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Recursive updating of geographic occupancy shapes path-dependent future alien floras

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Abstract

Biological invasions reshape the regional floras, yet how successive establishments alter opportunities for further spread and floristic composition remains unclear. We reconstructed alien-plant establishment histories across the 48 conterminous US states and used climate-driven simulations to test whether recursively updating geographic occupancy alters predictions of future establishment and regional floristic composition. Prior occupancy in neighboring states was associated with 34-fold higher odds of subsequent establishment in the focal state than when neighboring populations were absent. By the final simulation interval (2095-2099), recursive-updating simulations yielded approximately 17,800 new species–state establishments, compared with 6,800 when initial occupancy was fixed. After matching national establishment totals within

each five-year interval, the mean number of states occupied per realized species was 7.2% higher under updating. Compositional turnover between scenarios declined with increasing initial alien richness and future climatic compatibility, although the negative association with climatic compatibility weakened as initial geographic opportunity increased. These findings highlight the importance of accounting for changing geographic opportunities when forecasting alien-plant spread and regional floristic change.

Introduction

Alien species occur outside their native ranges as a result of human-mediated introductions (van Kleunen et al., 2015; Seebens et al., 2017). Although only a subset becomes invasive, those that do can alter biodiversity, ecosystem functioning and human well-being (Bacher et al., 2026; Chen et al., 2026; Zhu et al., 2026). The accumulation of alien species is projected to continue over the coming decades (Seebens et al., 2017). This leaves a growing pool of introduced species with unrealized potential for future establishment and spread (Essl et al., 2011; Rouget et al., 2016). Forecasts commonly use climatic suitability and other environmental or anthropogenic predictors to estimate future establishment while holding present geographic occupancy fixed throughout the projection (Bradley et al., 2015; Omer et al., 2026). However, each new establishment changes the geographic distribution of the species and may create opportunities for further spread. Whether incorporating these changes alters the projected composition of regional alien floras remains unclear.

When an alien species becomes established in a new location, the resulting population may serve as an additional source of propagules for nearby locations (Bertelsmeier et al., 2018; Zhang et al., 2023). Establishment in a new region may therefore bring propagule sources closer to previously unoccupied areas and increase opportunities for further geographic expansion (Brown & Barney, 2021; Pearson et al., 2018; van Kleunen et al., 2018). Because these opportunities depend on the

57 distributions generated by previous establishments, geographic occupancy may act as a
58 dynamic state variable in forecasts of further spread. Over successive establishment
59 intervals, earlier establishments may influence which species establish later, potentially
60 producing distinct regional floras (Fukami & Nakajima, 2011; Stroud et al., 2024).
61 The influence of earlier establishments on later spread is particularly relevant to
62 invasion debt—the delayed realization of invasions following historical introductions
63 (Duncan, 2021; Essl et al., 2011; Rouget et al., 2016). Climate change may increase the
64 climatic compatibility of particular regions for introduced species that have not yet
65 established in particular regions (Dullinger et al., 2017; Haeuser et al., 2018). For
66 example, the ornamental palm *Trachycarpus fortunei* had long been cultivated in
67 Europe before colonizing sheltered sites in southern Switzerland in the 1950s and forest
68 stands there in the 1970s. Its subsequent expansion was associated with warmer winters
69 and longer growing seasons (Walther et al., 2007). Whether an introduced species
70 establishes in a newly suitable region may also depend on the geographic distributions
71 produced by preceding establishments.
72 Although understanding how invasion debt unfolds over time is important for
73 forecasting alien plant invasions, two gaps remain (Duncan, 2021; Rouget et al., 2016).
74 First, the association between prior geographic occupancy and subsequent
75 establishment remains insufficiently resolved after accounting for climatic
76 compatibility, introduction history and observation effort (D'Antonio et al., 2017;
77 Fukami, 2015; Bradley et al., 2015; Omer et al., 2026; Robeck et al., 2024). Second,
78 the consequences of continuing geographic change remain poorly understood when
79 projections retain occupancy as a fixed starting condition (Fukami, 2015; Stroud et al.,
80 2024). A key uncertainty is whether geographic updating alters predicted future floristic
81 composition, rather than simply differences in local establishment totals or stochastic
82 variation.
83 In this study, we combined 655,520 introduction records from the United States
84 Department of Agriculture Office of Seed and Plant Introduction (SPI) with 24,821,238

cleaned occurrence records to reconstruct alien plant establishment histories across the 48 conterminous US states. We first tested whether prior establishment of the same species in neighboring states predicted its subsequent establishment in the focal state. We then developed climate-driven simulations to test whether projected establishment trajectories and regional floristic composition differed when geographic opportunities were updated after each five-year interval or keep fixed throughout the simulations. Finally, we assessed how initial alien richness, climatic compatibility, and geographic opportunity influenced the compositional differences between simulation scenarios.

Results

Previous occupancy predicts subsequent establishment

Previous establishment in a neighboring state was associated with 34-fold higher odds of subsequent establishment (95% CI 31.667–37.266; $P < 0.001$; Fig. 1a). Including previous neighboring-state establishment and recent establishment history substantially improved model fit relative to the model excluding both history terms ($\Delta AIC = 8,779$). The positive association persisted across alternative specifications of observation effort (OR = 30.49–30.96), establishment transitions (OR = 5.48–10.53), spatial connectivity (OR = 18.17–18.18), and anthropogenic pressure (OR = 34.42; Fig. 1b,c,e,f; Supplementary Tables S1 and S2).

Independent analyses of standardized observations from the National Ecological Observatory Network (NEON) provided further support at a finer spatial grain. Higher prior site-level prevalence was associated with increased odds of subsequent colonization under both the moderate definition (OR = 1.366) and the stricter persistence definition (OR = 1.379; Fig. 1g; Supplementary Table S3). These findings supported the role of prior geographic occupancy as a predictor of subsequent colonization, providing an empirical basis for its incorporation into future simulations.

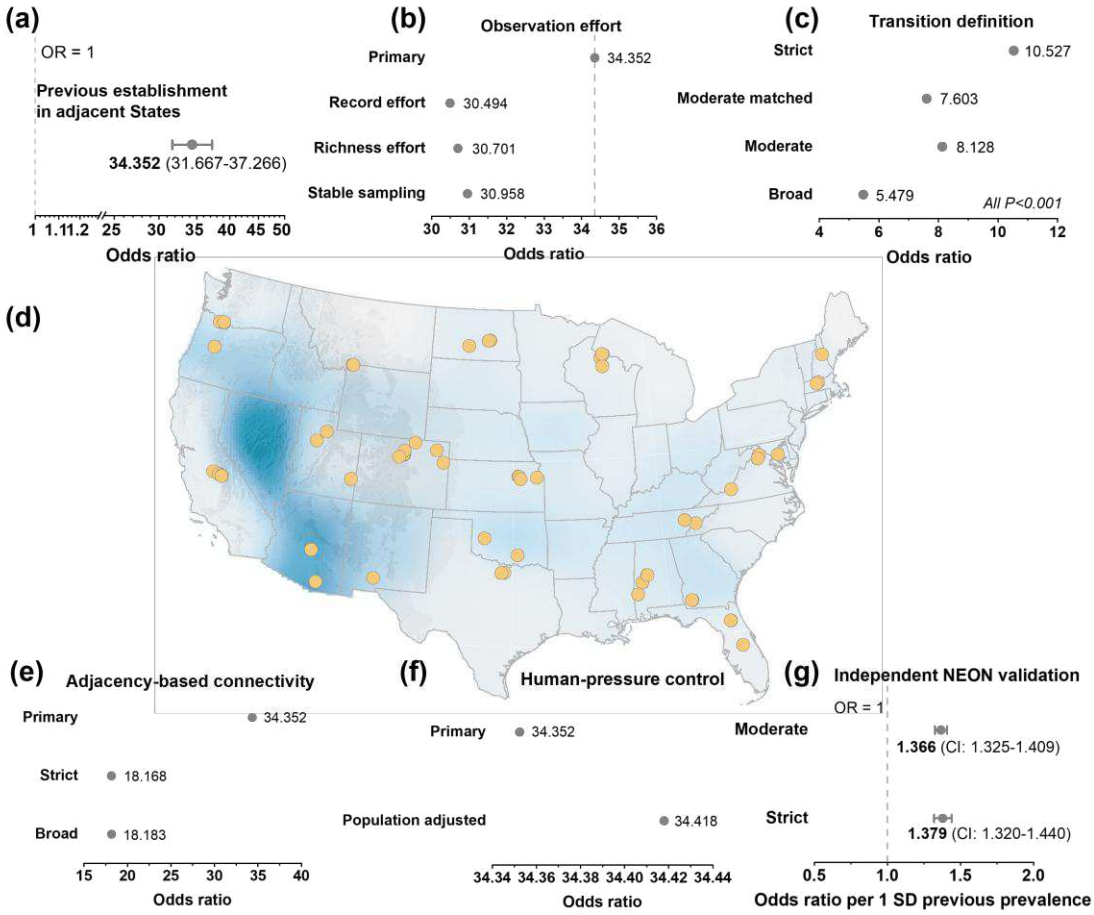

Fig 1 | Prior geographic occupancy predicts subsequent alien-plant establishment, with independent support from site-level observations. (a), Effect of previous neighboring-state establishment in the primary historical model. **(b)**, Sensitivity to alternative observation-effort measures. **(c)**, Sensitivity to alternative establishment-transition definitions. **(d)**, Distribution of NEON validation sites across the 48 conterminous US states. Yellow circles indicate NEON sampling sites. **(e)**, Sensitivity to alternative definitions of geographic connectivity. **(f)**, Sensitivity to additional anthropogenic-pressure controls. **(g)**, Independent NEON estimates of the change in colonization odds per standard-deviation increase in prior site-level prevalence under moderate and strict colonization definitions. Points show odds-ratio estimates. Horizontal bars in panels **(a)** and **(g)** show 95% confidence intervals. OR denotes the odds ratio. Dashed vertical lines in panels **(a)** and **(g)** mark an odds ratio of 1, indicating no association. The dashed vertical line in panel **(b)** marks the primary-model odds ratio for comparison with alternative observation-effort specifications. Axis ranges differ among panels.

Geographic updating alters regional species-pool reassembly

We compared three scenarios to assess the contribution of recursive geographic updating to future establishment including: (1) Dynamic, which updated the geographic occupancy after each five-year interval; (2) Frozen, which retained initial geographic occupancy; and (3) NoHistory, which excluded both previous neighboring-state establishment and recent establishment history. By the final five-year interval (2095–2099, labelled 2095), Dynamic produced approximately 17,800 new realized species–state pairs, compared with approximately 6,800 under Frozen and 2,300 under NoHistory (Fig. 2a). Dynamic produced more establishments than Frozen, and Frozen more than NoHistory, across all ten climate trajectories, although absolute realization totals varied among climate models and socioeconomic pathways (Supplementary Table S4). The additional species establishments associated with the recursive updating (Dynamic−Frozen) increased throughout the simulation, exceeding those associated with the historical predictors retained in Frozen (Frozen−NoHistory) around mid-century and reaching approximately 11,000 versus 4,400 by 2095 (Fig. 2b).

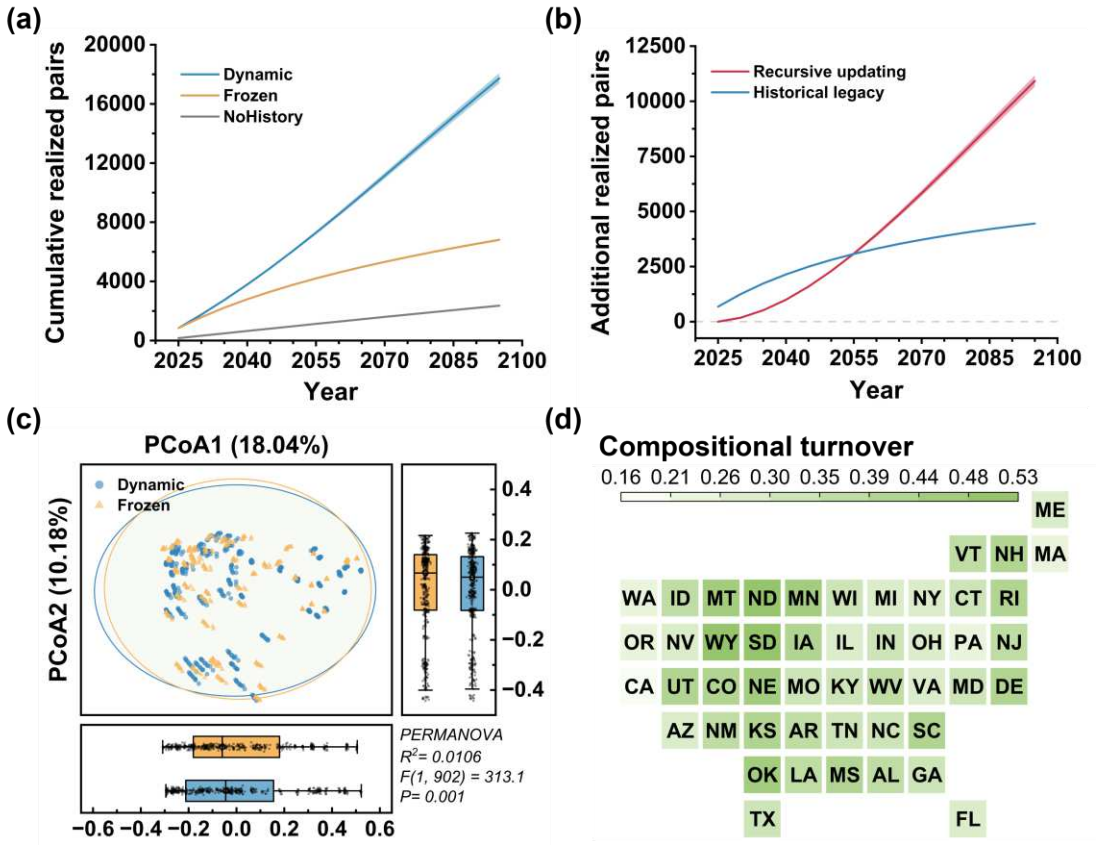

Fig 2 | Recursive updating increases future realization and alters terminal alien-flora composition. (a) Mean cumulative number of realized alien species–state pairs from 2025 to 2095 under Dynamic, Frozen and NoHistory scenarios. Dynamic updated geographic opportunity after each realization interval, Frozen retained initial geographic-opportunity values, and NoHistory excluded previous neighboring-state establishment and recent establishment history. **(b)** Additional realized pairs associated with recursive geographic updating (Dynamic − Frozen) and with the historical predictors retained in Frozen (Frozen − NoHistory). In **(a)** and **(b)** lines show means across ten climate trajectories and shaded bands indicate 95% confidence intervals. **(c)** Principal coordinates analysis of Bray–Curtis dissimilarities among terminal state-level species-occurrence probability profiles under Dynamic and burden-matched Frozen histories in 2095. Each symbol represents one state × climate-trajectory combination. Ellipses show 95% group ellipses, and marginal boxplots show the corresponding coordinate distributions. PCoA1 and PCoA2 explained 18.04% and 10.18% of the variation, respectively. After accounting for state and climate trajectory, the scenario-associated difference was statistically detectable but modest (Supplementary Fig. S4 and Table S15). **(d)** Mean State-level Jaccard turnover component between Dynamic and domain-wide burden-matched Frozen terminal floras, averaged across 200 paired replicates for each of ten climate trajectories. Years denote the starting years of five-year simulation intervals. Terminal results refer to 2095–2099, labelled 2095.

Dynamic and Frozen simulations showed slight differences in terminal floristic composition (Fig. 2c). Principal coordinates analysis (PCoA) showed substantial overlap between the two scenarios, although permutational multivariate analysis of variance (PERMANOVA) detected a significant difference between scenarios after accounting for variation among states and climate trajectories (R^2 = 0.0106, F = 313.107, P = 0.001). The low explanatory power of the scenario effect indicates that compositional differences between updating models were small relative to the broader variation among regional floras. Nevertheless, the compositional turnover effect varied among States (Fig. 2d), with the highest values in South Dakota and relatively high values in North Dakota and Wyoming, whereas California, Washington and Oregon

exhibited lower turnover effect. These differences indicate that matching national establishment totals did not produce a geographically uniform compositional response.

To determine whether recursive geographic updating altered species composition beyond stochastic variation, we constrained Dynamic and Frozen simulations to have identical establishment counts within each state and five-year interval. Compositional turnover between Dynamic and Frozen simulations slightly exceeded that among independent Dynamic simulations, both for whole floras (0.3960 and 0.3911, respectively) and for species established after 2025 (0.6879 and 0.6806, respectively). Although these additional differences were small (0.0049 and 0.0072, respectively), they were consistently positive across all ten climate trajectories (Supplementary Tables S16 and S17).

Recursive updating redistributes geographic occupancy

Under matched national establishment totals, recursive updating produced broader geographic occupancy among realized alien species (Fig. 3). Species occupied an average of 19.78 states under Dynamic compared with 18.45 under Frozen, representing a 7.2% increase (Fig. 3a). The ensemble-averaged median occupancy was also higher under Dynamic (18.04 and 15.17 states, respectively). This increase was consistent across all four census regions, with the largest difference in occupancy proportion in the Midwest (0.125) and the smallest in the West (0.061; Fig. 3b,c). Compared with Frozen, Dynamic increased the proportion of widely distributed species (occupying 37–48 states) by 1.71 percentage points. This difference remained positive (4.08 percentage points) when species occupying all 48 states were excluded, indicating that broader geographic occupancy under Dynamic was not solely driven by species reaching the geographic limit (Supplementary Fig. S2; Supplementary Table S8).

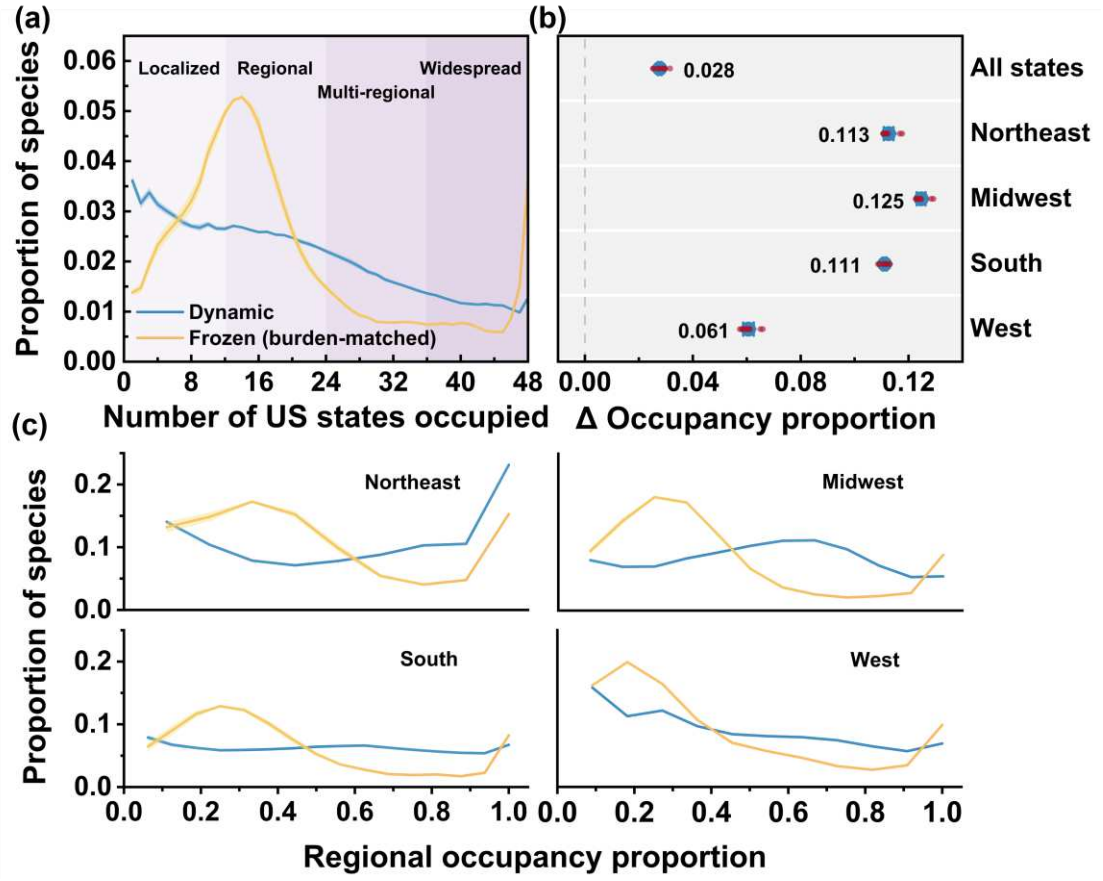

Fig 3 | Recursive updating redistributes future geographic occupancy under matched national establishment totals. (a), Distribution of the number of states occupied per realized alien species in 2095 under Dynamic and burden-matched Frozen histories. Background bands denote localized (1–12 states), regional (13–24 states), multi-regional (25–36 states) and widespread (37–48 states) occupancy classes. Lines show mean proportions and shaded bands indicate 95% confidence intervals across ten climate trajectories. **(b)**, Dynamic − Frozen difference in mean occupancy proportion for the 48 conterminous US states and four census regions. Symbols show climate-trajectory-specific estimates, horizontal bars show 95% confidence intervals, and annotated values give mean differences. Positive values indicate broader occupancy under Dynamic histories. **(c)**, Regional occupancy spectra for the Northeast, Midwest, South and West, expressed as the proportion of states occupied within each region. Dynamic and Frozen simulations were matched in national establishment totals within each interval; State-specific totals were not constrained. Accumulation at the 48-state boundary and sensitivity to alternative definitions of the high-occupancy tail are evaluated in Supplementary Fig. S2 and Supplementary Tables S8 and S9.

Under the original domain-wide matching design, compositional turnover between scenarios varied systematically with initial conditions (Fig. 4). Initial alien richness was the strongest single predictor of whole-flora turnover (marginal $R^2 = 0.636$), with turnover between scenarios declining as initial alien richness increased (Supplementary Fig. S1 and Supplementary Table S10). Future climate compatibility also showed a negative association with compositional turnover, but this decline became weaker as initial geographic opportunity increased (Fig. 4a,b). A higher proportion of early realizations was also associated with lower terminal compositional turnover (Fig. 4c). The full model, including all four predictors and the climate compatibility × initial geographic opportunity interaction, explained 78.9% of variation in whole-flora turnover through fixed effects. The climate compatibility × initial geographic opportunity interaction was supported in the whole-flora model, whereas the two interactions involving initial richness were not (Supplementary Fig. S3b and Supplementary Tables S11 and S12). Predictor explanatory power varied among the alternative response definitions (Supplementary Fig. S3a and Supplementary Table S10).

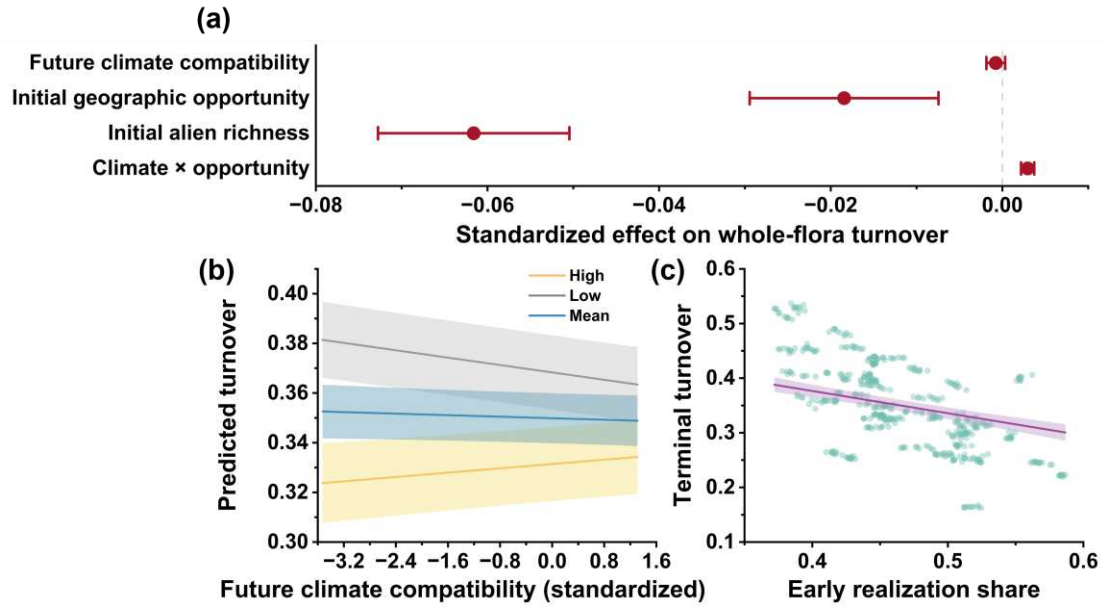

Fig 4 | Context dependence of compositional turnover under domain-wide burden matching. **(a)**, Standardized fixed-effect estimates from the multivariable mixed-effects model of whole-flora

turnover. Points show coefficient estimates and horizontal bars show 95% confidence intervals. The dashed vertical line denotes zero. The panel displays future climate compatibility, initial geographic opportunity, initial alien richness and the climate compatibility × initial geographic opportunity interaction. The association with early realization is shown separately in panel **(c)**. **(b)**, Fixed-effect predictions of whole-flora turnover along the standardized future climate-compatibility gradient. Low, mean and high initial geographic opportunity correspond to standardized values of −1, 0 and +1, respectively. Initial alien richness and early realization were held at their standardized means. **(c)**, Observed mean turnover for the 480 state × climate-trajectory combinations plotted against early realization share, with the fixed-effect prediction holding the remaining predictors at their standardized means. In both panels, random effects were set to zero and shaded bands indicate approximate 95% confidence intervals for the predicted means. Whole-flora turnover was quantified using the state-level Jaccard turnover component between Dynamic and burden-matched Frozen terminal floras. Models were fitted to means from states × ten climate trajectories, each based on 200 paired replicates, with random intercepts for different state and climate trajectory. Single-predictor marginal R^2 values are reported in Supplementary Fig. S1 and Supplementary Table S10. Sensitivity to alternative turnover definitions and interaction structures is reported in Supplementary Fig. S3 and Supplementary Tables S10–S13.

Discussion

Geographic occupancy links past establishment to future opportunities

Prior geographic occupancy may influence subsequent establishment by increasing the availability of potential source populations. Recurrent bridgehead effects demonstrate how introduced populations can contribute to further spread in alien ants (Bertelsmeier et al., 2018), while broader evidence links propagule pressure to establishment success across taxa and study settings (Lockwood et al., 2005; Cassey et al., 2018). Our historical analysis and independent NEON validation are consistent with this perspective, showing positive associations between prior occupancy and subsequent establishment or colonization at different spatial scales. However, occupancy is an

indicator of geographic opportunity, not a direct measurement of propagule supply. These associations do not identify the sources of individual establishments or demonstrate facilitation by other alien plants.

The simulations explore the consequences of carrying this historical association forward as geographic occupancy changes. Invasion debt describes delayed responses to historical introductions and other past drivers (Essl et al., 2011; Rouget et al., 2016). Our results suggest that its establishment and spread components may also depend on distributions generated by subsequent establishments. Earlier events can change the geographic opportunities available to later events, providing a potential link to historical contingency in community assembly (Fukami, 2015). Forecasting future alien floras may therefore require considering both the distributions inherited at initialization and the changes produced as additional establishments occur.

Recursive updating reorganizes composition and occupancy

Differences in species composition must be interpreted relative to both local richness and stochastic assembly, because dissimilarity can vary without a change in the underlying assembly process (Baselga, 2010; Chase et al., 2011). Our national matching experiment did not exceed the Dynamic stochastic baseline, whereas matching establishment counts within every state and interval revealed a small additional difference. Geographic updating therefore had a modest compositional effect under the imposed local counts. This result remains specific to the constrained sampling design and does not identify an independent effect of establishment order (Fukami, 2015).

Species counts alone can conceal compositional reorganization, as shown by assemblage time series in which species identities changed without systematic richness loss (Dornelas et al., 2014, 2019). Our simulations illustrate a related distinction at a regional scale: equal national establishment totals can be distributed among different species and locations. Recursive updating was associated with a higher proportion of widely distributed species, even after excluding those occupying all 48 states. This occupancy result applies to the national matching experiment and has not been

established under the additional local count constraints.

Initial conditions constrain compositional divergence

The negative relationship between initial richness and whole-flora turnover requires a metric-based interpretation. Compositional dissimilarity depends on the species shared between assemblages as well as those unique to each assemblage (Koleff et al., 2003). In our design, a larger shared initial flora can reduce proportional turnover for a given amount of subsequent species replacement. The weaker explanatory power of initial richness when the shared baseline flora was excluded supports this interpretation. Low whole-flora turnover should therefore not be equated with ecological resistance or an absence of future floristic change (Baselga, 2010; Chase et al., 2011).

The interaction between future climate compatibility and initial geographic opportunity is consistent with the broader expectation that realized geographic distributions depend jointly on environmental suitability and geographic accessibility (Soberón, 2007; Soberón & Nakamura, 2009). Broad climatic compatibility may make many of the same transitions feasible under both histories, reducing their divergence. Where geographic opportunity is already high, recursive updating may continue to alter which feasible transitions are realized (Supplementary Fig. S3b and Supplementary Tables S11 and S12).

The association between early realization and lower terminal turnover raises a temporal question related to historical contingency in community assembly (Vannette & Fukami, 2014; Fukami, 2015). One possibility is that early establishments involve transitions likely under both scenarios, whereas later establishments are more sensitive to distributions generated by preceding events. This remains a hypothesis because early realization was an outcome of the simulations, not an independently manipulated treatment.

Limitations and implications

Historical establishment was reconstructed from the first transition to sustained state-

level occupancy rather than the exact demographic establishment date. First records may lag behind establishment, and uneven spatial and temporal sampling can distort reconstructed distribution change (Delisle et al., 2003; Boakes et al., 2010; Isaac et al., 2014). Agreement with standardized NEON observations provides independent support for the historical association, but does not eliminate recording bias (Li et al., 2022). Neighboring occupancy also remains an indicator of geographic opportunity rather than evidence of a particular dispersal source. Because state-level incidence aggregates variation in climate, habitat, dispersal barriers and human activity, our conclusions apply to regional species-pool reassembly rather than individual dispersal events (Elith & Leathwick, 2009).

The simulations quantify the consequences of propagating a historically estimated association between geographic occupancy and subsequent establishment. They do not demonstrate that every simulated establishment will occur. Future trade, horticulture, transport and management could alter establishment processes beyond those represented here (Bradley et al., 2012; Essl et al., 2020). The primary experiment matched establishment totals across the complete domain. The additional control fixed totals within each state and interval, but used a different sampling design and did not isolate establishment order. Its Monte Carlo intervals describe uncertainty in simulation means under the specified model and count schedules, rather than uncertainty in historical coefficients or future conditions (Supplementary Tables S16 and S17).

Despite these limitations, our findings support considering geographic opportunity alongside climatic suitability in invasion forecasts. Dynamic range models provide an established framework for linking environmental responses with spatial population dynamics and dispersal (Pagel & Schurr, 2012). Our simulations address a related question at the regional species-pool scale by updating neighboring occupancy after successive establishment intervals. They propagate a historical occupancy–establishment association rather than explicitly modelling demographic rates or dispersal. Future regional alien floras may therefore reflect both inherited distributions

and the geographic opportunities generated by subsequent establishment.

Prevention and early detection are widely recognized as high-leverage points for invasion management (Keller et al., 2007; Reaser et al., 2020). Spatial assessments of forest pests likewise show how overlap between pest distributions and valuable ecosystem services can inform surveillance priorities (Qiao et al., 2026). Evidence that propagule pressure influences establishment success supports reducing introductions as a management objective (Cassey et al., 2018). Our simulations also motivate testing whether preventing establishment in potential source locations can reduce subsequent opportunities for regional spread. Incorporating dynamically updated occupancy into invasion forecasts could extend prediction beyond static suitability maps towards models in which climate, historical introductions and changing geographic opportunity jointly shape future regional floras.

Methods

Study design and data sources

We reconstructed the establishment histories of alien plants across the 48 conterminous US States by integrating records of plant introduction, alien status and historical occurrence. The candidate species pool was derived from the US Department of Agriculture Seed and Plant Introduction (SPI) archive. Taxonomic names were standardized against the World Checklist of Vascular Plants (WCVP; Govaerts et al., 2021), alien status was reconciled using GloNAF and national distribution records (Davis et al., 2025), and historical state-level occupancy was reconstructed from cleaned Global Biodiversity Information Facility records (GBIF; Edwards et al., 2000; Zizka et al., 2019).

Occurrence records were assigned to five-year intervals. Species–state combinations entered the analytical risk set after relevant historical introduction evidence became available and remained in the risk set until their first inferred establishment transition (Landes et al., 2020). An establishment transition was defined

as the first five-year interval in which a species–state pair had occurrence records from at least two distinct years. It represents the first detected transition to sustained state-level occupancy rather than the exact demographic date of establishment. Alternative definitions, including a stricter criterion requiring support in the next complete five-year interval, are described in Supplementary Methods (Lang et al., 2019). The primary historical panel contained 733,837 species–state–period observations for 1,392 species across 48 states and 14 five-year periods beginning in 1955–2020, including 3,693 inferred establishment transitions.

For each eligible species–state–period observation, we calculated climatic compatibility and observation effort for the focal interval. Historical introduction breadth, recent establishment history and previous occupancy in an neighboring state were defined using earlier information. Observation effort was measured using the log-transformed GBIF record count in the focal interval; a measure excluding records of the focal species was evaluated in sensitivity analyses. Previous establishment in an neighboring state was used as an indicator of geographic opportunity. This indicator describes the configuration of potential source populations but does not directly measure dispersal or local biotic facilitation (Lockwood et al., 2005; Daru et al., 2018; Meyer et al., 2016). Climatic compatibility was quantified as the negative Euclidean distance between state-level climate and each species' native-range climatic profile, using mean annual temperature and annual precipitation standardized by the corresponding species-specific standard deviations. Values closer to zero indicate greater compatibility. Climate aggregation and temporal interpolation are described in Supplementary Methods.

The historical transition model was fitted to 1,392 species using five-year periods beginning in 1955–2020. The reconstructed 2025 resident baseline contained 19,158 established species–state pairs representing 2,182 species. This baseline defined existing floras rather than the species eligible for future establishment. The future candidate pool contained 50,318 unoccupied species–state pairs representing 1,377

species, all of which were included in the historical training set. The same fitted coefficients were applied to candidate-specific predictor values, and baseline resident pairs were excluded from new establishment events. Initial geographic opportunity was carried forward from the 2020 historical predictor panel, whereas resident floras were defined from the 2025 baseline.

Prior geographic occupancy and independent validation

We tested whether previous geographic occupancy predicted subsequent establishment using discrete-time binomial regression, treating first establishment as a time-indexed event within an event-history framework (Juozaitienė et al., 2023; Landes et al., 2020). Let (Y_{ist}) indicate whether species (i) underwent its first inferred establishment transition in State (s) during interval (t). The primary model was (Capinha et al., 2023; Zhang et al., 2024):

$$logit[Pr(Y_{ist} = 1)] = \alpha + \beta_{adj} A_{is,t-1} + \beta^T X_{ist} + \gamma_s + \delta_t,$$

where $(A_{is,t-1})$ indicates prior establishment in an neighboring state, (X_{ist}) contains observation effort, climatic compatibility, historical introduction breadth and recent establishment history, and (γ_s) and (δ_t) denote state and period effects (Boakes et al., 2010; Meyer et al., 2015). We evaluated model support by comparing the primary model with a nested model excluding both previous neighboring-state establishment and recent establishment history. The coefficient and confidence interval for previous neighboring-state establishment quantified its adjusted association within the primary model. Effect sizes are reported as regression coefficients and odds ratios with 95% confidence intervals. Primary and human-pressure-adjusted estimates are reported in Supplementary Table S1.

We evaluated sensitivity to alternative observation-effort measures, broad, moderate and strict establishment definitions, alternative neighboring-state definitions, and additional controls for anthropogenic pressure. These analyses are reported in Supplementary Table S2.

We then used standardized repeated vegetation observations from the NEON as an

419 independent test at a finer spatial grain (Gill et al., 2021). Analyses were restricted to
420 fixed sampling units surveyed repeatedly between 2015 and 2022. For each non-native
421 species, we reconstructed absence-to-presence transitions and related colonization to
422 standardized prior site-level prevalence using binomial generalized linear mixed
423 models with random intercepts for species and sampling unit (Bolker et al., 2009;
424 MacKenzie et al., 2003).

425 Under the moderate definition, colonization was recorded at the first observed
426 absence-to-presence transition. Based on the strict definition, the species was
427 additionally required to remain present at the subsequent census. The strict analysis
428 included 539,908 observations, 1,269 colonization events, 262 species, 8,914 repeated
429 sampling units and 41 sites. This analysis evaluated the direction and consistency of the
430 association between prior occupancy and subsequent colonization rather than
431 reproducing the state-level historical process at the NEON sampling scale
432 (Supplementary Table S3).

433 **Future climate simulations and scenario design**

434 We simulated future alien-flora reassembly at five-year intervals from the reconstructed
435 2025 baseline to the final interval in 2095. Future climate was represented by ten
436 trajectories formed by crossing five general models with SSP126 and SSP585. The
437 climate models were ACCESS-CM2, BCC-CSM2-MR, IPSL-CM6A-LR, MIROC6
438 and MRI-ESM2-0 (Eyring et al., 2016; Tebaldi et al., 2021). Climate projections were
439 converted to trajectory-specific climatic-compatibility estimates for every eligible
440 species–state pair and simulation interval.

441 A realization event denotes a simulated establishment of one previously
442 unoccupied species–state pair. At each interval, the fitted historical model was used to
443 calculate realization probabilities for species–state pairs absent from the reconstructed
444 2025 baseline and not realized during an earlier simulation interval. Newly realized
445 pairs were retained in subsequent periods. The simulations propagated the historically
446 estimated association between prior geographic occupancy and subsequent

447 establishment. They were designed to compare alternative updating rules and should
448 not be interpreted as deterministic predictions that every simulated realization will
449 occur.

450 We first constructed an unconstrained scenario ensemble. For each climate
451 trajectory, we ran 20 stochastic replicates under Dynamic, Frozen and NoHistory
452 scenarios. Dynamic updated geographic opportunity after each realization interval.
453 Frozen retained its initial geographic-opportunity values throughout the simulation.
454 NoHistory set previous neighboring-state establishment and recent establishment
455 history to zero while retaining the remaining predictors.

456 We calculated differences in cumulative numbers of simulated species-state
457 establishments among scenarios. Dynamic-Frozen quantified the additional
458 establishments associated with updating geographic opportunity rather than keeping it
459 fixed. Frozen-NoHistory quantified the difference associated with retaining prior
460 neighboring-state establishment and recent establishment history rather than setting
461 these predictors to zero. Dynamic-NoHistory quantified the overall difference
462 associated with retaining both historical predictors and recursively updating geographic
463 opportunity. These are comparisons among specified simulation scenarios rather than
464 independent causal estimates of historical processes. Trajectory-specific terminal
465 summaries are reported in Supplementary Table S4.

466 Because realization burden differed between Dynamic and Frozen in the
467 unconstrained ensemble, we constructed a separate burden-matched Frozen null for
468 analyses of terminal composition and geographic occupancy. For each climate
469 trajectory, we generated 200 paired Dynamic and Frozen replicates, yielding 2,000
470 matched pairs. The Frozen member of each pair reproduced the exact number of
471 realization events in every five-year interval and the same terminal number of realized
472 species–state pairs across the 48 states (Chase et al., 2011; Kraft et al., 2011).

473 Candidate pairs in the burden-matched were sampled without replacement using
474 weights calculated from the fitted historical model, including climatic compatibility,

observation effort, introduction history, recent establishment history and the fixed initial geographic-opportunity indicator. Dynamic and Frozen histories could therefore differ in the identities, locations and sequence of realizations while having the same total burden. Matching was applied across the 48 US states. Null-model construction and matching validation are reported in Supplementary Table S5.

Terminal composition and geographic occupancy

We assessed scenario-associated terminal compositional divergence by comparing Dynamic and burden-matched Frozen histories under the same climate trajectory and identical period-specific realization totals across the 48 US states. Considering that establishment totals were matched nationally but not within individual states, we therefore examined differences in state-level establishment counts and compared turnover effect between different scenario.

To compare regional floristic composition between scenarios, we calculated the probability of each species occurring in each state. These probabilities were calculated as the proportion of the 200 replicates in which the species occurred in the terminal flora. The resulting 960 occurrence-probability profiles were compared using Bray–Curtis dissimilarity and summarized by PCoA (Bray & Curtis, 1957; Gower, 1966). We tested differences between Dynamic and burden-matched Frozen profiles using PERMANOVA (Anderson, 2001; Anderson, 2017). Statistical inference for the scenario term was based on 999 permutations restricted within the 480 matched state × climate-trajectory pairs (Anderson & Braak, 2003). Homogeneity of multivariate dispersion between scenarios was evaluated using Bray–Curtis distances to the corresponding scenario centroids (Anderson, 2006; Anderson et al., 2006). Statistical significance was assessed using 999 permutations restricted within matched state × climate-trajectory pairs (Supplementary Fig. S4 and Supplementary Table S15).

For each paired replicate and state, we also calculated total Jaccard dissimilarity as:

$$\left[d_J = \frac{b + c}{a + b + c},\right]$$

where (a) is the number of species shared by Dynamic and Frozen, and (b) and (c) are the numbers unique to Dynamic and Frozen, respectively. Total Jaccard dissimilarity was used for the supplementary compositional comparisons. The turnover component of Jaccard dissimilarity, defined in the next section, was used for the state-level map in Fig. 2d and as the primary response in Fig. 4 (Baselga, 2010). Domain-wide comparisons are reported in Supplementary Table S6, and state-level comparisons and local-burden diagnostics are reported in Supplementary Table S7.

To place cross-scenario divergence in the context of simulation variability, we also compared terminal floras from separate Dynamic replicates and from separate Frozen replicates within the same climate trajectory. For each comparison, we calculated total Jaccard dissimilarity and its turnover component for complete terminal floras and for species realized after 2025. We additionally controlled establishment totals within each state and five-year interval. For each climate trajectory, we recorded a target schedule of new establishments across 48 states and 15 intervals. A locally matched Frozen simulation sampled exactly these counts without replacement, using model-derived probability weights and fixed initial geographic opportunity.

To obtain comparable stochastic baselines, we generated two independent constrained Dynamic simulations and two independent Frozen simulations under each target schedule. Across ten climate trajectories and 2,000 schedules, this produced 8,000 constrained simulations. Both scenarios used fixed-count weighted sampling. Dynamic updated geographic opportunity after all States had been sampled within an interval, whereas Frozen retained its initial values. This constrained Dynamic procedure is not the exact conditional distribution of the original independent Bernoulli process given its establishment counts.

With establishment counts fixed for each state and five-year interval, we compared compositional turnover between scenarios with that between independent replicates within each scenario. State-level values were averaged within each schedule, and

overall summaries weighted climate trajectories equally. Monte Carlo standard errors quantified uncertainty in trajectory-specific mean contrasts across 200 schedules. Full definitions, matching checks and uncertainty summaries are provided in Supplementary Methods and Tables S16 and S17.

Geographic occupancy was defined as the number of states occupied by a realized species in 2095. For visualization, species were classified as localized when occupying 1–12 states, regional when occupying 13–24 states, multi-regional when occupying 25–36 states, and widespread when occupying 37–48 states. These categories were descriptive and were not used as inferential thresholds.

Regional occupancy was calculated separately for the Northeast, Midwest, South and West and expressed as the proportion of states occupied within each region. Dynamic minus Frozen differences in mean national and regional occupancy were calculated for each climate trajectory.

We further tested seven prespecified definitions of high occupancy, with and without species reaching all 48 states. Dynamic–Frozen contrasts were evaluated across the ten climate trajectories using exact sign-flip tests with Holm correction (Ernst, 2004; Holm, 1979). Results are reported in Supplementary Fig. S2 and Supplementary Tables S8 and S9.

Context dependence of compositional turnover

For each paired terminal flora, species were divided into those shared by Dynamic and Frozen and those unique to either scenario. The primary response was the turnover component of Jaccard dissimilarity (Baselga, 2010; Baselga & Orme, 2012):

$$\beta_{jtu} = \frac{2min(b,c)}{a + 2min(b,c)},$$

where (a) is the number of shared species and (b) and (c) are the numbers unique to Dynamic and Frozen. Unlike total Jaccard dissimilarity, this component emphasizes reciprocal species replacement and limits the contribution of differences in terminal richness (Anderson et al., 2011). Replicate-level values were averaged within each state

× climate-trajectory combination.

Future climate compatibility was the unweighted mean compatibility in the terminal interval across all species–state pairs in the fixed initial candidate pool. Initial geographic opportunity was the proportion of candidate species–state pairs with at least one neighboring state occupied. Initial alien richness was the number of alien species present in 2025 for each state. For each Dynamic replicate, early realization was calculated as the proportion of its terminal realization events that had occurred by 2060. These replicate-level proportions were then averaged within each state × climate-trajectory combination. Continuous predictors were standardized across the 480 state × climate-trajectory observations before model fitting (Schielzeth, 2010).

Predictions were calculated from the fixed effects, with random effects set to zero. Initial geographic opportunity was set to one standard deviation below the mean, the mean and one standard deviation above the mean for the climate-compatibility curves. Other predictors were held at their standardized means. Prediction settings and confidence-interval calculations are detailed in Supplementary Methods. Separate single-predictor models quantified the descriptive marginal explanatory power of future climate compatibility, initial geographic opportunity, initial alien richness and early realization. These marginal (R^2) values were not interpreted as mutually adjusted or causal effects (Nakagawa et al., 2017). Predictor construction and the complete model specification are provided in Supplementary Methods. Results are presented in Fig. 4, Supplementary Fig. S1 and Supplementary Table S10.

Robustness analyses and reproducibility

We evaluated the robustness of the context-dependence results using three alternative responses. Future-only turnover excluded species shared between Dynamic and Frozen in the 2025 baseline. Future-only Jaccard dissimilarity measured total compositional difference among species realized after 2025. Replacement-species richness was defined as $min(b, c)$, where b and c were the numbers of species unique to Dynamic and Frozen, respectively. Replicate-level values were averaged within each state ×

climate-trajectory combination, and the resulting mean was transformed using $\log(1 + x)$.

Each alternative response was analyzed using the same predictor set and random-effects structure as the primary model. We also fitted a model containing all three pairwise interactions among climate compatibility, initial geographic opportunity and initial alien richness. This tested whether the primary model omitted interactions between climate compatibility and initial richness or between geographic opportunity and initial richness.

Results across alternative response definitions are reported in Supplementary Fig. S3a and Supplementary Table S10. Interaction coefficients are shown in Supplementary Fig. S3b and Supplementary Table S11. Nested-model comparisons are reported in Supplementary Table S12, and predictor-collinearity diagnostics are reported in Supplementary Table S13.

All analyses were conducted in R. Data processing used the "*data.table*" , mixed-effects models were fitted using "*lme4*", and multivariate analyses were conducted using "*vegan*" package (Bates et al., 2015).

Data availability

We used the US Department of Agriculture Seed and Plant Introduction (USDA SPI) dataset (https://npgsweb.ars-grin.gov/gringlobal/search, last accessed March 2026), the Global Naturalized Alien Flora (GloNAF) dataset (https://zenodo.org/records/14696776, last accessed August 2026), the USDA PLANTS database (https://plants.sc.egov.usda.gov/, last accessed April 2026) and the World Checklist of Vascular Plants (WCVP; https://sftp.kew.org/pub/data-repositories/WCVP/, last accessed August 2026). Historical occurrence records were obtained from the Global Biodiversity Information Facility (GBIF; occurrence download DOI: https://doi.org/10.15468/dl.xgrhdz). Standardised vegetation observations were obtained from the National Ecological Observatory Network (NEON) Plant Presence and Percent Cover data product (DP1.10058.001), RELEASE-2024

(https://doi.org/10.48443/c50b-qx77). The processed analysis inputs, figure data, saved model objects and R scripts are available from Zenodo at https://doi.org/10.5281/zenodo.23283694. Additional data supporting the findings of this study are available from the corresponding author upon reasonable request.

Code availability

The R scripts for historical model validation, reconstructed simulation replay, terminal-flora analyses and figure-data generation are available with the processed inputs in the same Zenodo record (https://doi.org/10.5281/zenodo.23283694). The README specifies file assembly, dependencies and execution order.

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Author contributions

David P. Edwards, Renwu Wu, Silun Chen, Yuxin Qiao and Fabio A. R. Matos conceived the study. Silun Chen, Jiachen Liu, Hai Yan and Fan Yang collected and processed the data. David P. Edwards, Renwu Wu, Silun Chen, Yuxin Qiao, Fabio A. R. Matos, Peng Chen and Zhiyi Bao critically reviewed and revised the manuscript. All authors contributed to writing and revising the manuscript.

Competing interests

The authors declare no competing interests.

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