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The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches

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Forest restoration is being scaled-up globally to deliver critical ecosystem services and biodiversity benefits, yet we lack rigorous comparison of co-benefit delivery across different restoration approaches. In a global synthesis, we use 25,950 matched data pairs from 264 studies in 53 countries to assess how delivery of climate, soil, water, and wood production services as well as biodiversity compares across a range of tree plantations and native forests. Carbon storage, water provisioning, and especially soil erosion control and biodiversity benefits are all delivered better by native forests, with compositionally simpler, younger plantations in drier regions performing particularly poorly. However, plantations exhibit an advantage in wood production. These results underscore important trade-offs among environmental and production goals that policymakers must navigate in meeting forest restoration commitments.

As the UN Decade on Ecosystem Restoration gets underway (*1*), forest restoration on degraded and deforested land is being scaled-up globally, with far-reaching environmental and social implications (*2*–*4*). The Bonn Challenge alone pledges to restore 350 million hectares of land by 2030 (*5*), and many other initiatives are similarly ambitious (*6*, *7*). Large-scale programs to restore forests are frequently motivated by a desire to recover ecosystem services such as carbon storage (*8*), soil erosion control (*9*), water provisioning (*10*), and wood production (*11*). Based on an implicit assumption that these services can be effectively delivered by forests regardless of their composition, these programs frequently gravitate toward reforesting with compositionally simple tree plantations rather than restoring native forests (*7*, *10*, *12*). However, this premise has yet to be tested rigorously using paired data that limit potential confounding factors (*13*) (Supplementary Text). This is a critically important omission for reasons beyond the target ecosystem services per se, because by having limited (*14*) and at times negative (*9*) effects on native biodiversity, a focus on tree plantations risks severely limiting the conservation potential of large-scale forest restoration, in turn hampering progress toward global commitments to halt and reverse biodiversity loss (*15*–*17*) and ecosystem degradation (*1*).

We present a global synthesis of paired data from the world's main forest biomes to assess the merits of forest restoration approaches, in particular reforesting with tree plantations versus restoring native forests, on deforested land that would have been naturally forested in recent history (Materials and Methods) (*18*). We compare the performance of a range of compositionally simple tree plantations spanning a wide spectrum of management regimes ('tree plantations' hereafter) (*18*) versus native forests (including restored and pre-existing native forests) in delivering the key ecosystem services of carbon storage, soil erosion control, water provisioning, and wood production, as well as in supporting biodiversity. We further assess how variation in the relative performance of tree plantations versus native forests may be explained by plantation features and biophysical conditions. Our study aims to enable forest restoration to achieve co-benefits in addressing today's multiple environmental challenges (*4*), including the dual climate and biodiversity crises (*8*, *17*). By simultaneously considering forests' performance in carbon, soil, water, and biodiversity (i.e., environmental outcomes), plus in wood production, our study also provides a critical assessment of the trade-offs likely to confront forest restoration decision-makers.

For each environmental outcome, we identified the most informative metric with a reasonable amount of empirical data: aboveground biomass (Mg ha^{-1}), amount of eroded soil (kg m^{-2}

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y^{-1}), catchment- or plot-scale water yield (percent of rainfall), and species-specific abundance [individuals ha^{-1}, compiled for each species in a given ecological community; see (*18*) for rationale of metric choices]. Searching the peer-reviewed and gray literature and corresponding with authors, we compiled pairs of data that involved a tree plantation (classified into three types) and a matching native forest (classified into four types; Fig. 1A) from the same study system (*18*). For wood production, we compiled pairs of empirical data on wood yield (m^3 ha^{-1}) or profit (USD ha^{-1}) that involved a tree plantation and a matching restored native forest (Fig. 1A) over equal time horizons (*18*); we excluded native forests not resulting from restoration because the sustainability of their wood harvest could rarely be confirmed. Given the paucity of paired wood production data, we relaxed the matching requirement to also compile annualized yield data just from restored native forests (m^3 ha^{-1} y^{-1}) (*18*), which we compared with known annualized yields of some of the world's main monoculture plantations (*19*).

We assessed the rigor of matching for each data pair and weighed it accordingly in subsequent analyses (*18*). We calculated a log response ratio (RR) [ln(tree plantation over native forest)] from each data pair to represent the relative performance of tree plantations versus native forests; we reversed the RR signs for eroded soil to represent soil erosion control. In total, our searches (*18*) (fig. S1 and tables S1 to S3) yielded 25,535 RRs for species-specific abundance on 13 species groups from 405 plantation-native forest pairs, 146 RRs for aboveground biomass, 82 RRs for eroded soil, 167 RRs for water yield, and 20 RRs for wood production, from 264 studies in 53 countries (Fig. 1 and table S4). In addition, we collated 223 records on the standing wood volume of restored native forests with known age from 10 studies in six countries (fig. S2 and table S4).

We first asked how well tree plantations performed in environmental outcomes relative to reference native forests not resulting from restoration, namely old-growth forests and 'generic' native forests (i.e., other non-restored native forests not reported as old-growth). Not having undergone deforestation, these native forests represent reference environmental conditions (*20*) toward which forest restoration can aspire (Fig. 2A) (*18*). Consistent with prevailing understanding (*14*, *21*), tree plantations supported on average 29.3% lower species-specific abundance than did reference native forests (95% confidence interval ('CI' hereafter): 22.0 to 35.9%; Fig. 2B, upper panel; table S5; for differences among species groups, see fig. S3). This biodiversity contrast was echoed across the other three environmental metrics, with tree plantations delivering 32.8% lower aboveground biomass (95% CI: 16.5 to 45.9%), 60.6% lower soil erosion control (16.2 to 81.4%), and 13.4% lower water yield (4.1 to 21.9%; Fig. 2B, upper panel; table S5). These patterns were mainly driven by the poor performance of monoculture plantations, which exhibited the greatest contrasts with reference native forests (Fig. 2B, upper panel; table S5). Prolonged age (≥40 years) or abandonment appeared to somewhat improve the environmental performance of plantations (*18*), with water yield shortfall no longer significant (mean: 6.7%; 95% CI: –23.4 to 29.4%; Fig. 2B, lower panel; table S5). However, differences for the other metrics persisted, albeit less marked: 14.6% (2.3 to 25.3%) for species-specific abundance, and 24.0% (6.2 to 38.5%) for aboveground biomass; there were too few data to assess soil erosion control (Fig. 2B, lower panel; fig. S3 and table S5).

We next asked how well tree plantations performed relative to restored native forests of similar age (i.e., with ≤10 years of age difference), represented by secondary forests resulting from natural regeneration, as well as actively restored native forests resulting from the planting of a diverse native tree mix (typically ≥50 species; Fig. 1A, fig. S4, and Fig. 2A lower panel) (*18*). On environmental performance, tree plantations performed significantly more poorly than restored native forests of similar age in species-specific abundance (32.3% poorer; 95% CI: 15.7 to 45.7%; there were insufficient data to contrast between species groups; fig. S3) and marginally so for soil erosion control (80.2% poorer; –57.9 to 97.5%), but not aboveground biomass (4.1% greater; –23.1to 40.9% and spanning zero; Fig. 2C, upper panel; table S5; data paucity precluded analysis for water yield). The similarity in aboveground biomass appeared to be due to the strong performance of abandoned plantations that seemed to outperform both monocultures and mixed plantations (Fig. 2C, upper panel; although data paucity precluded formal analysis on this).

For wood production, the limited paired data showed that tree plantations had a clear advantage over restored native forests, with 222.7% (105.8% to 406.0%) higher wood volumes at comparable age (Fig. 2C, lower panel; table S5; data paucity precluded analysis of profits from wood production). This advantage was apparent for both intensively managed and abandoned plantations, and regardless of whether wood volumes included all woody species or only merchantable species (fig. S5). The same conclusion was reached using supplementary non-paired data on annualized wood yields of restored native forests and various prominent monocultures: average annual volume increments for restored native forests were 61.3% (Welch two-sample t test: $t_{28.8} = -6.40$, $P < 0.0001$) and 86.9% ($t_{26.4} = -9.76$, $P < 0.0001$) lower than the lower and upper bounds of the monocultures, respectively (Fig. 2D).

For all the above meta-analyses, we found high levels of heterogeneity (*18*), with I^2—the metric for heterogeneity—generally ≥80% (table S5). Findings were robust to publication bias (Supplementary Text; fig. S6) and various sensitivity analyses related to weighting schemes and model structure) (*18*) (table S5). They also showed that across the environmental metrics examined, tree plantations performed particularly poorly for soil erosion control (Fig. 2, right-hand panels). Because data for different metrics were obtained for different regions (Fig. 2, left-hand panels), the

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difference among environmental outcomes might reflect inherent biophysical differences among ecosystems. To address this potential geographical confounding effect, we next focused on a subset of our database in which data for different metrics could be geographically matched to a given ecosystem type whose biophysical conditions were largely coherent. Overlaying our data onto the Holdridge Life Zones map (*22*, *23*), we identified 'data bundles' for each forest biome where RRs were available for ≥2 metrics. In total, we identified 11 such data bundles for the comparison between tree plantations and reference native forests (Fig. 3A), and seven for the comparison between tree plantations and restored native forests of similar age (Fig. 3B). The patterns of how RRs for soil erosion control compared with other environmental metrics within each data bundle corroborated our earlier findings: relative to reference native forests, plantation shortfalls were almost always greatest for soil erosion control and the least for water yield (Fig. 3).

We also asked what factors might underlie the variation in environmental performance of tree plantations relative to native forests. For the comparisons of plantations versus reference native forests and plantations versus restored native forests of similar age, respectively, we assessed the relationship between RRs and a set of variables representing plantation features and site biophysical conditions [(*18*); analyses of wood production were dropped because of data paucity.] We considered plantation type, plantation age (except for the comparison involving restored native forests of similar age), and mean annual temperature (in °C; 'MAT' hereafter) (*18*). The rationale for considering MAT was that by supporting higher plant diversity (*24*), warmer climates may show greater contrasts between plantations versus native forests in vegetation complexity, and in turn, in delivery of carbon, soil, and water ecosystem services (*25*). We also considered mean annual precipitation (in mm y^{-1}; 'MAP' hereafter) for soil erosion due to its likely influence on protective ground cover, as well as MAP and the seasonality of native forests (evergreen or deciduous) for water yield due to their likely influence on the hydrological behaviors of forest ecosystems (*18*, *26*, *27*).

The most parsimonious models selected via small-sample corrected Akaike Information Criterion (AICc) scores (*18*); table S6) showed that increasing plantation age improved plantations' performance relative to that of reference native forests in species-specific abundance and aboveground biomass (table S7), although such improvement was limited (Figs. 4A): particularly for aboveground biomass, even old (≥40 years) plantations performed less well than reference native forests. Combined with the environmental shortfalls of old or abandoned plantations (Fig. 2B, lower panel), this finding suggests that old plantations no longer intended for productive use [e.g., (*28*)] would deliver environmental benefits more effectively if they were restored to native forests or native forest-like conditions. That such areas are common in our database (Figs. 1A and 2A) indicates the sizeable environmental gains that such 'forgotten lands' offer, underscoring the need to assess their global distribution and restoration potential (*29*).

We also found that increasing MAP (range covered by our data: 490 to 4210 mm y^{-1}) predicted more positive RRs for water yield when comparing tree plantations against reference native forests (Fig. 4B; table S7), indicating greater plantation shortfalls in water provisioning in drier climates. Clearly, water-oriented forest restoration initiatives should re-examine the practice of establishing large areas of tree plantations in the world's drier regions (*30*). We did not find evidence of other variables explaining variation in RR values, or for any variable explaining plantation performance relative to restored native forests of similar age (fig. S7 and table S6). These findings were again robust to various sensitivity analyses related to weighting schemes and model structure (*18*) (tables S6 and S7), with the exception of one sensitivity analysis on soil erosion control (table S6), which showed ameliorated plantation shortfalls relative to reference native forests in warmer or wetter climates (fig. S7 and table S7).

Our findings have important implications for forest restoration as it is scaled-up globally (*7*), providing a knowledge base for exploring how outcomes can be best delivered by alternative restoration approaches. We found that restoring native forests typically delivers greater—and certainly no less—environmental benefits than establishing tree plantations, in terms of biodiversity conservation and the key ecosystem services of aboveground carbon storage, soil erosion control, and water provisioning. However, delivering these outcomes will typically result in a trade-off with wood production because of the yield advantage of plantations over restored native forests (*31*–*33*), as measured in wood volumes (distinct from aboveground carbon storage, which in addition to wood volumes also factors in wood densities).

These findings provide evidence that if the goal of forest restoration is to recover environmental services on the land being restored, and if wood production is not a primary concern, native forest restoration should be prioritized, using site-appropriate measures including unassisted and assisted natural regeneration and active planting of diverse native species (*34*–*36*). Beyond biodiversity, the stakes are especially high for soil erosion control—given its far poorer delivery by tree plantations relative to native forests. Our synthesis refutes the implicit assumptions of ecosystem service-oriented forest restoration initiatives such as China's Grain-for-Green Program covering >34 million hectares (*37*, *38*), and a large collection of projects targeting carbon storage (*39*), soil conservation (*40*), and water provisioning (*41*) that have focused mostly on establishing (monoculture) tree plantations.

However, where the goals of forest restoration include wood production, decision-making must navigate the trade-off between environmental and production outcomes (*42*). Beyond weighing competing goals and adopting restoration approaches accordingly (*43*), larger-scale land-use planning must be invoked

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to also consider the 'leakage' of forgone production to land parcels elsewhere: such leakage could alter—and even reverse—the overall environmental gains of forest restoration (*44*). Ensuring environmental gains while meeting production goals under forest restoration hinges on understanding their trade-offs for a range of restored forest covers, making the acquisition of such information an urgent research priority.

Interpretation of our results and associated policy recommendations raises three additional issues. First, while the environmental metrics assessed were our best choices given data availability (*18*), they each characterize one aspect of a focal outcome. For example, beyond aboveground biomass, an assessment of forest carbon storage must also consider carbon stored belowground (*45*) as well as in long-lived wood products. Second, because our data came from established tree covers, they represent achievable outcomes of successful forest restoration (*13*). In reality, restoration approaches and outcomes are often constrained by factors including funding limitations, recurrent disturbances, livelihood needs, and regeneration stochasticity, etc. (*46*, *47*). Third, while we used paired data and accounted for the rigor of site matching in our analyses (*18*), we cannot rule out the potential influence of pre-existing site differences incurred by land-use history (*13*) and species turnover across space (beta-diversity) (*48*), both of which are often difficult to ascertain.

By presenting a global comparison between tree plantations and native forests that simultaneously assesses their impacts on biodiversity, climate, soil, water, and wood production based on rigorously paired data, our study provides insights into the alignment among these environmental goals and the trade-offs between environmental and production goals under forest restoration. Previous research on the co-benefits of forest restoration has focused on 'where to restore' (*29*, *49*). By addressing 'how to restore', our study will help to improve the realism of future spatial prioritization efforts. Finally, other forest restoration outcomes, such as food and nutrition security, will be important in some contexts (*50*). Future research should address how these outcomes fare under different restoration approaches, and their co-benefit opportunities and unavoidable trade-offs with other environmental and production goals.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S11
Tables S1 to S7
References (*51*–*535*)
MDAR Reproducibility Checklist

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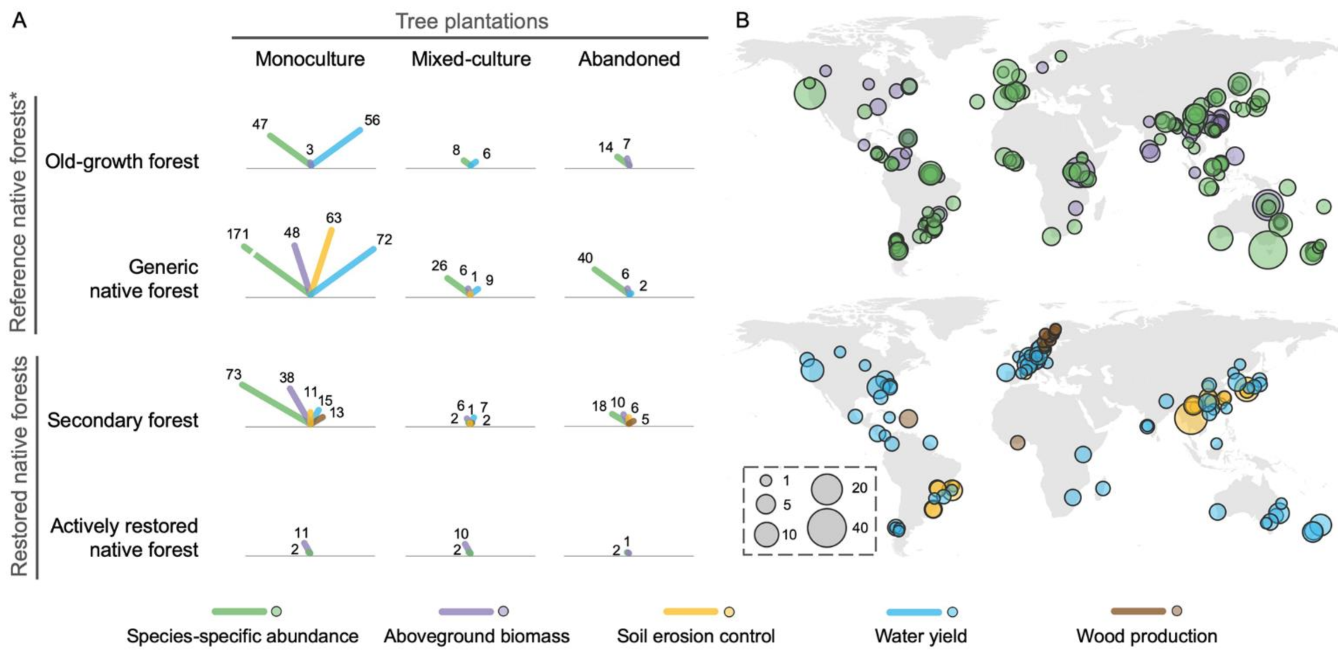

Fig. 1. Database overview. (**A**) The amount of paired data compiled into our database for different combinations of plantations and native forests. For species-specific abundance, the amount of data are represented by the number of plantation-native forest pairs that supplied species-level RRs for entire ecological communities; for all other metrics, it is represented by the number of RRs. (**B**) Geographical distribution of RRs of different metrics, displayed in two maps for better visualization: species-specific abundance and aboveground biomass in the upper panel, and soil erosion control, water yield, and wood production in the lower panel. Bubble size in maps is proportional to the cube root of the amount of data for a given geographical location. *: We did not compile paired wood production data for the comparison between tree plantations and reference native forests.

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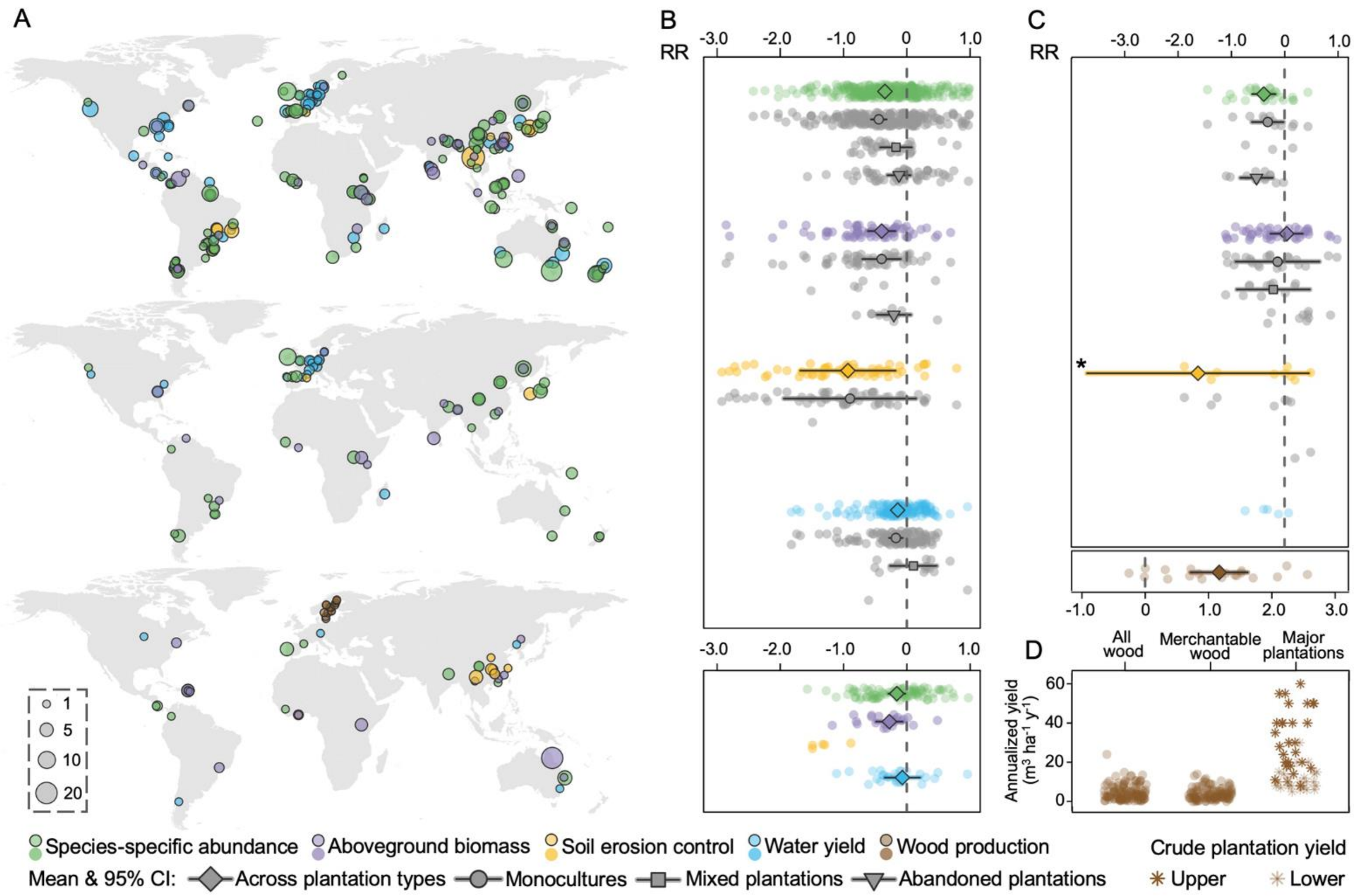

Fig. 2. Relative performance of tree plantations versus native forests across the metrics assessed. (**A**) Maps displaying the distribution and amount of data analyzed, for three types of comparisons: plantations versus reference native forests (upper panel), old (≥40 years of age) or abandoned plantations versus reference native forests (middle panel), and plantations versus restored native forests of similar age (i.e., with ≤10 years of age difference; lower panel). As with Fig. 1, bubble size is proportional to the cube root of the amount of data for a given geographical location. (**B**) Relative performance of plantations versus reference native forests (upper panel) and of old or abandoned plantations versus reference native forests (lower panel), in environmental metrics. Scattered dots in color represent RR from primary studies across all types of plantations, and diamonds and associated error bars represent the mean and 95% confidence intervals (CI) of RR values obtained from meta-analyses where the number of RR ≥10 (in the case of species-specific abundance, where the number of plantation-native forest pairs ≥10). For the comparison between plantations and reference native forests (upper panel), we also analyzed RRs separately for different types of plantations where the number of RR ≥10. For these analyses, we display their RR values from primary studies in grey, distinguishing among plantation types with different symbols for their meta-analysis-derived means and 95% CI. (**C**) Relative performance of plantations versus restored native forests of similar age in environmental (upper panel) and production (lower panel) metrics, with symbol use following that of (B). (**D**) Annualized wood volume increment of restored native forests compared with the lower and upper bounds of the annual wood increment of the world's major monoculture plantations. In our display, we differentiate between records on all woody plants and those on only merchantable species for restored native forests, and between the lower and upper bound for plantations. In panels (B) and (C), scattered dots for species-specific abundance data represent the average RR within the ecological community concerned in each plantation-native forest pair, and a small number of RR values are not displayed because they fell outside the display range, including five highly negative RRs for soil erosion control indicated by * in (C).

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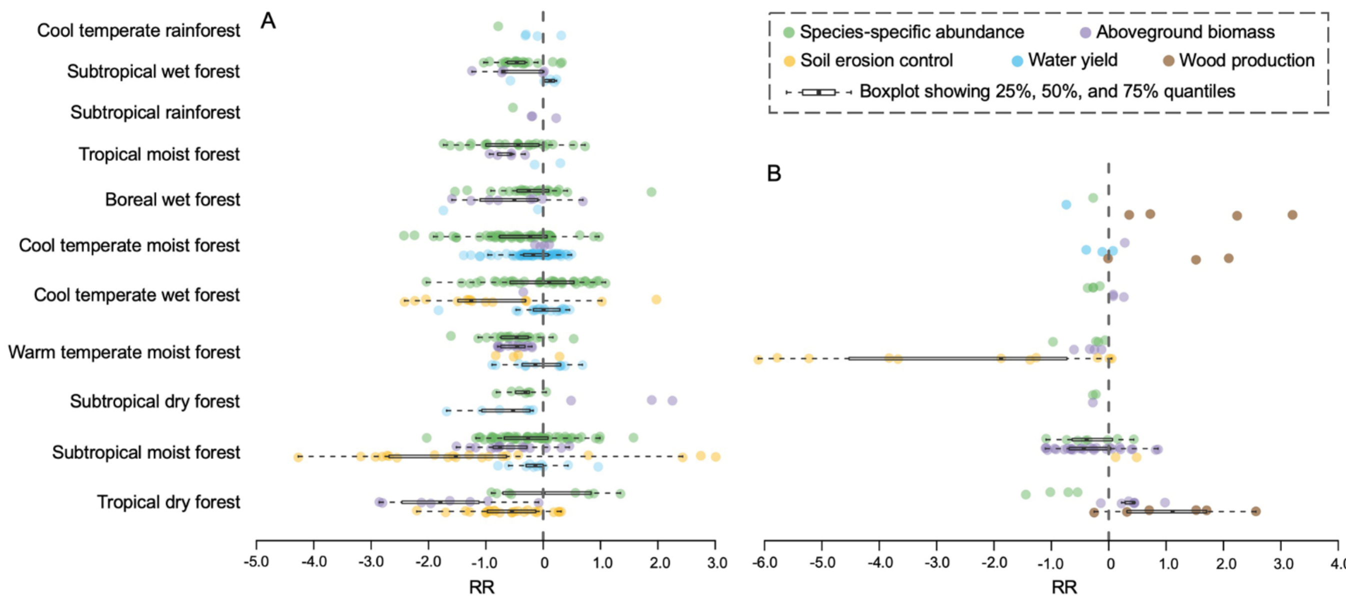

Fig. 3. Relative performance of plantations versus native forests compared among the metrics assessed, based on geographically matched data bundles for individual forest biomes. (**A**) Plantations versus reference native forests. (**B**) Plantations versus restored native forests of similar age (i.e., with ≤10 years of age difference). RR values (in the case of species-specific abundance, the average RR within the ecological community concerned in each plantation-native forest pair) are represented by scattered dots, and their quartiles by boxplots where the number of RRs ≥5. For the comparison between plantations and restored native forests of similar age, data bundles were not available for four forest biomes on the top.

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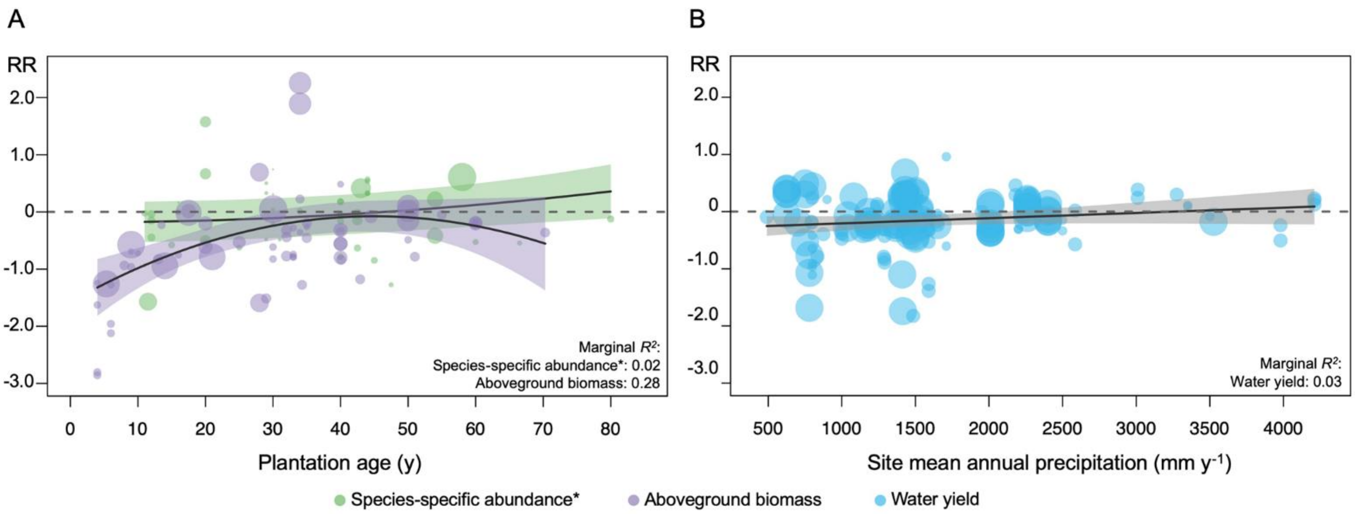

Fig. 4. Factors explaining the relative performance of plantations versus reference native forests. Best models selected based on AICc scores identified the following factors as explaining RRs: (**A**) plantation age for aboveground biomass and for species-specific abundance (*: the latter concerning the comparison between abandoned plantations and reference native forests only), and (**B**) MAP for water yield. Scattered dots represent RR values from primary studies (in the case of species-specific abundance, average RR within the ecological community concerned in each plantation-native forest pair), with dot size proportional to the weight of each RR in the meta-regressions, standardized within each metric to the RR with the greatest weight. Fitted curves (black lines) and 95% confidence bands (colored polygons; colored grey for water yield for better visualization) were generated from meta-regressions.

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