Title: Community-ecosystem interactions control plant biodiversity change before and after mangrove restoration.

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ABSTRACT:

Restoring biological diversity and ecosystem function requires understanding how introduced species interact with one another and their environments. The most prevalent and challenging scenarios involve multiple invasive species whose traits feedback through ecosystem processes. However, research into these systems often focuses on either community dynamics or ecosystem properties, rather than their interactions, limiting understanding of what causes biodiversity changes before and after restoration. Leveraging insights from theory and management of single-species invasions driven by feedback between plant litter and germination success, we documented the structure of a disturbed mangrove ecosystem and tested causal hypotheses for community and ecosystem change both in microcosms and across the landscape. Before restoration, competing invasive trees generated litter that facilitated the dominance of a single recently introduced species. After experimental restoration, native species seedling cover and richness increased only when removing invasive trees and their litter, supporting interacting community and ecosystem effects as the primary drivers of biodiversity change. Effective restoration of multiply-invaded ecosystems is possible when simple interventions follow causal hypotheses supported by theoretical mechanisms.

KEY WORDS: *Casuarina*; coexistence theory; dredge spoil; ecological succession; regime shift; *Schinus terebinthifolia*

INTRODUCTION

Since the onset of the Columbian Exchange, people have moved over 16,000 species across biogeographic barriers, with profound consequences for biodiversity and ecosystem function (Seebens et al. 2017). The most impactful invasive species alter feedbacks, causing sudden, dramatic changes in recipient communities (Gaertner et al. 2014). Some invaders form enduring monocultures, while others facilitate other exotic species, driving so-called “invasion meltdown” (Simberloff & Holle 1999). Either outcome provides strong tests for classical ecological theory with major management implications (Godoy 2019). Restoring transformed systems to more desirable states requires integrating theory, observation and experiments to identify what ecological mechanisms drive change, how new conditions influence establishment and whether practical interventions can increase biodiversity (Farrer & Goldberg 2014).

Ecological theory and empirical syntheses attribute many impactful plant invasions to ecosystem feedbacks involving dead plant tissue (Gaertner et al. 2014). Invasive litter may fuel fires, alter nutrient cycles, and suppress competitor germination, with major effects on biodiversity in both theory and practice. Using a mechanistic model with both community and ecosystem processes, Kortessis et al. (2022) found that introducing an annual grass into a woodland could entail stable coexistence, competitive exclusion, or priority effects, depending on how litter impacts germination. The same parameter influenced the simulated spread of an invasive tree through a diverse forest and implied that effective control requires not only removing living trees, but also their litter (Lu et al. 2022). Theoretical results reinforce empirical studies, mostly involving herbaceous plants, whose litter causes regime shift by promoting their own recruitment at the expense of native species (Eppinga et al. 2011). In wetlands surrounding the North American Great Lakes, hybrid cattail, *Typha×glauca*, forms monocultures by suppressing native seedlings with shade from litter (Farrer & Goldberg 2009; Vaccaro et al. 2009). Experimental litter removal is sufficient to increase plant species richness, phylogenetic and functional diversity (Farrer & Goldberg 2014; Lishawa et al. 2019).

While basic research has informed management of single high-impact invaders, scenarios with multiple co-occurring invasive species are far more prevalent, understudied, and difficult to manage. Over two-thirds of conservation areas reported multiple invasive species (Kuebbing et al. 2013), with cumulative abundance that often exceeds that of the single most dominant invader (Brandt et al. 2023). However, only a third of empirical studies mentioned more than one invasive species (Kuebbing et al. 2013), with little quantification of invasive species' interactions (Kuebbing 2020). The dearth of empirical data limits models and management. From a theoretical perspective, the criteria for invasive species' coexistence are clear; relatively rare species must have positive population growth to persist in a stable environment (Chesson 2000; Hallett et al. 2023). However, multispecies models require more data on demographic rates and interactions than empirical studies typically produce (Godoy 2019). Even the most sophisticated multispecies models lack representation for ecosystem feedbacks (Kortessis et al. 2022). Integrating community interactions involving multiple species with their ecosystem feedbacks is critical for translating theory into effective management.

Changes in biodiversity before and after experimental restoration can demonstrate the importance of community by ecosystem interactions in multispecies invasions. Consider a relatively simple system involving several invasive species that outcompete a pool of natives (Fig. 1). Community ecology theory predicts reduced native seedling richness and cover before invasive removal, which is necessary and sufficient to release natives from competition and restore diversity (Godoy 2019, Fig. 1A). However, this scenario lacks representation of ecosystem processes that may directly mediate competitive effects. Including ecosystem feedbacks in the form of germination-suppressing litter would also reduce native seedlings before restoration, while introducing the distinct prediction, supported by theory, that removing both invasives and their litter is necessary for biodiversity restoration (Kortessis et al. 2022, Lu et al. 2022, Fig. 1B). While litter may uniformly affect germination, community by ecosystem interactions generate distinctive predictions for biodiversity change (Fig. 1C). In this scenario, litter types have idiosyncratic effects of seedlings, including the possibility for either facilitation or suppression. Species with seedlings with higher net benefit from invasive litter may be overrepresented in the seedling community prior to restoration. While community by ecosystem interactions entail complex mechanisms, they generate distinct predictions for biodiversity change before and after experimental restoration that may apply broadly to multispecies invasions involving litter.

To test hypotheses for the importance of community by ecosystem interactions for restoring multispecies invasions, we examined invasive trees that dominate dredge spoil islands of southwest Florida, US. Before regulation in the 1970s, the creation of 16,000 km of navigation channels generated 2.3×10^8 m^3 yr^{-1} of sediments piled in nearshore habitats (Morton 1977). Invasive species then colonized nutrient-poor sands (Goldberg & Rillstone 2012). The most established species, *Schinus terebinthifolia* (Anacardiaceae, Brazilian peppertree) and *Casuarina* spp. (Casuarinaceae, Australian pine), were introduced in the 19th century and have caused major changes in Florida as they have worldwide (Gaertner et al. 2014). *Schinus* dominates more than 2% of terrestrial habitats in Florida using allelopathic compounds (Ferriter 1997; Nickerson & Flory 2015). *Casuarina* is particularly dominant in coastal sites where its senesced branchlets smother seedlings (Potgieter et al. 2014). A third invasive tree, *Cupaniopsis anacardioides* (Sapindaceae, Carrotwood), was more recently introduced and is among the only seedlings present in dredge spoil islands (Lockhart et al. 1999), suggesting some tolerance of *Casuarina* and *Schinus*, although the mechanisms and consequences are unknown (Oberle et al. 2023).

To identify what causes biodiversity change in this system, and whether community by ecosystem interactions influence multispecies invasions more broadly, we combined complementary multivariate analyses of observational data before restoration with multifactorial experiments both inside microcosms and across the landscape. Specifically, we explained variation in co-occurrence across life stages and edaphic conditions from a multiscale field inventory. After identifying the community and ecosystem interactions with the most explanatory power, we tested the hypothesis that community by ecosystem interactions drive changes in seedling diversity before restoration with a novel Bayesian analysis of a multifactorial germination experiment. We finally validated the results of our observational analysis and laboratory experiment with a randomized, controlled field experiment that compared biodiversity responses to realistic management methods. We show how simple interventions rooted in ecological theory and supported by detailed causal modelling of community by ecosystem interactions can effectively restore multi-species invasions.

MATERIALS AND METHODS

Community and ecosystem observations

We observed invaded plant communities at the Tidy Island Preserve, a channelized mangrove on the southwest coast of Florida, U.S.A with a mean annual temperature of 22.8 °C and annual precipitation of 1346 mm. The focal area spanned 1.7 ha and included a large spoil mound located at 27.4514°N, 82.6539°W. Between November 2019 and August 2020, we characterized plant communities in 24 12.5 x 8 m monitoring plots located every 25 m along the perimeter of the spoil mound. We previously characterized aboveground biomass in spoil habitats (50 m^2) using custom allometric growth equations for *Schinus* and *Cupaniopsis* (Oberle et al. 2023). *Casuarina* was the most important tree species (>7.5 cm DBH), accounting for 53.5% of aboveground biomass, and *Cupaniopsis* was the most numerous sapling (2 cm ≤ DBH ≤ 7.5 cm), accounting for 36.0% of stems while *Schinus* and seven native species accounted for the rest of the woody plant community (Table S1).

For this study, we further measured seedlings and substrates in 42 0.25m^2 quadrats. Of these, 24 were located within monitoring plots and 18 were located 6.25m further down the long axis from plots designated for restoration. We recorded percent cover for all plant species with foliage below 1.3m. We also measured substrates in 24 0.25 m^2 quadrats adjacent to the seedling quadrats within the monitoring plots. Litter consisted of all senesced plant material within quadrats. We measured litter depth by inserting a 1mm diameter steel rod through the litter to the soil surface at all four quadrat corners. We measured total litter dry mass after 3d at 60°C if less than 1L, or from the wet mass and moisture content of a subsample otherwise. We measured subsample carbon (C) and nitrogen (N) using a Thermo Electron Flash EA1112 (Waltham, USA). We characterized soil at 2.5-7.5 cm and 17.5-22.5 cm depth using an AMS Soil Bulk Density (SBD) sampler (American Falls, USA). We calculated SBD as the mass of the dry sample (3 d 60°C) divided by its volume (90.59 cm^3). We included duff and roots where present and removed coarse fragments that we could not homogenize by hand. Finally, we measured homogenized subsample C:N.

We estimated community interactions from patterns of co-occurrence using generalized linear latent variable models as implemented by R v. 4.3.1. (R Core Team 2020) package "gllvm" (Niku et al. 2019). We grouped all native species into a single category for comparison against each of the three dominant invasive species and distinguished trees from saplings in each species group. We modeled biomass per 50 m^2 plot using a Tweedie distribution (Dunn & Smyth 2005) and compared models with and without effects for SBD and C:N of lower soil strata. We also varied the number of latent variables from 1 to 4, both with and without soil covariates. Significant effects for soil covariates would support habitat filtering whereas latent variables alone would support community interactions (Niku et al. 2019). We identified the most adequate model based on the bias-corrected Akaike Information Criterion (Hurvich & Tsai 1989). We depicted residual correlations between species and size categories using chord diagrams as implemented in the R package "circlize" (Gu et al. 2014).

We quantified whether ecosystem variables mediate the effects of adults on seedling percent cover using Structural Equation Modeling (SEM). We log-transformed SBD at 5 cm, soil C:N at 20 cm and each species' aboveground biomass with a 1 kg offset. We also logit-transformed seedling percent cover after adding a 5% offset. Our first exploratory model included all ecosystem covariates, species' aboveground biomass, and indirect effects of aboveground biomass on every ecosystem covariate. We then simplified the model to include only statistically significant causal pathways and to meet three adequacy criteria: (1) a non-significant likelihood ratio (χ^2) test for overall model fit, (2) a root mean square error of approximation (RMSEA) estimate less than 0.08 and (3) a comparative fit index (CFI) greater than 0.95 (Oberle et al. 2022). We fitted SEMs using the "sem" function in R package "lavaan" (Rosseel 2012). We considered significant standardized path coefficients, β's, evidence for causal effects.

Germination experiment

We tested for community by ecosystem interactions in litter effects on seed germination using a multifactorial germination experiment. We included propagules and litter from all three invasive trees as well as a representative native tree, *Pinus elliottii*, which dominates uninvaded habitat. Microcosms consisted of 100 x 25 mm petri dishes (KORD MONO-AGRI-PLATE, Bioplast Manufacturing, Bristol, USA) with 60g sterile quartz sand and all pairwise combinations of species' seed and litter as well as controls with seed and sand only.

Because of differences in species' phenology and competitive mechanisms, we conducted two series of experiments. The first occurred from July to September 2020 and included treatments with *Casuarina*, *Cupaniopsis*, or *Pinus* propagules and litter, which we collected from the New College of Florida Campus (27.3850°N, 82.5640°W) except for *Pinus* seed, which we purchased from the Florida Forest Service. For *Casuarina*, which had low germination in a pilot experiment, we assembled 10 microcosms with 10 samaras per treatment. For *Cupaniopsis* and *Pinus*, we assembled eight microcosms with five seeds per litter treatment. The second series of experiments occurred from November 2020 to February 2021 and included all treatments with *Schinus*, which we collected on the New College of Florida Campus. We assembled six plates with six berries per litter treatment. We autoclaved litter for 20 minutes at 120°C and drying for 3d at 60°C. We added 5g of dry sterile litter per microcosm and watered with 6mL deionized water, adding water weekly to maintain the initial wet mass of the microcosms. We quantified *Schinus'* effects on other species' germination following Nickerson & Flory (2015), and applied 6mL of an aqueous extract of 5g of ground, dried *Schinus* leaves in 500mL of deionized water and reapplied in alternating weeks with deionized water. For seeds exposed to Schinus extracts, we included five replicate microcosms per species with 10 samaras of *Casuarina* or 5 propagules of other species. We placed all microcosms in lighted growth chambers with a 14h 28°C / 10h 23°C day/night schedule and rotated plates within the growth chamber weekly. We tallied all living and dead seedlings once or twice per week, with a mean interval length 4.87±2.16 (s.d.), for 11-13wk. Upon conclusion, we dissected every microcosm and identified whether seeds had died based on visible deterioration of the seed coat and embryo. We assumed that all other seeds were still viable.

We quantified community by ecosystem effects mediated by litter on seed germination in the context of the seed to seedling state transition matrix ***R***:

$$\boldsymbol{R} = \begin{bmatrix} s_{\sigma\_\delta} & s_{\mu\_\delta} & s_{\gamma\_\delta} & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & g_{\sigma\_\delta} & g_{\mu\_\delta} \\ 0 & 0 & 0 & 1 \end{bmatrix} \qquad \text{(Eq. 1)}$$

Where the columns from left to right represent the states of living seed, dead seed, living seedling or dead seedling in interval *i*, and the rows from top to bottom represent those same states following a short interval i+δ. The top row vector, $\boldsymbol{s}_{\tau\_\delta}$, represents the probabilities of three possible outcomes for viable seed: remaining alive, s_{σ_δ}, dying, s_{μ_δ}, or germinating s_{γ_δ}. The non-zero elements in the third row, $\boldsymbol{g}_{\tau\_\delta}$, represent the probabilities of a seedling either remaining alive, g_{σ_δ}, or dying, g_{μ_δ}. We estimated transition probabilities using a novel piecewise conjugate Bayesian approach implemented in the software "rjags" (Appendix S1, Plummer et al. 2022). We projected the probability that a seed survives as a seedling for one year, g_{σ_year}, by raising $\boldsymbol{R}$ to the 52nd power using the "matrix.power" function in the R package "matrixcalc" (Novomestky & Kelly 2022). We estimated uncertainty from 1000 random draws from the posterior distributions (Appendix S1). For a measure of absolute pairwise litter effects, we subtracted each species' estimated survival with litter from that estimated for bare sand, such that negative values indicate suppression while positive values indicate facilitation. We calculated species' aggregate germination sensitivity to litter as the absolute total difference for all litter treatments relative to bare sand. We depicted effects of litter on seedling germination relative to controls using chord diagrams. We excluded a treatment combination involving *Schinus* leaf extract on *Cupaniopsis* seeds, where no germination occurred in either the experimental microcosms or the controls, likely because the seeds had died during storage between the two experiments. In the context of the experiment, significant differences in seedling survival with different litter treatments supports community by ecosystem interactions as the mechanisms changing seedling community structure before restoration.

Experimental restoration

From March to April 2021, contractors implemented experimental restoration. In and around six plots designated as controls, contractors left all vegetation intact. In and around six plots designated as kill-in-place, contractors felled all invasive trees and saplings and treated stumps with 10% triclopyr ester herbicide. In and around the remaining 12 plots, contractors used a forestry mulcher to chip all invasive plants except *Casuarina* trees >25cm DBH, which were killed in place. Following mulching, we removed all deadwood, loose litter and mulched biomass from six plots designated for invasive and litter removal. In the final six plots designated for invasive removal and litter addition, we left *in situ* deadwood, litter and mulch and added more from adjacent litter removal plots. Across the entire project area, contractors left native trees intact and conformed to permit requirements.

Approximately eight months after experimental restoration, from January to March 2022, we re-inventoried all 42 seedling monitoring plots. We tested for effects of different restoration treatments on seedling percent cover and richness using paired *t*-tests against the null hypothesis of zero change. We further tested for a difference in difference between controls and treatments with ANOVA using the difference in controls as the reference category.

RESULTS

Different invasive species dominated alternative patches of uniform habitat, supporting competition as the primary mechanism structuring tree communities (Fig. 2). Subsurface soils were denser and had lower C:N than surface soils (Fig. S1). However, subsurface soil variables did not factor into the most adequate model for species importance, providing no evidence for habitat filtering (Table S2). Residual correlations between tree species were generally negative (n=6, mean=-0.11, sd=0.31), supporting a primary role for competition, although *Schinus* exhibited weakly positive residual correlations with other species across stages (n=12, mean=0.08, sd=0.19). Conspecific size classes tended to have positive residual correlations (n=4, mean=0.07, sd=0.47) and scored similarly on the first two latent variable axes, mapping each species onto a set of inventory plots where it dominated (Fig. S2).

While community processes explained why trees dominated different patches of uniform habitat, seedlings differed distinctly from adults and supported a strong mediating role for ecosystem processes (Fig. 3). *Cupaniopsis* was one of three plant species encountered among 42 0.25m^2 seedling plots surveyed over a 9-month period before restoration, and was the only species in 18/19 vegetated sites, where it covered up to 70% of the substrate (mean=23.7%±18.0%s.e). Variation in *Cupaniopsis* seedling percent cover depended on direct and indirect effects involving both community and ecosystem-level properties. The simplified SEM for 24 plots with paired aboveground biomass and substrate measurements met all model adequacy criteria (χ^2=0.05, p=0.82, RMSEA=0.00 [0.00-0.38 95%CI], CFI=1.00) and required only three variables and five causal paths to explain over two thirds of the variation in transformed seedling percent cover. Seedling cover increased with *Cupaniopsis* aboveground biomass (β=0.629, s.e.=0.106, p<0.001), which decreased with the biomass of its competitor, *Casuarina* (β=-0.443, s.e.=0.156, p=0.004). However, increasing biomass of both tree species increased litter depth (*Casuarina* β=0.640, s.e.=0.140, p<0.001, *Cupaniopsis* β=0.481, s.e.= 0.173, p=0.005), which correlated with higher percent cover of *Cupaniopsis* seedlings (β=0.421, s.e.=0.120, p<0.001), indicating that leaf litter accumulation facilitates *Cupaniopsis* establishment. In support of this hypothesis, we observed *Cupaniopsis* adventitious roots within the litter layer during sample collection (Fig. S3). No other variables describing communities (*Schinus* or Native AGB) or substrates (Litter C:N, Soil Bulk Density and C:N at 5 cm and 20 cm depth) explained variation in seedling cover before restoration.

Multifactorial germination experiments supported community by ecosystem interactions as the mechanisms driving the dominance of *Cupaniopsis* seedlings before restoration (Fig. 4). On bare sand, *Cupaniopsis* had the highest annual seedling survival, 39.2% ([6.2%-93.6%] 95%CI), nearly four times higher than projected for the second-best performing species, *Casuarina* (11.1% [0.1%-85.4%] 95%CI), and significantly higher than projected for either *Schinus* (0.7% [<0.1%-4.8%] 95%CI) or the representative native tree *Pinus* (<0.1% [<0.1%-0.1%] 95%CI). Supporting the hypothesis of facilitation, addition of *Casuarina* litter boosted *Cupaniopsis’* annual survivorship to 65.1% ([8.8%-99.9%] 95%CI), significantly higher than all but 3 of 20 experimental combinations (Table S3). *Cupaniopsis* also had higher seedling survival with added *Pinus* litter, although *Pinus* litter marginally reduced survivorship of both *Casuarina* and *Schinus* seedlings (Table S3). Conspecific litter generally reduced survivorship, with the exception of *Schinus*, which had significantly higher survival with addition of its own leaf extracts (Table S3). Other developmental transitions showed similar patterns, with *Cupaniopsis* generally exhibiting higher rates of germination and seedling survival that were increased by addition of heterospecific litter (Figs. S3-S5).

The importance of community by ecosystem interactions was reinforced by significant increases in seedling richness and percent cover following invasive biomass and litter removal. The total number of plant species increased from 3 to 19 after restoration, with 11/16 new occurrences considered native. Neither kill-in-place nor control treatments generated significant changes in species richness (kill-in-place n=12, p=0.05, control n=6, p=0.11). The greatest increase in richness, by 1.58 new species per 0.25 m^2 plot, occurred where both invasives and their litter were removed (Fig. 5A, paired *t*-test, n=12, *t*=5.479, p<0.001), with a slightly lower but still significant increase in richness by 1.01 new species per plot with invasive removal and litter addition (paired *t*-test, n=12, *t*=3.749, p=0.001). Only invasive and litter removal significantly increased seedling percent cover, by 20.4% on average (Fig. 5B, paired *t*-test, n=12, *t*=2.541, p=0.015). The differences in experimental treatment sites were only marginally greater than the differences in controls, which were less intensively sampled (Difference in difference ANOVA, control n=6, Richness p=0.09, Percent Cover p=0.10).

DISCUSSION

By combining multivariate analyses of observational data with multifactorial experiments, we validated ecological theory in showing that biodiversity change in a disturbed mangrove depends on community by ecosystem interactions involving distinct responses of seedlings to litter addition and removal. Our results illuminate how some of the world's worst invasive trees drive regime shift, connect subsequent biodiversity decline to the traits of an emerging invasive species, and inform management of understudied multi-species invasions, especially the many which involve litter-germination feedbacks (Gaertner et al. 2014).

Impactful invasive species drive regime shift by altering ecosystem feedbacks (Gaertner et al. 2014), as reinforced for globally important invasive species that interact on Florida dredge spoil mounds. The plant genera *Casuarina*, *Schinus* and *Pinus* all suppress competitors' germination and transform ecosystems (Potgieter et al. 2014; Simberloff & Rejmanek 2019). However, their effects on one another were not uniform. *Causuarina* suppressed other species and itself, suggesting that stands where it dominates now may not persist. In contrast, *Schinus* was less abundant despite evidence for facilitation, which would promote this species' characteristic monocultures (Ferriter 1997). The lack of co-occurrence between *Schinus* and

Casuarina may reflect priority effects, which are a potential outcome of litter-mediated competition (Kortessis et al. 2022) or asymmetrical competition between adults. *Pinus* includes globally significant invaders that transform ecosystems with litter (Sapsford et al. 2020), just as it did in our experimental microcosms. However, *Pinus* seedlings had very low survival and did not occur in the survey, suggesting poor habitat quality of disturbed mangroves and microcosms.

Decades of competition at our research site had resulted in an apparent stalemate among established invaders until ecosystem properties facilitated a new species. Subsurface soils, which may represent the original dredging material, were relatively dense and had low C:N ratios, within the range reported for sparsely-vegetated coastal habitats in the region (Radabaugh et al. 2018). However, surface soils directly received input from litter and had SBD and C:N values similar to undisturbed mangroves (Vaughn et al. 2021). The formation of organic soils from thick layers of litter favored the establishment of the most recently introduced species, *Cupaniopsis*, which dominated the seedling community. *Cupaniopsis* may be pre-adapted to establishing after *Casuarina* colonizes given their native range co-occurrence. Yet, *Cupaniopsis* germination also improved with litter from *Pinus*, a species with which it has no apparent co-evolutionary history. *Cupaniopsis* litter, in turn, strongly limited germination for all species including itself, suggesting that, like *Casuarina*, *Cupaniopsis* may not maintain long-term dominance. The apparent change in tree species composition based on both functional and demographic traits, strongly supports distinct responses of biodiversity to community by ecosystem interactions. To advance this field, piecewise analysis of factorial germination experiments can provide badly needed data to parameterize multi-species coexistence models (Godoy 2019). Further research should examine other aspects of coexistence, including dispersal and seed bank persistence, as well as priority effects. Given the prevalence of multispecies invasions, these results reinforce how understanding species' demographic properties and ecosystem impacts can yeild mechanistic insights into biodiversity change in unmanaged habitats

Just as community by ecosystem interactions drove a decline in biodiversity before restoration, the outcome showed how biodiversity recovery is possible in this system and many others where litter drives regime shift. As predicted by theory (Kortessis et al. 2022; Lu et al. 2022), and consistent with experimental restoration of other high-impact invaders (Farrer & Goldberg 2014), the only experimental removal technique that significantly increased both seedling percent cover and richness involved both killing invasive trees and removing their litter. The increase in diversity consisted primarily of native species and was of the same order of magnitude observed after removing invasive cattail litter from wetland ecosystems (Lishawa et al. 2019; Vaccaro et al. 2009). Furthermore, native species richness increased dramatically despite a much shorter duration for seedling inventory after restoration (2 months) compared to before restoration (9 months), minimizing potentially confounding effects of seedling phenology. The successes of litter removal in both systems, with very different plants (woody versus herbaceous) and edaphic characteristics (coastal upland versus freshwater marsh) indicates that litter accumulation is a prevalent and reversible property of highly invaded ecosystems. Moreover, differences between treatments reinforces the futility of restoration without addressing mechanisms underlying biodiversity decline (DiManno et al. 2023). Simply killing invasive trees and leaving their biomass in place did not generate changes in seedling cover or richness, just as alterations of wetland elevation without removing litter did relatively little to change invaded wetland community structure (Polzer & Wilcox 2022). While removing litter may effectively restore many invaded ecosystems, other mechanisms are significantly harder to address including changes in nutrient dynamics, allelochemical concentrations or microbial community structure (DiManno et al. 2023; Nickerson & Flory 2015).

While community by ecosystem interactions can inform biodiversity restoration where invasive litter germination feedbacks prevail, our results come with at least four important caveats. First, we observed significant gains in species richness in plots with added invasive tree mulch and litter, suggesting that the technique for controlling invasive trees—forestry mulching—may play some causative role in biodiversity recovery. Although we inferred that plant litter, and by extension mulch, should reduce seedling germination, forestry mulching also increases surface light availability compared to kill-in-place and control treatments, which has been shown to increase germination rates in a factorial experiment involving mulching of invasive common buckthorn in the temperate U.S.A (Anfang *et al.* 2020). Second, the gains in percent cover and species richness were not significantly different from the changes that we observed in the controls, which were less intensively sampled and may have benefitted from invasive removal increasing species' recruitment, for instance by increasing access by wind-dispersed seeds. Third, improvements occurred very shortly after experimental restoration. Whether or not native species persist and resist reestablishment of invasive plants will require monitoring over longer time horizons or predictive models for community and ecosystem change. Finally, increased plant richness is just one among many ecosystem services. Removing large invasive trees generated a huge influx of deadwood and greatly diminished primary productivity, likely resulting in significant C loss (Dickie et al. 2014; Mascaro et al. 2012). Measuring that loss and comparing it to gains in species richness over longer time horizons will be necessary for a more holistic sense of the costs and benefits of using community by ecosystem interactions to manage invasive species.

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REFERENCES

Anfang, C., Schuster, M.J., Wragg, P.D. & Reich, P.B. (2020). Increased light availability due to forestry mowing of invasive European buckthorn promotes its regeneration. *Restoration Ecology*, 28, 475–482.

Brandt, A.J., Png, G.K., Jo, I., McGrannachan, C., Allen, K., Peltzer, D.A., et al. (2023). Managing multi-species plant invasions when interactions influence their impact. Frontiers in Ecol & Environ, 21, 370–379.

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. Annu. Rev. Ecol. Syst., 31, 343–366.

Dickie, I.A., Bennett, B.M., Burrows, L.E., Nuñez, M.A., Peltzer, D.A., Porté, A., et al. (2014). Conflicting values: ecosystem services and invasive tree management. Biol Invasions, 16, 705–719.

DiManno, N., Ostertag, R., Uowolo, A., Durham, A., Blakemore, K., Cordell, S., et al. (2023). Functional trait-based restoration alters nutrient cycling and invasion rates in Hawaiian lowland wet forest. Ecological Applications, 33, e2894.

Dunn, P.K. & Smyth, G.K. (2005). Series evaluation of Tweedie exponential dispersion model densities. Stat Comput, 15, 267–280.

Eppinga, M.B., Kaproth, M.A., Collins, A.R. & Molofsky, J. (2011). Litter feedbacks, evolutionary change and exotic plant invasion. Journal of Ecology, 99, 503–514.

Farrer, E.C. & Goldberg, D.E. (2009). Litter drives ecosystem and plant community changes in cattail invasion. Ecological Applications, 19, 398–412.

Farrer, E.C. & Goldberg, D.E. (2014). Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. Aquatic Botany, 116, 35–43.

Ferriter, A. (1997). Brazilian Pepper Management Plan for Florida. Florida Exotic Pest Plant Council.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J. & Richardson, D.M. (2014). Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions, 20, 733–744.

Godoy, O. (2019). Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. Functional Ecology, 33, 1190–1201.

Goldberg, N.A. & Rillstone, R.J. (2012). Comparison of plant diversity on spoil and natural islands in a salt marsh habitat, northeastern Florida. The Journal of the Torrey Botanical Society, 139, 226–231.

Gu, Z., Gu L., Eils R., Schlesner M. & Brors B. (2014). "Circlize" implements and enhances circular visualization in R." Bioinformatics 30: 2811-2812.

Hallett, L.M., Aoyama, L., Barabás, G., Gilbert, B., Larios, L., Shackelford, N., et al. (2023). Restoration ecology through the lens of coexistence theory. Trends in Ecology & Evolution, 38, 1085–1096.

Hurvich, C.M. & Tsai, C.-L. (1989). Regression and time series model selection in small samples. Biometrika, 76, 297–307.

Kortessis, N., Kendig, A.E., Barfield, M., Flory, S.L., Simon, M.W. & Holt, R.D. (2022). Litter, Plant Competition, and Ecosystem Dynamics: A Theoretical Perspective. The American Naturalist, 200, 739–754.

Kuebbing, S.E. (2020). How direct and indirect non-native interactions can promote plant invasions, lead to invasional meltdown and inform management decisions. In: Plant invasions: the role of biotic interactions (eds. Traveset, A. & Richardson, D.M.). CABI, Wallingford, pp. 153–176.

Kuebbing, S.E., Nuñez, M.A. & Simberloff, D. (2013). Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. Biological Conservation, 160, 121–129.

Lishawa, S.C., Lawrence, B.A., Albert, D.A., Larkin, D.J. & Tuchman, N.C. (2019). Invasive species removal increases species and phylogenetic diversity of wetland plant communities. Ecology and Evolution, 9, 6231–6244.

Lockhart, C.S., Austin, D.F., Jones, W.E. & Downey, L.A. (1999). Invasion of Carrotwood (*Cupaniopsis anacardioides*) in Florida Natural Areas (USA). Natural Areas Journal, 19, 254–262.

Lu, Y., DeAngelis, D.L., Xia, J. & Jiang, J. (2022). Modeling the impact of invasive species litter on conditions affecting its spread and potential regime shift. Ecological Modelling, 468, 109962.

Mascaro, J., Hughes, R.F. & Schnitzer, S.A. (2012). Novel forests maintain ecosystem processes after the decline of native tree species. Ecological Monographs, 82, 221–228.

Morton, J.W. (1977). Ecological effects of dredging and dredge spoil disposal: a literature review (Report No. 94). Technical Paper.

Nickerson, K. & Flory, S.L. (2015). Competitive and allelopathic effects of the invasive shrub Schinus terebinthifolius (Brazilian peppertree). Biological Invasions, 17, 555–564.

Niku, J., Brooks, W., Herliansyah, R., Hui, F.K.C., Taskinen, S. & Warton, D.I. (2019). Efficient estimation of generalized linear latent variable models. PLoS ONE, 14, e0216129.

Novomestky, F. & Kelly, S. (2022). Matrixcalc: Collection of Functions for Matrix Calculations.

Oberle, B., Breithaupt, J., McTigue, A. M., Stryker, R., Cladas, M., Raulerson, G., & Young, D. F. (2022). Restoration objectives create surface carbon cycle trade-offs in coastal habitats. Restoration Ecology, 30(4), e13563.

Oberle, B., Cole, P.O., Frank, G., Gates, A., Hall, B., Harvey, D., et al. (2023). Multilevel allometric growth equations improve accuracy of carbon monitoring during forest restoration. Trees, Forests and People, 14, 100442.

Plummer, M., Stukalov, A. & Denwood, M. (2022). rjags: Bayesian Graphical Models using MCMC. R package version 4.

Polzer, E.L. & Wilcox, D.A. (2022). Testing restoration methods for Lake Ontario wetlands at a wetland scale. Journal of Great Lakes Research, 48, 756–767.

Potgieter, L.J., Richardson, D.M. & Wilson, J.R.U. (2014). *Casuarina*: biogeography and ecology of an important tree genus in a changing world. Biol Invasions, 16, 609–633.

R Core Team. (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Radabaugh, K.R., Moyer, R.P., Chappel, A.R., Powell, C.E., Bociu, I., Clark, B.C., et al. (2018). Coastal Blue Carbon Assessment of Mangroves, Salt Marshes, and Salt Barrens in Tampa Bay, Florida, USA. Estuaries and Coasts, 41, 1496–1510.

Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. J. Stat. Soft., 48.

Sapsford, S.J., Brandt, A.J., Davis, K.T., Peralta, G., Dickie, I.A., Gibson, R.D., et al. (2020). Towards a framework for understanding the context dependence of impacts of non-native tree species. Functional Ecology, 34, 944–955.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., et al. (2017). No saturation in the accumulation of alien species worldwide. Nat Commun, 8, 14435.

Simberloff, D. & Holle, B.V. (1999). Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions, 1, 21–32.

Simberloff, D. & Rejmanek, M. (Eds.). (2019). 100 of the World's Worst Invasive Alien Species: A Selection From The Global Invasive Species Database. In: Encyclopedia of Biological Invasions. University of California Press, pp. 715–716.

Vaccaro, L.E., Bedford, B.L. & Johnston, C.A. (2009). Litter accumulation promotes dominance of invasive species of cattails (Typha spp.) in Lake Ontario wetlands. Wetlands, 29, 1036–1048.

Vaughn, D.R., Bianchi, T.S., Shields, M.R., Kenney, W.F. & Osborne, T.Z. (2021). Blue Carbon Soil Stock Development and Estimates Within Northern Florida Wetlands. Front. Earth Sci., 9, 552721.

Figure Legends:

Fig. 1: Community by ecosystem interactions predict distinctive changes in biodiversity before and after experimental restoration. Community processes alone (**A**) predict that strong competition reduces native seedling percent cover and diversity before restoration, which recovers after reducing invasive biomass. Including ecosystem processes (**B**) via seedling-suppressing litter supports the prediction that native seedling recovery also requires litter removal. Community by ecosystem interactions (**C**), whereby litter facilitates some species while suppressing others, supports a prediction of distinctive seedling communities before restoration.

Fig. 2: Interspecific competition predominates in community interactions before experimental restoration as indicated by residual correlations from generalized latent variable mixed models of species biomass. Connection width is proportional to the cumulative residual correlations from all other species and size class categories and color indicates the direction and absolute strength of residual correlations. Outer tracks indicate the proportion contributed by each species and size class to 30 kg m^{-2} of aboveground biomass in 24 50 m^2 inventory plots.

Fig. 3: Litter facilitates dominance of *Cupaniopsis* seedlings. Simplified structural equation model illustrating hypothesized causal pathways among measured variables in boxes, with R^2 values below endogenous variables, and causal pathways illustrated as arrows with direction, strength and statistical significance indicated by color (magenta = negative, green = positive), standardized effect size and asterisks (**$p<0.01$,***$p<0.001$) respectively.

Fig. 4: Heterospecific litter enhances a germination advantage for the only invasive species present as a seedling in a disturbed mangrove. Lower sector sizes correspond to estimated annual survival probabilities for seeds on bare sand. Upper sector sizes correspond to aggregate effects of each species' litter on seedling survival. Arrow color corresponds to the direction of the pairwise litter effect with magenta decreasing and green increasing. Arrow width corresponds to the proportion of the total pairwise litter effects relative to the rate estimated for

bare sand. Litter sensitivity is calculated as the sum of absolute differences in survival probabilities for litter treatments relative to bare sand controls.

Fig. 5: Invasive species biomass removal significantly increases richness (A) and also removing mulch significantly increases seedling percent cover (B) in 42 0.25 m^2 monitoring plots measured before and after experimental restoration. Asterisks indicate statistical significance of paired *t*-tests (*p<0.05,***p<0.001).

549 **FIGURES**

550 **Fig. 1:**

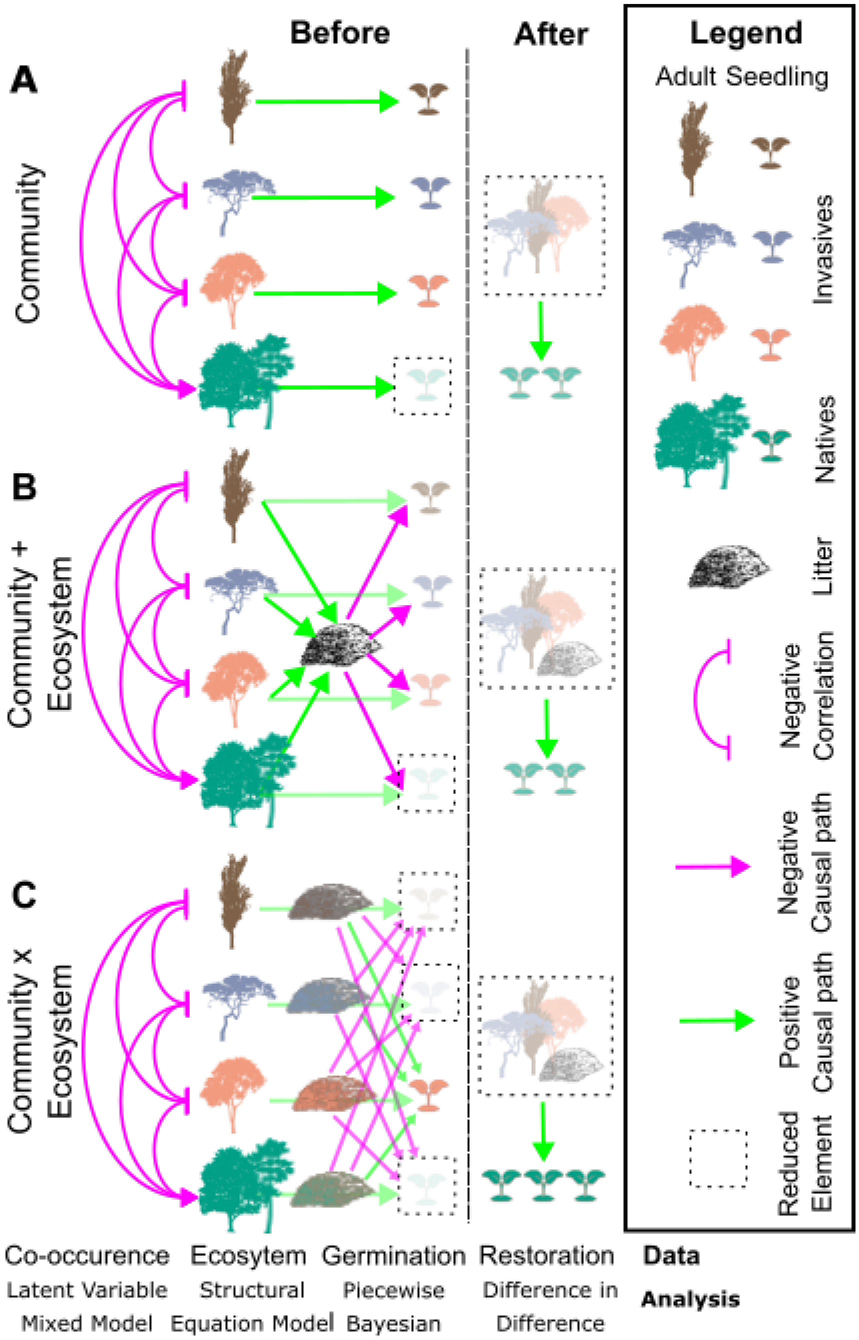

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Fig. 2:

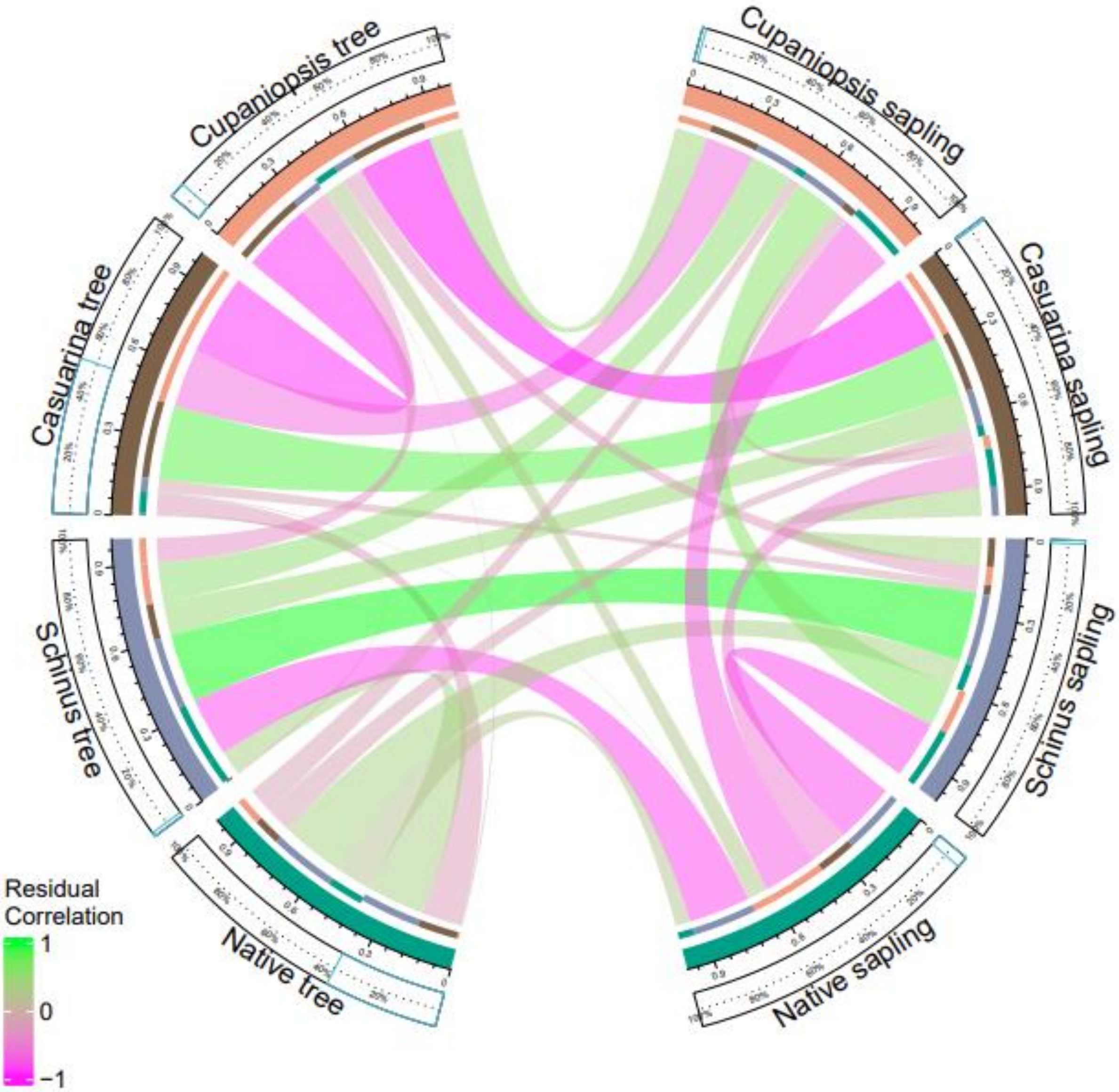

Cupaniopsis tree
Cupaniopsis sapling
Casuarina tree
Casuarina sapling
Schinus tree
Schinus sapling
Native tree
Native sapling
Residual Correlation
1
0
−1

Fig. 3:

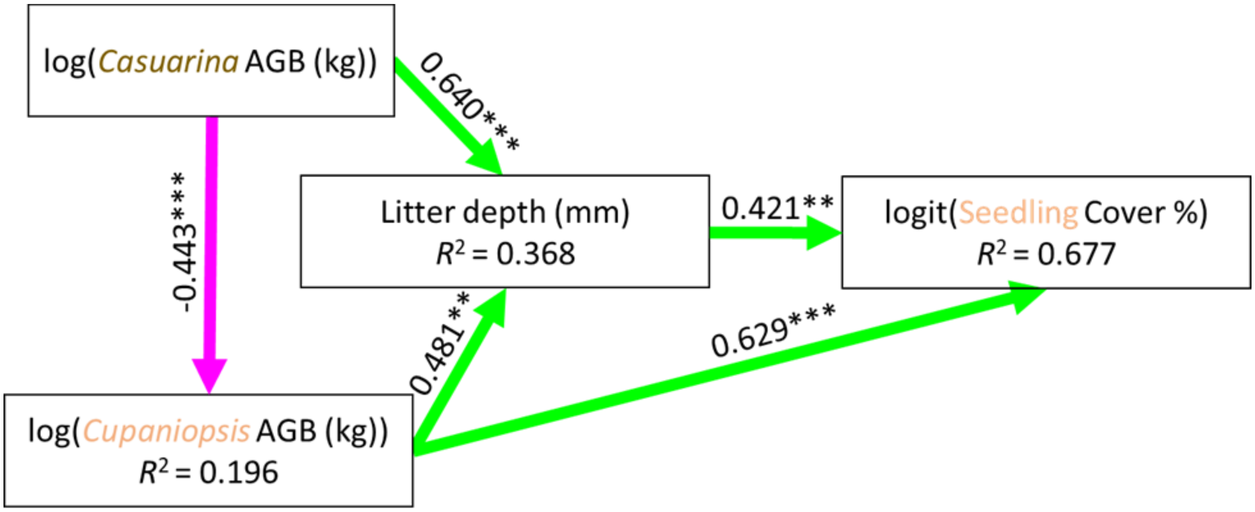
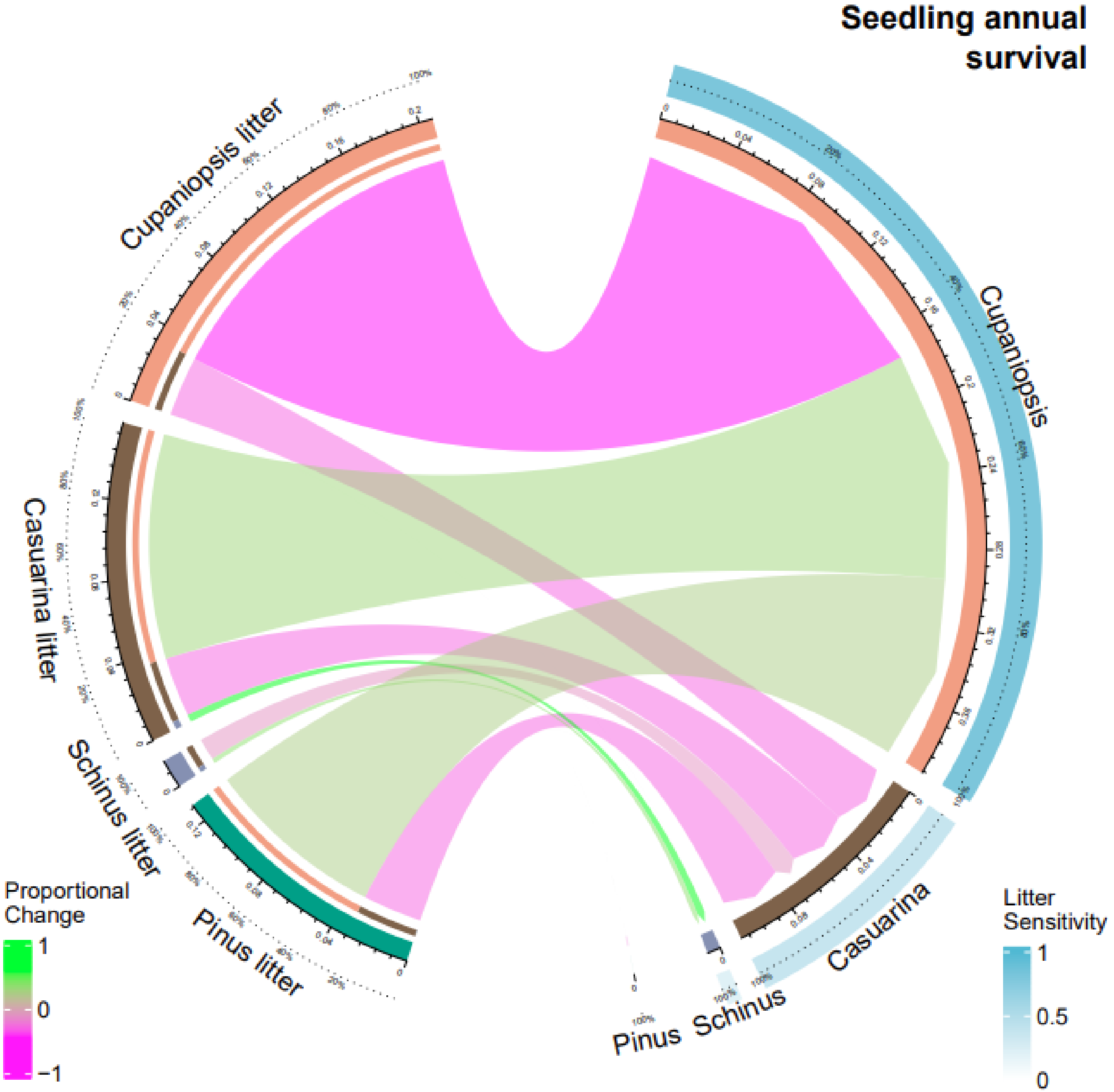
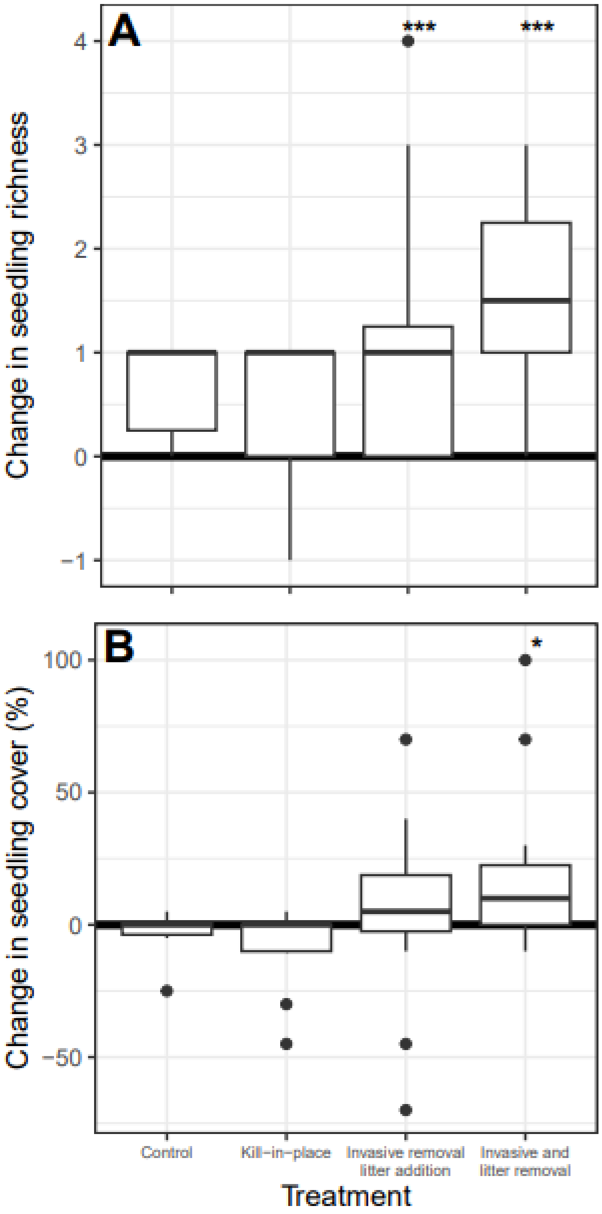

log(*Casuarina* AGB (kg))
0.640***
-0.443***
Litter depth (mm)
R^2 = 0.368
0.421**
logit(Seedling Cover %)
R^2 = 0.677
0.481**
0.629***
log(*Cupaniopsis* AGB (kg))
R^2 = 0.196

Fig. 4:


Seedling annual survival
Cupaniopsis litter
Casuarina litter
Schinus litter
Pinus litter
Cupaniopsis
Casuarina
Schinus
Pinus
Proportional Change
1
0
−1
Litter Sensitivity
1
0.5
0

566 **Fig. 5**:


A
Change in seedling richness
4
3
2
1
0
−1
***
***
B
Change in seedling cover (%)
100
50
0
−50
*
Control
Kill−in−place
Invasive removal litter addition
Invasive and litter removal
Treatment

567

ONLINE SUPPLEMENTARY INFORMATION

Table S1: Cumulative aboveground biomass (ABG) and abundance for trees (DBH > 7.5cm in 24 50 m^2 plots) and saplings (7.5 cm > DBH > 2 cm in 24 6.25 m^2 plots) before experimental restoration.

Species	Status	Tree ABG (kg)	Tree Abundance	Sapling ABG (kg)	Sapling Abundance
Casuarina equisitifolia	Invasive	17951	72	36	2
Cupaniopsis anacardioides	Invasive	1853	30	55.3	18
Schinus Terebinthifolia	Invasive	492	19	51.4	6
Avicennia germinans	Native	198	3	41.2	4
Conocarpus erectus	Native	4534	26	40.6	2
Forestiera segregata	Native	18.8	1	33.8	11
Guilandina bonduc	Native	0	0	9.51	1
Laguncularia racemosa	Native	80.6	3	22.9	4
Quercus virginiana	Native	8423	2	0	0
Rhizophora mangle	Native	0	0	18.8	2

Table S2: Bias-corrected Akaike Information Criterion (AICc) for generalized latent variable mixed models for aboveground biomass modelled as a Tweedie distribution for four species groups before restoration with soil variables measured at 20cm depth and 1-4 latent variables.

Environmental Variables	Latent Variables	AICc
None	1	1204.630
None	2	1192.353
None	3	**1176.571**
None	4	1191.508
Subsurface soil C:N, SBD	1	1216.580
Subsurface soil C:N, SBD	2	1203.892
Subsurface soil C:N, SBD	3	1209.461
Subsurface soil C:N, SBD	4	1224.797
Subsurface soil C:N	1	1200.526
Subsurface soil C:N	2	1187.705
Subsurface soil C:N	3	1205.791
Subsurface soil C:N	4	1199.470
Subsurface soil SBD	1	1213.886
Subsurface soil SBD	2	1204.071
Subsurface soil SBD	3	1194.022
Subsurface soil SBD	4	1206.212

Table S3: Posterior mean and 95%CI for seedling transition probabilities from pairwise germination experiments calculated over an annual (Yr1) or weekly (Wk) basis

Propagule	Litter	Yr1 seedling survival mean	Yr1 seedling survival 2.5%	Yr1 seedling survival 97.5%	Wk seed survival mean	Wk seed survival 2.5%	Wk seed survival 97.5%	Wk seed germination mean	Wk seed germination 2.5%	Wk seed germination 97.5%	Wk seedling survival mean	Wk seedling survival 2.5%	Wk seedling survival 97.5%
Casuarina	Control	0.1107	0.0007	0.8545	0.9322	0.9103	0.9514	0.0119	0.0042	0.0228	0.9586	0.8759	0.9969
Casuarina	*Casuarina*	0.0000	0.0000	0.0727	0.9273	0.9040	0.9473	0.0086	0.0019	0.0186	0.8229	0.6344	0.9530
Casuarina	*Schinus*	0.0688	0.0002	0.7968	0.8828	0.8429	0.9168	0.0221	0.0132	0.0362	0.9498	0.8485	0.9961
Casuarina	*Cupaniopsis*	0.0000	0.0000	0.1099	0.8584	0.8209	0.8912	0.0023	-0.0018	0.0103	0.6132	0.1647	0.9605
Casuarina	*Pinus*	0.0010	0.0000	0.1752	0.9000	0.8714	0.9248	0.0194	0.0086	0.0337	0.8763	0.7330	0.9681
Schinus	Control	0.0066	0.0004	0.0478	0.7788	0.6940	0.8463	0.1526	0.0988	0.2207	0.9079	0.8651	0.9430
Schinus	*Casuarina*	0.1312	0.0058	0.6920	0.6910	0.5296	0.8015	0.0789	0.0364	0.1417	0.9617	0.9032	0.9935
Schinus	*Schinus*	0.0861	0.0115	0.3285	0.7897	0.6792	0.8722	0.1787	0.1064	0.2776	0.9539	0.9189	0.9792
Schinus	*Cupaniopsis*	0.0056	0.0000	0.3597	0.8044	0.7310	0.8637	0.0361	0.0138	0.0679	0.9052	0.7698	0.9833
Schinus	*Pinus*	0.0041	0.0000	0.1848	0.7489	0.6413	0.8299	0.0593	0.0269	0.1051	0.8997	0.7987	0.9679
Cupaniopsis	Control	0.3917	0.0622	0.9361	0.9209	0.8862	0.9496	0.0651	0.0391	0.0965	0.9821	0.9446	0.9987
Cupaniopsis	*Casuarina*	0.6509	0.0881	0.9995	0.8535	0.7993	0.8997	0.1149	0.0744	0.1635	0.9918	0.9588	1.0000
Cupaniopsis	*Schinus*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Cupaniopsis	*Cupaniopsis*	0.0356	0.0002	0.5706	0.8857	0.8411	0.9231	0.0901	0.0569	0.1307	0.9379	0.8463	0.9894
Cupaniopsis	*Pinus*	0.5740	0.0781	0.9994	0.8788	0.8318	0.9184	0.1047	0.0681	0.1489	0.9894	0.9489	1.0000
Pinus	Control	0.0000	0.0000	0.0006	0.7046	0.5773	0.8021	0.2520	0.1642	0.3657	0.8109	0.7425	0.8710
Pinus	*Casuarina*	0.0000	0.0000	0.0000	0.9208	0.8863	0.9491	0.0615	0.0366	0.0920	0.5877	0.4016	0.7594
Pinus	*Schinus*	0.0000	0.0000	0.0000	0.7896	0.6795	0.8728	0.2025	0.1221	0.3099	0.3180	0.1729	0.4801
Pinus	*Cupaniopsis*	0.0000	0.0000	0.0000	0.9156	0.8797	0.9454	0.0591	0.0344	0.0904	0.6387	0.4900	0.7754
Pinus	*Pinus*	0.0000	0.0000	0.0000	0.8625	0.8101	0.9064	0.0981	0.0617	0.1433	0.6304	0.4815	0.7659

Fig. S1: Soil bulk density (**A**) and C:N ratios (**B**) at 5 cm and 20 cm below the soil surface in 24 spoil mound monitoring plots prior to experimental restoration.

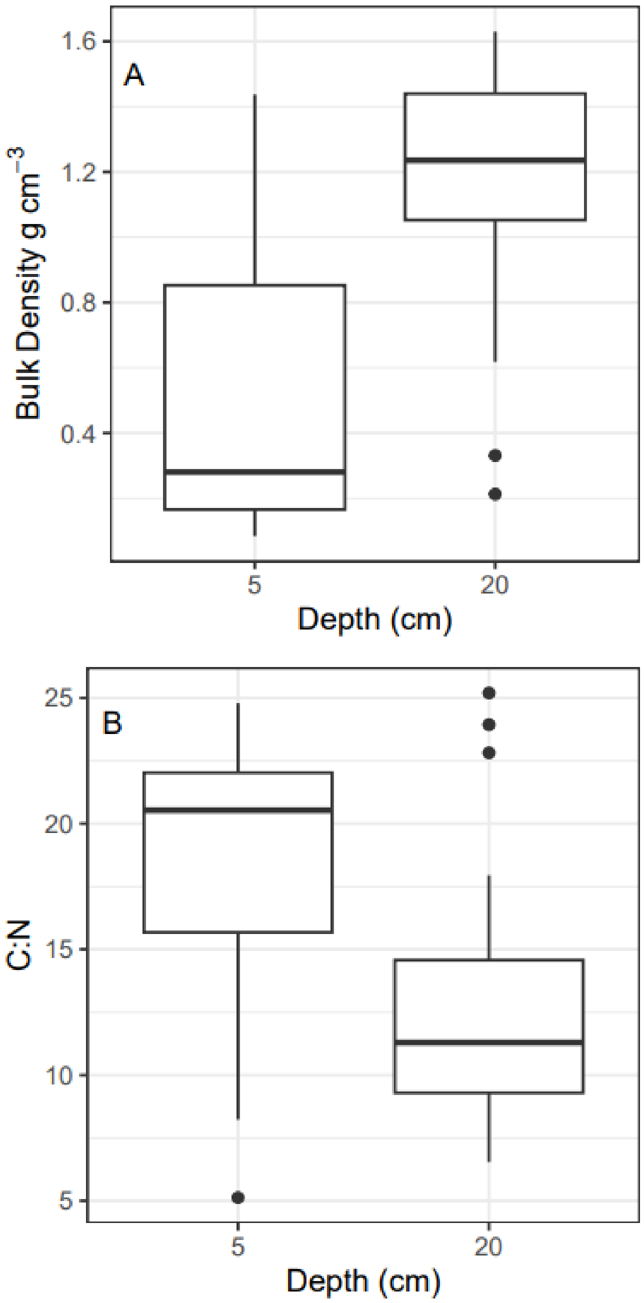


Fig. S2: Competition between invasive trees maintains diversity among patches of uniform habitat. Results from the most adequate generalized latent variable mixed model represented by (**A**) residual correlations between all species group by size class combinations where circle color indicates interaction direction and size corresponds to absolute value and (**B**) ordination of 24 monitoring plots with respect to the first two latent variables.

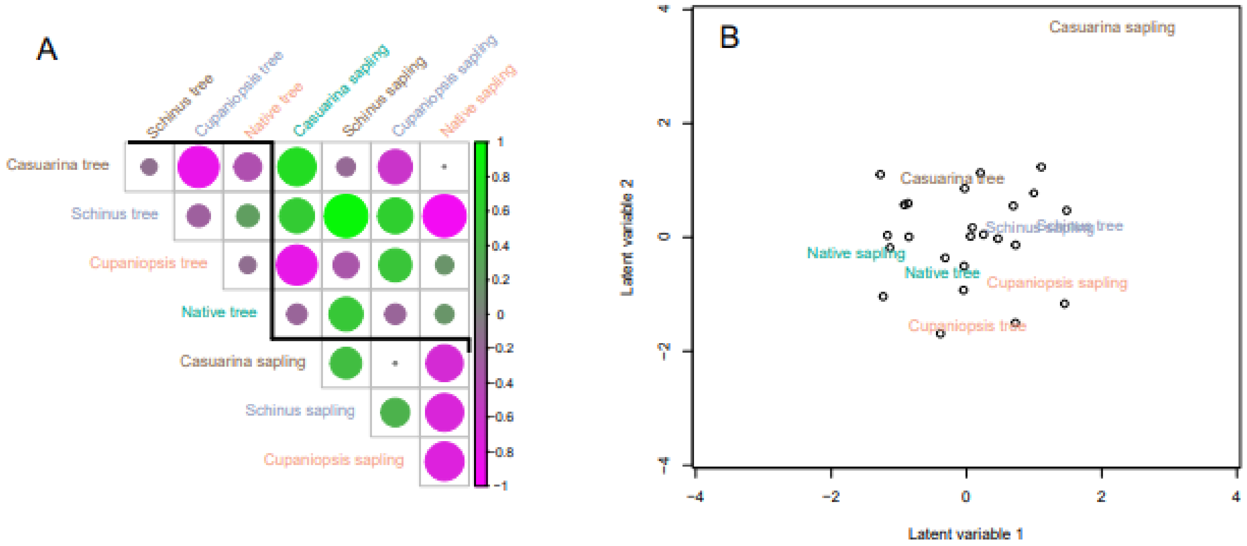


Fig. S3: Adventitious root emerging from *Cupaniopsis anacardioides* sapling shoot directly into duff (removed). Discoloration along the stem indicates the original height of the duff layer where the stem diameter is 6.2 cm.

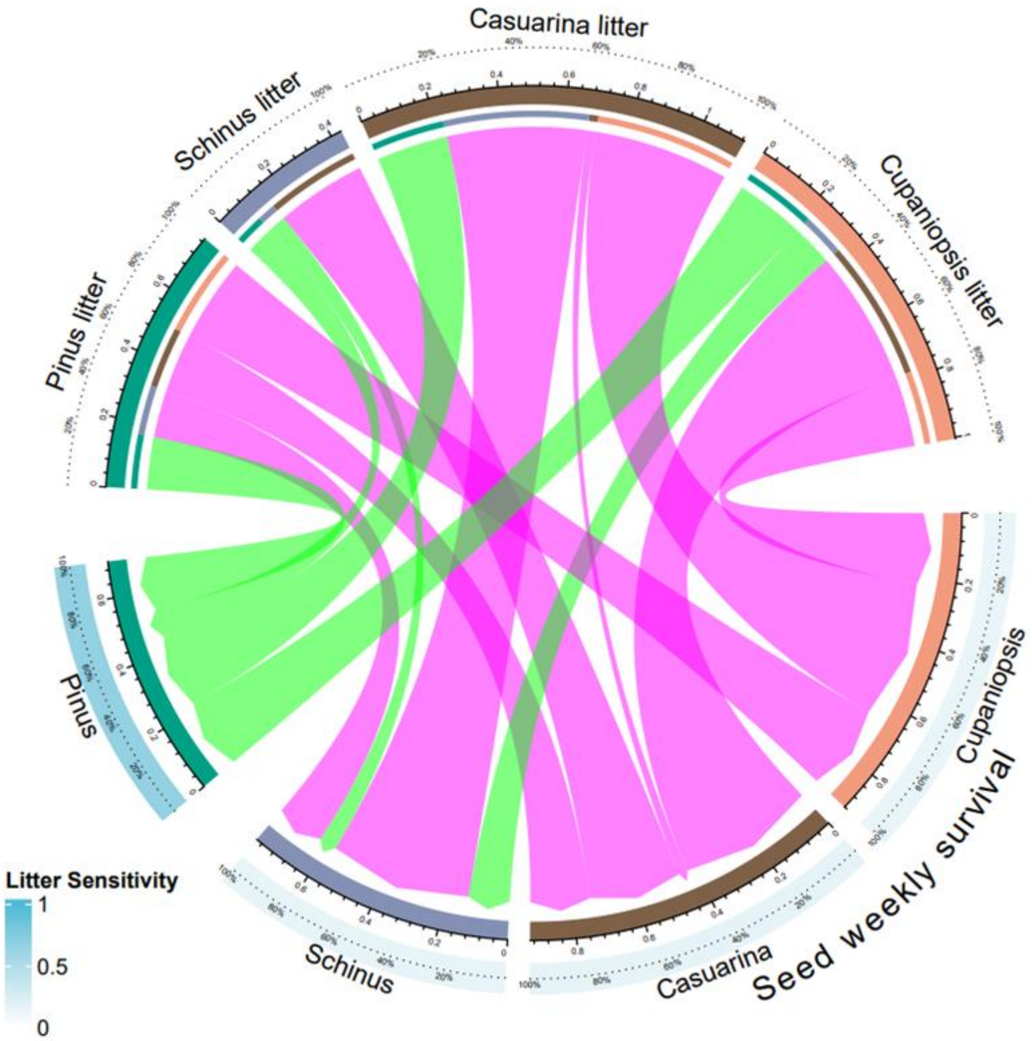


Fig. S3: Litter effects on weekly seed survival rates (i.e. Eq. S2) in pairwise microcosm experiments. Lower sector sizes correspond to estimated weekly survival probabilities for seeds on bare sand. Upper sector sizes correspond to aggregate effects of each species' litter on seed survival. Arrow color corresponds to the direction of the pairwise litter effect with magenta decreasing and green increasing. Arrow width corresponds to the proportion of the total pairwise litter effects relative to the rate estimated for bare sand. Litter sensitivity calculated as the sum of absolute differences in survival probabilities for litter treatments relative to bare sand controls.

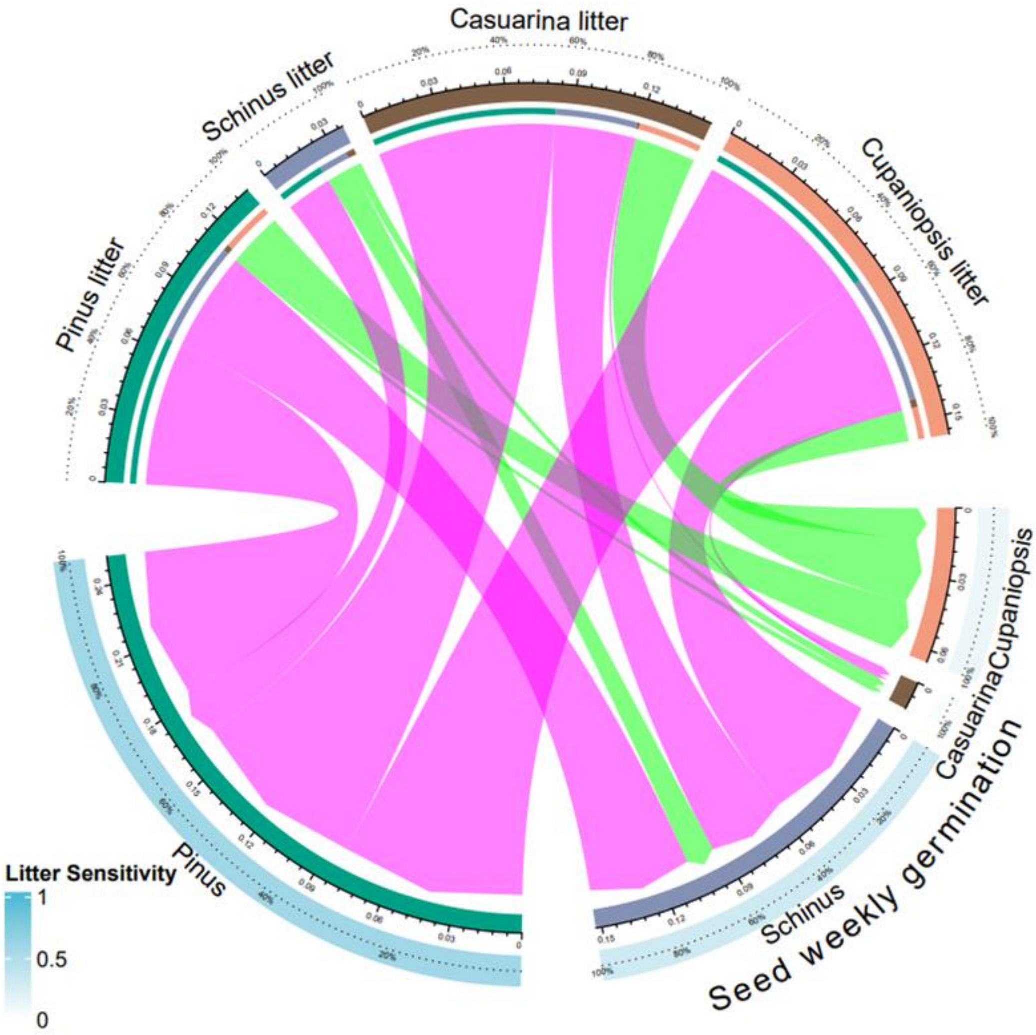


Fig. S4: Litter effects on weekly germination rates (i.e. Eq. S4) in pairwise microcosm experiments. Lower sector sizes correspond to estimated weekly germination probabilities for seeds on bare sand. Upper sector sizes correspond to aggregate effects of each species' litter on germination rates. Arrow color corresponds to the direction of the pairwise litter effect with magenta decreasing and green increasing. Arrow width corresponds to the proportion of the total pairwise litter effects relative to the rate estimated for bare sand. Litter sensitivity calculated as the sum of absolute differences in survival probabilities for litter treatments relative to bare sand controls.

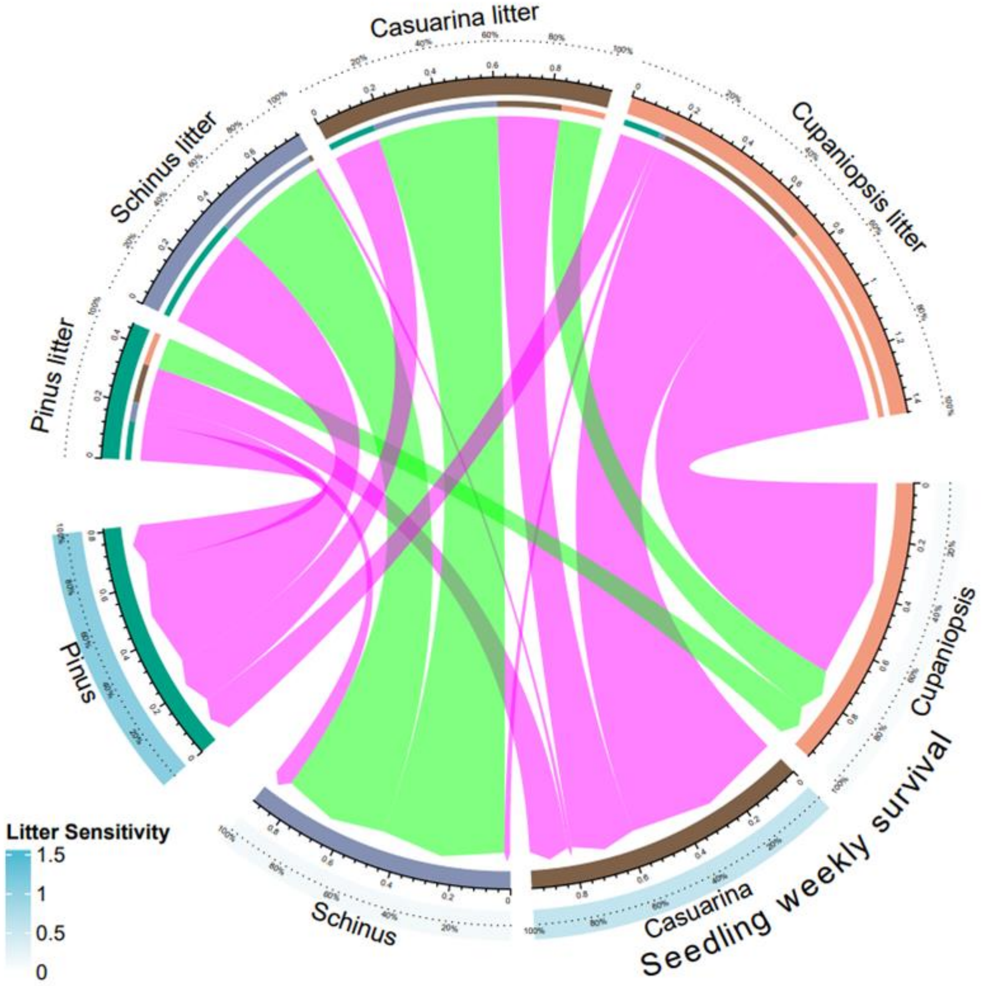


Fig. S5: Litter effects on weekly seedling survival rates (i.e. Eq. S5) in pairwise microcosm experiments. Lower sector sizes correspond to estimated weekly survival probabilities for seedlings on bare sand. Upper sector sizes correspond to aggregate effects of each species' litter on seedling survival. Arrow color corresponds to the direction of the pairwise litter effect with magenta decreasing and green increasing. Arrow width corresponds to the proportion of the total pairwise litter effects relative to the rate estimated for bare sand. Litter sensitivity calculated as the sum of absolute differences in survival probabilities for litter treatments relative to bare sand controls.

Supplementary Methods:

Piecewise Bayesian model for estimating seed to seedling transition probabilities from germination time series.

To parameterize ***R*** (Eq. 1) for each seed by litter combination, we used a piecewise Bayesian approach. To estimate the elements of $\boldsymbol{s}_{\boldsymbol{\tau}\_\delta}$, we used final state assessments as living, dead or germinated, and assumed that the transition probabilities were constant for the duration of the experiment. Under these assumptions, the counts of seeds in each state, $\boldsymbol{s}_{\mathbf{obs\_dur\_k}}$, in each dish, *k*, for the duration of the experiment in days, *dur*, follows a multinomial likelihood of the form:

$$\boldsymbol{s}_{\boldsymbol{obs}\_\mathbf{dur}\_\boldsymbol{k}} \sim \mathrm{multinomial}\left(\boldsymbol{s}_{\boldsymbol{\tau}\_dur}, \mathrm{n}_k\right) \qquad \text{(Eq. S1)}$$

Where n_k is the total number of viable seeds added to dish *k*. To facilitate interpretation, we rescaled the transition probabilities to weekly intervals using the three relations:

$$s_{\sigma\_week} = s_{\sigma\_dur}{}^{\frac{7}{dur}} \qquad \text{(Eq. S2)}$$

$$s_{\mu\_week} = \frac{s_{\mu\_dur}}{1 + s_{\sigma\_week} + s_{\sigma\_week}{}^{2} + \ldots s_{\sigma\_week}{}^{\left\lfloor\frac{dur}{7}\right\rfloor - 1} + s_{\sigma\_week}{}^{\left(\left\lfloor\frac{dur}{7}\right\rfloor - 1 + \frac{dur\ modulo\ 7}{7}\right)}} \qquad \text{(Eq. S3)}$$

$$s_{\gamma\_week} = 1 - s_{\sigma\_week} - s_{\mu\_week} \qquad \text{(Eq. S4)}$$

For estimating the elements of $\boldsymbol{g}_{\tau\_\delta}$, we analyzed the time-series observations of seedling states, assuming that seedlings could not germinate and die in the same interval and that survival probabilities were constant. Under these assumptions, the number of newly dead seedlings in interval *i* in plate *k*, follows a binomial distribution:

$$g_{dead\_obs\_i\_k} \sim \text{binomial}\left(1 - g_{\sigma\_\text{week}}{}^{\frac{int\_i\_\text{k}}{7}}, g_{alive\_obs\_i-1\_\text{k}}\right) \quad \text{(Eq. S5)}$$

Where e $g_{dead\_obs\_i\_k}$ is the sequence of newly dead seedlings created from counts of total dead seedlings minus the count of total dead seedlings in the preceding interval on plate *k*, int_i_k is a sequence of interval lengths in days, $g_{alive\_obs\_i\_k}$ is a sequence of living seedling counts, and the exponent for the survival probability converts transitions to weekly equivalents. In 11 of 3210 sequential observations, seedlings appeared to germinate and die within the same interval, violating an assumption of the model. We adjusted these observations to maintain the germination event in the recorded interval and postpone the mortality event to the subsequent interval. We estimated transition probabilities for every seed by litter combination, including bare sand, in a Bayesian context using vague conjugate priors for the multinomial and binomial probabilities, Dirichlet(1,1,1) and beta(0.5,0.5), respectively. We calculated the posterior distributions in the software “rjags” (Plummer et al. 2022) and represented uncertainty using posterior 95% CI.