RESTORATION ECOLOGY

Diverse and larger tree islands promote native tree diversity in oil palm landscapes

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In monoculture-dominated landscapes, recovering biodiversity is a priority, but effective restoration strategies have yet to be identified. In this study, we experimentally tested passive and active restoration strategies to recover taxonomic, phylogenetic, and functional diversity of woody plants within 52 tree islands established in an oil palm landscape. Large tree islands and higher initial planted diversity catalyzed diversity recovery, particularly functional diversity at the landscape level. At the local scale, results demonstrated that greater initial planting diversity begets greater diversity of native recruits, overcoming limitations of natural recruitment in highly modified landscapes. Establishing large and diverse tree islands is crucial for safeguarding rare, endemic, and forest-associated species in oil palm landscapes.

Many tropical forests are being converted into large-scale monoculture plantations, simplifying Earth's most biodiverse ecosystems. Southeast Asian forests are biodiversity hotspots (*1*) that have undergone large-scale conversion into plantations of African oil palm (*Elaeis guineensis* Jacq.). This has resulted in alarming losses of biodiversity, evolutionary history, and ecosystem function (*2*, *3*). To safeguard tropical biodiversity, it is imperative to protect remaining forests (*4*). It is also crucial to improve agricultural practices (*5*) and restore human-modified landscapes with seminatural habitats (*6*). Such measures can maintain some tropical biodiversity outside of protected areas while providing ecological, social, and economic benefits (*6*–*8*).

Recent research highlights the importance of viewing restoration approaches as a continuum from minimal, “passive” interventions (e.g., allowing natural plant regeneration) to more intensive, “active” interventions (e.g., tree planting or soil modification) that promote ecosystem recovery (*9*). Although natural regeneration can be applied at large scales (*10*, *11*), assisted restoration, such as tree planting, is a more resource-intensive method for promoting rapid forest regeneration (*9*, *12*, *13*). Tree islands, strategically planted patches of native vegetation within agricultural or degraded landscapes, offer a middle ground (fig. S1) (*14*–*16*).

Tree islands can facilitate seed dispersal by animals, improve microclimatic conditions, and promote succession without the need to plant large areas (*14*). Although these benefits may be restricted to local scales in oil palm plantations and other highly managed landscapes (*17*), landscape gains in biodiversity may be achieved when tree islands host distinct species (*18*). By reducing intensive management practices in the agricultural matrix surrounding tree islands (*5*), positive effects on ecosystem services, such as crop pollination and biological pest control, can be expected through spillover effects (*19*). When oil palm plantations are no longer economically viable, tree island expansion and coalescence over time (i.e., applied nucleation) can be envisaged to restore tropical forests (fig. S1). Despite previous studies showing that tree islands enhance species richness through natural recruitment (*17*), it remains unclear to which degree they also recover the evolutionary history (i.e., phylogenetic diversity) and functional attributes (i.e., functional diversity) of restored areas at local and landscape scales (*17*, *20*). This is crucial when aiming to restore diversity and ecosystem processes (*21*, *22*) and gain a mechanistic understanding of restoration, e.g., filtering of evolutionary clades or ecological strategies (*13*, *20*). Increasing functional and phylogenetic diversity in restored ecosystems also ensures long-term resilience and the ability to respond to environmental change (*23*–*25*).

The optimal tree island design for maximizing restoration outcomes remains debated (*14*, *17*). For instance, tree islands can be implemented with different planting diversities and sizes, and their effectiveness is likely influenced by landscape context (*14*, *16*, *26*). Locally, diverse tree plantings can enhance vegetation structural complexity, i.e., the three-dimensional distribution of plants within an ecosystem, owing to variations in ecological and architectural characteristics among trees (*27*). Higher vegetation structural complexity is associated with more heterogeneous environmental conditions (*27*). These conditions may promote the recruitment of species with complementary strategies, including shade-tolerant, slow-growing, or fast-growing pioneer species. By contrast, natural regeneration alone might favor the recruitment of functionally similar species, e.g., fast-growing species associated with open habitats, potentially limiting the recovery of functional diversity (*20*). We expect that tree island area affects recruiting diversity mainly because larger islands have higher colonization and lower extinction rates (as predicted by island biogeography theory) (*28*). Larger islands may provide more niches and reduce edge effects, promoting tree recruits with various ecological strategies. Owing to proximity to seed sources, areas closer to forests typically receive more seeds and experience higher plant colonization rates (*11*, *29*, *30*). Further, trees scattered in the agricultural matrix can act as stepping stones for seed dispersers (*31*). Understanding the relative importance of local versus landscape factors contributing to natural recruitment is therefore crucial for predicting successional trajectories and for guiding restoration efforts worldwide (*11*, *32*).

In this study, we assessed the recovery of taxonomic, phylogenetic, and functional diversity of native woody species at local and landscape scales in a large restoration experiment (EFForTS-BEE, Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems: Biodiversity Enrichment Experiment). In EFForTS-BEE, 52 tree islands were embedded in an industrial-scale oil palm plantation in Sumatra, Indonesia (*33*). Tree islands varied in planted tree diversity (zero, one, two, three, or six species, with zero corresponding to natural regeneration only) and area (25, 100, 400, or 1600 m^2) (Fig. 1B). Additionally, four 100-m^2 control plots were demarcated within conventional oil palm

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management areas, resulting in 56 plots. Before planting trees, 40% of oil palms were removed from treatment plots, except for the 5 × 5 m plots that were established in between oil palm rows (*33*). Weed control was stopped one year after establishment to allow for natural recruitment within the tree islands (see the supplementary materials for more details on the experimental design). We aimed to determine whether tree islands promote functional and phylogenetic diversity in addition to taxonomic diversity of woody plants (*17*) and to test whether the diversity of the native recruiting species is driven by local (i.e., planting diversity, tree island area, or soil properties) or landscape factors (i.e., distance to the nearest forest patch or number of scattered trees). We further assessed whether the effects of planting diversity and tree island area act indirectly through vegetation structural complexity and canopy dominance of

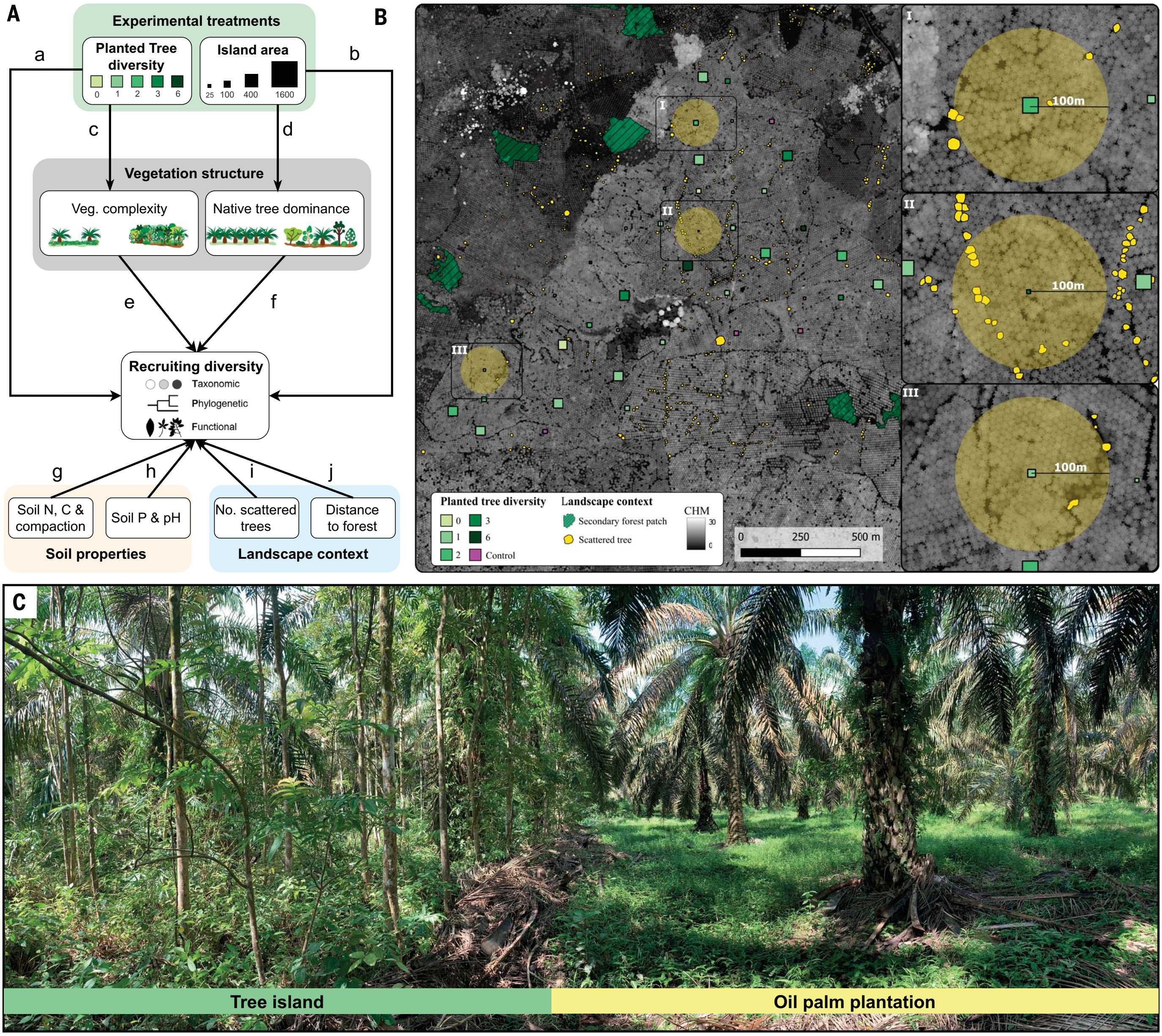

Fig. 1. Conceptual model and EFForTS-BEE study area. (**A**) Path diagram describing the mechanistic links between different drivers and recruiting diversity (taxonomic, phylogenetic, and functional diversity). Colored boxes represent groups of drivers: experimental treatments, vegetation structure, soil properties, and landscape context (distance to nearest forest and number of scattered trees). White boxes represent measured variables. Arrows represent hypothesized unidirectional causal links between variables. Potentially missing links were evaluated as part of the model fit through the d-separation test. Mechanistic relationships for each path code (lowercase letters) are described in table S1. Veg., vegetation; N, nitrogen; C, carbon; P, phosphorus. (**B**) The landscape map illustrates the spatial distribution of tree islands [squares], secondary forest patches (larger than 0.5 ha), and scattered trees. Control plots are indicated in magenta, whereas the experimental tree islands are represented by a green gradient, with darker green indicating higher planted tree diversity (0, 1, 2, 3, or 6 species, with 0 corresponding to natural regeneration only). Square size corresponds to tree island area (25, 100, 400, or 1600 m^2). The buffer area (100 m) used to calculate the number of scattered trees is shown in subpanels (I) to (III). The canopy height model (CHM) represents the maximum canopy height (meters) derived from airborne light detection and ranging scans. (**C**) Picture showing the edge between a 40 × 40 m tree island (left) and the conventional oil palm plantation (right). The picture was taken in May 2023 on the plantation PT Humusindo in Jambi province, Sumatra, Indonesia. [Image credit: Gustavo B. Paterno]

native trees (hereafter, native tree dominance), respectively (Fig. 1A; see table S1 for details on the mechanistic framework and predictions).

We hypothesized that large tree islands with higher planted diversity enhance native recruiting diversity in oil palm landscapes, e.g., by attracting seed dispersers, improving local conditions, and increasing environmental heterogeneity. Yet, we hypothesized that taxonomic, phylogenetic, and functional diversity respond differently to island design. For example, without dispersal limitation, taxonomic diversity was expected to be mostly driven by island area, consistent with the species-area relationship. Increasing planting diversity and tree island area may be more relevant for recovering functional and phylogenetic diversity (when ecological strategies are phylogenetically conserved) owing to their combined effects on environmental heterogeneity. In other words, larger and more diverse islands should provide more niches, allowing a wider range of species with different ecological strategies to establish and survive. We hypothesized that tree islands closer to forest patches and surrounded by more scattered trees will have greater recruiting diversity owing to reduced dispersal limitation.

We found that 6 years after their establishment, tree islands hosted a wide range of recruiting species. Specifically, we identified 2788 woody plant recruits (i.e., excluding planted trees), which belong to 58 species from 28 plant families and reflect different plant ecological strategies (Fig. 2, table S2, and figs. S2 and S3 for the distribution of species traits). The most species-rich families were Euphorbiaceae ($N = 8$ species), Moraceae ($N = 7$), Rubiaceae ($N = 5$), and Fabaceae ($N = 5$). Recruiting woody species represented various life forms, including trees ($N = 35$), treelets ($N = 8$), shrubs ($N = 7$, including 1 bamboo species), and lianas ($N = 8$)

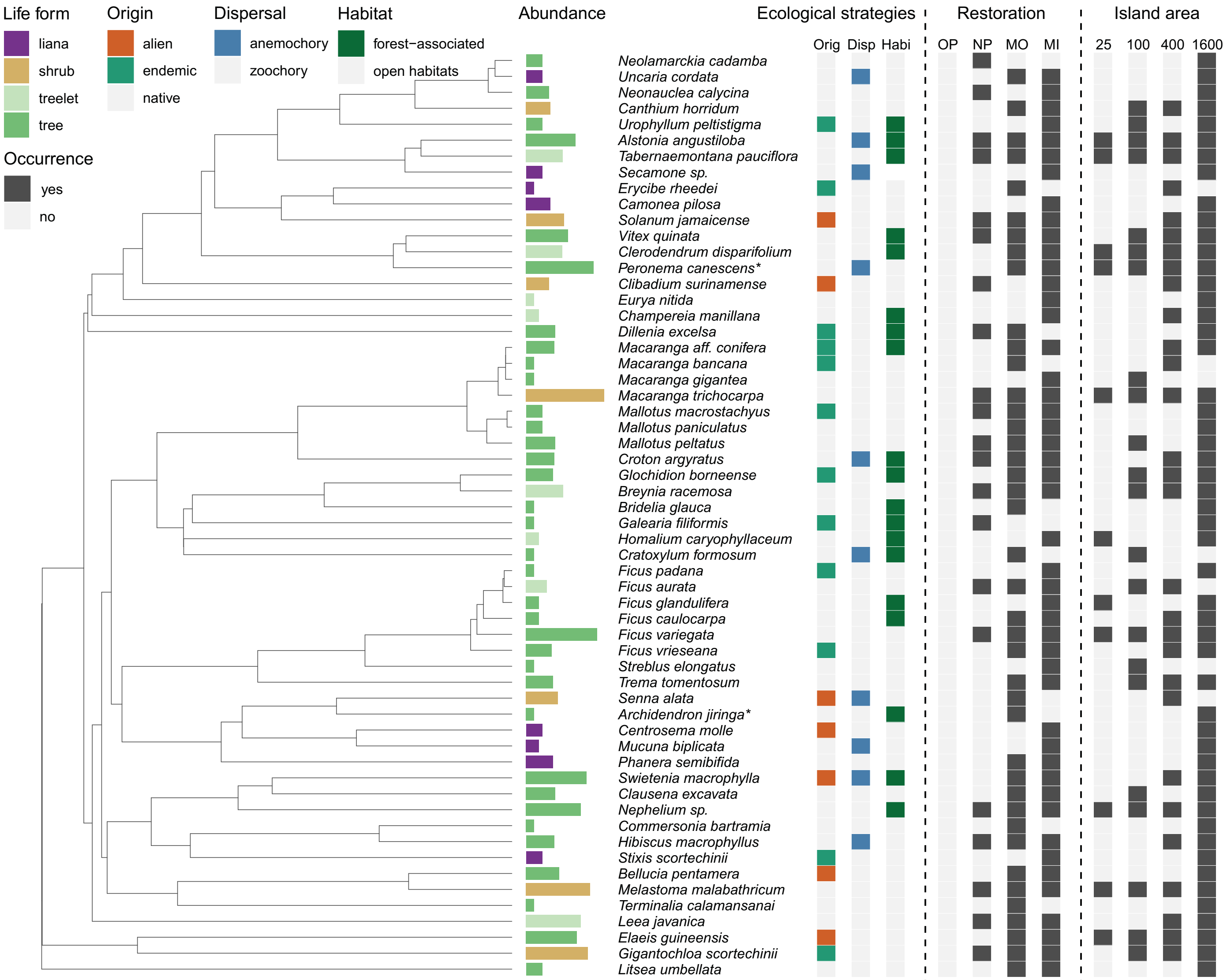

Fig. 2. Phylogenetic relationships, abundances, ecological strategies, and occupancy of recruiting species. Bar colors represent life forms (liana, shrub, treelet, and tree) of all 58 woody species regenerating in the EFForTS-BEE experiment in Sumatra, Indonesia. Bar length represents the species' total abundance across plots (log-scale), ranging between 1 and 774 individuals. Species origin (alien, endemic, and native), dispersal type (anemochory versus zoochory), and habitat (forest versus open habitat) are highlighted in the columns Orig, Disp, and Habi, respectively. The open/forest habitat classification was assigned to species based on where they typically occur. Asterisks indicate planted tree species. Black rectangles indicate occurrence in different restoration treatments: OP, conventional oil palm; NP, no planting; MO, monoculture (only one planted native tree species); MI, mixture plantations (two to six planted native tree species); and tree islands with different areas of 25, 100, 400, and 1600 m^2.

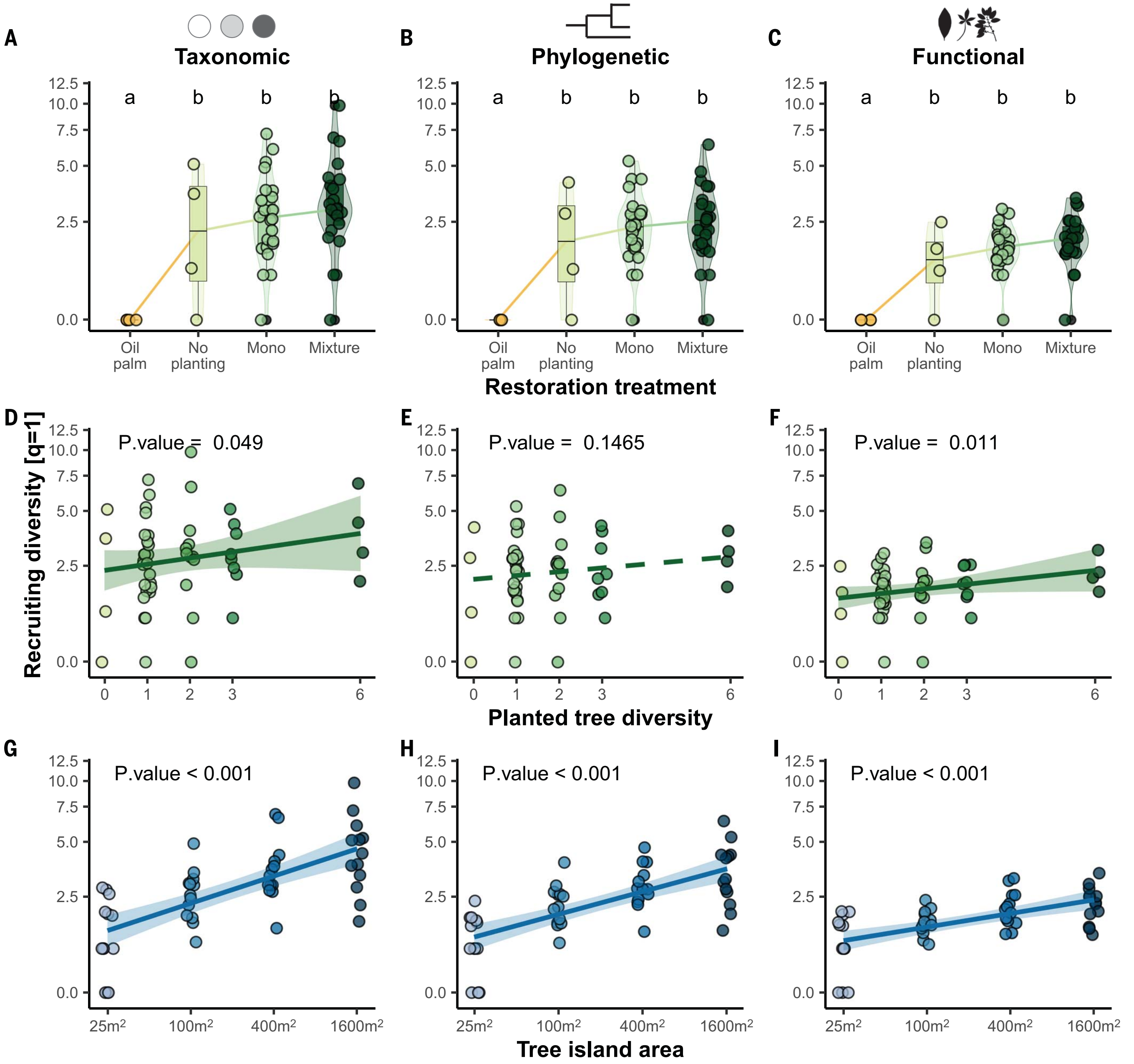

Fig. 3. Experimental effects on local diversity of recruiting woody species. Observed taxonomic (**A**), phylogenetic (**B**), and functional diversity (**C**) of recruiting species (excluding planted trees) ($q = 1$) in conventional oil palm plantations against restoration treatment [(A) to (C); $N = 56$]. Restoration treatments included conventional oil palm (control), no planting, monoculture (only one planted native tree species), and mixture plantations (two to six planted native tree species). Within tree islands, recruiting diversity was plotted against planted tree diversity [(**D** to **F**), $N = 52$] and tree island area [(**G** to **I**), $N = 52$]. Darker green represents higher planted tree diversity, and lighter green represents plots with no planted trees (no planting). Letters indicate statistical pairwise differences ($P < 0.05$) based on least-squares means, with P values adjusted with the Tukey method. The shaded area represents a 95% CI of regression lines. The P values for regression lines are from ordinary least-squares models, including Hill diversity as the response variable against tree diversity and tree island area.

(Fig. 2). Although most species ($N = 38$) were associated with secondary forests and disturbed habitats, one-third were forest-associated species ($N = 19$), which were characterized by higher maximum height ($F_{1,\,55} = 5.69$, $P = 0.021$), higher wood density ($F_{1,\,49} = 4.18$, $P = 0.046$), but similar specific leaf area (SLA; $F_{1,\,50} = 0.80$, $P = 0.377$) compared with species associated with open habitats (fig. S3). Twenty percent of species were endemic ($N = 12$), and a smaller fraction were nonnative to Sundaland ($N = 7$, ~ 10% of recruiting individuals) (Fig. 2). Zoochory was the most prevalent dispersal strategy, accounting for 79% of all individuals ($N = 2196$) and 83% of species ($N = 48$). The primary dispersers of recruiting species were birds, bats, and other mammals. Although high levels of zoochory (i.e., >70%) are expected in secondary forests of Sundaland (*34*), our results underscore the need to protect functioning seed disperser communities to ensure successful restoration (*29*). The diversity of native tree species is modest compared with typical values for degraded forests in the region (*34*, *35*),

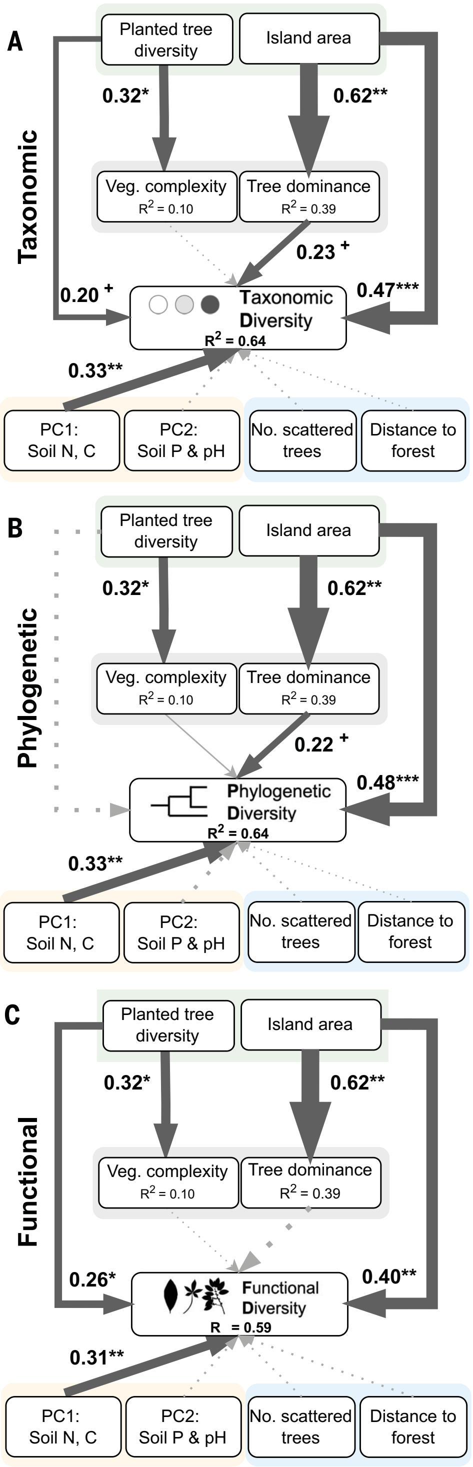

Fig. 4. Local and landscape drivers of recruiting native species diversity. Results from piecewise structural equation models (Fisher's C = 27.4, d.f. = 22, P = 0.197, N = 52) explaining the main drivers of observed taxonomic (**A**), phylogenetic (**B**), and functional diversity (q = 1) (**C**) of the native recruiting plant community (excluding planted trees). Dark gray arrows indicate positive effects. Light gray arrows indicate paths with no evidence of an effect ($P > 0.10$). Path thickness reflects standardized model coefficients (in bold). $^{+}P < 0.10$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

confirming that any further destruction of the few remaining forests should be prevented for their exceptional conservation value (*4*).

Planting diversity begets local and landscape recruiting diversity in larger tree islands

We examined differences in recruited diversity at local scale (i.e., α diversity) by comparing (i) conventional oil-palm plantations (control) and the restoration treatments: no planting, monoculture (only one planted native tree species), and mixture (two to six planted native tree species), (ii) planted tree diversity and tree island area, and (iii) controlling for local and landscape factors with Structural Equation Models (SEMs). Additionally, we examined differences in recruited diversity at landscape scale (γ diversity) by comparing the cumulative diversity across tree islands grouped by treatments (restoration treatments and tree island area). For those analyses, only species native to Sundaland, which are considered most relevant for restoration, were considered. We used the Hill-Chao numbers unified framework, calculating the effective number of species or functional groups or divergent lineages irrespective of their abundance (Hill number $q = 0$, i.e., richness), weighted by the abundance of common ($q = 1$, i.e., exponential of Shannon entropy) or most abundant species ($q = 2$, i.e., inverse of Simpson concentration index) (*36*).

Locally, native recruited species richness ranged from 0 to 16, with an average of 5.3 species/plot ± 4.6 SD (fig. S4). Tree islands greatly improved recruitment diversity compared with conventional oil palm plantations (control) (Fig. 3, A to C, and table S3). Tree island area and planted tree diversity both affected recruited species diversity, but effects varied across diversity measures. Planted tree diversity had a positive effect on functional [Fig. 3F; standardized model coefficient (Std. beta) = 0.28, $P = 0.011$; 95% confidence interval (CI) [0.07, 0.50]; table S4], a weak positive effect on taxonomic (Fig. 3D; Std.beta = 0.20, $P = 0.049$; 95% CI [0.00, 0.41]), and no clear effect on phylogenetic (Fig. 3E; Std.beta = 0.15, $P = 0.146$; 95% CI [−0.05, 0.35]) local diversity of recruiting species. These results were consistent with our SEMs (Fig. 4, A to C). After standardizing diversity through coverage-based rarefaction, planted diversity still had a positive effect on functional diversity (tables S4 and S5). Island area had a strong positive effect on recruitment diversity of native species for all diversity measures (Fig. 3, G to I). The positive effect of island area on taxonomic, phylogenetic, and functional diversity was consistent when more weight was given to locally rare (i.e., $q = 0$) or abundant species (i.e., $q = 2$) and even after accounting for sampling effort by standardizing recruiting diversity to the same sample coverage (tables S4 and S5). Furthermore, for forest-associated recruiting species, island area was the only relevant driver of taxonomic, phylogenetic, and functional diversity (table S6).

Although local estimates of diversity facets were correlated (coefficient of determination $R^2_{\text{phy-tax}} = 0.95$; $R^2_{\text{fun-tax}} = 0.85$), functional diversity was less correlated and saturated faster than phylogenetic diversity with increasing taxonomic diversity (fig. S5) due to weak phylogenetic signal on functional traits (Bloomberg's K statistic $K_{\text{max.height}} = 0.18$, $P = 0.144$; $K_{\text{SLA}} = 0.30$, $P = 0.020$; $K_{\text{wood.density}} = 0.24$, $P = 0.050$). This explains why the different facets responded differently to our experimental treatments.

At landscape scale, the cumulative recruitment diversity of native woody species ($q = 1$) across tree islands was, overall, higher for larger tree islands with planted trees (either single species or mixtures) (Fig. 5, A to F, and fig. S6) compared with no species recruiting in conventionally managed control plots. Mixed plantings had the highest functional diversity at landscape scale (Fig. 5C and fig. S6E). Differences between small and large tree islands were more pronounced for diversity measures of lower *q* order (i.e., increasing the weight of locally rare species) (figs. S6 and S7). Larger tree islands (≥400 m^2) hosted 94% of all native species found in our study, 75% of locally rare species (i.e., represented by a single individual), 89% of forest-associated species, and all endemic species. By contrast, smaller islands (<400 m^2) hosted less than half of all native species (45%) and only one-quarter of the endemic species. Notably, 37% of native species, 42% of endemic species, and 21% of forest-associated species were only found in the largest tree islands (i.e., 1600 m^2), whereas no recruiting species were exclusively found in the smallest islands (i.e., 25m^2) (Fig. 2).

Island area was the most important driver of recruit diversity, positively affecting native woody species diversity both directly and indirectly. The strong positive direct effect of tree island area on woody species diversity aligns with theoretical and empirical evidence

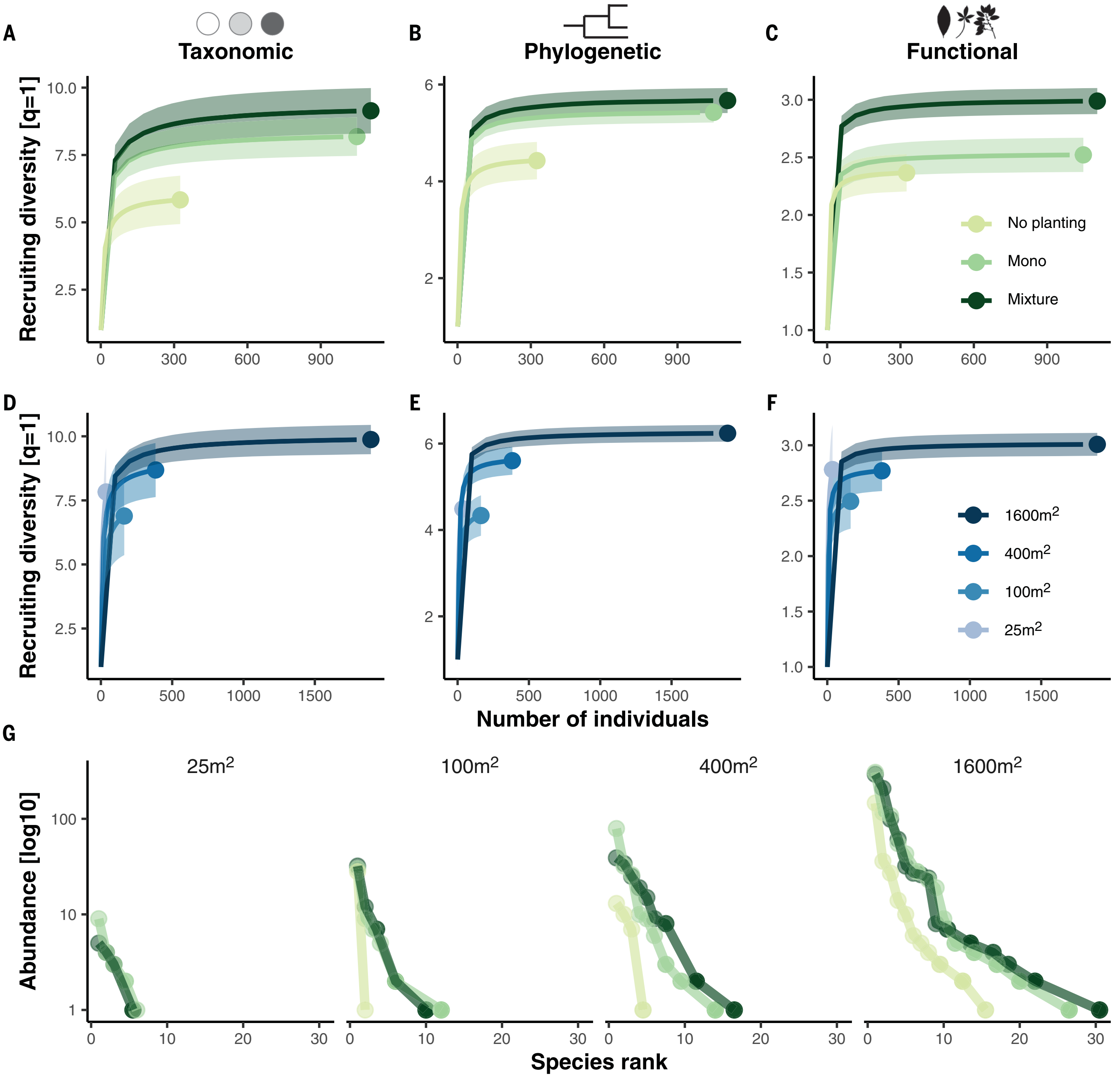

Fig. 5. Mixed-tree plantings and larger tree islands enhance native recruiting diversity at the landscape scale. (**A** to **F**) Sample size–based rarefaction curves for taxonomic (left), phylogenetic (middle), and functional recruiting diversity (right) (*q* = 1) for different restoration treatments [(A) to (C)] and across tree island areas [(D) to (F)]. Solid lines represent rarefaction curves based on a complete census of the tree islands. Solid points represent observed recruiting diversity. Error bars represent 95% CIs from bootstrapping (*N* = 500 randomizations). (**G**) Rank-abundance curves for different restoration treatments [no planting, monoculture (only one planted native tree species), and mixture (two to six planted native tree species)] and across tree island area sizes (25, 100, 400, and 1600 m^2). Abundances are shown in $\log_{10}$ scale.

suggesting that species diversity increases with area, consistent with the species-area relationship (*21*, *32*). Tree island area also had a net positive effect after controlling for sampling effort (i.e., coverage-based standardized diversity) (tables S3 and S4), pointing to ecological mechanisms and not only passive sampling. Our SEMs revealed that this effect was mediated by enhanced native tree dominance in larger islands (i.e., a higher fraction of the canopy covered by native trees rather than oil palms) (Fig. 4, A to C; fig. S8; and table S5), leading to increased taxonomic, phylogenetic, and functional local diversity. The positive effect of tree dominance on recruiting diversity may be explained by higher relative tree cover providing better habitat quality through effects on light and microclimate (*14*, *37*) and also increased litter cover (*17*). Furthermore, larger islands attract more seed dispersers than oil palm (*14*, *15*, *38*), have a more heterogeneous environment (*39*), and provide more stable microclimatic conditions (*40*). Together, this may increase seedling survival and recruit diversity. Our results highlight that increasing the restoration area (i.e., by creating larger tree islands) leads to greater biodiversity gains per unit area.

Local drivers play a greater role than landscape drivers on recruiting species diversity

When considering local and landscape contexts simultaneously, the distance to the nearest forest and the number of scattered trees surrounding tree islands had little or no detectable effect on recruitment diversity (Fig. 4, fig. S8, and table S5), with no spatial autocorrelation across tree islands (fig. S9). Whereas some studies have reported that proximity to primary forests or increased forest cover increases biodiversity by facilitating dispersal (*29*, *41*, *42*), others have found little or no landscape effect on restoration outcomes (*14*, *16*, *43*). The conditions under which landscape context is more or less relevant are still debated (*10*, *32*) and may vary with taxon, ecological context, spatial scale, successional stage, and species composition of remnant forest patches (*14*, *26*, *41*, *44*). The lack of landscape influence in our study may be explained by the absence of primary forests and low secondary forest cover in our study region (~4%) (Fig. 1B). Another reason might be the presence of abundant generalist animal species, such as long-tailed macaques (*Macaca fascicularis*) and common palm civets (*Paradoxurus hermaphroditus*), which thrive in oil palm landscapes and facilitate long-distance seed dispersal (*45*).

Local soil properties played an important role in native recruit diversity. Soil properties reflecting higher carbon and nitrogen and lower soil compaction (PC1; fig. S10) had a strong positive effect on taxonomic (Std.beta = 0.33, P = 0.002; 95% CI [0.13, 0.53]), phylogenetic (Std.beta = 0.33, P = 0.002; 95% CI [0.13, 0.53]), and functional diversity of native recruiting species (Std.beta = 0.31, P = 0.005; 95% CI [0.10, 0.53]). This suggests that reduced soil fertility and increased soil compaction in oil palm plantations (*46*) hinder natural regeneration.

Implications for restoration ecology

Increased diversity of recruiting trees due to tree planting supports growing evidence that tree planting can accelerate natural recruitment compared with no planting (i.e., natural regeneration only) (*13*, *14*, *20*, *47*). Planted trees can promote recruitment by alleviating environmental stress and improving local conditions for recruiting species that otherwise would not establish (*12*, *20*). Furthermore, different planted tree species modify environmental conditions and resource availability differently, promoting the recruitment of species with contrasting growth and survival requirements (*48*). The consistent effect of planted diversity on functional diversity supports the idea that higher planted tree richness creates small-scale biotic and abiotic heterogeneity (*27*, *48*), promoting functionally diverse communities. In other words, planted diversity begets recruited diversity.

We show that different restoration strategies can maximize distinct facets of diversity at multiple scales. For example, large tree islands are crucial to maximize the taxonomic and phylogenetic diversity at the landscape scale by supporting locally rare, endemic, and forest-associated species. On the other hand, to maximize local or landscape-scale functional diversity, we also suggest increasing the number of planted tree species.

As large areas currently under oil palm cultivation are approaching replanting age [e.g., in Indonesia, 3.5 Mha are older than 20 years (*49*)], a second wave of biodiversity loss is expected to occur (*50*), driving the need for fast and effective restoration. Within a portfolio of different options, tree islands, particularly larger and more diverse plantings, have the potential to contribute to multiple restoration goals at different temporal and spatial scales.

REFERENCES AND NOTES

1. L. Cai *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2300981120 (2023).
2. M. Qaim, K. T. Sibhatu, H. Siregar, I. Grass, *Annu. Rev. Resour. Econ.* **12**, 321–344 (2020).
3. Y. W. C. Kusuma, K. Rembold, S. S. Tjitrosoedirdjo, H. Kreft, *J. Appl. Ecol.* **55**, 2216–2226 (2018).
4. J. E. M. Watson *et al*., *Nat. Ecol. Evol.* **2**, 599–610 (2018).
5. N. A.-A. Iddris *et al*., *Nat. Sustain.* **6**, 683–695 (2023).
6. H. P. Jones *et al*., *Proc. Biol. Sci.* **285**, 20172577 (2018).
7. W. A. Foster *et al*., *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 3277–3291 (2011).
8. M. D. Pashkevich *et al*., *Trends Ecol. Evol.* **37**, 963–975 (2022).
9. R. L. Chazdon *et al*., *Restor. Ecol.* **2021**, 13535 (2021).
10. R. Crouzeilles *et al*., *Conserv. Lett.* **13**, e12709 (2020).
11. R. L. Chazdon, M. R. Guariguata, *Biotropica* **48**, 716–730 (2016).
12. D. Lamb, P. D. Erskine, J. A. Parrotta, *Science* **310**, 1628–1632 (2005).
13. L. Li, M. W. Cadotte, C. Martínez-Garza, M. De La Peña-Domene, G. Du, *J. Appl. Ecol.* **55**, 986–996 (2018).
14. K. D. Holl *et al*., *J. Appl. Ecol.* **57**, 2316–2328 (2020).
15. J. M. R. Benayas, J. M. Bullock, A. C. Newton, *Front. Ecol. Environ.* **6**, 329–336 (2008).
16. R. J. Cole, K. D. Holl, R. A. Zahawi, *Ecol. Appl.* **20**, 1255–1269 (2010).
17. D. C. Zemp *et al*., *Nature* **618**, 316–321 (2023).
18. V. Montoya-Sánchez *et al*., *Commun. Earth Environ.* **4**, 1–9 (2023).
19. I. Grass *et al*., *People Nat.* **1**, 262–272 (2019).
20. L. K. Werden *et al*., *Front. For. Glob. Change* **5**, 935011 (2022).
21. C. Messier *et al*., *Conserv. Lett.* **15**, e12829 (2022).
22. L. Poorter *et al*., *Science* **374**, 1370–1376 (2021).
23. M. W. Cadotte, K. Carscadden, N. Mirotchnick, *J. Appl. Ecol.* **48**, 1079–1087 (2011).
24. S. Schmitt *et al*., *J. Ecol.* **108**, 831–843 (2020).
25. G. G. Mazzochini *et al*., *Glob. Ecol. Biogeogr.* **28**, 1430–1439 (2019).
26. J. L. Reid *et al*., *Ecosphere* **12**, e03868 (2021).
27. T. C. Coverdale, A. B. Davies, *J. Ecol.* **111**, 1378–1395 (2023).
28. R. H. MacArthur, E. O. Wilson, *Evolution* **17**, 373–387 (1963).
29. C. Bello *et al*., *Nat. Clim. Chang.* **14**, 636–643 (2024).
30. S. Sloan, M. Goosem, S. G. Laurance, *Landsc. Ecol.* **31**, 601–618 (2016).
31. A. D. Manning, J. Fischer, D. B. Lindenmayer, *Biol. Conserv.* **132**, 311–321 (2006).
32. V. Arroyo-Rodríguez *et al*., *Biol. Rev. Camb. Philos. Soc.* **92**, 326–340 (2017).
33. M. Teuscher *et al*., *Front. Plant Sci.* **7**, 1538 (2016).
34. S. Rahayu *et al*., *For. Ecosyst.* **9**, 100030 (2022).
35. K. Rembold, H. Mangopo, S. S. Tjitrosoedirdjo, H. Kreft, *Biol. Conserv.* **213**, 234–242 (2017).
36. A. Chao *et al*., *Methods Ecol. Evol.* **12**, 1926–1940 (2021).
37. R. A. Zahawi, C. K. Augspurger, *Ecol. Appl.* **16**, 464–478 (2006).
38. R. D. Fink, C. A. Lindell, E. B. Morrison, R. A. Zahawi, K. D. Holl, *Restor. Ecol.* **17**, 479–486 (2009).
39. K. D. Holl, V. M. Stout, J. L. Reid, R. A. Zahawi, *Oecologia* **173**, 569–578 (2013).
40. L. S. Donfack *et al*., *For. Ecol. Manage.* **497**, 119480 (2021).
41. R. Crouzeilles, M. Curran, *J. Appl. Ecol.* **53**, 440–448 1(2016).
42. J. I. Watling *et al*., *Ecol. Lett.* **23**, 674–681 (2020).
43. K. D. Holl, J. L. Reid, J. M. Chaves-Fallas, F. Oviedo-Brenes, R. A. Zahawi, *J. Appl. Ecol.* **54**, 1091–1099 (2017).
44. J. L. Reid, J. M. Chaves-Fallas, K. D. Holl, R. A. Zahawi, *Appl. Veg. Sci.* **19**, 508–517 (2016).
45. R. T. Corlett, *Glob. Ecol. Conserv.* **11**, 1–22 (2017).
46. M. Pérez-Sato *et al*., *Heliyon* **9**, e16302 (2023).
47. K. Shono, E. A. Cadaweng, P. B. Durst, *Restor. Ecol.* **15**, 620–626 (2007).
48. G. B. Paterno, J. A. J. A. Siqueira Filho, G. Ganade, *J. Veg. Sci.* **27**, 606–615 (2016).
49. A. Descals *et al*., *Earth Syst. Sci. Data* **13**, 1211–1231 (2021).
50. A. Ashton-Butt *et al*., *Ecol. Evol.* **9**, 6433–6443 (2019).
51. G. B. Paterno *et al*., Data and code for: Diverse and larger tree islands promote native tree diversity in oil palm landscapes, GRO.data (2024); https://doi.org/10.25625/GUWXUX.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S10
Tables S1 to S6
References (*52*–*97*)
MDAR Reproducibility Checklist

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