

RESEARCH ARTICLE

Inverse priority effects: The order and timing of removal of invasive species influence community reassembly

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Abstract

1. An ongoing restoration challenge is to recover native communities after the removal of invasive species. Because priority effects (i.e. the order and timing of species arrival) can strongly determine the trajectory of community assembly, their intentional manipulation is gaining attention to manage invasive plants and achieve restoration goals. Yet, ecologists and conservationists rarely consider how the order and timing of species removal—*inverse priority effect*—may impact future plant communities.
2. Here, we evaluated the dependence of community reassembly on inverse priority effects by experimentally removing the target invasives Sweetbriar rose (*Rosa rubiginosa*) and Scotch broom (*Cytisus scoparius*) in field and mesocosm communities. We manipulated removal order (rose before broom vs. broom before rose) and timing (simultaneously early vs. simultaneously late in the season). We performed a hierarchical modeling of species community to assess differences in community structure in response to order and timing of removal, and to evaluate whether species origin and leaf and seed traits were associated with species responses.
3. We found that the order of removal was as important as timing driving community reassembly. Simultaneous removal favoured nonnatives, more so when performed early. Sequential removals led to contrasting communities. Rose before broom removal also favoured nonnative grasses at expense of native species, whereas the inverse order produced small changes in communities. In general, species with high specific leaf area were boosted, regardless of their seed size.
4. *Synthesis and applications.* Inverse priority effects are neglected mechanisms that can drive variability in the reassembly of plant communities and can potentially upgrade invasive species management. These historical contingencies suggest the existence of an optimal order of removal that facilitates the recovery of the native community. We found that simultaneous removal promoted secondary invasions to a greater extent than sequential removals. Furthermore, removal order affected post-removal community structure. In our system, we suggest removing

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the rose before the broom to hinder nonnatives and pave the way for restoration of native communities. Our results show that manipulation of the order and timing of removal can help to achieve restoration goals.

KEYWORDS

community disassembly, hierarchical modelling of species communities, historical contingencies, priority effects, removal experiment, secondary invasions, trait-based community assembly

1 | INTRODUCTION

In the face of increasing invasion of nonnative species worldwide (Van Kleunen et al., 2015), managements designed to encourage the recovery of native communities have become a priority in ecological restoration (Weidlich et al., 2020). In particular, the removal of invasive species is one of the most common management practices towards ecosystem restoration (Kettenring & Adams, 2011; Weidlich et al., 2020). However, restoration of native communities is challenging, since the removal of invasive species frequently favours the establishment and growth of other nonnatives through secondary invasions (Pearson et al., 2016; Prior et al., 2018). To face this challenge, we examined the role of historical contingencies (i.e. the effect of the order and timing of past events on community assembly, Fukami, 2015) during invasive species removal. It has been demonstrated that the order and timing of species arrival, known as priority effects, can shape community assembly (Chase, 2003; Drake, 1991; Fukami, 2015). Yet, ecologists rarely (see below) consider how the order and timing of species removal—what we call *inverse priority effect*—could impact future plant communities.

Unlike *priority effects*, which are the historical contingencies associated with the order and timing at which species arrive to a community, we use *inverse priority effects* to refer to those associated with the order and timing at which species are lost/removed from the community (see Young et al. (2017) for an alternative meaning). Removal of species can modify resources available or environmental conditions for the remaining species, something that can reshuffle species interactions favouring some species over others (Zavaleta et al., 2009). In other words, the biotic and abiotic filters of community assembly can change after species loss, modulating the ability of species in the regional pool to colonize and grow in the new community (HilleRisLambers et al., 2012). As biotic (e.g. interaction strength due to changes in species phenology, Herold et al., 2011) and environmental conditions (e.g. temperature, rainfall) fluctuate over time, it is expected that the filters of community assembly and, consequently, the response of remaining species to removals will be contingent on seasonal timing. If removal timing influences the success of invasive species management, it would be worthwhile to consider it in restoration plans. A handful of studies of nonnative species removals during ecosystem restoration have suggested that the

order in which species are removed from a system can have lasting consequences for ecosystem structure and function (Bergstrom et al., 2009; Collins et al., 2009; Courchamp et al., 1999; Zavaleta et al., 2001). These studies suggest the existence of historical contingencies during species removal and were focused mainly on trophic interactions, leaving the question of whether these contingencies operate within communities structured by other interactions such as competition. The large scale of most of these studies provides valuable information in terms of management, but poses challenges in interpreting the data due to the difficulty in controlling relevant variables at play. As a result, they are subject to alternative interpretations because species identity and removal timing can obscure interpretation of results. We build on these studies by conducting experiments with a greater degree of control while providing a conceptual framework for inverse priority effects, which likely represent an important and underappreciated historical contingency in community reassembly.

An important aspect of removal experiments is unveiling the mechanisms that drive community reassembly. By providing a greater measure of control over field experiments, mesocosm experiments aid in controlling specific variables (e.g. resource availability, propagule pressure, environmental conditions) and, therefore, in identifying such mechanisms. Thus, mesocosms allow us to focus on the role of biotic interactions, while field experiments provide a more comprehensive and realistic overview of community reassembly, considering the interplay of biotic interactions with the spatial and temporal context of the removal. By combining both approaches, we can gain a more comprehensive understanding of how species interactions and the environmental context influence community reassembly. Furthermore, species traits can affect their responses to environmental conditions as well as their biotic interactions (Keddy, 1992; McGill et al., 2006). Understanding the functional response of species to the removal history will help predict the most likely reassembly trajectory, reducing the uncertainty of the success of restoration strategies. If functional traits are explicitly incorporated into assembly models, we can infer the characteristics determining species-specific responses (e.g. resource acquisition strategies, fecundity, growth rates, Diaz et al., 2004; Westoby, 1998). Moreover, including traits can facilitate generalization across species (Drenovsky et al., 2012; Funk et al., 2008) allowing us to translate findings to new species and engaging in more efficient species management.

Our goals were (1) to determine the effect of the order and timing of invasive species removal on community reassembly, (2) to explore the role of species origin and functional traits in modulating species responses to histories of removal and (3) to unravel the contribution of environmental and biotic factors in the effects of the order and timing of removal, if any. We conducted removal experiments in field and mesocosm communities of two highly invasive shrubs, sweetbriar rose (*Rosa rubiginosa*, Rosaceae) and scotch broom (*Cytisus scoparius*, Fabaceae). In both settings, we removed the target species in different timing (simultaneously early vs. late) and order (rose before broom vs. broom before rose) and compared community structure to a no-removal situation (control). We used hierarchical modelling of species community (Ovaskainen et al., 2017) to assess changes in community structure following contrasting removal histories and to assess whether species origin and leaf and seed traits shaped such responses.

2 | MATERIALS AND METHODS

2.1 | Study system

In northwest Argentinian Patagonia, humid forests of *Nothofagus* spp. are replaced by forests and shrublands of *Austrocedrus chilensis* (matorral) as precipitation decreases eastward (Cabrera & Willink, 1973). The study region is also characterized by high seasonality. Rainfall concentrates in the colder months (April–September). Mean annual temperature is 7.9°C. We conducted our field study on Isla Victoria (40° 58' 20" S, 71° 31' 6" W, 800 m a.s.l.), an island (20 km long × 4 km wide) located within the Nahuel Huapi National Park (research activities conducted within the National Park were authorized by the Dirección Regional Patagonia Norte, Administración de Parques Nacionales, permit 1496 2016–2020). Its vegetation is dominated by primary or secondary forests of native trees *Nothofagus dombeyi* and *Austrocedrus chilensis* (Simberloff et al., 2002, 2003). The understorey consists mainly of shrubs (*Aristotelia chilensis*, *Schinus patagonicus*, *Berberis darwinii*) and perennial herbs (*Chusquea culeou*, *Carex* spp.). The island has experienced several disturbances (e.g. forestry) and deliberate introductions of nonnative species (including target species) during the 20th century, triggering the invasion of multiple plants and mammals that currently threatens native communities (Simberloff et al., 2002, 2003).

Disturbed sites are dominated by the sweetbriar rose and scotch broom target shrubs with a mix of native and nonnatives herbs and grasses (Sample et al., 2019; Torres et al., 2018). Target species are fast-growing shrubs native to Europe that can reach up to 3 m (Bossard & Rejmanek, 1994; Damascos & Gallopin, 1992). They lose most leaves in winter and flower in spring–summer (rose December–January, broom October–December). These invasive plants produce abundant seeds sexually or asexually (Bossard & Rejmanek, 1994; Damascos & Gallopin, 1992). The rose is characterized by its resistance to harsh conditions. The broom is a

N-fixing mesic shrub that can affect neighbouring species through plant–soil feedbacks (Bossard & Rejmanek, 1994; Grove et al., 2012, 2015).

2.2 | Field experiment

Our experimental setup consisted of four removal treatments of both target species (broom or rose), which involved manipulating timing and order of removal. To do so, we chose two contrasting seasonal times of removal: early (summer) and late (fall) removal. To manipulate the seasonal timing of removal, we removed both species simultaneously early and late in the growing season. To manipulate the order of removal, we simply removed one species before the other in the two possible sequences (rose before broom vs. broom before rose). Concurrently the simultaneous removal dates, the first removal of the sequence took place in early summer, followed by the second removal in late fall. Our design allows us to unravel the overall effect of removing species at different times of the growing season from removing them in different order, as well as to explore the potential effect of removing species simultaneously versus sequentially. We explored community trajectories (cover trend %) of each removal compared to a no-removal control ($\text{cover}_{\text{removal}} - \text{cover}_{\text{control}} / \text{cover}_{\text{control}} * 100$). Controls simulated a pre-removal situation given the difficulty to define a native community of reference due to long-standing anthropogenic disturbances on the island. We established 12 replicate plots each containing all five treatments (60 in total) in areas dominated by the target species. Plots were randomly located at seven sites scattered throughout the island and characterized by different clear-cut ages (between 2009 and 2013) (see Table S1 in Supporting Information). Therefore, plots represented spatial variability in the reference community and the presence of nonnative species throughout the landscape.

We established circular core plots (1 m diameter, 0.8 m²) that were fenced with 1-m-high woven wire (10 × 5 cm mesh size) to prevent herbivory by nonnative ungulates occurring at high densities in Isla Victoria (deer and wild boar, Barrios-García & Simberloff, 2013). To avoid edge effects, we established a 0.5 m buffer belt where we also removed target species, extending the influence of removals to 3.1 m² (extended plot). In the extended plot, we carefully cut and removed the above-ground biomass of target species at ground level to minimize disturbance in the soil and co-occurring plant species. Although we registered the initial biomass of target species (Table S1), we did not include it as a covariable in our model because a previous study in the same communities found that the initial biomass did not modulate species responses to removals (Torres et al., 2023b). To evaluate removals under contrasting environmental conditions within a growing season, early and late removals were performed in the austral summer (February 2018) and fall (May 2018) respectively. To reduce the influence of the target species to a minimum, we removed new seedlings (broom) or occasionally resprouts (rose) every 4 months if present. In January 2020 (almost

2 years from early removal), we quantified community composition by recording species-specific aerial cover (%) in the core plots.

2.3 | Mesocosm experiment

We conducted mesocosm experiments in the greenhouse of the Universidad Nacional del Comahue at Bariloche (41°08'36" S, 71°18'56" W) as a complement to our field study. Mesocosms were assembled in 15-L pots (28 cm diameter × 25 cm tall) with the same composition and density of seedlings of similar age (3–4 months old, Table S5). Each mesocosm had two seedlings from each of the target species (broom and rose), and two seedlings from each of six nontarget species (three native and three nonnative species, Table S5), totalling 16 seedlings per mesocosm. Nontarget species were selected among those commonly co-occurring with target species in the study area. One month and two months after planting seedlings, we performed removals of the target species following four distinct removal histories: early simultaneous, late simultaneous, rose before broom and broom before rose. We explored community trajectories (biomass trend %) of each removal compared to a random-removal control ($\text{biomass}_{\text{removal}} - \text{biomass}_{\text{control}} / \text{biomass}_{\text{control}} * 100$). To

control for differences in density between the control and removal treatments, we removed four random individuals from four different nontarget species from the control pots. Early removal occurred in January and late removal in February to ensure variation in plant size. Random removals occurred 15 days after early removal (Figure 1). After 1 year, we harvested above-ground and below-ground material by species and weighted total biomass after drying (48 h at 65°C).

2.4 | Data analysis

2.4.1 | Field experiment

We evaluated changes in field community composition through Hierarchical Modeling of Species Community (HMSC, Ovaskainen et al., 2017). Species cover was modelled using a zero-inflated Beta regression to separate the probability of being present from treatment effects on cover (if present). The probability of occurrence of species at a site was treated as a random factor, whose expected values depended on site age (time since clear-cut). If present, species cover was a function of a baseline cover (defined by controls) and species-specific responses to removal histories. Responses of all species came

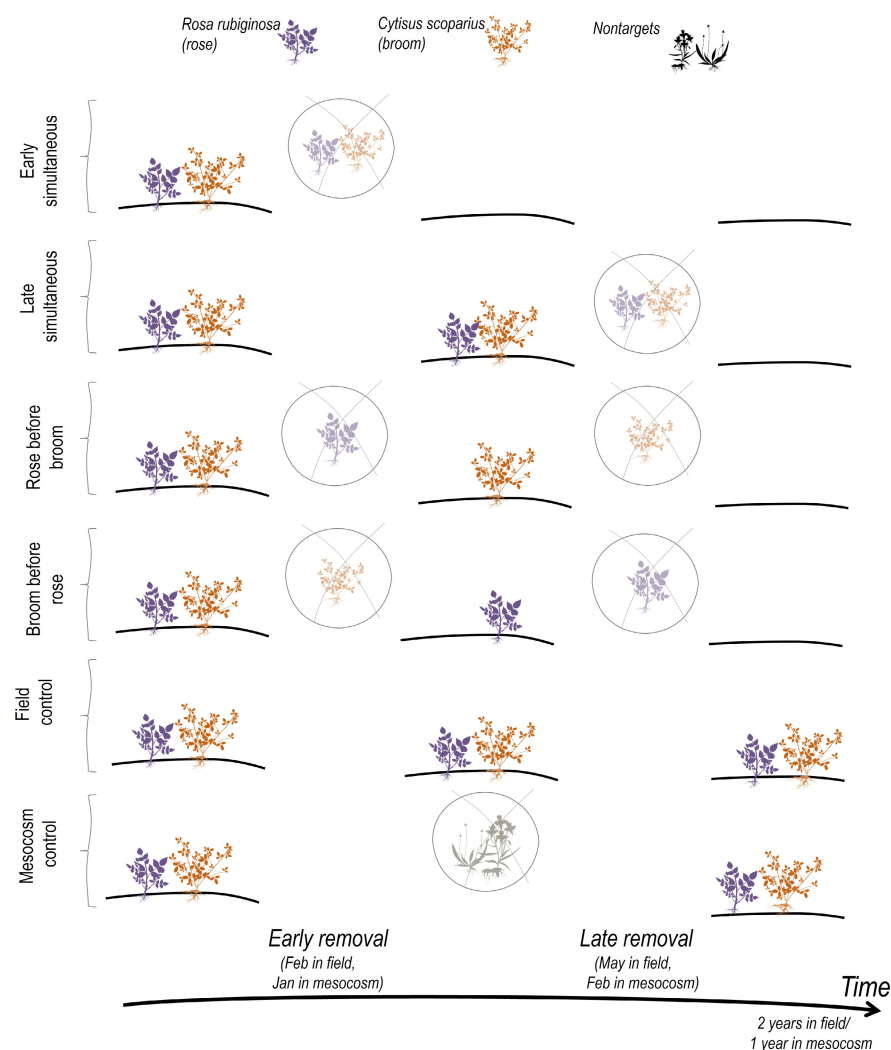


FIGURE 1 General outline of the study. We removed target species in different timing (early and late) and order (rose-before-broom and broom-before-rose). The post-removal community was compared to a no-removal (field) or random-removal (mesocosm) control. Circles with shaded species indicate the type and time of removal. For simplicity, nontarget species are not shown (except to exemplify random removals in mesocosm controls).

from a multivariate normal distribution with mean $\gamma_{..}$ and variance-covariance Σ . Expected species responses ($\gamma_{..}$) to site- and plot-level variables (site age and history of removal respectively) depended on the origin of the species (native/nonnative) and traits. The rationale for HMSC models is that species responses to the environment depend on a set of characteristics that may share a common evolutionary history (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017). In the context of removals, it allows detecting which type of species is more likely to be favoured in newly reassembled communities. We chose specific leaf area (SLA, mm²/mg) and seed size (mg) (Table S2) as functional traits capturing main axes of evolutionary specialization (Diaz et al., 2004). SLA reveals whether successful species have rapid acquisition strategies typical of rich environments (Wright et al., 2004), and seed mass informs whether successful species have higher competitive ability at the seedling stage or high reproduction rates (Moles et al., 2005; Moles & Leishman, 2008). Finally, the variance-covariance Σ was modulated by species phylogeny through the parameter ρ (when close to 1 phylogeny modulates species responses and when close to 0 it is independent of it). More details on model parameterization are given in HMSC section in Supporting Information.

We extracted species origin (native/nonnative) from Zuloaga et al. (2008), and SLA and seed mass from TRY database (Kattge et al., 2011; Table S2). Given that the ranking of species remained relatively stable despite the variability of trait values (Garnier et al., 2001; Kazakou et al., 2014), we obtained averaged trait values. For species whose traits were not recorded in TRY, we used traits reported in the bibliography (de Paz, 2014) or TRY mean by genus, assuming that traits are relatively well conserved by phylogenetic groups (Freckleton et al., 2015; Li et al., 2017; Moles et al., 2005; Table S2). To test this assumption, for all species with information at the species level ($n=67$), we regressed reported values for the species against the mean of the genus using the *lm* function in R. Both traits showed a good match between imputed and observed values (see Figure S1 in Supporting Information). The phylogenetic correlation matrix was obtained from published megaphylogeny using the S.PhyloMaker R package (Qian & Jin, 2015; Zanne et al., 2014). We ran 30,000 iterations in two chains and checked for convergence ($R_{hat} < 1.1$) and effective sample size ($N_{eff} > 100$; Table S3). To assess the predictive power of our models, we performed posterior predictive checks (PPCs) of species cover (Gelman & Hill, 2006; Figure S2). HMSC was implemented using uninformative priors (HMSC section in Supporting Information) in Stan (Stan Development Team, 2020).

2.4.2 | Mesocosm experiment

To evaluate the effects of removal histories on mesocosms, we again conducted a log-normal (conditional on presence) HMSC. The response variable was the log-transformed biomass of surviving individuals. The fixed effects were the control (intercept) and removal histories. We only included species origin in the trait matrix and no phylogenetic effects because the number of species ($N=6$) limited our ability to infer trait and phylogenetic effects

(Ovaskainen & Abrego, 2020). We ran 70,000 iterations (thin=50, transient=3000) in three chains and used uninformative default priors for model parameterization (Ovaskainen & Abrego, 2020). We checked for convergence and effective sample size (Figure S7) and assessed the predictive and explanatory power through PPC (Figure S8). Mesocosm HMSC was implemented with the *Hmsc* package in R (Ovaskainen et al., 2017; Tikhonov et al., 2020).

3 | RESULTS

3.1 | Field experiments

The timing of removal of invasive species affected nontarget species responses. In general, the effects were more pronounced when we removed both target species early in the growing season as opposed to later (Figure 2 and Figure S5). In early removals, nonnative species cover had an overall positive response, while moderate evidence supports that some native species had negative responses to early removals compared to no-removal controls (Figures 2 and 5). In late removals, nonnative species also increased their cover, but to a lesser extent (Figures 2 and 5, Table S4). Species with higher SLA tended to increase their cover in early removals, but not significantly in late removals (Figure 4 and Figure S6). Seed size did not significantly affect species cover in any treatment (Table S4, Figure S4).

The order of removal changed the ranking of cover trends (Figure 3 and Figure S3). Species covers were more affected when the rose was removed before the broom than the other way around (Figure 3). Such differences were reflected in the composition of the reassembled community and the abundance of nonnative species. Rose before broom removal favoured two nonnative grasses: *Dactylis glomerata* and *Holcus lanatus*. Their cover increased by ~80% compared to control plots, which, together with other rearrangements in the community, made them the most abundant species in the plots (Figure 3a and Figure S3). On the contrary, approximately 30% of the species in the community, mostly natives, reduced their cover after rose before broom removal (Figure 3a and Figure S5, Table S3). Removal of broom before rose did not reduce the cover of any species (Figure 3b). Yet, we found moderate evidence that a subgroup of six nonnative species increased their cover (Figure 3b, Table S3). We found moderate evidence that species with higher SLA tended to increase their cover in sequential removals, especially after rose before broom removal (Figure 4 and Figure S6, Table S4). Responses to order of removal were not significantly modulated by species origin or seed size (Figure 5 and Figure S4, Table S4).

3.2 | Mesocosm communities

Species biomass generally increased after target species removals in mesocosms, compared to controls. History of removal modulated some species responses, but to a lesser extent than in the field (Figure 6 and Figure S9, Table S6). In general, species were more

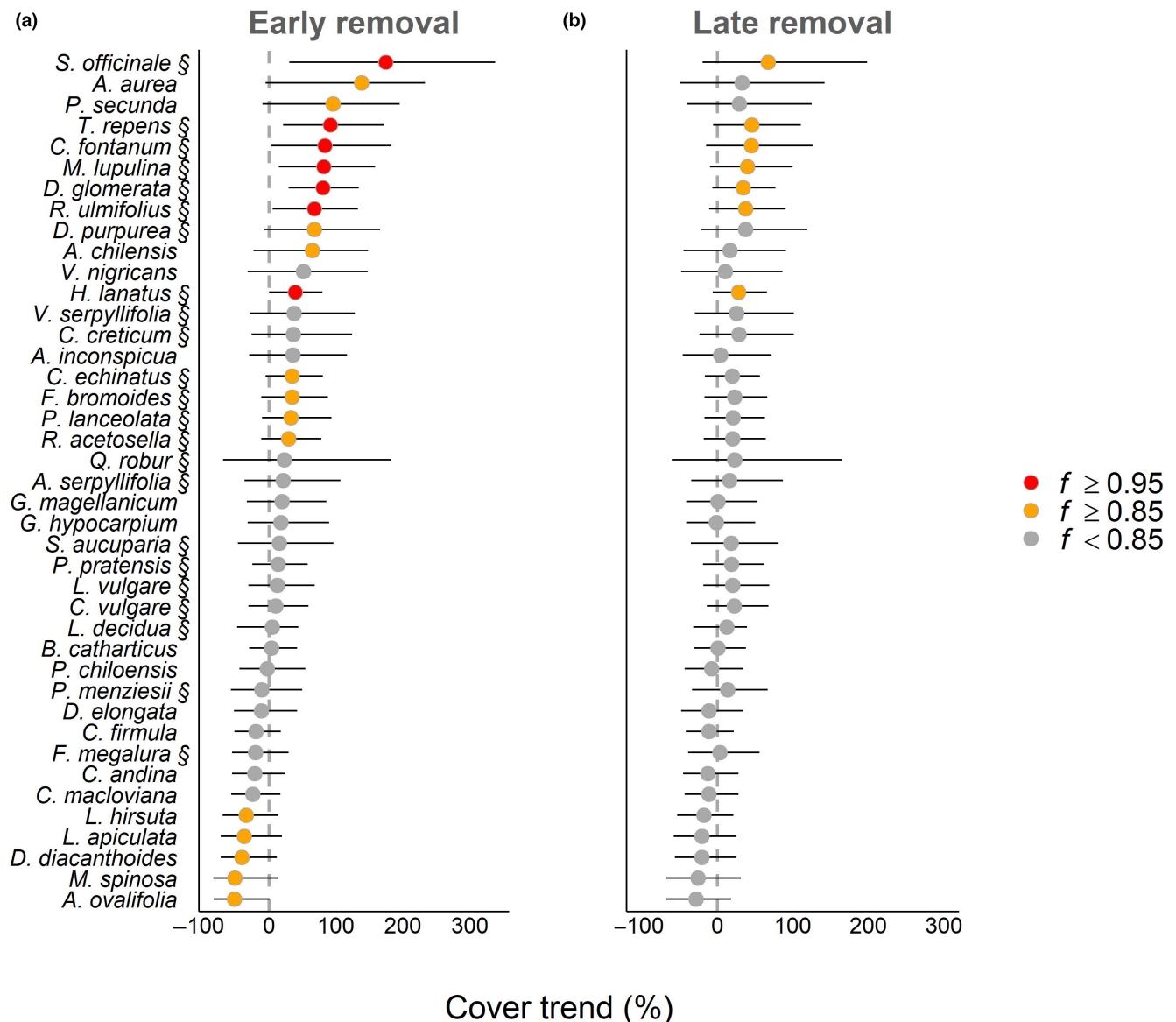


FIGURE 2 Changes in the cover of nontarget species (relative to a no-removal control) for different timing of removals in field experiment: (a) early, and (b) late. The circles indicate the mean percentage of change relative to control ± 0.95 credibility interval. f is the proportion of the posterior distribution with the same sign as the mean. Evidence supporting increase/decrease in cover: $f \geq 0.95$ strong, $0.95 > f \geq 0.85$ moderate, $f < 0.85$ weak. § indicates nonnative species. Species are arranged in descending order according to their responses in early removal.

responsive to simultaneous early removals and to removal of rose before broom (Figure 6, Table S6). The most responsive species were the nonnative herbs *Cirsium vulgare* and *Cynoglossum creticum* which, compared to the control, doubled their biomass when the rose was removed before the broom or simultaneously early. *Festuca arundinacea* dominated mesocosms and was the least reactive species (Figure S9). Species responses did not depend on their origin (Figure S10).

4 | DISCUSSION

Our work challenges the generally held idea that removing all invasive species at the same time is the most effective way to recover

native communities (Bergstrom et al., 2009; Zavaleta et al., 2001; Zenni et al., 2020). Overall, simultaneous removals benefited non-native plant species to a greater extent than sequential removals, especially in the field experiment. Furthermore, the order of removal affected species responses, showing that inverse priority effects can influence community reassembly and secondary invasions after management. The timing of removals was also an important factor in modulating community composition. Early removals benefited nonnative species with rapid growth, a trend that was absent late in the growing season. Both order and timing effects are processes frequently overlooked when designing management actions that could be manipulated to improve management actions.

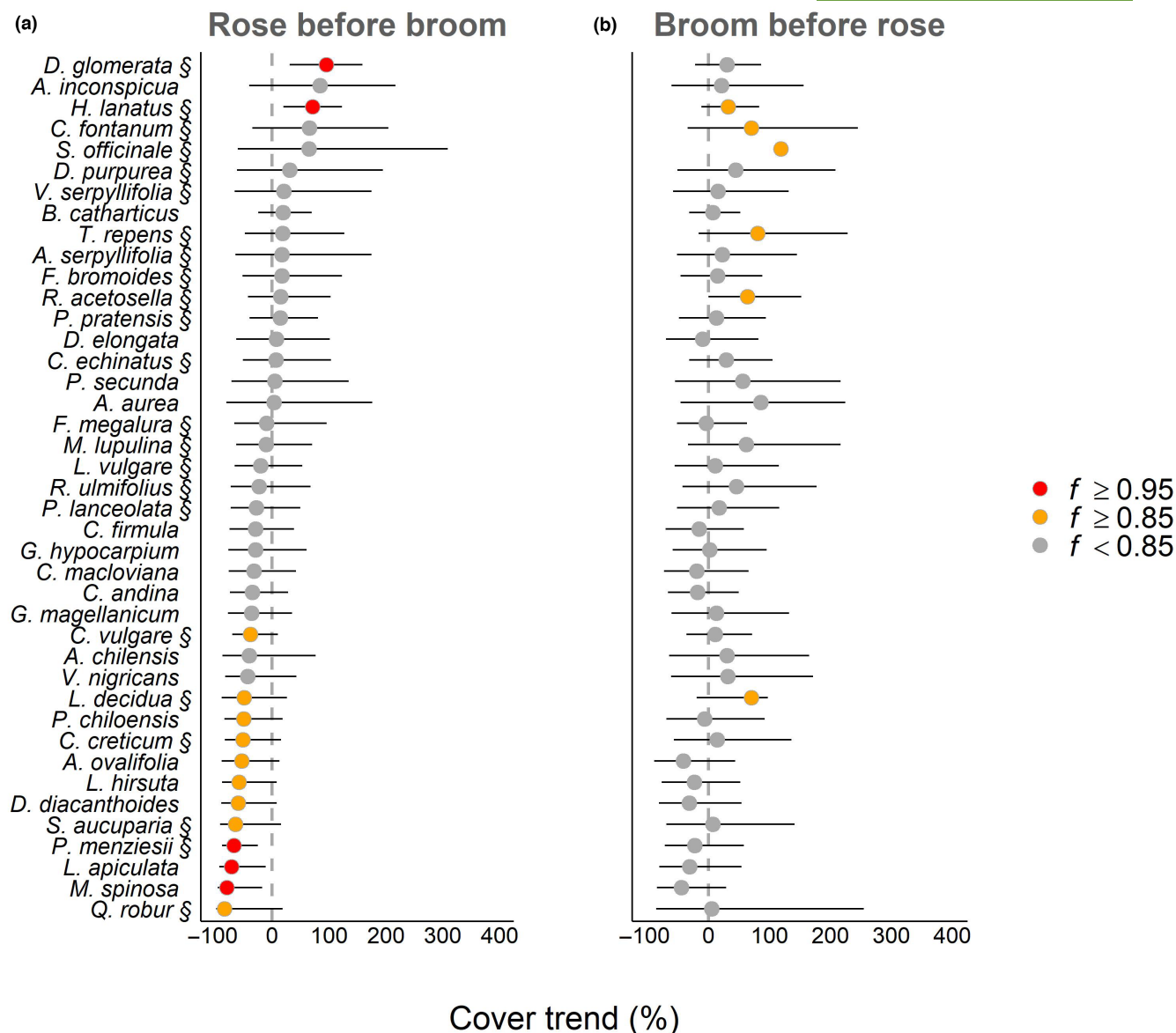


FIGURE 3 Changes in the cover of nontarget species (relative to a no-removal control) for different order of removal in field experiment: (a) rose before broom, and (b) broom before rose. The circles indicate mean percentage changes ± 0.95 credibility interval. f is the evidence supporting increase/decrease in cover (see Figure 2). § indicates nonnative species. Species are arranged in descending order according to their responses in rose-before-broom removal.

Simultaneous removal favoured nonnative species to a greater extent than sequential removal. Simultaneous removals represent a major disturbance that can trigger a high pulse of resources that can be capitalized by nonnative rather than native species (Jauni et al., 2015; Leishman et al., 2007). However, the strength of the response depended on the seasonal timing of removal (see below). This was not the case when sequential removal occurred whereby some kind of resistance to invasions mediated by the presence of at least one of the dominant co-invaders occurred (Torres et al., 2023b). Although native species tended to be more hindered by sequential than by simultaneous removals, this was likely driven by rose before broom removals. However, broom before rose removal caused the least harm to natives and provided the least advantage to nonnatives.

Thus, our results challenge the notion that simultaneous removal is the most effective management technique to increase the chances of recovering native communities (e.g. Courchamp et al., 1999; Zavaleta et al., 2001; Zenni et al., 2020), suggesting management could benefit from removing one species at the time as long as the temporal context of removals (e.g. environmental conditions, interaction strength) is properly considered.

Our results highlighted that removal order can influence the outcome of restoration actions. Overall, the field community was more responsive when the rose was removed before the broom than vice versa. On average, rose before broom removal reduced native species cover by 30% (compared to no-removal), while broom before rose removal had minor effects. Previous work in this system

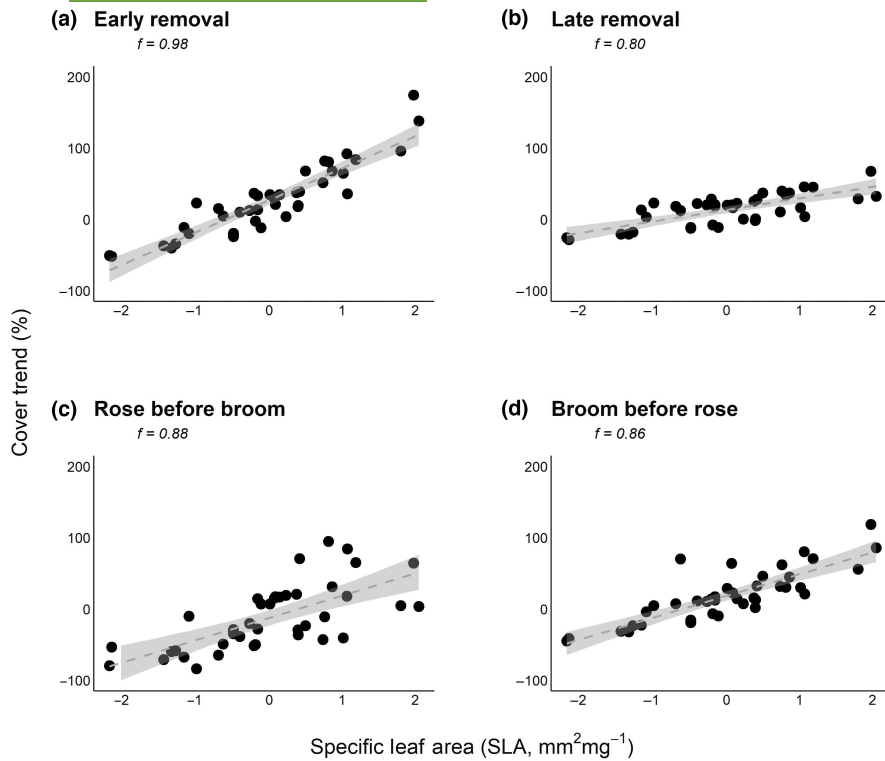


FIGURE 4 Changes in the cover of nontarget species (relative to a no-removal control) as a function of specific leaf area (δ) for different histories of removal in field experiment: (a) early, (b) late, (c) rose before broom, and (d) broom before rose. The regression slope represents the effect of SLA on the response of the species to treatments. f is evidence supporting SLA effect on cover (see Figure 2).

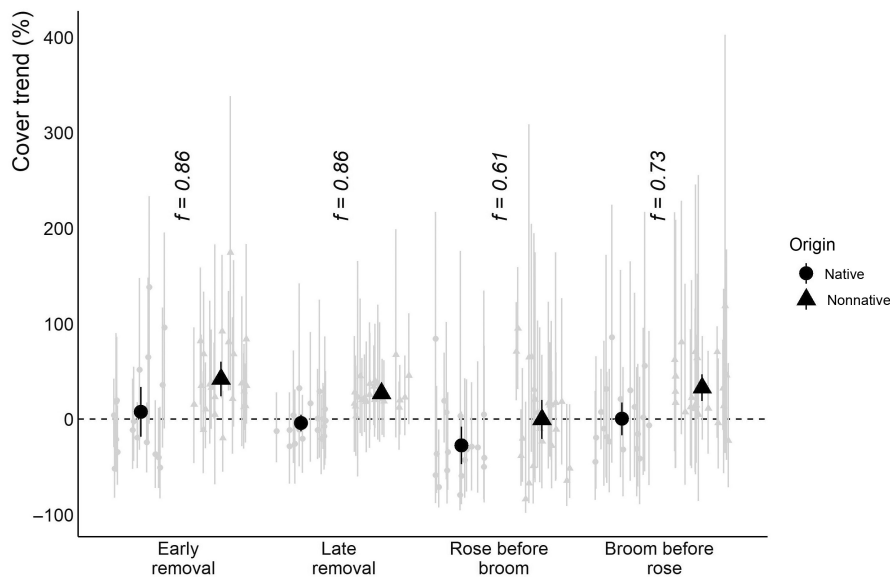
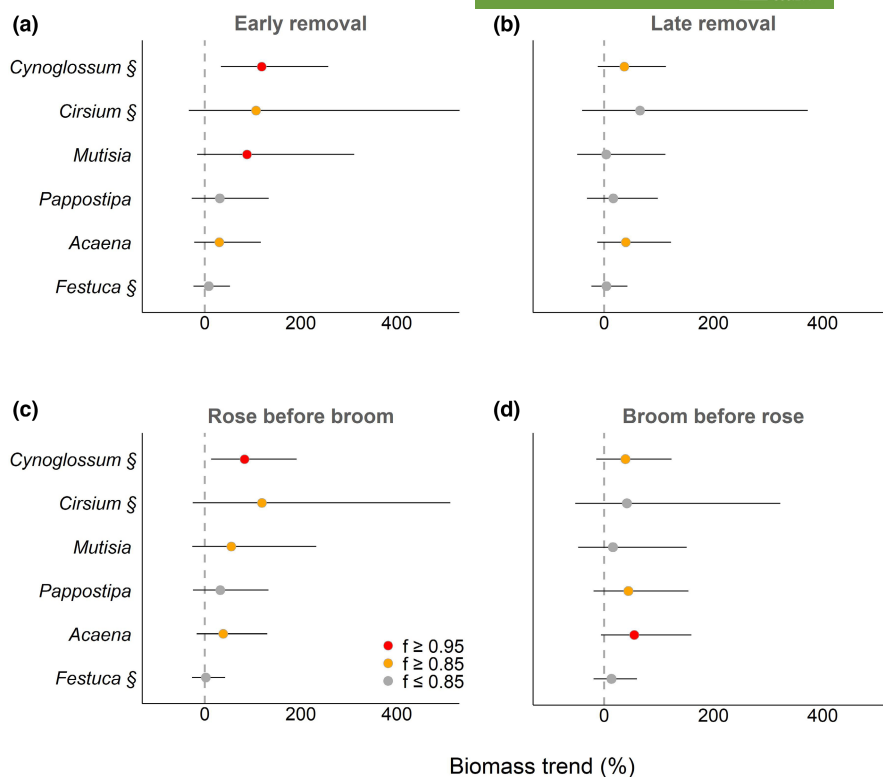


FIGURE 5 Changes in the cover of nontarget species (relative to no-removal control) as a function of biogeographic origin (δ) for different histories of removal in field experiment. Grey circles depict species-specific estimated responses ± 0.95 credible intervals. Shapes represent mean values across species of the same origin (native or nonnative) ± 0.95 credible intervals. f is evidence supporting the origin effect on cover (see Figure 2).

has shown rose-to-broom suppression whereby broom increased its cover by 46% and natives were hindered after rose removals (Torres et al., 2023b). Such patterns suggest that the broom rapidly capitalized resources and outcompeted co-occurring species after rose removal; that is, establishing temporary interactions that exert a lasting influence on reassembly (Amor et al., 2020; Temperton et al., 2016). Although rose before broom removals produced an overall disadvantage on nonnative species compared to the inverse order of removals, two remnant species capable of rapidly growing and hoarding released resources (e.g. nitrogen) increased their cover (Carter et al., 2019; Shaben & Myers, 2010). These species were mainly nonnative grasses *H. lanatus* and *D. glomerata* characterized

by high SLA values (70th percentile). As previously suggested in food webs (Bergstrom et al., 2009; Collins et al., 2009), plant community reassembly was also influenced by removal order. Therefore, by simply changing the removal order, managers could limit secondary invasions and pave the way for the recovery of natives. Species-specific and trait-based approaches like ours can provide valuable information for more targeted restoration actions. Although species with higher SLA seem to be boosted by removals, the consequences for restoration depend on which species are present at that moment. Depending on their identities, removals that favour species with high SLA can be desired (e.g. if fast-growing native species hinder further invasions) or not. Furthermore, if reassembly is dependent

FIGURE 6 Changes in the biomass of nontarget species (relative to a random-removal control) for different removal histories in mesocosms: (a) early, (b) late, (c) rose before broom, and (d) broom before rose. Circles indicate the mean percentage of change relative to control ± 0.95 credibility interval. f is evidence supporting increase/decrease in biomass (see Figure 2). § indicates nonnative species. Species are arranged in descending order according to their responses in early removal.



on the temporal context, as shown here, the species phenology can counteract the trait-based effect. If winners are not 'available' to recruit/grow, other species can manage to do it, changing the course of reassembly (see below).

The timing of removal shaped community reassembly. Early simultaneous removal strongly increased the performance of fast-growing nonnatives (e.g. *S. officinalis* and *T. repens*), while late removal had moderate effects and was not mediated by leaf traits. In early summer removals, suitable conditions for growth combined with the release of resources after removals could have fostered species of rapid growth (Jauni et al., 2015; Leishman et al., 2007). In late fall removals, opportunistic species may already have completed their germination/growth when resources were released. Depending on timing, phenology can either boost or limit the ability of nonnative species to hoard the resources released after removal (Grove et al., 2015; Marushia et al., 2010). Our findings are in line with previous work showing that the environmental context in which reassembly takes place can determine the composition of new communities (Groves & Brudvig, 2019; Marushia et al., 2010; Stuble et al., 2017). From an applied standpoint, we highlight that accounting for timing of removals and species phenology can be important when removals result in an important pulse of resources.

Mesocosms provided further evidence on inverse priority effects while allowing deeper exploration of the underlying mechanisms due to the better control over experimental conditions. In mesocosm, nonnatives were most responsive to simultaneous early removals, and some species responses were influenced by order. Although of lesser magnitude, similarity to field patterns

suggests complementary mechanisms to those operating in the field. The weaker effects observed in mesocosms may result from a reduced release of resources after the removal of seedlings, in contrast to the removal of adult shrubs. Alternatively, since variables such as environmental variability and propagule pressure were controlled, it becomes evident that certain species' responses may be seasonally structured due to their phenology, which determines their interactions with co-occurring species (Rudolf, 2019). In such cases, inverse priority effects could occur even under conditions of low environmental variability or low density of invaders.

Reducing secondary invasions is key to achieving sustained restoration after invasive species management. While a great deal of attention has been paid to priority effects as a tool to manipulate competitive interactions to reduce the establishment of nonnative species in reassemblies (Hess et al., 2019; Weidlich et al., 2021; Yannelli et al., 2020), decisions related to the order and timing of invasive species removal can also affect community reassembly. Given that broom before rose removal mitigated negative effects on natives, we suggest that an optimal order of removal could maximize restoration success, even to a greater extent than simultaneous removal. In this line, we provide evidence on the existence of inverse priority effects, which, when adequately managed, could reduce secondary invasions and maximize restoration success. We aim to encourage the development of a conceptual framework that facilitates the incorporation of inverse priority effects on restoration plans. We also aim to stimulate research into the dynamics of species removal/loss and to delve into the mechanisms by which reassembly could vary when species are lost in a different order/timing. In such

a context-dependent process, the role of functional traits remains to be unravelled.

AUTHOR CONTRIBUTIONS

Agostina Torres, Mariano A. Rodríguez-Cabal and Martín A. Núñez conceived the idea. Agostina Torres led the study, conducted the experiments, and wrote the first manuscript draft. Teresa Morán-López designed the models and analysed the data with Agostina Torres. All authors wrote and revised the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Martín Núñez is a Senior Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.80gb5mkws> (Torres et al., 2023a).

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SUPPORTING INFORMATION

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

Table S1. Field site information and initial biomass of target species.

Table S2. Field species list with traits.

Table S3. Effect of history of removal on species cover.

Table S4. Effect of traits on history of removal effect.

Table S5. Initial composition of mesocosm communities.

Table S6. Biomass of nontarget species for different histories of removal.

Figure S1. Posterior predictive check of missing trait imputation by genus.

Figure S2. Posterior predictive check of the HMSC in field communities.

Figure S3. Estimated final cover of nontarget species for different histories of removals and no-removal control in field experiment.

Figure S4. Mean species as a function of seed size for different histories of removals.

Figure S5. Mean cover trend of native and nonnative species in early vs. late simultaneous removals, rose before broom vs. broom before rose removals, and sequential vs. simultaneous removals.

Figure S6. Mean trend of the SLA effect in early vs. late simultaneous removals, rose before broom vs. broom before rose removals, and sequential vs. simultaneous removals.

Figure S7. MCMC convergence of the HMSC of biomass response in the mesocosm communities.

Figure S8. Posterior predictive check of the HMSC of biomass response in the mesocosm communities.

Figure S9. Estimated final biomass of nontarget species for different histories of removals and random-removal control in mesocosm communities.

Figure S10. Mean biomass trend (relative to control) as a function of biogeographic origin for different histories of removals in mesocosm communities.

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