showed a decrease with an increasing sample size during the lag period (Supplementary Fig. 6). This suggests that species with larger population sizes during the lag phase may experience smaller shifts in their climate conditions during subsequent expansion. Alternatively, an increased sample size could also indicate that the species' climate space has been more accurately delineated. Using a multivariate approach[42], we found that annual mean temperature is the most influential climatic variable, leading to differences between the lag and post-lag phases in most regions (Table 3). For almost all regions, the post-lag period can be described by lower annual mean temperatures than the lag period, implying that most species have dispersed to colder areas as they expanded their range limits (Fig. 4). A colder climate during post-lag can result from moving to higher altitudes, as found in another study[56]. Despite the partial temporal mismatch of the climate data concerning the time range of the occurrence records, it is necessary to use the climate data from a single period[55] to avoid the confounding effect of climate change. If climate data are extracted according to the time of specimen collection, then the difference between lag and post-lag climatic niches will not be the pure result of invasion dynamics but also the climate changes over time. Climate change, however, might have contributed to the termination of the lag phase, perhaps by making previously climatically unsuitable regions more suitable, particularly in species with long lag times and generation cycles.

While several cases of improved habitat suitability and associated range extensions were studied using species distribution models (SDMs)[57,58], none account for the temporal dynamics of invasions. There is also evidence of niche shifts through post-introduction evolution,

**Table 3 | Climate niche differences between lag and post-lag periods in naturalized plant species from nine regions and Blomberg's K test results for detecting phylogenetic signals**

| Region | Number of species analysed for climate comparison[c] | Number of species with significant climatic niche shift[d] | MIV[e] | Blomberg's K test | |
|---|---|---|---|---|---|
| | | | | K for climate novelty[f] | P value |
| Australia | 124 | 98 (79.0%) | Annual mean temperature (25.0%) | 0.06 | 0.77 |
| Ireland[a] | 23 | 16 (69.6%)[b] | Annual mean temperature (18.2%) | 0.33 | 0.10 |
| Japan | 21 | 13 (61.9%) | Precipitation seasonality (19.1%) | 0.35 | 0.42 |
| Madagascar | 5[g] | 4 (80.0%) | Precipitation of wettest quarter (40.0%) | 1.13 | 0.06 |
| New Zealand (North Island) | 0 | NA* | NA* | NA | NA |
| New Zealand (South Island) | 5[g] | 4 (80.0%) | Annual mean temperature (40.0%) | 1.00 | 1.00 |
| South Africa | 27 | 6 (22.2%) | Annual mean temperature (37.0%) | 0.83 | 0.15 |
| United Kingdom[b] | 119 | 106 (89.1%) | Annual mean temperature (20.2%) | 0.05 | 0.24 |
| United States | 229 | 199 (86.9%) | Annual mean temperature (22.7%) | 0.04 | 0.83 |
| All regions | 553 | 446 (80.7%) | Annual mean temperature (23.3%) | 0.02 | 0.35 |

A randomization test with 1,000 iterations was used for statistical significance of the climatic niche shift. MIV, most influential variable. *No data available after filtering. [a]Including Northern Ireland. [b]Excluding Northern Ireland. [c]From the species pool with significant lag phases (Table 1), only those with 15 records per invasion phase were analysed. [d]Values in parentheses indicate the percentage of species with a significant climatic niche difference between the lag and post-lag phases. [e]MIV is the climate variable with the most significant contribution to climate differences (novelty) between the lag and post-lag phases. MIV was determined for each species, and the most frequent MIVs for each region are reported in the table. Values in parentheses indicate the percentage of species with the same MIV. [f]The larger value of K, the stronger the phylogenetic signal; that is, close relatives are more similar than expected under a Brownian motion evolutionary model. [g]The phylogenetic results may be unreliable and are not considered in the conclusion as the assessment has been made using a low number of species.

allowing some aliens to establish beyond their preadapted environments reflected by the fundamental niche[22,37,59,60]. Our study points towards niche shifts as a potential driver of terminating the lag phase.

Our understanding of the early phases of biological invasions is poor and retrospective, and recognizing the lag and its potential drivers is essential to predict and manage biological invasions better. Our findings show that 'sleeper weeds'[9] can become 'awake' once moved to new locations, highlighting the necessity of better quarantine legislation to minimize the chance of propagule dispersal to climatically suitable areas. Our results show that many species with lags have undergone very long time lags. Such lag periods make predictions about the full potential invasion extent highly unreliable. Any judgement about the fate of an introduction based on its past and present status can be underestimated as a lag phase will mask the true spread potential of an alien species. Risk assessment schemes should not take the status of aliens for granted, as they can give rise to future invasive problems once they land in the right place. As changes in the climate niche can be associated with the ending of the lag phase, incorporating invaded range data into SDMs[58] is deemed beneficial to project suitable habitats at the risk of post-lag colonization. Incorporating the temporal dynamics of invasions and their phases into SDMs may yield more realistic predictions of the fate of invasions[61]. Understanding the complex interplay between biotic factors, evolution and climate is crucial for comprehending the mechanisms underlying invasion success and predicting the potential impacts of invasive species on ecosystems. The consistency of our results across regions suggests the existence of general patterns in invasion dynamics. This finding challenges the prevailing notion that invasions are idiosyncratic phenomena[62,63]. This shared pattern across regions supports the notion that certain underlying mechanisms and processes may drive invasion dynamics more generally than previously assumed. By highlighting these findings, we contribute to the growing body of evidence[64] that challenges the view of invasions as purely idiosyncratic events.

## Methods

We obtained 12,538 time series of naturalized alien plant species based on herbaria data for Australia, New Zealand, Ireland land-mass (the Republic of Ireland and Northern Ireland), United Kingdom (excluding Northern Ireland), Japan, Madagascar, South Africa and the United States. For Australia, a list of naturalized alien plants (2,416 species) was acquired from the compendium of the introduced flora of Australia[65]. This species list, adopted in previous studies[66], was used to obtain historical (date of specimen collection) and geographical (longitude and latitude) information from Australia's Virtual Herbarium[67]. For New Zealand's North Island and South Island, previously studied[41,47] occurrence records of 387 species from the Allan Herbarium database[68] were analysed separately. A subset of the global naturalized alien flora (GloNAF) database[69] was queried to extract naturalized alien species for the remaining six regions. Georeferenced occurrence records from the Global Biodiversity Informatics Facility[70] were verified for consistency and completeness in taxonomic names, geolocation and collection dates. Species names were taxonomically validated using the Integrated Taxonomic Information System (http://www.itis.gov), and synonyms, subspecies and varieties merged to the species level while infraspecific taxonomic ranks (for example, hybrids, cultivars, forms) were removed. We also discarded duplicates, non-georeferenced records and records without a collection date for each species. The analysis was restricted to pre-2014 data to account for the potential delay between the data collection and database entry[41,47,71]. The lag phase analysis included only species with a minimum of 15 occurrence records[41,72,73]. A total of 5,711 time series satisfied all the above requirements (Table 1).

We obtained information on plant traits using the TRY plant trait database[74], Traitbank of the Encyclopaedia of Life[75], BioFlor[76], The Ecological Flora Database[77], the PLANTS Database[78], the Apomixis Database[79] and an online assisted literature research. The compiled data from online and offline databases are available upon request from the authors.

The cumulative number of herbarium records (or occupied grid cells) plotted against time is often used to interpret the temporal trajectories of invasions, including the possibility for the existence of lag phases[44,47,72,73,80]. However, both logical and statistical problems exist with parametric regression models fitted to these data to detect a lag and estimate its length[41]. For example, the first part of an exponential[7] or logistic[80] model has been mistakenly regarded as a lag phase, while these models are monophasic and do not include two distinct periods of slow and rapid growth. A recently suggested method[47] resolves this problem by fitting a two-segmented regression in which the first phase has a smaller slope (depicting slower growth during the lag phase) than the second phase (depicting more rapid growth during the expansion

phase). However, the use of cumulative data violates the assumption of independence in statistics[81], and the use of asymptotic models as their best candidates implies that the rate of specimen collection drops to zero after the second phase of the invasion, which does not seem logical[41].

Perhaps the most serious challenge in modelling time series to estimate time lags in invasions relates to biases in sampling intensity over time and space of herbarium records, which is particularly poor and sparse during the early stages of invasions[82]. Using herbarium data to construct invasion histories or as a surrogate for the abundance of a species assumes that the collection is constant. However, collection efforts can vary over time owing to changes in awareness, the number of collectors, and environmental protection or invasive species management policies, leading to a temporal trend that may resemble phases of slow and rapid increase[41,47,83,84]. We have developed an improved statistical method for detecting and estimating lags from herbarium data, which directly models the annual collection rate rather than using the cumulative number of records. The model uses the total number of specimens of alien plant species collected each year as a covariate to allow for variability in the overall alien species collection effort. Our model accounts for the multiphasic nature of invasions by fitting a generalized additive model with piecewise linear splines and a log-link function (see ref. 41 for more details). A separate model was fit to the time series of each species (within a region) individually, and the number and position of knots were determined through a model selection procedure that aims to minimize the Akaike information criterion[41].

Differences in climate envelopes can be measured based on either the position of the centroids or the degree of overlap between climate envelopes.

We have recently developed a novel multivariate statistical method for comparing climate envelopes that use the Mahalanobis metric, $D$[85], to calculate the distance between the centroids of two multidimensional climate envelopes[81]. An ellipsoid encompassing the data is drawn using Mahalanobis $D$[85]. For each point ($x_i$) in the multivariate space of climate data, its distance ($D_i$) from the centroid ($\underline{x}$) is calculated using Mahalanobis distance: $D_i = \sqrt{(x_i - \underline{x})^T C^{-1}(x_i - \underline{x})}$, where $C^{-1}$ is the inverse of the covariance matrix (superscript $T$ indicates the transposed vector-matrix). The maximum $D$ values ($D_{max}$) were used to delineate an ellipsoid that includes all data points. As mentioned above, climate difference can be measured with respect to the position of centroids and the magnitude of overlap between two climate envelopes. To test for a shift in the position of centroids, we first calculate $D$ between the two centroids (that is, lag versus post-lag niche): $D = \sqrt{(\underline{y} - \underline{x})^T S^{-1}(\underline{y} - \underline{x})}$, where $\underline{x}$ and $\underline{y}$ are the centroids of two climatic envelopes (lag and post-lag niches, respectively), and $S$ is a pooled covariance matrix of the two climate envelopes. $D$ varies from 0 to infinity, with larger $D$ values indicating larger differences (distances) between the two climate envelopes. A randomization test was used to test for the statistical significance of $D$ the centroids of two climatic envelop. To test whether the distance between the two climatic niches cannot be obtained by chance, the combined data of two climate envelopes (lag and post-lag phases) were split randomly, preserving the original number of records per phase. This process was repeated 1,000 times, calculating the distance between these two new groups. The distance between the two climatic envelopes is concluded to be significant if the original $D$ value is larger than or equal to the 95th percentile in randomly generated $D$ values. A $P$ value is also estimated as the proportion of $D$ values from randomized datasets smaller than or equal to the observed $D$.

The deviation of post-lag climate from that of the lag might have resulted simply from the species sampling of new climates as they colonize new areas and hence may have no bearing on the role of climate in terminating the lag phase. To address this issue, we conducted a similar climate analysis, as described above, on non-lag species that had at least 30 records ($n = 1,849$). We randomly split the time series of these non-lag species into two subsets (while maintaining the chronology

of records) as if their invasions have undergone a biphasic trajectory, that is, lag and expansion phases. We then calculated the Mahalanobis distances between the centroids of the climate envelopes associated with these two subsets and repeated this randomization 1,000 times. We then compared the Mahalanobis distances for non-lag species against those for species with true lags. If Mahalanobis distances for non-lag species are smaller than those of the lag species, then there is compelling support that climate shifts in lag species cannot solely be obtained through the sampling of new climates during the range expansion, but rather, climate has played a role in terminating the lag phase.

To calculate the degree of novelty (overlap) of the post-lag climate relative to the climate of the lag period, we calculated the proportion of data points from the post-lag period that falls within the climate ellipsoid of the lag period. The lag climate ellipsoid was drawn using the $D_{max}$, which is the maximum Mahalanobis distance observed within the climate space of the lag period. To determine whether a record ($x_i$) from the post-lag climate falls inside the lag ellipsoid, we need to calculate the distance of that point ($D_i^x$) from the centroid ($\underline{y}$) of the lag data: $D_i^x = \sqrt{(x_i - \underline{y})^T C_y^{-1}(x_i - \underline{y})}$, where $C_y$ is the covariance matrix of lag data. If $D_i^x > D_{max}$, it means that the post-lag record $i$ is outside the lag ellipsoid and thus represents a novel point (that is, climate niche extension). If $D_i^x \leq D_{max}$, the post-lag record $i$ locates within the ellipsoid of the lag climate. Therefore, post-lag climate novelty is the number of post-lag records satisfying $D_i^x \leq D_{max}$ divided by the total number of post-lag records.

For species with significant climate differences, we identified the climate variable that contributes the most to the differences in climate spaces of lag versus post-lag phases following a previous study[42]. The Mahalanobis distance (between the centroid of two climate spaces) will attain its largest value if all covariates are used to construct the climatic niche and will decrease with the number of covariates removed. A climate variable has a high contribution to climate difference if its omission (while keeping all other variables) results in a large reduction of the Mahalanobis distance compared with the climate comparison that includes all variables. We iteratively dropped climate variables (one at a time). We recalculated the magnitude of reduction in Mahalanobis distances between the lag and post-lag centroids to identify the most influential variable in driving the lag versus post-lag climate differences. All analyses were conducted in MATLAB (R2020a) and R[86,87].

Climate data representative of current conditions (1950–2000) were extracted from the WorldClim database at a spatial resolution of 2.5 arc minutes[88]. For each occurrence record, we extracted the climatic values from eight Bioclim variables that are reflective of the average (annual mean temperature and precipitation), extreme (mean temperature of the warmest and coldest quarter, precipitation of wettest and driest quarter) and variability (temperature and precipitation seasonality) of hydrothermal conditions. These climate variables are considered relevant to the ecology of plant species and have been widely used in modelling their distributions[89–91]. It may be desirable to use more detailed climatic data; however, such data are not widely available or not thoroughly tested, especially for a comparative study across 12,538 time series. Despite the partial temporal mismatch of the climate data to the time range of the occurrence records, it is necessary to use the climate data from a single period to avoid the confounding effect of climate change. Suppose climate data are extracted according to the time of specimen collection. In that case, the difference between lag and post-lag climatic niches will not be the pure result of invasion dynamics but also that of changes in climate over time. All previous studies have used the climate conditions of a single period (current) for testing niche shifts in invasive species (for example, refs. 37,38,92,93).

Dispersal of the invader into different geographical regions can result in differences between the lag and post-lag niches through exposure to novel climate conditions. Based on the georeferenced occurrence data, we quantified the post-lag points that occur outside the

geographical range of the lag records, calculating kernel densities for ten levels of the lag points. To remove low-density areas encompassing outliers, we selected the third-lowest density level, comprising about three-fourths of all lag records as a polygon delimiting the geographical range of lag occurrences. We calculated the ratio of post-lag records falling outside this density level.

We test the hypothesis that species with a lag phase or climate shift during the expansion phase are more phylogenetically related than species with no significant lag or climate shift. Species shared across the nine regions were used as a yardstick of the robustness of predictions made using phylogeny analysis.

A phylogenetic analysis was used to summarize phenotypic (dis) similarity, given that the evolutionary divergence times correlate with ecological differences[94,95]. First, a composite phylogeny of all species was constructed using the publicly available 'supertree' from the 'brranching' package in R[96]. Next, the branch lengths were calculated using Grafen's method[97] using the 'compute.brlen' function of the R package 'ape'[98]. After species were pruned from this tree depending on data availability, we used Blomberg's $K$[53,54] to test for phylogenetic signal, a quantitative measure of the degree to which phylogeny predicts the ecological similarity of species, here magnitude of lag phase or niche shift. $K$ values near 0 indicate a lack of phylogenetic signal.

By contrast, values close to or above 1 indicate a strong signal for Brownian trait evolution, that is, a tendency for related species to resemble each other. To construct 95% confidence intervals around the observed $K$, the lag length (or climate novelty) was permuted across the tips of the phylogenetic tree (that is, among species) 1,000 times. The corresponding $K$ is recalculated[54,99]. The comparative trait analysis needs to be corrected for phylogeny, as closely related species violate the assumption of statistical independence. We used generalized estimating equations to account for evolutionary history, incorporating a phylogenetic distance matrix into a general linear model[100].

A summary of the major steps to collate and analyse the data is given in the flow chart shown in Supplementary Fig. 3.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

For Australia, a list of naturalized alien plants was acquired from the compendium of the introduced flora of Australia[65] and the corresponding occurrence records were extracted from Australia's Virtual Herbarium (https://www.ala.org.au)[67]. New Zealand's data were obtained from literature[41,47,68]. The GloNAF database is available in the literature[69,101] and was queried to extract species lists for the remaining six regions. Georeferenced occurrence records were extracted from the Global Biodiversity Informatics Facility (https://www.gbif.org)[70]. Trait data were extracted from TRYDB (https://www.try-db.org). Climate data were downloaded from the second version of the WorldClim dataset (https://www.worldclim.org/data/worldclim21.html). All data are available online and in the literature.

The minimum dataset comprises the naturalized species lists sourced from the GloNaf database, the compendium of the introduced flora of Australia[65] and previous studies[41,47] and is available under the CC BY 4.0 licence (https://doi.org/10.26188/24782898).

## Code availability

The analysis has been implemented using existing packages referenced in the text. Implementation scripts are available on request.

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## Author contributions

M.B.M. conceived the idea; M.B.M. and P.R. designed the research, performed the analysis and wrote the first draft of the paper; F.E., M.V.K., P.P., J.P. and P.W. provided data, edited the paper and provided comments.

## Competing interests

The authors declare no competing interests.

## Additional information

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| ☒ | ☐ | For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
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*Our web collection on statistics for biologists contains articles on many of the points above.*

## Software and code

Policy information about availability of computer code

| Data collection | No computer code was used in data collection. All data were collected manually through website downloads. |
|---|---|
| Data analysis | All analytical methods utilised in this study have been described in prior literature and are elaborated upon, with accompanying citations, in the Supplementary Information (SI) methods section. All analyses were conducted using the R programming language. We employed Hyndman's (2015) script for assessing the lag phase and adapted Mesgaran's (2014) multivariate metrics for comparing climate spaces. The phylogeny for all the species was derived from the publicly accessible 'supertree' in the 'brranching' R package. Branch lengths were determined using the 'compute.brlen' function in the 'ape' R package. |

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All sources are available online and in the literature. For Australia, a list of naturalised alien plants was acquired from the compendium of the introduced flora of Australia and the corresponding occurrence records were extracted from Australia's Virtual Herbarium (https://www.ala.org.au). New Zealand's data was obtained from literature. The GloNAF database is available in the literature and was queried to extract species lists for the remaining six regions. Georeferenced occurrence records were extracted from the Global Biodiversity Informatics Facility (https://www.gbif.org). Trait data was extracted from TRYDB (https://www.try-db.org). Climate data was downloaded from the second version of the WorldClim dataset (https://www.worldclim.org/data/worldclim21.html). The minimum dataset comprises the naturalised species lists sourced from the GloNaf database, the compendium of the introduced flora of Australia and previous studies and is available under the CC BY 4.0 licence (https://doi.org/10.26188/24782898).

## Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender (identity/presentation), and sexual orientation](#) and [race, ethnicity and racism](#).

| | |
|---|---|
| Reporting on sex and gender | N/A |
| Reporting on race, ethnicity, or other socially relevant groupings | N/A |
| Population characteristics | N/A |
| Recruitment | N/A |
| Ethics oversight | N/A |

Note that full information on the approval of the study protocol must also be provided in the manuscript.

# Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences      ☐ Behavioural & social sciences      ☒ Ecological, evolutionary & environmental sciences

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# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|---|---|
| Study description | Assessment of time lags and changes in realised climate spaces of naturalised plants |
| Research sample | 3,505 naturalised plant species from nine regions (i.e., Australia, North and South New Zealand, Madagascar, South Africa, Japan, Great Britain, Ireland landmass, and the USA) were analysed. The regions are selected to cover diverse climate zones in both hemispheres and have a sizeable invasive flora well represented in biodiversity data. |
| Sampling strategy | No sampling was conducted. However, we filtered the data before each assessment to ensure a minimum sample size for statistical power. |
| Data collection | For Australia, we sourced a list of 2,416 naturalised alien plant species from the compendium of Australia's introduced flora. This list, referenced in prior studies, facilitated the retrieval of historical data (such as the date of specimen collection) and geographical coordinates (longitude and latitude) from Australia's Virtual Herbarium. For the North and South islands of New Zealand, we analyzed occurrence records of 387 species derived from the Allan Herbarium database. For the other six regions, we utilized a subset of the GloNAF database to identify naturalised alien species and subsequently downloaded occurrence data from GBIF. |
| Timing and spatial scale | The data ranges from 1611 to 2014 and encompasses nine regions: Australia, New Zealand's North Island, New Zealand's South Island, Madagascar, South Africa, Japan, Great Britain, the Ireland landmass, and the USA. |

| | |
|---|---|
| Data exclusions | The lag phase analysis only included species with a minimum of 15 occurrence records, while the climate space comparison only included lag species with a minimum of 15 records per phase (lag and post-lag). |
| Reproducibility | While the majority of the analysis is deterministic, some randomised simulations (e.g., calculating D2 values for non-lag species) might produce results that vary slightly from those presented in the SI figure. However, for all other analyses, the results can be consistently reproduced. |
| Randomization | Permutations were conducted using 1000 replicates to calculate a p-value, which served as the foundation for determining significant differences between lag and post-lag climate spaces. A randomised simulation was also executed to produce D2 values for non-lag species. |
| Blinding | Since there was no human interpretation of the data or results, blinding was deemed irrelevant and was not applied. |

Did the study involve field work? ☐ Yes ☒ No

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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| n/a | Involved in the study |
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| ☒ ☐ | Palaeontology and archaeology |
| ☒ ☐ | Animals and other organisms |
| ☒ ☐ | Clinical data |
| ☒ ☐ | Dual use research of concern |
| ☐ ☒ | Plants |

## Methods

| n/a | Involved in the study |
|---|---|
| ☒ ☐ | ChIP-seq |
| ☒ ☐ | Flow cytometry |
| ☒ ☐ | MRI-based neuroimaging |