Species richness accelerates marine ecosystem restoration in the Coral Triangle

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Ecosystem restoration aims to restore biodiversity and valuable functions that have been degraded or lost. The Coral Triangle is a hotspot for marine biodiversity held in its coral reefs, seagrass meadows, and mangrove forests, all of which are in global decline. These coastal ecosystems support valuable fisheries and endangered species, protect shorelines, and are significant carbon stores, functions that have been degraded by coastal development, destructive fishing practices, and climate change. Ecosystem restoration is required to mitigate these damages and losses, but its practice is in its infancy in the region. Here we demonstrate that species diversity can set the trajectory of restoration. In a seagrass restoration experiment in the heart of the Coral Triangle (Sulawesi, Indonesia), plant survival and coverage increased with the number of species transplanted. Our results highlight the positive role biodiversity can play in ecosystem restoration and call for revision of the common restoration practice of establishing a single target species, particularly in regions having high biodiversity. Coastal ecosystems affect human well-being in many important ways, and restoration will become ever more important as conservation efforts cannot keep up with their loss.

biodiversity | Coral Triangle | restoration | seagrass | species richness

The exceptional marine biodiversity in the Coral Triangle (1, 2) provides fisheries resources for more than 350 million humans, many of whom live in the coastal zone in close proximity to coral reefs, seagrass meadows, and mangrove forests (3, 4). In addition to fisheries resources, these coastal ecosystems provide other valuable ecological services and functions, including coastal defense against flooding; habitat and food for marine species of conservation concern, such as sharks, dugongs, and sea turtles; and carbon storage (5–7). These important functions are put at risk as coral reefs, seagrass meadows, and mangroves decline due to unrelenting coastal development in the region; fisheries overexploitation and destructive practices; and ocean warming and acidification associated with global climate change (4, 8–12). To date, conservation efforts have focused primarily on coral reef fisheries management and establishment of marine protected areas (10, 13–15). These conservation measures are critically important, but they do not address mitigation of coastal ecosystems already degraded or lost; thus, ecosystem restoration is an important complement to fisheries management and habitat protection (15). Despite this obvious need, restoration of coral reefs, seagrass meadows, and mangroves has not advanced very far in the Coral Triangle (16, 17). Of this ecosystem triad, seagrasses in particular have been understudied (18–20), despite their importance for providing food and livelihoods (21, 22). Seagrasses straddle mangroves lining the shore and coral reefs farther offshore, linking these interdependent ecosystems in an integrated coastal seascape wherein the mangroves and seagrasses intercept terrestrially derived sediments, nutrients, and pathogens, reducing their loading on sensitive corals, and provide nursery habitats for coral reef fisheries species (23–27).

The Coral Triangle hosts more seagrass species than virtually anywhere else on earth, and across the region they naturally grow together in mixed species communities (28). We investigated the role of this biodiversity in ecosystem restoration, which here refers to the deliberate establishment of a founder community. Biodiversity often determines ecosystem function and resilience (29, 30), but its role in restoration is relatively unexplored in both marine and terrestrial environments (17, 31–35). Species diversity tends to be a goal, rather than a means, of restoration, although intraspecific genetic diversity has been examined for seagrass, salt marsh, and mangrove restoration, which have focused largely on single species (36–43) (Results).

Planting monocultures in coastal vegetation restoration practice and research emanated in part from targeting a conspicuous or "climax" species, the most impacted or stress-tolerant species, or one desired for silvaculture, even in tropical regions where species grow intermixed naturally (44–49). Planting monocultures of the mangrove Rhizophora has led to failed projects (50, 51), yet the practice has not evolved (52). As part of our study, we confirmed the pervasive monospecific approach for seagrass, mangroves, and salt marshes by taking advantage of recent reviews of restoration practice and research (17, 43, 51, 53) (Results).

The monospecific rationale is understandable, but at odds with the idea that biodiversity often confers ecological benefits. Species diversity can enhance ecosystem function and services in established (29, 30), but also nascent, communities, as in a seminal study of a salt marsh restoration (54). Species diversity in the founding community can set the pace of restoration through negative

Significance

The exceptional diversity of species in the coral reefs, seagrass meadows, and mangrove forests of the Coral Triangle and the many ecological functions and benefits to humans they provide have made them a high priority for conservation and fisheries management. Nevertheless, their degradation continues and calls for effective restoration. In an experimental restoration, we demonstrated that planting mixtures of diverse seagrass species improves their overall survival and growth and thus the trajectory toward successful restoration. Incorporating species diversity into restoration heralds a shift in practice from establishing a single founder species, and recognizes the widely documented positive effects that biodiversity has on ecosystem function and services. Biodiversity is often a restoration goal, but it also promises a means to improve success.

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(inhibition, competition) or positive (facilitation) interactions of one or more species with others, as in succession (55–59). Concern about both intra- and interspecific competition helped shape restoration practice in aquatic ecosystems (50, 60–62). However, facilitative interactions could benefit restoration early on or in fluctuating or stressful environments (34, 61), as demonstrated intraspecifically for a salt marsh species (62). Interspecific facilitation has been proposed to spread predation risk (52) or hasten colonization of a climax target species, i.e., succession could be "compressed" by planting a single nurse or pioneer species (50, 63–65). However, empirically testing the effect of species richness on restoration trajectories has remained a research gap highly relevant to restoration goals and costs (17, 66) (*Results*), which is particularly true in the Coral Triangle where much is at stake environmentally and socially.

To test the effect of seagrass species richness on the restoration trajectory, we conducted a field experiment using a proven restoration technique (67). We transplanted six common Indo-Pacific seagrass species (*Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Syringodium isoetifolium*, *Halodule uninervis*, *Halophila ovalis*) of ~15 occurring in the Coral Triangle (28), at four species richness levels (monocultures, two, four, and five species). We randomly drew unique species combinations for replication at the higher richness levels (68) (Fig. 1 *A* and *B* and

Tables S1 and S2). To assess differences in early restoration trajectories, we analyzed the survivorship of the initial transplants and their collective rate of expansion or contraction (percent cover) for more than a year.

Results

The success of the seagrass transplantations improved with the number of species planted, indicating that species richness can play a positive role in restoration. Both survivorship (Fig. 2) and the rate of change in percent cover (Fig. 3) increased with species richness (survival: Kruskal–Wallis $\chi^2 = 7.88$, $P = 0.024$, df = 3; percent cover: GLM, $F_{1,30} = 5.991$, $P = 0.021$), i.e., overyielding occurred (68–71). We also examined the variability in survival and change in cover as a measure of stability (72). Although the variances were homogeneous, i.e., they did not differ across the richness levels (survival Levene's $F = 0.904$, $P = 0.452$, cover Levene's $F = 1.81$, $P = 0.169$), the coefficients of variation revealed that monoculture survival, and possibly cover, was more variable (theoretically less stable) when contrasted against all mixtures (GLM survival $F_{1,28} = 6.879$, $P = 0.014$; cover $F_{1,28} = 3.055$, $P = 0.091$).

Positive species richness effects are typically attributed at least statistically to either the random inclusion of a high-performing species or richness itself through complementation or facilitation among species, although these mechanisms are not exclusive

Fig. 1. Transplanting seagrasses using SCUBA (*A*), a mixed-species plot posttransplantation (*B*) (*Enhalus*, *Cymodocea*, *Syringodium*, *Halodule*), and disturbances of plots by algae (*C*) and marine debris (*D*). Photos courtesy of D. Trockel, University of California, Davis, CA (*A*), J.M.A. (*B*), C.S. (*C*), and K. DuBois, University of California, Davis, CA (*D*).
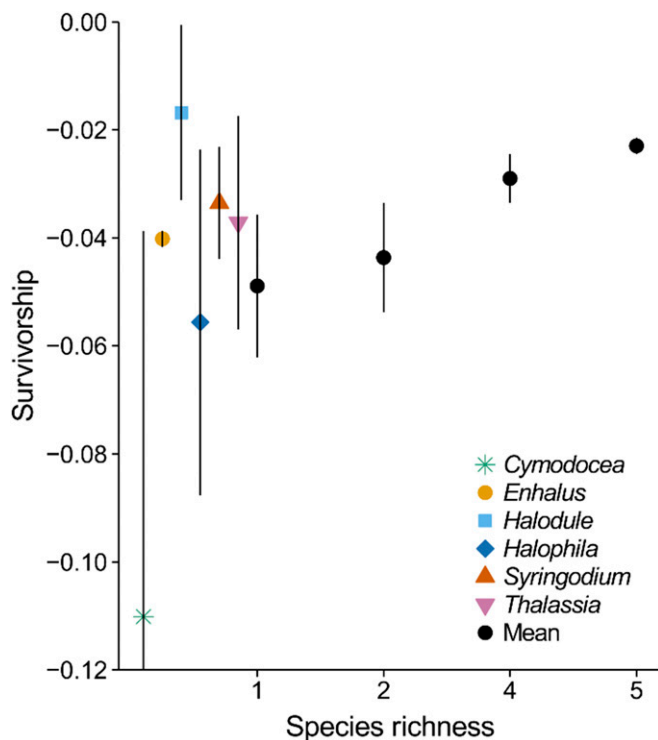
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Fig. 2. Species richness and restoration trajectories: survivorship increased with species richness ($\chi^2 = 7.88$, $P = 0.024$, df = 3). Mean, SE bars, $n = 6$ monocultures and five-species combinations, $n = 10$ two- and four-species mixtures; $n = 32$ assemblages. Individual species did not differ ($\chi^2 = 3.68$, $P = 0.597$, df = 5), mean and SE bars, $n = 2–4$.

(73–75). In our experiment, partitioning the variance pointed to the random inclusion of a high-performing species (species identity, sampling, selection effect, or nontransgressive overyielding), which necessarily would be in most of the five-species assemblages (68–71) (ω^2; Table 1). Although *Halodule uninervis*, which attained the highest mean survival and increase in cover (Figs. 2 and 3 and Tables S1 and S2), was the most likely candidate for the identity effect, we detected no differences in survival (Kruskal–Wallis $\chi^2 = 3.68$, $P = 0.597$, df = 5) or the rate of change in cover ($F_{5,10} = 2.41$, $P = 0.111$) among species grown in monoculture. Despite no monoculture differences (68), we calculated commonly reported log response ratios (70, 71) to compare the five-species mixtures to the average monoculture and to *Halodule*. These ratios also supported an identity effect of including *Halodule*. The five-species mixtures survived better than the average monoculture (non-transgressive overyielding, $LR_{mean} = 0.0009$, two-sided $t = 16.576$, $P < 0.0001$, df = 5) but not better than *Halodule* (transgressive overyielding, $LR_{max} = -0.0002$, two-sided $t = -4.00$, $P = 0.010$, df = 5; Tables S1 and S2). The cover in the five-species mixtures increased faster than the average monoculture ($LR_{mean} = 0.034$, two-sided $t = 3.436$, $P = 0.019$, df = 5) but not faster than *Halodule* ($LR_{max} = -0.026$, two-sided $t = -2.645$, $P = 0.046$, df = 5). Neither *Halodule* nor any other species took over the mixtures, just as they naturally grow together (28) (Tables S3 and S4). Having replicated each unique assemblage, we contrasted changes in cover with and without *Halodule* among all mixtures or only the four- plus five-species mixtures and were unable to document differences (Tables S3 and S4). Altogether, the results could indicate a possible richness effect not captured by some of the statistics (68, 73–75).

Our experiment contrasts strongly with much restoration-oriented practice and research. Restoration databases (17, 42, 51, 53) confirmed our collective experience that monocultures are the norm in both restoration practice and research (Dataset S1).

Of 253 seagrass, mangrove, and salt marsh studies, we identified 71 (28%) in which multiple species were actually planted in the field. Most of the rest were temperate studies where seagrass and salt marsh species effectively form monocultures. Of the 71 applicable studies, 30 (42%) reported planting species in mixtures in at least some part of the study. Seagrass species were mixed in only five of 29 studies (17%). Nineteen of 36 mangrove studies (53%) included species mixtures; however, *Rhizophora* composed 97% of the mixtures in 10 of these studies (51). Of the six applicable salt marsh studies of 42 total, species were planted in mixtures but the species richness effect was tested in only one (54, 76). Across systems, species richness was not a factor in the design of nearly all of the multispecies plantings (Dataset S1).

Discussion

Establishing a diverse founder community holds promise for enhancing restoration of seagrasses, where efforts have focused largely on a single species (48, 49), and coastal vegetation in general (Dataset S1). The mechanisms underlying the seagrass diversity effect are hypothetical, because supporting evidence in the form of ω^2, log ratios, and the like are merely statistical proxies for the ecological interactions occurring among species (68–75). We found evidence for and against *Halodule uninervis* as driving better performance in the mixtures. Although ω^2 points to *Halodule*, we could not document differences between mixtures with or without it, or among monocultures, and it did not dominate the plots or the naturally diverse bed (Tables S3 and S4).

Ecologically, facilitative interactions and niche partitioning to reduce competition could have been operating as the seagrasses established and grew, along with identity (selection) effects (73–75). Early facilitation followed by niche partitioning and continued coexistence is reasonable given the diverse morphologies
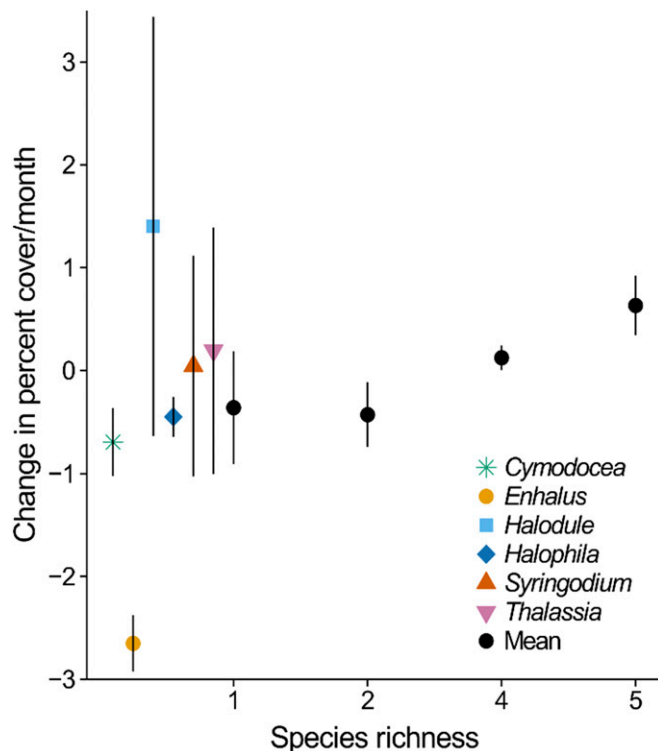

Fig. 3. Species richness and restoration trajectories: rate of change in percent cover increased with species richness ($F_{1,30} = 5.99$, $P = 0.021$). Mean, SE bars, $n = 6$ monocultures and five-species combinations, $n = 10$ two- and four-species mixtures; $n = 32$ assemblages. Individual species did not differ ($F_{5,10} = 0.894$, $P = 0.521$), mean and SE bars, $n = 2–4$.

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Table 1. Seagrass species diversity vs. identity effect sizes (ω^2)

Effect	SS	df	MS	P	ω^2	η^2	R^2
Model	0.0873	86	0.0028	0.0067	0.2892	1.000	0.550
Diversity	0.0013	1	0.0873	0.0001	0.0002	0.008	
Identity	0.0860	30	0.0029	0.0061	0.2890	0.539	
Error	0.0723	55	0.0013			0.453	
Total	0.1596						

Partitioning of variance into species diversity and identity effects (effect size ω^2) on changes in percent seagrass cover for 32 unique replicated species assemblages (Table S2). Effects of species richness vs. identity on changes in percent seagrass cover over time (linear regression coefficients) were partitioned through orthogonal planned contrasts of mixed species vs. single species (69). η^2 is the proportion of the total variance attributable to each effect, R^2 is proportion of the variance explained by the model.

and growth strategies within Indo-Pacific seagrasses (77, 78). For example, small, shallow-rooted species (e.g., *Halodule uninervis*, *Halophila ovalis*) colonize quickly and stabilize sediments, allowing nutrient pools to build by minimizing resuspension, thus facilitating succession (58, 79, 80). These species can then coexist within canopies of taller, slow-growing species such as *Enhalus acoroides*, which has roots extending ≥20 cm into the sediments. By layering their roots (79), seagrasses can partition sediment nutrients (58), thus alleviating competition as density increases. Taller canopies shade and potentially reduce photoinhibition to facilitate smaller, more-sensitive species (81). Mixtures of morphologically different species perhaps stabilize sediments and prevent uprooting and nutrient release better than single species (58, 82). Thus, mixtures could more fully utilize nutrients and light, leading to enhanced overall seagrass production (77) and potentially to higher animal diversity (83–85). This scenario is in line with the positive biodiversity effects demonstrated in many studies (29, 30, 68–71), and could imply that multispecies restoration efforts might perform better based not only on plant survival and cover but also on the ecosystem functions they provide (e.g., stabilizing sediments).

Regardless of the mechanisms for its effect, species richness clearly had a positive influence on the restoration trajectory (Figs. 2 and 3). Understanding the biological basis for the richness effect requires going beyond the statistical indicators and investigating the potential mechanism(s) proposed above. Without detailed mechanistic information, there is good reason to include multiple species in restorations of diverse communities when the best-performing species cannot be definitively identified, as in this study, and particularly in tropical regions where species coexist naturally.

Diverse transplantations certainly did better, but overall survival was low and cover increased slowly, which is typical in seagrass restorations and highlights a critical restoration issue (43). Small chronic disturbances to our plots, which were close to an inhabited shoreline, undoubtedly contributed to a slow restoration trajectory. The plots suffered from boat traffic and anchoring, trampling, mariculture installations, smothering by marine debris and sediments, and algal overgrowth, presumably stimulated by sewage inputs in the absence of a sanitation system on the island (Fig. 1 *C* and *D*). However, transplants were not destructively cropped by herbivores; sea urchins were almost absent from our study site, and we observed herbivorous fishes feeding primarily on algal epiphytes and less directly on seagrasses. Anthropogenic disturbances to seagrasses are not unique to Coral Triangle locales (6, 11, 12, 17, 19, 23, 28, 43), but the attention and resources to address them lag behind coral reef and mangrove conservation and management efforts (4, 18–20). Managing human disturbances in the Coral Triangle clearly will be necessary for the ultimate success of restoration, but meanwhile a speciose founding community offers good results in the face of such disturbances. It could very well be that the species richness effect is most evident in disturbed

habitats, but verification awaits experiments deployed across a disturbance gradient.

Given the exceptional biodiversity in the Coral Triangle (1, 2) and the grave threats to its coastal ecosystems and human dependence on them (3, 4, 8, 9, 21, 22), it is imperative to begin restoration efforts in earnest to complement the existing focus on fisheries management and habitat conservation (12–15), reconnect broken linkages in the seascape (24–27), and capture and store carbon (86). Diverse founding communities can accelerate the pace of seagrass restoration, a finding that should also be tested explicitly in other ecosystems (17, 51, 53) (Dataset S1). Biodiversity is not only critical to ocean-dependent peoples, but in itself provides a means to enhance restoration results.

Methods

Transplantation Design. We cut standardized seagrass transplants (15-cm rhizomes with terminal meristem, roots, and leaf shoots) of *Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Syringodium isoetifolium*, *Halodule uninervis*, and *Halophila ovalis*. We randomly drew unique assemblages at each richness level to control for species composition bias (68), yielding $n = 6$ monoculture treatments, $n = 10$ for two- and four-species, and $n = 6$ for five-species treatments (all possible combinations). We randomly assigned richness treatments to plots (60 × 60 cm, divided into 16 equal grids) separated by at least 1 m in which total transplant density ($n = 16$) was constant across treatments and the number of transplants of each species was equal within a plot. We standardized transplants by rhizome length and meristem, as done in restoration practice; therefore, biomass differences across species were part of random experimental error. Each monoculture and unique species combination was replicated ($n = 3$) except for the following replication errors during transplantation: *Halodule* ($n = 2$ plots), *Halophila* ($n = 4$), *Cymodocea* plus *Halophila* ($n = 2$), *Syringodium* plus *Halophila* ($n = 4$) (Tables S1 and S2). We anchored transplants in plots ($n = 96$) in unvegetated sediments in 2- to 3-m water depth within a seagrass bed growing behind the barrier reef on Pulau Badi (S 5°2′44.9–5°3′0.53′′, E 119°19′42.38′′–119°19′49.17′′), Spermonde Islands, South Sulawesi, Indonesia.

Our site was a typical Indonesian small island where inhabitants maintained traditional lifestyles and used the seagrass meadow for various purposes, including artisanal fishing, mariculture, anchorage, swimming, bathing, and waste disposal, including human. Our plots followed the seaward edge of the meadow where it abuts the reef at ~50 m from shore. We engaged the community with outreach about seagrasses and our experiment.

We monitored plots every 2 wk for the first 4 mo and then every 4 wk for a total of 19 times over 57 wk. We estimated survival as the proportion of the original transplants ($n = 16$) that were alive in each plot at each census. We estimated percent cover by taking a photograph from 1 m above each plot and summing the percent cover in 320 equal-sized subdivisions. Plots invaded by other species or lost were deleted from analyses, leaving $n = 87$ to analyze. Because rates of change encompass variation due to seasons, storms, and other disturbances, our analyses differ from biodiversity experiments that test effects at a single point typically at the end of an experiment, which might misrepresent the overall trajectory.

Data Analysis. Survival of the initial transplants declined exponentially (a typical survivorship curve), and we estimated survivorship as the slope of log (survival + 1) vs. time for each plot (average $R^2 = 0.81 \pm 0.15$ SD, $n = 87$ plots). We averaged the slopes of replicate plots ($n = 2–4$; see above) within each unique species assemblage ($n = 32$ monocultures and polycultures). The mean was used as the response variable in the nonparametric Kruskal–Wallis test for species richness effects (four levels) after transformations did not meet parametric assumptions (examination of residuals, normal Q-Q, and log-likelihood plots using R 3.0.1). Mean slopes of linear regressions of percent cover vs. time were also tested but in a general linear model; linear regressions were the best-fit function (higher R^2 compared with exponential functions except for a few plots). We compared species survivorship and changes in percent cover in monocultures using Kruskal–Wallis tests and within and among species using ANOVA (after examining residual plots using SYSTAT 11), respectively (68). We used Levene's test for homogeneity of variances and tested differences in coefficients of variation between all monocultures and all mixtures in a general linear model.

To assess whether the positive relationship between species richness and percent cover (overyielding) was likely due to species richness itself (diversity effect) or inclusion of a high-performing species in the mixtures (identity effect), we partitioned the total variance into the two effects (ω^2) by performing

Williams et al.

contrasts between the poly- and monocultures to yield the diversity effect, which then yields the identity effect when subtracted from the total sum of squares (69) (Table 1). Because ANOVA was inappropriate for survivorship, we could not partition the variance. We also calculated log response ratios as a commonly reported test of species richness effects (70, 71), acknowledging the challenge of ascribing mechanisms to overyielding effects (68, 73–75). These ratios compare species mixtures to species grown alone (monocultures). The nontransgressive overyielding log ratios, LR_{mean}, were calculated as the natural log of the ratios of the mean of replicate plots for each unique five-species mixture ($n = 6$) to the mean of all monocultures calculated from the average of the replicate plots for each species (Tables S1 and S2). The transgressive over-yielding log ratios, LR_{max}, were similarly calculated based on the averages of replicated plots of each unique five-species combination ($n = 6$) divided by the mean of the highest-performing species in monoculture (*Halodule uninervis*). We performed two-sided t tests (df = 5) to assess whether LR_{mean} and LR_{max} were different from zero. All data are provided in *Supporting Information*.

To assess multispecies approaches in seagrass, mangrove, and salt marsh restoration projects and experiments, we considered four restoration supplemental databases for mangroves, seagrass, and salt marshes (17), seagrasses (43), mangroves (51), and all ecosystems (53). After excluding freshwater and terrestrial studies (53), we culled all studies that potentially included >1 species. After reading all papers from this subset, we selected the applicable studies that provided information on transplantations or sowings in field restoration projects or experiments where the natural vegetation comprises multiple species (primarily tropical regions) and deleted those that did not, e.g., ones on natural recolonization, economic analyses, and general review papers without planting details. From the applicable papers, we calculated the percentage in which >1 species were actually planted mixed together in the field in at least some part of the study (Dataset S1).

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