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First come, first served: arrival order shapes competitive outcomes among co-occurring alien plants

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Abstract

Multiple alien plant species commonly co-occur in disturbed habitats, yet how arrival order shapes competition among them is largely untested. Previous work has examined priority effects between alien and native species, but the case in which co-occurring aliens compete with each other after arriving at different times has received little attention. We used a greenhouse experiment in Stuttgart, Germany, with nine annual alien species common to Central Europe, factorially manipulating neighbour identity and order of arrival, to test whether arriving first confers a competitive advantage among aliens and whether arriving second reduces establishment. Because pots were not thinned to single individuals, we used per-capita biomass to separate per-individual growth from density. Across all nine species, plants that arrived three weeks before their neighbour produced 41% more per-capita biomass than those arriving simultaneously, and we found no evidence that this advantage differed among species. Arriving second into already-occupied pots roughly halved the number of established individuals. Species also differed strongly in their competitive effect on neighbours, and this suppressive effect was closely correlated with species size, forming a size-structured competitive hierarchy. The priority advantage operated through increased per-capita growth rather than through higher establishment, whereas the cost of arriving second acted primarily on establishment. These results show that among co-occurring alien plants, arrival order confers a broad competitive advantage, and suggest that the timing of colonisation may be as important as species identity in determining which alien species gains an early competitive advantage in newly disturbed ground.

Introduction

Biological invasions are a leading driver of biodiversity change worldwide (Vilà et al. 2011; Pyšek et al. 2020), and the number of non-native species continues to rise across all taxonomic groups and regions (Seebens et al. 2017). Because most research has focused on the interactions between a single non-native species and the resident community, far less is known about what happens when several non-native species share the same habitat (Kuebbing et al. 2013). Yet co-occurrence among alien plants is common, particularly in disturbed and ruderal environments, and the interactions among them can determine which species come to dominate a site (Kuebbing and Nuñez 2015; Ferenc and Sheppard 2020). Understanding these among-alien interactions is therefore important both for predicting invasion outcomes and for managing co-occurring alien species in practice (Hess et al. 2019; Weidlich et al. 2021).

One factor likely to govern these interactions is the order in which species arrive. Priority effects, in which early-arriving species affect the establishment, growth, or fitness of later arrivals, are increasingly recognised as a strong structuring force in plant communities (Von Gillhaussen et al. 2014; Fukami 2015). An early arrival can preempt resources and space, gaining a competitive advantage that may persist even after competitors establish (Kardol et al. 2013), while a late arrival faces the cost of entering ground that is already occupied (Cleland et al. 2015; Stuble and Souza 2016). Priority effects are not always uniform: their strength can depend on the identity and functional traits of the species involved,

and competitive hierarchies can change when arrival order is manipulated (van Steijn et al. 2025). Whether a head start confers a general advantage among co-occurring alien plants, or one that is contingent on species identity, remains an open question.

Most experimental work on priority effects in the context of plant invasions has manipulated arrival order between native and alien species, asking whether giving natives a head start can suppress invaders or, conversely, whether early-arriving aliens preempt natives (Dickson et al. 2012; Stuble and Souza 2016; Ferenc et al. 2021). These studies have shown that arrival order can be at least as important as species identity or diversity in determining competitive outcomes. However, priority effects among the alien species themselves, the case in which two or more non-native species colonise the same disturbed patch and compete with each other, have received almost no experimental attention (Ferenc and Sheppard 2020). This is a relevant gap, because alien species are not a random subset of the regional flora: they tend to share suites of traits associated with disturbance tolerance and fast growth (Van Kleunen et al. 2010), and the phenological advantage that aliens often hold over natives, such as earlier germination, does not apply when both competitors are alien. Priority effects among co-occurring aliens may therefore operate differently from those observed in native-alien pairs.

A second factor is the competitive hierarchy among the co-occurring species. Recent work has shown that interactions among alien plants are driven primarily by hierarchical differences in traits related to competitive ability, with taller species and those with greater biomass suppressing their neighbours more strongly (Sheppard 2019; Ferenc and Sheppard 2020). Size-based competitive hierarchies are well established in plant ecology more broadly (Gaudet and Keddy 1988; Weiner 1990; Keddy et al. 2002), but their interaction with arrival order among aliens has not been tested. Specifically, it is unknown whether arriving first benefits all species equally or whether larger, competitively dominant species gain disproportionately from a head start (van Steijn et al. 2025).

We used a greenhouse experiment with nine annual alien plant species common to Central Europe to test the role of arrival order in among-alien competition. Building on previous experiments that assessed trait-based competition among alien plants (Sheppard 2019; Ferenc and Sheppard 2020) and priority effects in alien-native interactions (Ferenc et al. 2021), we manipulated both the identity of the neighbour and the relative timing of arrival in all pairwise combinations. We tested three hypotheses:

1. *Priority advantage among aliens.* Arriving before a neighbour, rather than simultaneously, increases per-capita growth, and this advantage is consistent across species rather than contingent on identity.
2. *Establishment cost of late arrival.* Arriving into a pot already occupied by an established competitor reduces establishment success, imposing a consistent cost on late-arriving species.
3. *Size-structured competitive hierarchy.* The presence of a neighbour reduces per-capita growth, and a species' suppressive effect on its neighbours scales with its own size, consistent with a trait-based hierarchy.

Methods

Study system and experimental design

We selected nine annual alien plant species from five families that co-occur in ruderal habitats in Central Europe (Table 1). The species are annual fast-growing grasses or forbs with a range of adult sizes. They originate from the Americas, the Mediterranean, southern Africa, and western to central Asia. Seeds were obtained from botanical gardens in Germany (see Table 1 for provenance) and in one case from a commercial supplier (Saatgutshop, Volkmarsen, for *Vicia villosa*).

Table 1
The nine annual alien plant species used in the experiment, their families, native ranges, growth habits, seed provenance, and the abbreviations used in the analysis and supplementary tables. Abbreviations are the six-letter codes formed from the first three letters of the genus and species epithet. Native-range information was obtained from Plants of the World Online (Royal Botanic Gardens Kew 2026). BG = Botanical Garden of the respective university. Seeds were collected or obtained from the botanical gardens' living collections over the three years preceding the experiment.

Species	Family	Native range	Growth habit	Seed provenance
Amaranthus albus L.	Amaranthaceae	North America	Forb	BG Halle
Cosmos bipinnatus Cav.	Asteraceae	North America	Forb	BG Frankfurt
Datura stramonium L.	Solanaceae	North America	Forb	BG Potsdam
Dittrichia graveolens (L.) Greuter	Asteraceae	Mediterranean, Middle East, Central Asia	Forb	BG Konstanz
Galinsoga parviflora Cav.	Asteraceae	North and South America	Forb	BG Hohenheim
Nicandra physalodes (L.) Gaertn.	Solanaceae	South America	Forb	BG Greifswald
Panicum capillare L.	Poaceae	North America	Grass	BG Potsdam
Tragus racemosus (L.) All.	Poaceae	Mediterranean, Middle East, Africa, Central Asia	Grass	BG Halle
Vicia villosa Roth	Fabaceae	Mediterranean, Middle East, Central Asia	Forb	Saatgutshop, Volkmarsen

The experiment was conducted over six weeks, from 28 October to 16 December 2019, in a greenhouse at the Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany. Day and night temperatures were held at approximately 20 and 10 degrees Celsius. We grew plants in 270 plastic

pots (two litre volume) filled with sterile compost, with five seeds sown per species per pot. Seedlings were not thinned, so each pot could contain one to five established individuals per species, and the biomass harvested per species per pot is therefore the total produced by all surviving individuals. Pots were assigned random positions in the greenhouse and watered three times per week.

We manipulated two factors: the identity of a plant's neighbour and the relative timing of arrival, through four treatments (Table S1). In the *monoculture* treatment (18 pots), a single species was sown alone (five seeds) and grown for the full six weeks. In the *simultaneous* treatment (90 pots), two species were sown together at the start and grown side by side for six weeks; this treatment included both interspecific pairs (36 unordered species combinations, each replicated twice: 72 pots) and intraspecific pairs (each of the nine species paired with itself, replicated twice: 18 pots). In the *interspecific combination* treatment (144 pots), one species (first arrival) was sown at the start, followed three weeks later by a second, different species (second arrival), so that the two grew together only during the final three weeks; this treatment covered all 72 ordered pairwise combinations (species A first and B second, plus B first and A second), each replicated twice. In the *intraspecific combination* treatment (18 pots), the design was identical to the interspecific combination, but the second-sown species was the same as the first; because biomass was harvested per species per pot, first- and second-sown individuals could not be distinguished in these pots, and they therefore contribute only to the pooled species-level analyses and not to the first-arrival versus second-arrival contrast. In total, the design comprised 270 pots, each containing five seeds per species (five seeds in monoculture pots, ten in all two-species pots).

We note that the monoculture treatment differs from the competition treatments not only in the absence of a heterospecific neighbour but also in initial sowing density (five seeds versus ten). The competition contrast (monoculture versus simultaneous) therefore compares growth without a neighbour to growth with a neighbour at twice the initial density. This is a standard design feature of pairwise competition experiments (e.g. Ferenc and Sheppard 2020), but it means that the 51% reduction in per-capita biomass we report for the competition contrast includes any density-dependent effect of the additional five seeds, and the true effect of heterospecific competition alone may be smaller. The priority contrast (first arrival versus simultaneous) is not affected, because both treatments have the same initial density of ten seeds per pot.

At the first sowing on 28 October 2019, all monoculture, simultaneous, and first-arrival seeds were sown. At the end of the third week, on 18 November, we recorded germination (the number of emerged seedlings out of five) and plant height, and then carried out the second sowing. Final measurements of germination and height were taken at harvest on 16 December. All aboveground plant material was then harvested, dried at 60 degrees Celsius for 48 hours, and weighed to obtain aboveground dry biomass per species per pot, using a balance reading to 0.0001 g for small samples and to 0.01 g for larger ones. Because the experiment ran for only six weeks under greenhouse conditions, few plants reached the reproductive stage, and our results therefore capture the establishment and early growth phase rather than lifetime fitness.

The monoculture, simultaneous, and first-arrival treatments all involved six weeks of growth and differed only in whether a neighbour was present and when it arrived, so comparisons among them isolate competition and the benefit of early arrival from growth duration. The second-arrival treatment, by contrast, combines a shorter growth window (three weeks) with arrival into occupied ground, and we therefore restrict comparisons involving second arrivals to establishment, where the confounding effects with growth duration is less consequential because, for these species, most seeds germinate within the first three weeks.

Statistical analysis

All analyses were carried out in R version 4.5.2 (R Core Team 2025). We tested the three hypotheses stated in the Introduction, presented here in the order they appear in the Results.

Hypothesis 1

priority advantage. To test whether arriving before a neighbour increases per-capita growth, we compared the first-arrival and simultaneous treatments (both six weeks of growth) with a linear model of log per-capita biomass on treatment and focal species. We tested whether the priority effect depended on focal species by comparing this additive model with one including a treatment-by-species interaction using a likelihood-ratio test, and retained the additive model if the interaction was not supported. We report the priority effect as a back-transformed proportional change in per-capita biomass.

Hypothesis 2

establishment cost of arriving second. To test whether arriving second reduces establishment, we modelled the number of established individuals (out of five) as a binomial generalized linear model with treatment and focal species as predictors, using the simultaneous treatment as the reference category.

Hypothesis 3

size-structured competitive hierarchy. To test whether the presence of a neighbour reduces per-capita growth, we compared the monoculture and simultaneous treatments (both six weeks) with a linear model of log per-capita biomass on treatment and focal species. Within the simultaneous treatment, we tested whether the identity of the neighbour affected focal per-capita biomass beyond the focal species' own identity by adding neighbour identity as a term to a species-only linear model and comparing the two with an F test. The full focal-species-by-neighbour interaction was not estimable given the replication (two pots per combination) and was therefore not fitted. To test whether a species' suppressive effect as a neighbour scaled with its own size, we extracted each species' centred neighbour coefficient from the simultaneous-treatment model and correlated it with that species' mean log per-capita biomass grown alone, using Spearman's rank correlation. Height was analysed under the same set of contrasts using linear models.

Because each pot contained two species in the simultaneous and combination treatments, biomass observations within a pot are not independent. We accounted for this by computing cluster-robust (sandwich) standard errors with pot as the clustering unit (R packages sandwich, Zeileis et al. 2020; and lmtest, Zeileis and Hothorn 2002). Linear mixed models with a random intercept for pot returned among-pot variance estimates of effectively zero, confirming that the cluster-robust fixed-effects approach is appropriate. Factor-level significance was assessed with Type II tests (R package car, Fox et al. 2019). All tests used a significance threshold of 0.05.

Results

A general priority advantage among aliens

Arriving first conferred a clear per-capita growth advantage. Plants that grew for six weeks with a neighbour arriving three weeks later (first arrival) produced 41% more per-capita biomass than plants of the same species that grew for six weeks with a neighbour present from the start (simultaneous) (log per-capita biomass coefficient = + 0.340, cluster-robust SE = 0.137, P = 0.014; back-transformed ratio 1.41; Fig. 1, Table 2). Because both groups grew for the same duration and differed only in when the neighbour arrived, this difference is a priority effect rather than an artefact of growth duration.

Table 2

Summary of the main statistical results. Each row gives the estimated effect of one treatment contrast on one response variable, with its 95% cluster-robust confidence interval and P value. Per-capita biomass was natural-log transformed for analysis; effects are back-transformed and expressed as multiplicative ratios (values below 1 indicate a reduction relative to the reference treatment). Establishment effects are odds ratios from a binomial generalized linear model of the number established out of five seeds (values below 1 indicate lower odds of establishment). Height effects are differences in centimetres from a linear model. All models included focal species as a covariate. The reference treatment is simultaneous arrival for all contrasts except competition, where the reference is growing alone. Standard errors are cluster-robust with pot as the clustering unit.

Hypothesis	Response	Contrast	Effect	CI_low	CI_high	P
H1	Per-capita biomass (ratio)	First arrival vs simultaneous	1.405	1.073	1.841	0.014
H3	Per-capita biomass (ratio)	Neighbour present vs alone	0.488	0.316	0.755	0.001
H2	Establishment (OR, n/5)	Second arrival vs simultaneous	0.463	0.345	0.622	< 0.001
H1	Establishment (OR, n/5)	First arrival vs simultaneous	1.286	0.982	1.683	0.067
H3	Establishment (OR, n/5)	Alone vs simultaneous	1.463	0.765	2.797	0.249
H1	Height (cm)	First arrival vs simultaneous	1.698	-0.015	3.411	0.052
H3	Height (cm)	Alone vs simultaneous	4.161	0.250	8.073	0.037

We found no evidence that the priority effect differed among focal species: adding a treatment-by-species interaction did not improve the model ($F(8, 272) = 1.06$, $P = 0.39$; Table S3), indicating that the advantage of arriving first was general across the nine species. First arrival did not significantly increase height relative to simultaneous arrival (contrast = + 1.698 cm, $P = 0.11$; Fig. S1, Table S5), nor establishment (binomial GLM, odds ratio 1.29, $P = 0.067$; Table S5), suggesting that the priority advantage operated mainly through per-capita biomass accumulation rather than through earlier or more successful germination.

Considering the three six-week treatments together, per-capita biomass followed the expected ordering: highest when grown alone (mean 0.63 g per plant), intermediate with a late-arriving neighbour (0.65 g), and lowest with a neighbour present from the start (0.57 g) (treatment Type II test, $F(2, 294) = 4.19$, $P = 0.016$; Fig. 1). This ordering was consistent across species (treatment-by-species interaction $F(16, 278) = 0.76$, $P = 0.73$; Table S3).

Establishment cost of arriving second

Arriving into a pot already occupied by an established competitor reduced establishment. Second arrivals established on average 1.5 out of 5 sown seeds, compared with 2.2 in the simultaneous treatment (binomial GLM, odds ratio 0.46, $P < 0.0001$; Fig. 2, Table 2). Establishment did not differ significantly between the simultaneous treatment and either growing alone (OR 1.46, $P = 0.25$) or arriving first (OR 1.29, $P = 0.067$), so the penalty was specific to second arrivals.

Because second arrivals also had only three weeks of growth rather than six, this establishment penalty combines the shorter growth window with arrival into occupied ground. However, most of the study species germinate within the first three weeks under greenhouse conditions, so the contribution of the shorter window to the establishment count is likely minor relative to the true effect of arriving into already-occupied space.

Competition and the size-structured competitive hierarchy

The presence of a neighbour reduced per-capita growth. Plants grown with a neighbour from the start (simultaneous) produced 51% less per-capita biomass than plants of the same species grown alone (coefficient = -0.717, cluster-robust SE = 0.220, $P = 0.001$; back-transformed ratio 0.49; Table 2). This reduction was confirmed with total biomass and the number of established individuals as a covariate ($P = 0.002$; Table S3).

The species differed strongly in both their per-capita biomass and their effect as neighbours. Grown alone, per-capita biomass ranged from 1.38 g in *Datura stramonium* down to 0.006 g in *Dittrichia graveolens* (Fig. 3a; Table S2). Four species formed a large-statured group (*D. stramonium*, *Galinsoga parviflora*, *Nicandra physalodes*, and *Cosmos bipinnatus*, all above 1.0 g per plant), whereas the remaining five were markedly smaller (Fig. 3a).

Within the simultaneous treatment, the identity of the neighbour significantly affected focal per-capita biomass beyond the focal species' own identity ($F(8, 133) = 5.21$, $P < 0.0001$; Table S4). This suppressive effect was strongly rank-correlated with the neighbour's own per-capita size grown alone (Spearman's rho = 0.83, $P = 0.008$; Pearson's r = 0.76, $P = 0.017$; Fig. 3b), indicating a size-structured competitive hierarchy consistent with that described for a larger set of alien species by Ferenc and Sheppard (2020). The most suppressive neighbours were *N. physalodes* and *C. bipinnatus*, and the least suppressive were *D. graveolens* and *P. capillare* (Fig. 3b; Table S4).

Discussion

Arriving first conferred a consistent per-capita growth advantage across all nine alien species, and arriving second reduced establishment. These priority effects operated on top of a size-structured competitive hierarchy in which larger species suppressed their neighbours more strongly, consistent with the hierarchy described for a broader set of alien species by Ferenc and Sheppard (2020). Together, these results show that among co-occurring alien plants, competitive outcomes are shaped jointly by species size and by order of arrival.

A general priority advantage among aliens

The priority effect we observed, a 41% increase in per-capita biomass for first arrivals relative to simultaneous arrivals, is among the first demonstrations that arrival order structures competition among alien species themselves, rather than between aliens and natives. Previous work has shown that early arrival benefits plants in native-alien (Dickson et al. 2012; Stuble and Souza 2016; Ferenc et al. 2021), native-native (Von Gillhaussen et al. 2014; van Steijn et al. 2025), and restoration contexts (Young et al. 2017; Weidlich et al. 2021), and our results extend this to the alien-alien case. The finding matters because co-occurring alien plants are not a random sample of the flora: they tend to share fast-growth, disturbance-adapted strategies (Van Kleunen et al. 2010), and the phenological advantage that aliens commonly hold over natives, such as earlier germination (Reeb and Kuebbing 2024), does not apply when both competitors are alien. That a three-week head start still yielded a measurable advantage under these conditions suggests that priority effects among co-occurring aliens are robust and do not depend on the trait asymmetries that often separate aliens from natives.

A notable feature of the priority effect is its generality. We found no evidence that the advantage of arriving first differed among focal species, meaning that all nine species, spanning a wide range of sizes and families, benefited similarly from early arrival. This contrasts with studies in which priority effects were contingent on species identity or functional group (Cleland et al. 2015; van Steijn et al. 2025), and may reflect the relatively uniform trait space occupied by the annual ruderals in our study. We note, however, that the absence of a significant interaction does not rule out species-level variation; with two replicate pots per combination, the power to detect interaction effects is limited.

The cost of arriving second

Second arrivals established roughly half as many individuals as simultaneously sown plants, confirming that arriving into occupied ground carries a substantial cost (Kardol et al. 2013; Stuble and Souza 2016; Ferenc et al. 2021). Because second arrivals also had only three weeks of growth rather than six, the establishment penalty we observed combines a shorter growth window with true preemption by the resident. However, the contribution of the shorter window is likely minor for these species, because most of them germinate within the first three weeks under greenhouse conditions, so the count of established individuals at harvest largely reflects survival rather than failure to germinate. The asymmetry between a moderate benefit of arriving first (a per-capita growth advantage with no detectable effect on establishment) and a steep cost of arriving second (a large reduction in establishment) suggests that for these species, being preempted is more consequential than preempting.

This pattern is consistent with recent work showing that phenological timing mediates interactions among co-occurring alien species: Reeb and Kuebbing (2024) found that seasonal priority effects, arising from phenological separation, can weaken competition among dominant invaders and help explain why multiple alien species coexist. Our results complement theirs by showing that even without

natural phenological separation, an experimentally imposed head start is enough to shift competitive advantages among aliens.

The competitive hierarchy as context

The competitive hierarchy we observed, in which a species' suppressive effect as a neighbour scaled with its own per-capita size (Spearman's rho = 0.83), is consistent with the trait-based hierarchy reported by (Ferenc and Sheppard 2020) for a larger set of alien species, using a broader suite of functional traits. That the pattern holds when measured with a single variable, per-capita biomass, and on a partially overlapping but independently grown set of species, provides additional support for the view that hierarchical trait differences related to competitive ability, rather than niche differences, drive interactions among co-occurring alien plants (Sheppard 2019; Ferenc and Sheppard 2020). We here used per-capita biomass as it more closely reflects the competitive ability of individual plants and is therefore the more appropriate measure for assessing competitive hierarchies (Gaudet and Keddy 1988; Weiner 1990; Keddy et al. 2002). However, we note that the per-capita ranking of species differed from the total-biomass ranking, because in unthinned, multi-individual pots the total biomass confounds per-individual size with density.

Implications for the management of co-occurring alien species

The priority advantage and the establishment cost of late arrival suggest that, where multiple alien species colonise the same disturbed site, the first to arrive is likely to gain a competitive edge that is broadly independent of which species it is. Two practical points follow. First, in early-detection and rapid-response programmes, the timing of colonisation may be as important as species identity in determining which alien species comes to dominate, and monitoring disturbed sites soon after disturbance may be critical for anticipating the trajectory of multi-species invasions. Second, the same priority mechanism could be turned to advantage in restoration: sowing desired species, possibly if necessary, even alien non-invasive species, ahead of alien invasive arrivals exploits the same preemption effect, and our results suggest this approach should be effective even against a broad range of alien ruderals, not only against specific target species (Young et al. 2017; Hess et al. 2019; Weidlich et al. 2021). However, we note that the experiment was a single greenhouse run of six weeks in sterile compost, with two replicate pots per treatment combination. It is therefore best understood as a controlled screening of mechanism rather than a field test. Climate-driven changes in the timing and predictability of growing seasons may further increase the importance of arrival order, as shifts in phenology can alter which species arrives first at a site and how large its head start is.

Conclusions

Among nine co-occurring alien plant species, the order of arrival shaped competition: arriving first increased per-capita growth across all species, while arriving second reduced establishment. These priority effects operated on top of a size-structured competitive hierarchy in which larger species

suppressed their neighbours more. Both patterns, the general priority advantage and the size-based hierarchy, are predictable features that could help anticipate which alien species gains an early competitive advantage in disturbed ground and identify when management can most effectively intervene. Testing whether these greenhouse patterns hold in the field, over full life cycles and in the presence of resident vegetation and soil communities, is a natural next step.

Declarations

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Competing Interests

The authors declare they have no competing financial or non-financial interests.

Author Contribution

C.S.S. and V.F. conceived and designed the study. V. F. supervised data collection. R.R.C.T. collected the data, performed the analysis, and wrote the manuscript. All authors contributed to interpretation and critically revised the manuscript, and all authors read and approved the final version.

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Data Availability

The datasets generated and analysed during the current study, as well as the R code, are available from the corresponding author on reasonable request and will be deposited in a public repository upon acceptance.

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Figures

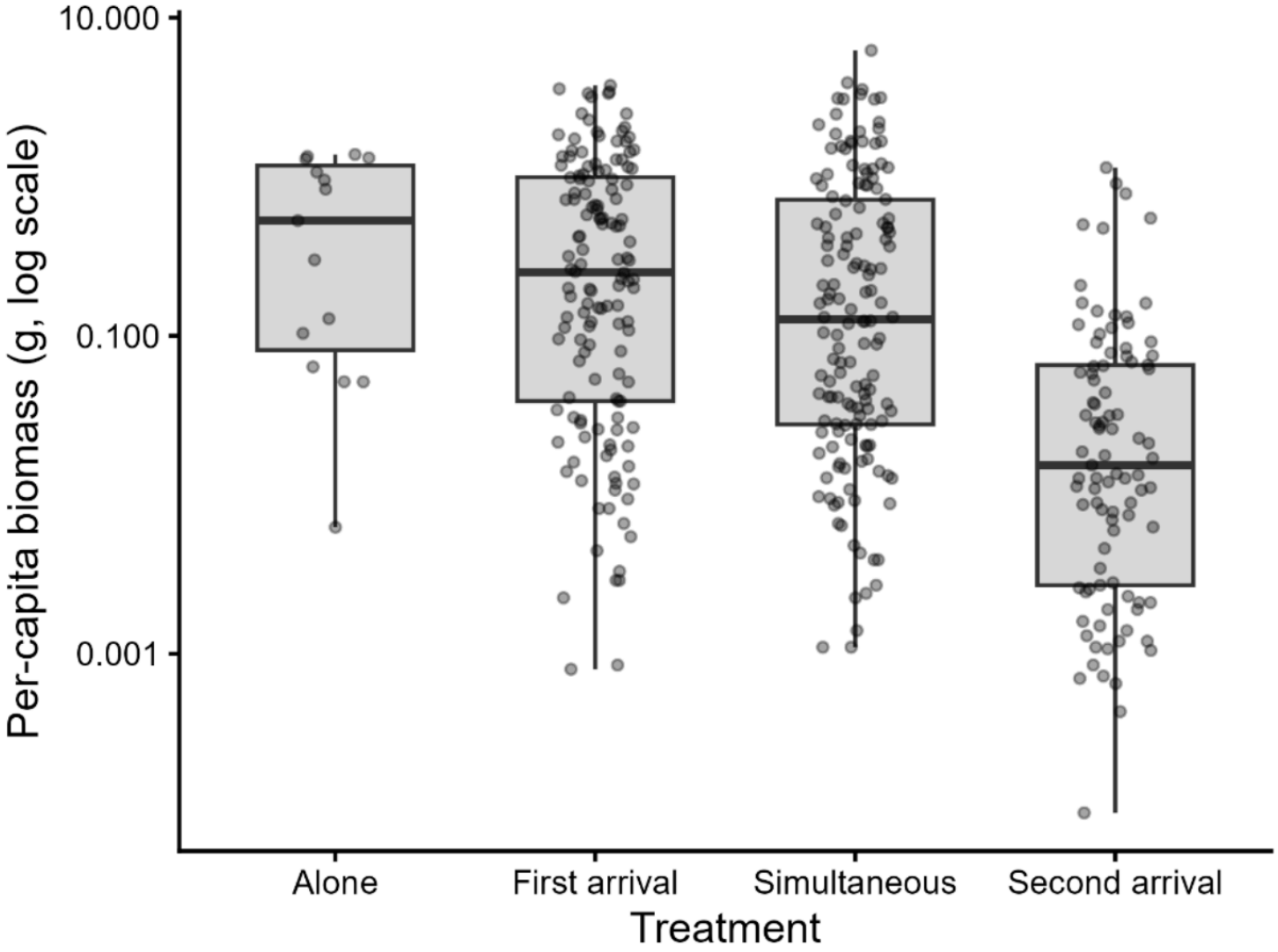


Figure 1

Per-capita aboveground biomass (g, log scale) across the four treatments. Alone: grown without a neighbour for six weeks. First arrival: a neighbour arrived three weeks after the focal species; six weeks of growth. Simultaneous: a neighbour present from the start; six weeks of growth. Second arrival: the focal species sown three weeks after an established neighbour; three weeks of growth. Boxes show the median and interquartile range, whiskers extend to 1.5 times the interquartile range, and points show individual pots. Per-capita biomass is the total aboveground dry biomass of the focal species in a pot divided by the number of its established individuals.

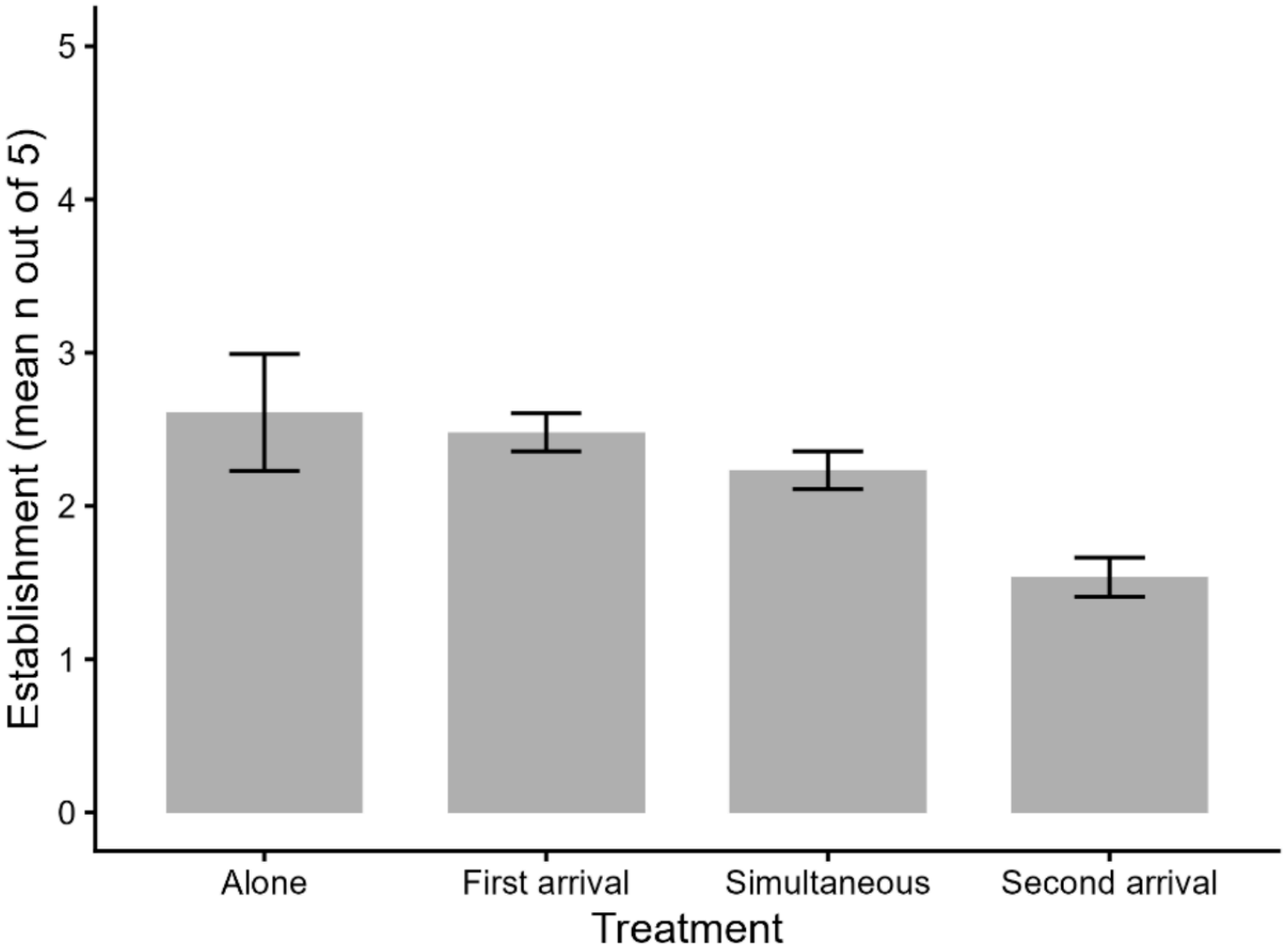


Figure 2

Establishment across the four treatments (defined in Fig. 1). Establishment is the number of seeds (out of five sown) that produced a surviving individual at harvest. Bars show treatment means and error bars show plus or minus one standard error. Second arrivals established markedly fewer individuals than plants in the other three treatments.

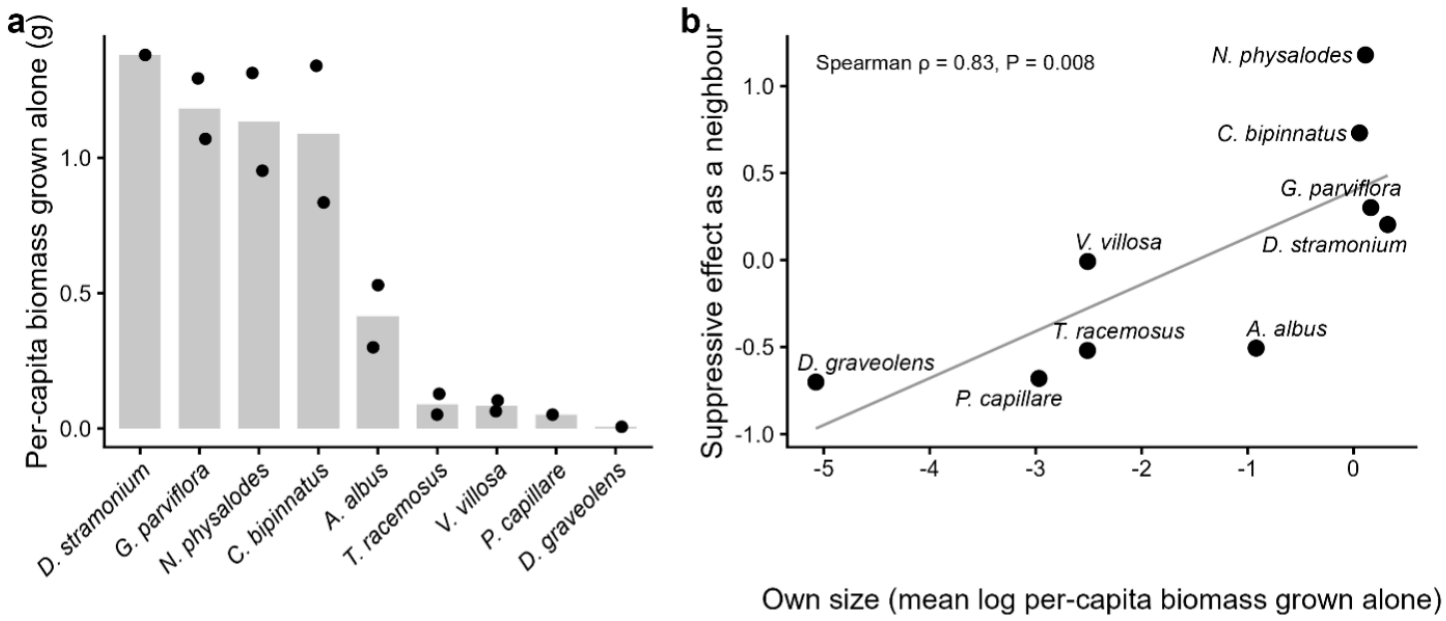


Figure 3

Size-structured competitive hierarchy among the nine alien species, measured on a per-capita basis. (a) Mean per-capita aboveground dry biomass (g) of each species grown alone (monoculture) for six weeks, ordered from largest to smallest. Bars show treatment means; points show the individual monoculture replicates (one or two pots per species with at least one established individual). (b) Each species' suppressive effect as a neighbour plotted against its own size measured as mean log per-capita biomass grown alone. The suppressive effect is the species' centred neighbour coefficient from a linear model of log per-capita biomass in the simultaneous treatment (higher values indicate stronger suppression of focal plants). The line shows the linear fit. Species that produced more per-capita biomass when grown alone also suppressed their neighbours more strongly (Spearman's rho = 0.83, P = 0.008; Pearson's r = 0.76, P = 0.017).

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