The role of community assembly processes in the biodiversity-production relationship: tests of theory on real gradients

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Abstract

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Understanding spatiotemporal variation in net primary productivity (NPP) continues to be of fundamental importance to basic ecology and to applied conservation and management efforts for human well-being. Diversity is an important driver of NPP variation, but its effect is variable depending on ecosystem context and spatial scale as well as more closely linked to functional traits. Explicitly considering processes of trait-based community assembly and maintenance at relevant scales at which they occur can potentially resolve some of this variation. In my thesis, I address this gap by considering various processes that structure and maintain diversity in communities and analyze NPP as an outcome of these processes. I examine processes in high diversity tropical forests, relatively less explored in the context of biodiversity-ecosystem functioning. In **Chapter 1**, through a manipulated experiment, I show that diversity effect on biomass gain in seedling communities is modulated by light. This interactive effect holds across different functional groups that are known to respond uniquely to light. In **Chapter 2**, I expand the spatial scale of inquiry to community assembly processes that maintain diversity at regional spatial scales – dispersal and competition, akin to island biogeographic contexts. Through simulations, I show that dispersal and competition acting on correlated traits explain a range of variation in BEF curves observed in nature. Finally, in **Chapter 3**, expanding the focus of inquiry to include human aspects, I consider the impact of a biodiversity-driven human intervention, protected areas, in maintaining NPP. I show that at the landscape scale, mean annual NPP and temporal stability are both influenced by protection status, but the effectiveness

of protection is contingent on environmental factors. Taken together, my thesis suggests that understanding the combined drivers of diversity and NPP can improve predictions for spatiotemporal variation of this ecosystem function. Further inquiry integrating diversity-gradients at multiple scales can improve process-based understanding of the effect of biodiversity on ecosystem functioning.

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Acknowledgements

It took a village to write this thesis. The introduction focuses on what "I" did and showed, like the hero's journey narrative of a PhD, and yet, my largest learning through this time was the importance of collaboration. Although the actual thesis has near-polished language, graphs and tables, attempting (really hard) to tell a cohesive story, this journey has been far from linear.

For the actual thesis, I have several people to thank, starting with my advisor Shahid Naeem. Shahid took a chance on a young person from across the world, in India, who had little in the way of experience, no publication record, without even having met them, and I will always be infinitely grateful for this opportunity. Although Shahid would have loved for me to work on ecosystems closer to Columbia University, he allowed me the freedom to work in the Andaman Islands, which was where my heart was. More than that, despite being half way across the world, Shahid and his partner Sara took the time to visit me on field and experience the dynamics of the system and its limitations, demonstrating supportive mentorship at its finest. He continues to believe, though, that this thesis and indeed everything else I do "is shadowed by" my first first-author paper based on his data on experimental grassland mesocosms. It will be my life-long mission to prove him wrong.

The rest of my committee too have been available and accommodating. Maria Uriarte has always made time to discuss statistics and analytical methods; the courses she taught have translated directly into methods and figures in this thesis. Ruth DeFries has been continually challenging why and how we do science and has been an anchor for the place-based approach to science that I aspire to pursue. Robert Bagchi has been incredibly supportive and generous with his time, scheduling regular meetings across time zones to collaborate on a chapter in the middle of the initial waves of the pandemic. I will be eternally grateful to Mahesh Sankaran, for

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My real family has been patient and supportive champions of my career. I lived my life in the last six years adrift between two continents and not truly belonging anywhere. My mother helped retain a sense of place and home. When I was frustrated with academia, she encouraged, championed, and collaborated on creative science writing projects that resurrected my joy for scientific inquiry. My father, who believes is financial security and stability now has to continually rechart his expectations from me and is bravely dealing with it. He did fill the house with nature field guides when I was young; this was almost inevitable. Backyard adventures with my nephews and niece, and time with my larger extended family, were reminders that there is more to life than productivity.

I write this thesis, standing on the shoulders of giants – my great grandmother was the first woman in her family to get a college degree. A family history of wealth and privilege is fairly common in the circles I move in, and this journey has been an immense one in acknowledging and being aware of that privilege. While from the outside, a woman of colour finishing a PhD in a premier university in the US, might seem like a significant achievement in the face of adversity, it is in fact built on the foundation of centuries of oppression. Most pertinently, ancestral wealth and social privilege accumulated through caste-based oppression in my country has allowed me higher education and mobility. Columbia University itself is built on past and continued oppression of Black and indigenous lives. In the Andamans, where much of this data is from, it is past genocide and dispossession of indigenous communities that has allowed settler-colonials like me to travel and work there. Perhaps closer to home, power inequalities within scientific research teams that produced the pages of this thesis continue to reek of imperial-colonial and sexist-misogynistic legacies. While my work for this thesis did little to address these, I have learned vastly and reflected widely on some of these issues and my complicity in them. I hope to use the voice afforded this PhD degree in actively dismantling some of these structures.

Introduction

Understanding the patterns of spatiotemporal variation in ecosystem functions and the processes that generate them, or their "drivers," has been a focus of fundamental population and community ecology, and has emerged as the cornerstone of many applied issues in contemporary ecology. In particular, it has become an important part of designing effective strategies to ensure the stability of globally relevant functions, local ecosystem services and human well-being. Net primary productivity (NPP), or the primary production per unit area and time, not only reflects the importance of a region in the global carbon cycle (Bonan, 2008) but also determines the level of most ecosystem functions (EFs) governs the capacity of an ecosystem to deliver provisioning, supporting, regulating and cultural ecosystem services, being foundational to the pathways that result in these quantities (Carpenter et al., 2009). The productivity of ecosystems varies widely across spatial and temporal scales with biotic (e.g., local extinction, trophic structure), abiotic (e.g., precipitation, insolation) and human drivers (e.g., land use, resource extraction) (Chu et al., 2016; Lohbeck et al., 2015; Piao et al., 2009; Sutton et al., 2016). A key relationship to consider, in the face of widespread anthropogenic extinctions across taxa, is the dependence of productivity on biodiversity.

Despite biodiversity being frequently reported as having a positive association with many ecosystem functions, especially productivity, the nature and strength of the biodiversity-ecosystem-function (BEF) relationship can vary widely across ecosystems and scales of inquiry (Isbell et al., 2018). Productivity is strongly regulated by abiotic factors like temperature, rainfall or disturbance, but controlling for these factors, diversity has ubiquitous and strong effects on productivity across ecosystems (Duffy et al., 2017). Biodiversity is expected to increase productivity by either increasing the probability of high functioning species (selection effect), reducing competition for resources (complementarity effect), or by differences in species traits leading to alternating performance under different conditions over time (spatial or temporal insurance) (Isbell et al., 2018). However, factors relating to individual species traits, their distribution across sites, species interactions, as well as the scale of inquiry can alter this relationship, leading to positive, negative or neutral relationships under different combinations of conditions (Chisholm et al., 2013; Connor et al., 2017; Laughlin, 2014; Seabloom et al., 2017). In the face of global change, in particular, climate change, NPP and the dominant role forests play in local and global productivity, have taken center stage in global change biology, environmental science, and environmental policy. However, this large, often unexplained variation in the biodiversity effect on productivity, hinders the translation of this theory into effective policy and management, and presents an immediate need to disentangle mechanisms.

To predict the future of NPP and continued provisioning of associated ecosystem services, it is imperative to investigate the contribution of species diversity to NPP over scales at which species assembly and loss occur. Understanding the role of past, present, and future contributions of forests to NPP has led to numerous theoretical, observational, and experimental studies. The different factors that affect biodiversity and production have been traditionally studied in isolation even though it is well known that they are not independent. Landscape factors like habitat size, shape and isolation can influence the abundance and diversity of species and through these, productivity. Specifically, increased habitat size can support higher number of species, increasing the likelihood of high productive species (De Groote et al., 2017). Moreover, both biodiversity and productivity gradients are structured by environmental factors, such as gradients in light, water, temperature, nutrient inputs or anthropogenic influences (Prager et al., 2017). Additionally, BEF relationships are scale-dependent, often showing patterns that change as one expands the scale of investigation (e.g., from local to global patterns) (Chisholm et al., 2013). At the regional scale, where human interventions for biodiversity conservation and natural resource management are most often focused, the drivers of biodiversity, production and their interactions are poorly understood. This issue is the focus of my dissertation; how do extrinsic ecological processes that influence diversity alter the BEF relationship at the regional scale?

Tropical forests are the largest contributors to terrestrial NPP (Bonan et al. 2008) and have the highest values of biodiversity (Pimm & Raven 2000), but the role of species diversity in maintaining NPP within these hyperdiverse forests is poorly understood compared to other biomes. At the two extremes of spatial scale, BEF mesocosm experiments (Isbell et al. 2018) and global analyses (Poorter et al. 2015; Liang et al. 2016) reveal that plant species diversity is an important driver of NPP. However, at the intermediate, regional scale - the scale at which species assembly and loss occurs, and at which management is usually implemented - the contribution of species diversity to variation in NPP is less clear, beyond studies of manipulated diversity (Huang et al. 2018; but see Oehri et al. 2017). If species diversity within tropical forests contributes significantly to regional NPP, observed high rates of biodiversity loss can exacerbate NPP loss from tropical forests beyond direct loss from deforestation.

In this dissertation, I explored and measured productivity as a complex outcome of the different factors that drive or generate and maintain diversity across scales. I wanted to use the triad of methodologies that defines ecological, and indeed most scientific research; experiment, modeling/theory, and observation. Chapter 1 is an experimental test of the influence of abiotic factors on the relationship between diversity and ecosystem functioning. Chapter 2 is a modeling/theoretical exploration of island biogeographic influences on diversity and ecosystem functioning. Chapter 3 is an observational study of the outcomes of anthropogenic influences protected and non-protected areas and ecosystem functioning. Below, I provided a brief overview of each chapter.

In **Chapter 1**, I tested the combined influence of light and species diversity on biomass gain in tropical forest communities. Seedling recruitment in carbon-rich tropical forests is a result of biotic and abiotic drivers, but their combined outcomes at the community-level remain poorly understood. For this chapter, I focused on the first year of growth of tree seedling communities because of two reasons: a) survival and growth outcomes in the first year predict long-term survival, affects the adult tree community and therefore, future productivity and b) this stage experiences the highest heterogeneity in light environments, depending on their spatial location on the forest floor. I experimentally tested the combined effects of light and species diversity on the growth of mixed communities of tropical evergreen and deciduous seedlings and compared the patterns with long-term plots from the landscape. I found that diverse seedling communities gained more biomass and this effect was enhanced under high light. Moreover, I found that these patterns held across both evergreen and deciduous functional types, supporting expectations from complementarity with non-random overyielding across species. Through these results, I show that environmental conditions that are known to structure biodiversity in high diversity tropical forests can have strong effects on BEF relationships. If these effects accrue through time, they can have significant impacts on the composition and functioning of adult tree communities.

Chapter 2 expands on this inquiry from a controlled environment and into natural communities at the regional scale by employing mechanistic understanding of community assembly. In natural systems, processes of dispersal and competition, that structure communities as a function of both site and species characteristics can influence the strength of the biodiversity effect on production and its change over time. In Chapter 2, I modelled the effect of community assembly processes, specifically, dispersal and competition on the biodiversity-production relationship at the regional scale, akin to the construct used in island biogeographic studies. These relationships can also depend on inherent correlations between traits that drive dispersal and productivity. Starting with a regional species pool with positive, negative or no correlations among the dispersal and productivity trait. I modelled waves of dispersal, competition-driven mortality and subsequent replacement through both dispersal and in situ reproduction. I modelled these using a mechanistic, lottery framework with dispersal, competition and abundance compensation based on well-defined probability functions (D'Andrea and Ostling, 2019). I found BEF relationships at the regional scale were influenced by community assembly processed through their action on correlated traits. Specifically, assembly from a regional species pool with a negative correlation between dispersal and productivity trait was the only case that consistently results in positive, saturating curves. Through this work, I was able to show that basic ecological processes and relationships observed in communities could result in varying, yet predictable BEF relationships, providing a starting point to understand the relevance of the biodiversity effect at the regional scale, where interventions are often focused.

Finally, in **Chapter 3**, I expanded the scope of inquiry beyond a pure focus on ecological processes. Biodiversity and productivity at the regional scale are a cause and consequence of human interventions within the landscape. Through the last century, protected areas have been important human interventions in preventing loss of tropical biodiversity and forest cover (Bruner et al., 2001). Despite substantial ethical and moral concerns in where they are demarcated (DeFries et al., 2005), and who are the stakeholders and decision makers, protected areas have been effective in preventing both biodiversity and forest loss from large anthropogenic drivers (Gray et al., 2016). However, as many protected areas shift in their vulnerabilities from primarily anthropogenic concerns to combined anthropogenic and climate concerns, the effectiveness of protected areas in preserving ecosystem functioning is poorly resolved. In Chapter 3, I tested the effect of landscape processes and protection on the magnitude and stability of NPP across a tropical forest landscape experiencing climate stress. I model the temporal stability of remotely sensed Enhanced Vegetation Index, EVI, a proxy for NPP, from 2000-2021 across the landscape of the Andaman Islands, India, and ask whether protection affects the stability of productivity while controlling for spatial and environmental factors. I find that controlling for environmental variation, protected areas were associated with lower means and higher stability of productivity. Moreover, protection status interacted with environmental variables, suggesting that protection can rescue productivity where ecological factors are unfavorable. Broadly, the results of this chapter suggest that protected areas that are primarily focused on biodiversity conservation are effective in maintaining ecosystem functioning in tropical landscapes contingent on spatial and environmental factors.

Taken together, this dissertation advances our fundamental understanding of the potential effects of biodiversity loss on ecosystem functioning at multiple scales through a framework that considers processes that structure and maintain biodiversity. Results of the experimental study and theoretical approach suggest that policies that target maintaining ecosystem functions in the face of biodiversity loss need to consider ecological processes that structure and maintain biological diversity at the regional scale. On the other hand, the landscape ecology study suggests that interventions for preventing biodiversity loss can have positive outcomes for ecosystem functions under specific ecological conditions. My dissertation identifies key links among these fields that are often studied in isolation. I hope this body of research creates the groundwork for future synthetic inquiry on the assembly, maintenance and effects of biodiversity on key ecosystem functions and the services they provide for humanity.

Chapter 1: Biodiversity effects on seedling biomass growth are modulated by light environment across functional groups

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1.1 Introduction

Diverse forests consistently store more carbon than low diversity stands, but these ecosystem functions can be destabilized by changing environments (Ammer, 2019; Hutchison et al., 2018). At global and regional scales, higher tree diversity in forests is associated with greater productivity and higher contributions towards reducing atmospheric carbon (Liang et al., 2016; Osuri et al., 2020). However, with global environmental change increasing spatial and temporal environmental heterogeneity and driving compositional shifts, the future of forest-associated carbon storage remains uncertain (Feeley et al., 2011). In forested ecosystems, where large, long-lived trees have disproportionate contributions to biomass, productivity and associated ecosystem functions, future functioning depends on mortality and recruitment processes that shape community composition (Bunker et al., 2005). Although the responses of tree mortality to global environmental change are actively studied, recruitment processes have received relatively less attention in this context (but see Zhao et al., 2018). Understanding the importance of diversity to the community function of recruited tree communities under heterogenous environments is crucial for understanding and predicting the future of ecosystem functioning under scenarios of co-occurring environmental change and biodiversity loss.

The contribution of species diversity to ecosystem functioning under varied environmental conditions depends on how these conditions affect species performance. Diverse communities could have higher yield compared to monocultures either due to increased probability of selecting species that are high yielding across all conditions (selection effect), higher yield across all species in mixtures across all conditions (complementarity), each species performing better in a suitable condition (spatial insurance), or differences in species yield but species overyielding in mixtures (complementarity with non-random overyielding) (Isbell et al., 2018). Depending on the mechanisms, trait differences between species and their performance under different conditions can therefore contribute significantly to the biodiversity effect, with larger spatial heterogeneity requiring higher species richness to maintain biodiversity (Thompson et al., 2018, 2021). Tests of these basic theoretical frameworks have mostly involved grassland communities with annuals or short-lived perennials. On the other hand, tropical forests store roughly 55% of terrestrial carbon with 56% of this stored in live biomass (Badgley et al., 2019; Pan et al., 2011). In these forests with long-lived species, the relative importance of diversity mechanisms, fine-scale environmental heterogeneity and high species richness remains unknown.

Intraspecific competition plays an integral role in structuring seedling communities and neighborhood biodiversity can therefore increase growth. Studies with tropical tree species show that species richness and functional diversity in communities have the potential to increase the relative growth rate of individual seedlings and cause overyielding in communities (Kuptz et al., 2010; Sapijanskas et al., 2013; Shen et al., 2021; Van de Peer et al., 2018). Seedling diversity in the neighbourhood can alter seedling root traits directly, altering resource niches and acquisition patterns, and increasing growth at the community level (Madsen et al., 2020). However, seedling competition occurs in an environmental context for limiting resources, and the outcomes of interspecific interactions can change as the environment varies (Butterfield & Callaway, 2013). Biodiversity can therefore increase spatial and temporal insurance, leading to more consistent growth (lower variation over time), and higher biomass accumulation compared to single-species stands (Hutchison et al., 2018; Isbell et al., 2018; Tuck et al., 2016).

In forests with high diversity, light differentially affects growth across functional groups of tree seedlings, potentially structuring local communities and affecting standing biomass along natural gradients. As a result of pervasive light limitation in forest understories, seedlings respond to increased light intensity with increased growth (Kuptz et al., 2010; Lu et al., 2021; Sangsupan et al., 2021; Sovu et al., 2010). Fundamentally, growth plasticity and the ability to utilize increased light is mediated by species identity or functional identity (Kuptz et al., 2010; Tomlinson et al., 2014; Tripathi et al., 2020). Deciduous species grow faster under increased light conditions while evergreen species have slower growth and are sensitive to drought in high light conditions (Tripathi et al., 2020). Mixed deciduous forests, a type of seasonally dry tropical forests, have both broad-leaved evergreen and deciduous species in the same canopy, leading to seasonal heterogeneity of microclimates in the forest floor. These differences can determine the distribution of seedlings in the understory; deciduous species in the canopy increase the abundance and diversity of light-demanding species in the understory by increasing light availability (Souza et al., 2014). Since evergreen and deciduous species are adapted to low and high light respectively, potential diversity effects under different light conditions are likely driven by mechanisms of spatial insurance. However, with increased tree mortality in tropical forests due to drought and extreme climatic events (Aleixo et al., 2019; Uriarte et al., 2019), light environments in the understory are potentially undergoing large-scale shifts, affecting both biodiversity and its effects on ecosystem functioning.

We experimentally assessed the combined influence of light and species diversity on the growth of tropical forest seedling communities and compared dynamics with field communities under natural regeneration in a high diversity tropical forest. We expected that (i) light would increase overall seedling growth and lead to overyielding (increased biomass in diverse communities) in high light treatments compared to shade treatments (ii) decreased intraspecific competition in mixed cultures would lead to higher biomass with increasing species richness and combined with expectation (i), lead to higher overyielding in high diversity, high light treatments (iii) light responses of evergreen and deciduous species would be different, with evergreen species performing better under low light and deciduous species performing better under high light environments, i.e., overyielding through spatial insurance.

1.2 Methods and Materials

We measured the combined influences of two key factors structuring forests – light and species diversity – through experimental methods and long-term data from a tropical forest landscape. The study was conducted in the Andaman Islands, India, an archipelago in the Bay of Bengal. It is part of the Indo-Burma biodiversity hotspot with high species diversity, high endemism and >80% forest cover. Many forests in the archipelago are mixed deciduous forests, where tropical evergreen and tropical deciduous tree species co-exist in the canopy. This has the potential to create heterogeneity in microclimate in the understory. A shadehouse experiment was conducted at the Silviculture Research nursery, Nayashahar, maintained by the Department of Environment and Forest, Andaman and Nicobar Islands. We matched the design of the experimental plots (plot size, range of species richness, abundance) and census methods closely with seedling plots at a permanent forest dynamics plot at Alexandra Island, about 10 km from the experiment site and with mixed deciduous forest type. This plot is part of the Long-term Ecosystem Monitoring Network (LEMoN) in India established to set baselines for forest dynamics and carbon storage across various biomes in India.

Experimental Methods

In a fully crossed experiment, we planted similarly sized evergreen and deciduous seedlings under 3 shade conditions (simulating an evergreen canopy that is closed throughout the year – “closed”, a deciduous canopy that is closed in the wet season and open in the dry season - “deciduous” and a consistently open condition – “open”) and in 3 levels of diversity (1 species, 3 species and 6 species from a pool of 10 species) and measured growth for 1 year (Fig 1.1). Each treatment had 6 replicates each, totaling 54 plots. Each plot of 1 m x 1 m plot was planted with 18 individually tagged seedlings belonging to 1, 3 or 6 species from a pool of 10 species in March 2019. Seedling plots of $1m^2$ in the landscape contained an average of 16 seedlings and had a maximum of 7 species and the planting numbers were matched to these naturally occurring values. Experimental plots were set up using natural, well-mixed soil from an abandoned plot nearby and demarcated as regular rows using bamboo and other locally available building material. Over each plot, standard shade nets of 50% shade were used to cover the canopy at 1.8 m height to mimic either a closed canopy (closed throughout the year) or a deciduous canopy (closed in the wet season and open in the dry season) or they were left fully open throughout the year. The plots were arranged in regular rows with a spacing of 30 cm between adjacent plots and the 9 treatments were randomly distributed spatially among the 54 plots in the experiment.

We used seedlings of ten native forest tree species germinated by ANI forest department nurseries from seeds collected from nearby forests and for the purpose of replanting into selectively logged forests in the area. Six common species – 3 evergreen (*Dipterocarpus griffithii*, *Myristica andamanica* and *Mangifera andamanica*) and 3 deciduous (*Terminalia procera*, *Pterocarpus dalbergioides* and *Planchonia valida*) were chosen as the primary experimental species to make up the monocultures, while the other 4 species (*Artocarpus chaplasha*, *Diospyros sp.*, *Planchonella longipetiolata*, *Walsura* sp.) were planted in a few of the 3 and 6 species plots, to increase variation in species combinations in polycultures. For the 6 primary species, monocultures were planted under each of the 3 canopy treatments. Seedlings were planted into the experiment when approximately 30 cm tall and within the height range in which these are usually replanted into forests. During transplanting, we removed the plants from the potting soil and measured root length, shoot length, basal area and total biomass, allowing us to create allometric equations of this life history stage. Eighteen individually tagged seedlings were planted into each plot in a random order but with equal spacing, 15 cm apart. After transplanting, we watered the plots for two weeks to reduce mortality specifically from transplanting. Other than weeding every month to maintain planting conditions, the plots were left unmanaged until the end of the experiment.

Two months after replanting, we initiated monthly censuses of the plots for 11 iterations. During each census, the height and basal area of every tagged individual seedling was measured. Height of the seedlings were measured using a standard measuring tape (carpentry tape) with an accuracy of 1 mm. Basal area of seedlings was measured using an Insize digital caliper with an accuracy of 0.01 mm. We report values from the final census, conducted in June 2020 throughout this study.

Observational data

Seedling data from long-term plots with comparable species composition and microclimate heterogeneity in the landscape were analyzed to validate experimental results. Under the LEMoN network, a 1-hectare long-term monitoring plot was set up at Alexandra Island in the Andaman archipelago. This site is in a mixed deciduous forest with no recent logging history and protected as part of the Mahatma Gandhi Marine National Park. Within the 1 ha plot, 25 seedling plots of 1 m^2 have been set up on a uniform grid covering the extent of the plot. Within these subplots, naturally regenerating seedlings are tagged, identified to the best possible degree and measured at monthly intervals. For comparing the light environments of the 25 different seedling plots, the canopy cover at each location was measured in December 2020, using a Forestry Suppliers Spherical Crown Densiometer, Convex Model A. At each seedling plot, the percent of canopy cover was calculated as the number of grid cells in the densiometer with canopy cover as an average over four replicate measures. Since much of the canopy cover in these plots is determined by the upper canopy where dynamics are slow, these light environments were assumed to be stable through the years of measurements.

For comparison between observational and experimental data, basal diameter and height of individual seedlings in these plots measured using similar equipment and from three censuses done in June 2016, 2017 and 2018 were used. Height was measured for all individuals in the seedling plot, while basal diameter was measured only for seedlings with height > 1m. For those instances where basal area was not recorded as part of monitoring protocol, basal area was calculated as a function of height using a fit for basal area to height from experimental communities. The allometric equation was $basal\ diameter = 2.34 + 0.08 * height$. Being under natural regeneration, the abundance, species richness and species composition varied across these plots. Over the three censuses, 585 seedlings were recorded, out of which 310 were unique individuals, while the rest were repeated encounters. Gaps in species IDs within the data were filled to the best possible extent using other information in the data sheet – like local names and remarks, but unidentified individuals with no further information were considered as a single species to avoid overcounting of richness. Out of these, 254 of these individuals remained unassigned to species. Identified species belonged to genera that were used in the manipulated experiment, including *Myristica spp.*, *Terminalia bialata*, *Diospyros spp.*, *Dipterocarpus spp.*, and *Planchonia andamanica*.

Statistical methods

All statistical analyses were performed in R version 4.1.3 (R Core Team 2020). For both experimental communities and field communities, we analyzed the effects of experimental treatments of light and species richness on basal area and height using generalized linear models using the *lme4* package (Bates et al., 2015). To avoid the confounding effects of differential survival on total final biomass, we modelled treatment effects on the mean values of surviving individuals in the experiment (n=651) and on observed individuals in the field. Mean basal area and height being continuous, non-zero variables were modelled with gamma errors for continuous, non-zero variables, and because it best fit the distribution.

For the final communities, we assessed the degree of overyielding with species richness and the relative contribution of complementarity and selection effects using methodology from Loreau M. & Hector. A., 2001. We used data from the tenth census of the experiment as one of the monocultures (of *D. griffithii*) had all died by the last census. We used 49 of 54 replicates for this analysis, excluding mixed communities planted with species for which monocultures were not planted in the experiment (see above section). For each species, we calculated the average basal area in a monoculture across all three light treatments (*M*). We calculated relative yield (ΔY) in mixed communities as the difference of the observed yield (*Y*) from the expected simple sum. Further, for each plot, we partitioned this difference into selection effects ($cov(\Delta RY, M)$, where $\Delta RY = {}^{Y}/_{M} - {}^{1}/_{N}$) and complementarity effects ($N\overline{\Delta RY}\,\overline{M}$), where *N* is the planted species diversity. We also used generalized linear mixed models to assess the relative effects of the experimental treatments on basal area and height at the community and individual level at the end of the year. We modelled community basal area and height as a generalized linear model with a gamma family of errors (best fit function and positive definite) with light and diversity treatment as fixed effects. We modelled individual basal area and height as a generalized linear mixed model with a gamma family of errors, using light and diversity as fixed effects and with species slopes allowed to vary across light treatments. We evaluated the goodness-of-fit of each model using R^2.

For observed communities in the field, we modelled total basal area and height of individuals as a generalized linear mixed effects model with a gamma family of errors. We modelled each of these with separate quadratic models of species richness and canopy openness, with intercepts allowed to vary with the year of observation. We compared models with the linear only model (without the quadratic term) using AIC values.

All figures were created using *ggplot2* and *sjPlot* (Lüdecke, 2021; Wickham, 2016).

1.3 Results

Growth at the community level

Seedlings in experimental communities with greater species richness and greater light levels accumulated more biomass on average. Individual wet weight at the initial time point was more strongly associated with basal diameter than height (linear model for weight adjusted R^2 with height=0.26, basal diameter=0.40). Mean basal area in the plant community, indicative of biomass, significantly increased with increasing levels of light and species richness; the 6 species treatment and the deciduous canopy treatment had significantly higher mean basal area than the closed, monocultures (Fig 1.2). Mean height of the seedlings, however, was only influenced by light; the deciduous treatment significantly increased mean height, while other treatments were not significantly different from the closed canopy monocultures (Fig 1.2). Moreover, there were no significant interactive effects of light and species richness treatments on either mean basal area or mean height of the seedlings (Fig 1.2). The differences between communities also persisted through time when analyzed at the monthly timescale (repeated measures ANOVA, Fig S1.2). More trivially, regardless of treatment, higher values of final abundance were strongly associated with higher mean basal area and mean height in these communities (Fig 1.2). Summed across all individuals in a $1m^2$ plot, total height and basal area in final communities were highly correlated (Pearson's correlation coefficient r=0.96). The survival of seedlings in plots was not significantly predicted by either planted species richness or by canopy treatment, but communities with higher proportion of evergreen species had significantly lower survival at the end of the experiment (Fig S1.1).

Species richness in communities increased overyielding and complementarity effect and decreased the magnitude of selection effect across the light environments (Fig 1.3). At the end of 10 months of the experiment, the observed total basal area in many plots was higher than from the expectation from monoculture averages; relative yield was largely positive. The relative yield increased with both light and diversity treatments; two-way ANOVA of observed – expected total basal area was significant for both species richness treatments (F=13.6, df=1, $p<0.001$***)

and canopy treatments ($F=3.4$, $df=2$, $p=0.04$*). Further, the effect of complementarity increased and selection effect decreased with increasing species richness (Fig 1.3). At the highest level of species diversity, the six species treatment, the magnitude of complementarity effect across all light treatments in all communities was positive while the selection effect was negative for all communities. The magnitude of the complementarity effect was positive and significantly different across light and diversity treatments (two-way ANOVA: species richness $F=24.23$, $df=1$, $p<0.001$***, canopy treatment $F=3.74$, $df=2$, $p=0.03$*), while selection effect was significantly different only with species richness ($F=23.3$, $df=1$, $p<0.001$***, canopy treatment $F=1.121$, $df=2$, $p=0.33$).

Predictors of growth at the individual level

Accounting for differences in species identity, individual seedlings that survived until the end of the experiment showed higher gain in basal diameter and height in mixed communities and in the deciduous treatment as compared to counterparts in closed monocultures ($n=651$, $RMSE=3.21$, marginal $R^2=0.11$; Fig 1.4). However, the open canopy treatment was not significantly different from the closed treatment. Models also revealed significant negative interactions between the species richness and light treatments for individual seedling growth (Fig 1.4). Although species richness increased basal diameter and height across light treatments, this gain was lower in the deciduous treatment than in the closed treatment. Basal area and height at planting significantly increased corresponding gains in these response variables within a year of the experiment (Fig 1.4).

Individual growth varied with species in the experiment and under different canopy conditions, but the differences remained consistent across light treatments. The model with species specific slopes, varying with canopy, had the lowest AIC, lower than the random intercept model (ΔAIC (for df=17 and df=12) =2.05). All other models - with no random effects and with only random effects – performed much worse. The response of biomass to species diversity and light dependent on species identity; in the full model with species richness, canopy treatment and slopes varying with species, the random effect of species on slopes was significant (SD of random effect species identity at closed canopy = 1.89; deciduous canopy = 1.09, open canopy = 1.20, residual =3.26). Deciduous species – *T. procera*, *P. valida*, *P. dalbergioides* and the evergreen *D. griffithii* had higher than average growth rates, demonstrated by positive values of the random effect, while *Myristica andamanica* and *Mangifera andamanica* were slower growing species (Fig 1.5). These patterns were consistent between basal diameter and height. Moreover, these differences were consistent across light treatments, although starker under lower light.

Species functional identities affect total basal area and total height of the community. Although functional diversity levels were not fully replicated in the experimental design, the proportion of evergreen species in the community affected the final biomass across all experimental treatments. Overall, increased proportion of evergreen species was associated with lower total basal area and total height across different light treatments (Fig S1.3). In the open canopy treatment, however, a 0.3 proportional abundance of evergreen species had the highest total basal area and total height. Due to a lack of replication of this combination in the closed and deciduous treatments, further tests of this pattern are not possible.

Convergence with observational data

Higher values of biomass accumulation in seedling communities in observational plots was associated with higher species richness and canopy openness. For 25 plots across a range of light conditions and species richness, separate models of total basal area and height in seedling communities showed significant non-linear effects of canopy openness and species richness on these variables. AIC values of all quadratic models were lower than for models with linear terms alone; except for height and species richness, where there was no clear best-fit model (Table S1.1). Total basal area in communities increased with species richness, but peaked at intermediate levels; for a model with observation year as a random effect, the positive linear and negative quadratic term were significant (RMSE=0.5, marginal R^2=0.99, Fig 1.6A). Total basal area had a quadratic relationship with canopy openness (RMSE=0.50, marginal R^2=0.89, Fig 1.6B). Similarly, total height of seedling communities was highest at intermediate openness; a quadratic model of canopy openness was significant (RMSE=0.49, marginal R^2=0.94, conditional R^2=0.99, Fig 1.6D). However, a quadratic model of total height with species richness only showed marginal effect of the linear term of species richness (RMSE=0.51, marginal R^2=0.99. Fig 1.6C). Across all treatments, the values of total basal area and total height in the field observations were lower than the experimental communities, but total height was closer in magnitude (Fig 1.6).

1.4 Discussion

We found that light modulates the positive effect of species diversity on biomass accumulation in seedling communities. In even-aged, experimental tree seedling communities, representing the onset of regeneration, community growth was increased by both light levels and species diversity. Further, we show that this increase in growth at the community level is mirrored at the individual seedling level as well, even across species varying in functional types and growth rates. Ultimately, we show that complementarity with non-random overyielding likely drives biomass accumulation in seedling communities under combined biotic and abiotic influences in seedling communities. Taken together, our results demonstrate a critical need to integrate biotic and abiotic factors that structure diversity and ecosystem functioning. Our results lay groundwork to further understanding of future forest diversity and ecosystem functioning by disentangling processes that structure tree communities under regeneration.

Our results show that in the first and most crucial year for seedling performance, biomass accumulation in seedling communities can be influenced independently and additively by light and species diversity. Seedling communities planted with higher species richness and under canopies with higher light had higher values of basal area and height after a year of the experiment (Fig 1.2) (Sapijanskas et al., 2013; Shen et al., 2021). This demonstrates a potential additive influence of diversity and light on community-level seedling growth. However, the increase in biomass was clearly observable only at the higher level of species richness or in the deciduous canopy treatment indicating that growth responses to these factors are not linear at the community level (Fig 1.2). Lending weight to experimental results, such non-linear responses of plot-level biomass to light were also observed in the naturally regenerating communities; although light increased standing biomass of seedlings, a single plot with the most open canopy had low values of biomass (Fig 1.6). Although there were clear biomass gains with species richness in experimental plots, standing biomass increased weakly along the observed species diversity gradient (Fig 1.2, Fig 1.6). Under natural regeneration, species composition varies with microclimate conditions; for example, deciduous canopies with higher light have higher abundances of deciduous seedlings below them (Souza et al., 2014). Such niche partitioning by these functional groups and associated differences in growth rates could potentially explain weak relationships with species richness in natural communities.

We show that in seedling communities, overyielding with increasing richness can be explained by species complementarity rather than the increased probability of sampling faster growing or higher yielding species (Fig 1.3). Increasing diversity led to overyielding in communities (Fig 1.3), as expected from other studies on forest ecosystems (H. Pretzsch et al., 2015; Sapijanskas et al., 2013; Van de Peer et al., 2018). Beyond species richness, species functional composition influenced the survival and growth of communities (Fig S1.1, Fig S1.2) (Potvin & Gotelli, 2008; Salisbury & Potvin, 2015; Shen et al., 2020; Yang et al., 2013). However, despite considerable differences in growth rates among experimental species, inclusion of fast-growing species alone did not explain the observed increase in biomass in high-diversity treatments (Fig 1.3). In fact, selection effects decreased progressively from low to high species treatments, while complementarity effects increased (Fig 1.3). Such evidence about biodiversity-driven mechanisms in early life history stages of trees is lacking, but our results extend emerging evidence of complementarity in seedlings of forest species under constant environments (Bastias et al., 2021) and suggest that under heterogeneous environments, too, complementarity drives regeneration dynamics.

Deviating from purely competition-driven (complementarity) or probabilistic (selection) effects, our results indicate that the positive effect of biodiversity in heterogeneous environments can be driven by complementarity with non-random overyielding (Isbell et al., 2018). Contrary to expectations of differential responses by functional groups across different light conditions, individuals across species, on average gained more biomass with higher light and higher species richness in the community (Fig 1.4). In other words, fast-growing, high yielding, deciduous species continued to outperform slower growing evergreen species across all conditions, but species diversity and light increased yield for all species, leading to higher biomass in high light, high diversity treatments (Fig 1.5). Light and diversity-mediated increases in individual growth across species suggests strong resource and light competition within these communities, in agreement with other studies on tree seedlings (Lu et al., 2021; Madsen et al., 2020; Promis & Allen, 2017).

Grassland species as well as mature trees show significant spatial and temporal insurance effects, which we did not detect on tree seedlings (Bunker et al., 2005; Isbell et al., 2018; and as reviewed in Loreau et al., 2021). This implies that although functional differences in mature trees might stabilize production through differential growth under heterogenous environments, these differences do not produce similar asynchrony in seedling communities. Instead, strong complementarity in seedling communities is a possible consequence of high intraspecific competition in these stages or growth suppression by plant enemies (Inman-Narahari et al., 2016). Our initial results indicate the need to explore these mechanisms further across diverse ecosystems and life history stages.

Broadly, we show that the potential for diversity to maintain ecosystem functioning is affected by changing environmental conditions. In the highest light conditions in our experiment, biomass at the community level was not improved significantly or consistently with increasing diversity (Fig 1.2). Moreover, for individual seedlings, the proportional gain with increasing light was lower in high diversity treatments, indicating the limits of these positive outcomes, potentially due to other competitive interactions (Fig 1.4) (Rüger et al., 2011). These patterns may be driven by altered aboveground competition for light in high diversity communities, resulting from fast growth by some species and rapid vertical stratification observed during the experiment (Lu et al., 2021; Sapijanskas et al., 2014). Further, although light treatments in our study represent a strong driver of community structure in these forest understories, increased light could lead to both increased photosynthesis and increased water stress with consequent divergent effects on growth, that could interact with species diversity (O'Brien et al., 2017). While our results hold for both these processes acting together and represent realism to understand within-stand dynamics, these effects may be dissociated across forest stands and need further disentangling. More generally, multiple abiotic factors, including light, soil nutrients and soil moisture affect seedling dynamics in these forests. The strength of the biodiversity effect and the mechanisms through which it affects yield are likely to vary across forests structured by different environmental factors (García et al., 2018; Thompson et al., 2018, 2021).

Our findings have broad implications for understanding the interaction between multiple drivers and their influence on ecosystem functioning. Altered environmental conditions through global and local drivers combined with biodiversity loss across biomes have heightened the vulnerability of several ecosystem functions and services (Delzon et al., 2012; Heilpern et al., 2018). However, many mechanistic and simulation models that quantify forest futures continue to deal with single-species stands, simplified dynamics with light and focus largely on tree mortality than regeneration (Hans Pretzsch et al., 2015; Strigul et al., 2008). Our study adds to the understanding of future forest composition through by experimentally disentangling mechanisms that affect early growth stages (Shen et al., 2021; Uriarte et al., 2018). We show that biodiversity effects on biomass gain in early growing stages of long-lived tree species can be modulated by abiotic factors. In the light of renewed understanding from this study, predictions of future composition and ecosystem functioning need to include community-based approaches and regeneration dynamics. Updated models for regeneration that include interactions between biotic and abiotic drivers and outcomes at the community level are crucial for predictions of ecosystem functioning in a changing world.

1.5 Figures and Tables

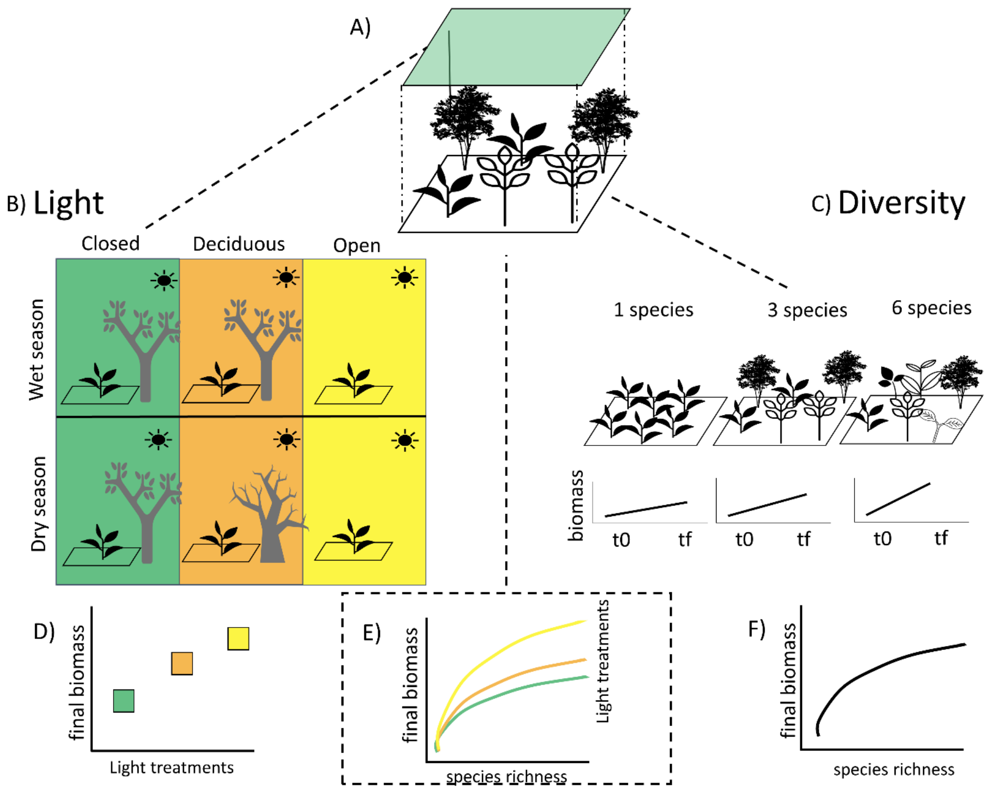

Figure 1. 1 Schematic of experimental setup and expectations

A) Experimental setup with fully crossed light and diversity treatments B) Light treatments in detail – closed, deciduous and open canopy treatments and with colour codes – in the wet and dry season and D) final biomass expectations for each of these based on increased growth in the presence of light. C) Three levels of diversity treatments – 1, 3 and 6 species and biomass expectations between initial and final communities and F) expectations for final biomass between the three treatments – an increasing, saturating curve. And finally, E) combined expectations for community biomass under the combined influence of light and diversity treatments; the influence of species diversity on growth is expected to be modulated by light conditions. Icons from The Noun Project.

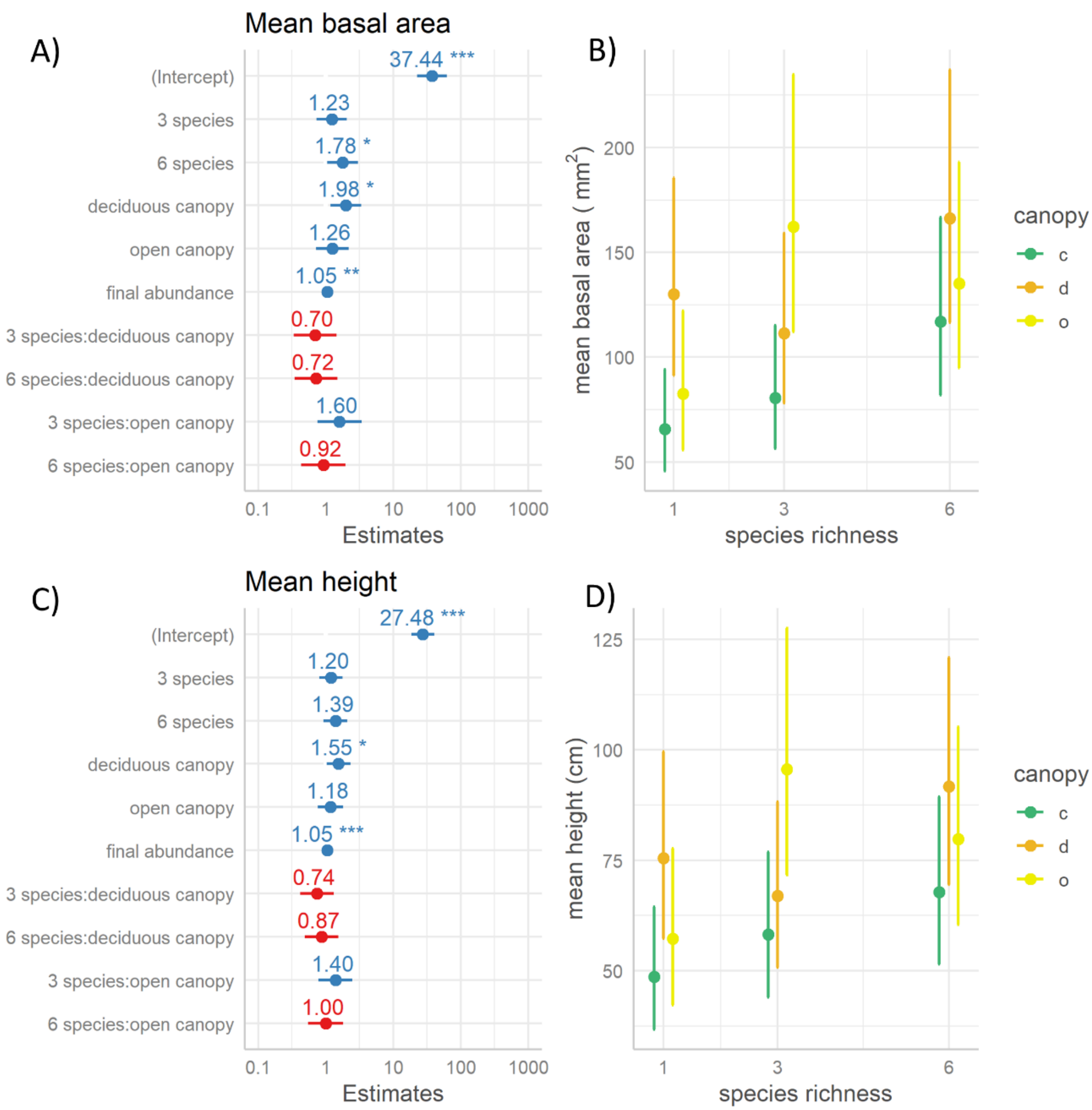

Figure 1. 2 Generalized linear model of mean basal area and mean height of a seedling in a 1m x 1m plot in the experiment.

For mean basal area, deviance is 12.96, df=47, p=0.999, R2=0.41. For mean height, deviance =8.24, df=47, p=1, R2=0.48.

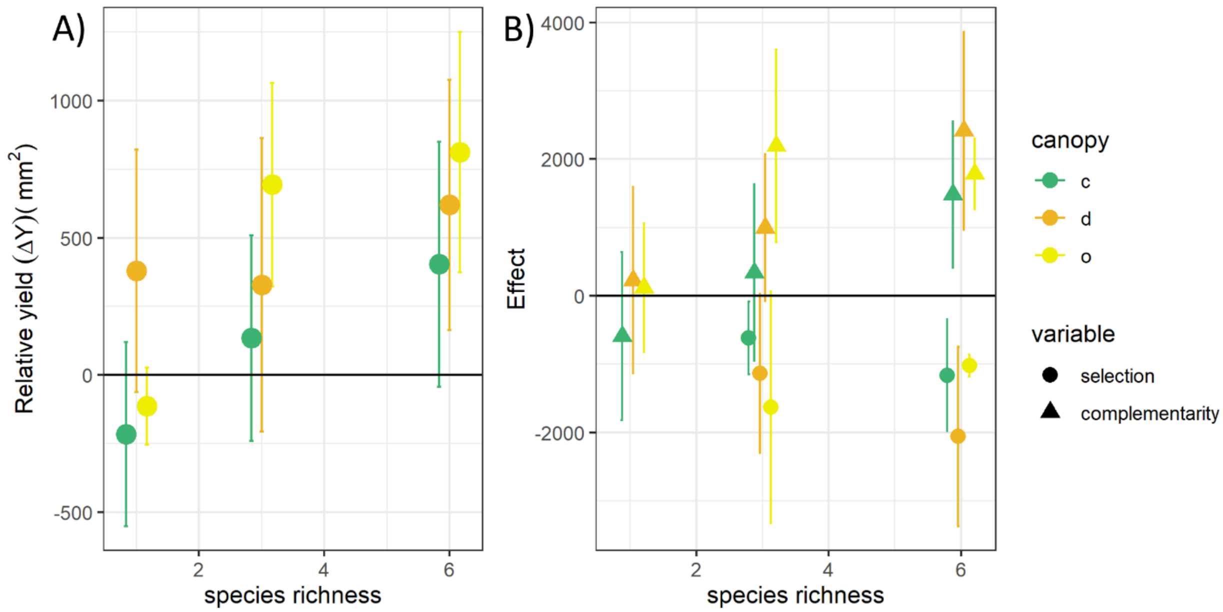

Figure 1. 3 Relative contributions of complementarity and selection effect to relative yield (*ΔY*) of multispecies communities.

A) Plot of the relative yield (*ΔY*) for different treatments, based on basal area measurements. B) The magnitude of complementarity and selection effects, as calculated by the Loreau-Hector method (details in methods). Points represent means and errors bars represent 95% confidence intervals.

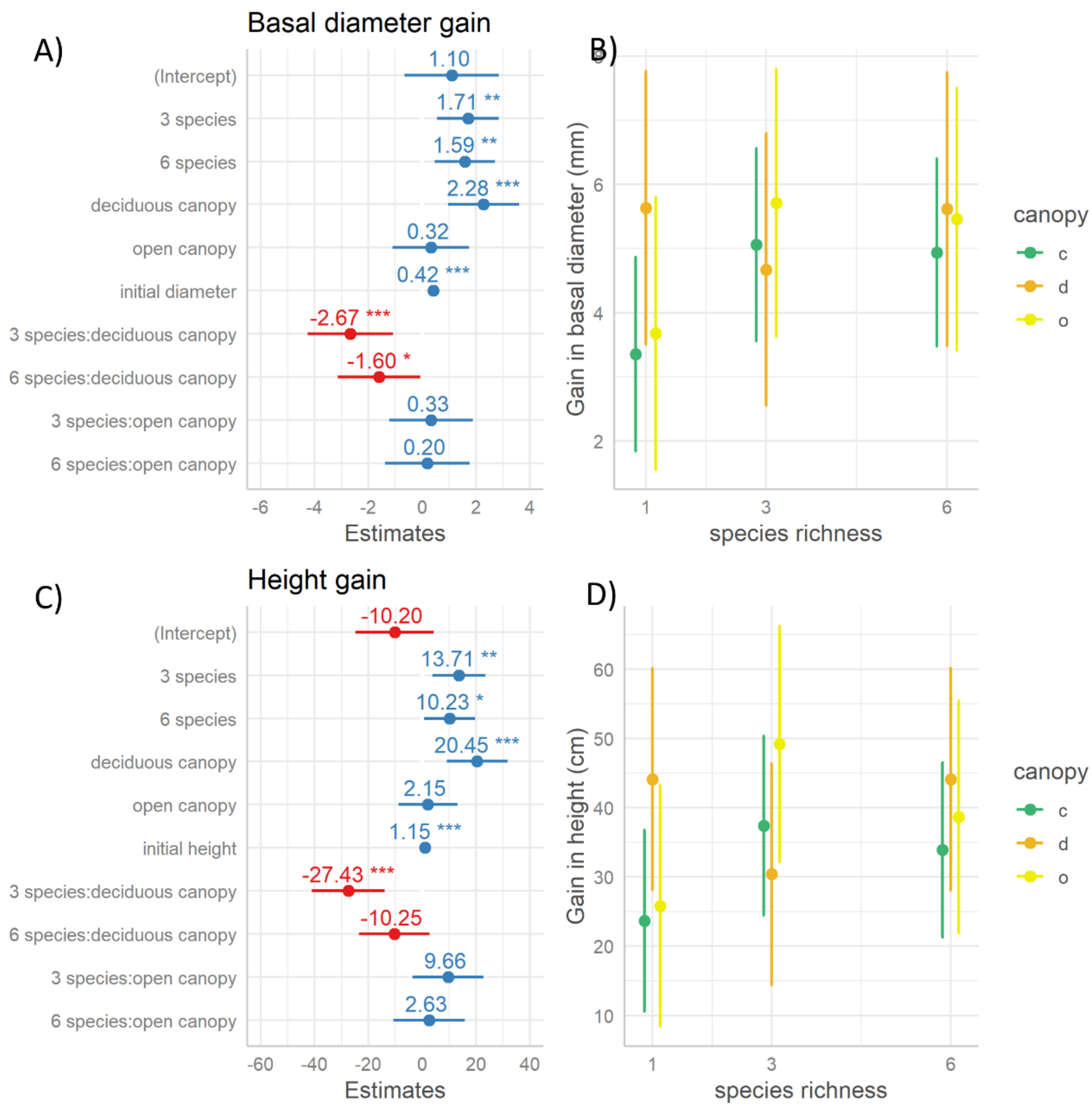

Figure 1. 4 Linear mixed effects models for gain in basal diameter and height between the first and the last census for individual seedlings; random slope model with variable slopes for each species with canopy treatment.

For basal diameter, deviance=3414, total R^2=0.44, fixed effect R^2=0.16; for height, deviance=6200, total R^2=0.50, fixed effect R^2=0.29. For basal diameter and height respectively, A) and C) represent estimated effects of different predictors, B) and D) show predicted responses from the model for species richness and canopy conditions

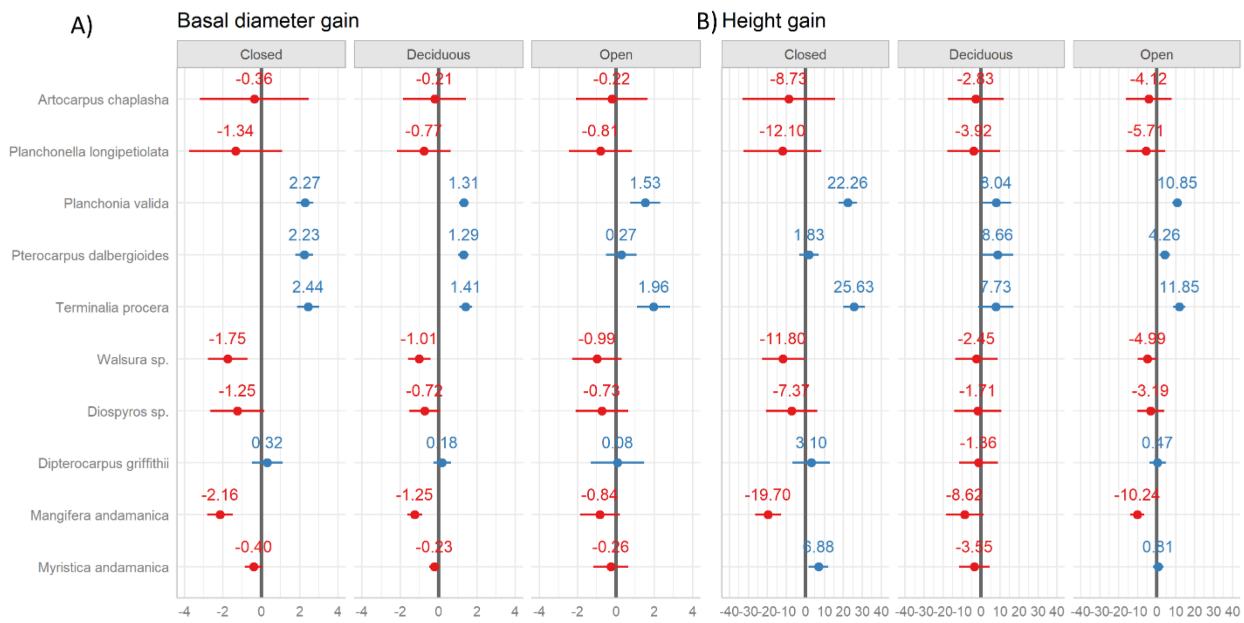

Figure 1. 5 Random slopes of species under different canopy conditions

A) shows random effects for each species for gain in basal diameter and B) for height gain. The top six species represent fast-growing, deciduous species, followed by slower growing, evergreen species towards the bottom.

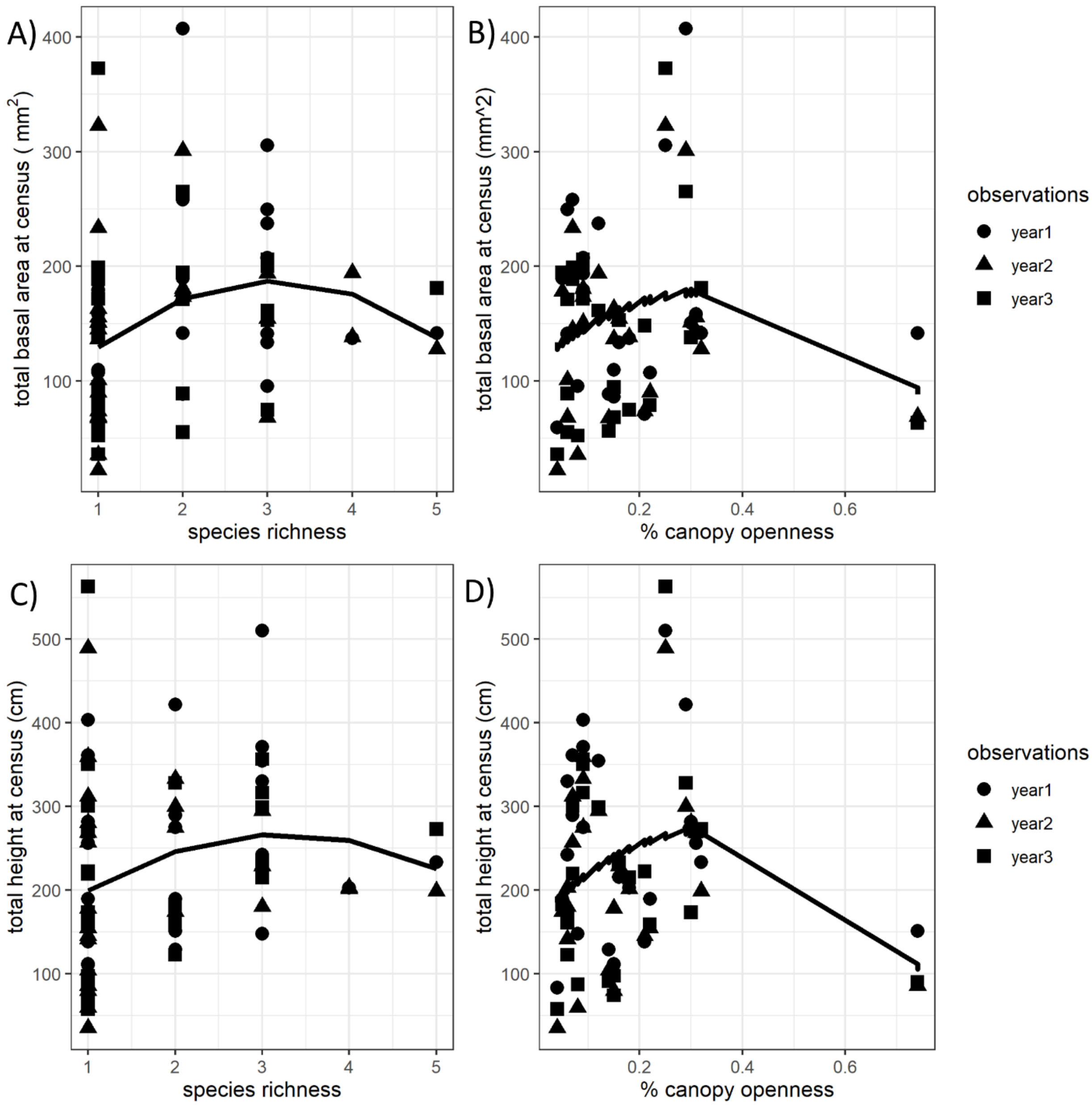

Figure 1. 6 Observational data from long term plots.

Generalised linear models of total basal area as a function of A) species richness and B) canopy openness and total height as a function of C) species richness and D) canopy openness.

Chapter 2: Community assembly processes alter the nature and strength of regional biodiversity-production relationships through trait correlations

Krishna Anujan, Robert Bagchi, Sebastian Heilpern, Shahid Naeem

2.1 Introduction

Although higher levels of biological diversity often yield greater magnitudes of ecosystem functioning (EF), the nature and strength of this relationship is variable across ecosystem contexts (Duffy et al., 2017; Liang et al., 2016). Simultaneously maximizing biodiversity and EFs like carbon sequestration is an emerging focus of natural resource policy and improving mechanistic understanding of biodiversity-ecosystem functioning (BEF) relationships is crucial for this goal (Phelps et al., 2012). This is challenging because BEF relationships that are strongly positive and observable in small-scale empirical studies either disappear or become negative at regional scales of measurement, where multiple processes (e.g., dispersal, competition, disturbance) influence EFs (Chisholm et al., 2013; Thompson et al., 2018). Further, BEF relationships are often stronger when functional diversity is considered, rather than the more ubiquitous taxonomic diversity (Cadotte, 2017; Lefcheck & Duffy, 2015). Understanding how taxonomic diversity correlates with functional trait diversity at the regional scale where natural resources are managed can potentially lend insights into understanding the variability of BEF relationships at this scale (Gonzalez et al., 2020; Thompson et al., 2018).

Predictions for the biodiversity effect on EFs in natural communities can be improved by explicitly considering the processes that structure and maintain diversity gradients at regional scales. Community assembly of species from a regional pool to specific sites occurs through probabilistic processes often conceptualized as hierarchical filters of dispersal and biotic interactions (Knelman & Nemergut, 2014; Laughlin, 2014; Laughlin et al., 2012). Biodiversity gradients at the regional scale are structured and maintained by these sequential and iterative processes that are influenced by both site factors and species factors and result in unique community compositions (Laughlin et al., 2012; Laughlin & Joshi, 2015). Primary production is an additive function of species traits, i.e., the total magnitude of the EF at the community level is the abundance-weighted sum of productivity traits across all species at a site. In the absence of intraspecific variation, high values of production can be linked to either the selection of species with high values of a production trait (selection effect) or by the sum across many species moderate values (complementarity effect) (Ulrich et al., 2021). Diverse communities are both likely to contain high performing species and also average out the effects of low performing species, leading to higher levels of production than low diversity stands (Cadotte, 2017). Production is therefore influenced by species abundances, total diversity and trait values at the site (Kunstler et al., 2016). Scaling this inference across sites, how productivity traits are distributed across the richness gradient as a result of community assembly can influence the BEF relationship.

Along with community assembly processes, functional composition across sites and functional diversity can depend on the relationship among species traits. In general, considering functional diversity and the degree of these correlations among various traits considered can affect BEF relationships (Flynn et al., 2011; Heemsbergen et al., 2004; Lefcheck & Duffy, 2015; Meyer et al., 2018; Mora et al., 2014; Wolf & Zavaleta, 2015). However, species traits are generally linked by physical and evolutionary constraints, leading to correlations and covariation (Mason et al., 2016; Maynard et al., 2015). Specifically examining richness gradients, correlations between traits that predict species vulnerability and traits that influence EFs alter BEF relationships under biodiversity loss (Heilpern et al., 2018). Conversely, correlations among traits that predict community assembly and traits that predict EFs can affect the biodiversity-production relationship. If traits that influence arrival and survival probabilities of species from the regional species pool correlate positively with traits that influence production, diversity gradients may lead to strong production gradients. On the other hand, if diversity gradients are structured by processes that exclude high performing species, it is likely that production either decreases or has no relationship with diversity (Cadotte, 2017).

Finally, community assembly processes can alter BEF relationships over time across empty habitats. Sequential dispersal, competition and compensation in the context of site and species pool can structure species richness, dominant functional traits, biomass and the relationships between them over time (Lasky et al., 2014; Meyer et al., 2016; Mori, Lertzman, et al., 2017; Mori, Osono, et al., 2017; Qiu & Cardinale, 2020). Early successional communities are likely to be composed of species with high dispersal ability and therefore, BEF relationships would be driven largely by correlations between dispersal and production. As communities diversify through mortality and compensation, the BEF relationship is expected to change as well. Natural ecosystems in early successional stages often have high productivity even at low species richness and therefore have flat or negative biodiversity-production relationships as compared to later stages (Grossman et al., 2017; Mori, Osono, et al., 2017). To understand the long-term stability of EF in natural communities, community assembly in relation to landscape factors need to be considered explicitly.

As community assembly processes that generate diversity gradients indirectly impact diversity-production relationships, a trait-based framework that explicitly links the influence of community assembly on diversity and production can potentially provide predictive inferences for BEF relationships, which we illustrate in Figure 2.1. Biodiversity and composition at a location is affected by the interaction between species traits and site properties that influence processes permit or hinder the arrival and persistence of species at different locations (Laughlin et al., 2012). This trait-based assembly framework for biodiversity and ecosystem functioning at a landscape level consists of three fundamental components. First, the dispersal filter determines the colonization probability of a site by a species as a function of both site distance to seed sources and the species dispersal trait. The dispersal distance of a species relative to the distance of the seed sources determines the probability of arrival of a species in a community. Second, following dispersal, we assume that species that colonize a specific site will be in competition with other species at the site, with higher overlap resource-use traits leading to more negative interactions between species. The probability of competition-driven mortality is determined by the sum of negative interspecific competitive interactions each species experiences. Third, post-dispersal mortality through biotic interactions leaves empty spots within a site that are filled by a combination of further trait-driven dispersal from the mainland or source and through *in situ* reproduction from the surviving community, cyclically altering composition over generations. Within this framework, the pattern of diversity across the sites at any time point is determined by two intrinsic factors (dispersal and competition traits), an extrinsic factor (distance of site from mainland), as well as the assembly history of the community.

To test the hypotheses that landscape-level factors influence biodiversity-production relationships, we simulated communities following the trait-based assembly framework presented in Figure 2.1. Specifically, focusing on productivity, we ask how do community assembly processes influence BEF relationships over time? We aim to understand

1) How does colonization of sites through trait-linked dispersal influence the biodiversity-production relationship at the landscape scale?

2) How do biodiversity-production relationships change over time with mortality, compensation and further dispersal post initial colonization?

3) How do positive, negative and null correlations between traits affecting dispersal ability and production in the regional species pool influence the biodiversity effect on production?

We consider a set of equal-area sites with different distances from the mainland and a regional species pool with four traits - two assembly traits, a productivity trait and a regional density (Fig 2.1). The dispersal and productivity traits are further considered to be positively correlated (disp:prod +ve), negatively correlated (disp:prod -ve) or uncorrelated (random); in all cases the competition trait is negatively correlated with dispersal. From a regional pool, we apply assembly processes repeatedly for several iterations and record local community composition across sites. At each time step, we compute the biodiversity effect as the slope of the model between log-transformed production and log-transformed taxonomic or functional diversity across sites.

2.2 Methods

We constructed and analyzed mechanistic models of community assembly for a set of M sites from a regional pool of S species to generate communities that differed in diversity. Here, M was set to 10. Sites of equal area were defined along distances that increased linearly from the mainland; distance from the mainland increased from 5 units (l_5) to 50 units (l_{50}) in increments of 5. In other words, the resultant community at site 1 (nearest) was always closest in species richness and composition to the regional species pool, and the site more favorable for dispersal. At each of these sites, we simulated initial colonization from a regional species pool through dispersal. A species s is present and can contribute to production in the local community Li at a time point if it disperses to the location and survives the effect of competitive interactions from other species also present in the community. The probability of the presence of a species s in a local species pool L at a given time, is given by the conditional probability:

$$P(s \in L) = P(competitive\ success \mid occurrence)$$

Over subsequent time steps, we then simulated mortality through interspecific competition and replaced dead individuals through recruitment from the local species pool or further dispersal from the regional pool. The probability of these events were determined by a fixed parameter, m. We calculated community biomass at each location based on species-specific productivity values and modelled the relationship between this biomass and biodiversity across sites. Site properties and species traits therefore, together determine site-specific probabilities for each species to "pass" through each stage of the filtering process. For each of these processes, we simulated the abundance of each species passing through the filter as a binomial process that resulted in the number of successes in n_s trials where n_s is the species abundance at the previous step, determined by iterative processes of dispersal competition and replacement after initial colonization.

Specifying the regional species pool

We defined a regional species pool of N species, each with 3 traits – each species s is defined by its dispersal trait d_s, biotic trait b_s, linked to the filtering process and the productivity trait p_s, all picked from independent normal distribution as

$$d_s = N(\mu, \sigma)$$

$$b_s = N(\mu, \sigma)$$

$$p_s = N(\mu, \sigma)$$

We set μ =0.5 and σ=0.15 for all three traits and converted all negative trait values to 0. In addition to the traits, each species also has a regional density, k_s, that determined the number of dispersing propagules per unit area. This value was picked from a uniform distribution as the simplest possible case,

$$k_s = uniform(min = 0, max = 150)$$

We picked the minimum and maximum values to be comparable to the regional species richness N, to prevent hyper-dominance of any single species at any site. At values of N that were higher orders of magnitude than the regional species richness, communities were likely to heavily dominated by species with high dispersal, undermining our ability to evaluate the effect of species richness.

Species abundance effects on biomass production are important, however it is not the focus of this study. Although abundances are often distributed non-uniformly across species, we used the uniform distribution to reduce potential impact of species abundance on distribution and contribution to production, and to make the effects of relevant gradients more directly comparable. Moreover, we maintained each local community at constant abundance over each time step through recruitment and dispersal. Although site area can lead to significant differences in dynamics by regulating the number of incident propagules and niches available, we analyze only the effects of distance in this study. By removing all confounding effects of abundance, we are able to isolate true biodiversity effects on production.

Assembling communities through dispersal

We assembled the initial community at each site through dispersal from the regional species pool. We assume isotropic dispersal, uniform in all directions from the mainland, limited only by the dispersal distance of the species and the number of propagules produced. Therefore, the probability of each species arriving at a site is a function of the mean dispersal distance of the propagule (dispersal trait), d_s, the distance l_i to the site and the relative abundance of conspecific propagules in the regional pool, k_s. The strength of the dispersal filter defined the probability of occurrence of a species *s* at a location *i*.

$$P(occurrence)_{s,i} = f(dispersal\ trait, distance)$$

$$= e^{-\frac{l_i}{d_s}}$$

where d_s, the dispersal trait, is the inverse of the exponential rate of decline in dispersal probability with distance, l_i is the distance of the site *i* from the mainland. We assumed total propagule abundance to be much larger than number of sites – making colonization only dispersal limited and not propagule limited. Probability distributions along dispersal trait and dispersal distance from these functions is provided in Figure S2.3. At each site, we sampled the regional species pool (n=300) with different site-specific dispersal probabilities for each species, to get site specific values of n_s for each species *s*.

Competition, mortality and replacement

In the next time-step, we simulated inter and intraspecific competition-based mortality at each site. For simplicity, we focused on competitive success as the main biotic process affecting filtering although trophic interactions and mutualisms are other important biotic factors that might determine the persistence of a dispersed species at a new site. Once a species arrives at a site, biotic filtering defines the probability of competitive success of a species *s* at site *i*. The competitive effect of species r on species s is given by the coefficient A_{sr}. We link this to traits through an equation from (D'Andrea and Ostling, 2019) by

$$A_{sr} = e^{-\left(\frac{|b_s - b_r|}{w}\right)^4}$$

where b_s and b_r are trait values for species s and r linked to biotic competition and w is the niche width across all species. We assumed a uniform niche width for all species in the pool. Therefore, the total value of intraspecific competition on species s is the sum of A_{sr} across all species r in the local species pool, and the competitive success of the species is the inverse of this probability. Following this,

$$P(competitive\ success)_{s,l} = f(biotic\ trait, trait\ composition)$$

$$= 1 - \frac{\sum_r A_{sr} n_s n_r}{\sum_s \sum_r A_{sr} n_s n_r}$$

Where n_s and n_r are relative abundances for species s and r. The denominator is the normalizing factor – the sum of the pairwise competition coefficients across all species in the community. The probability distribution function for a community with equal abundance of each species is given in Figure S2.4. Using this probability for each species at each site, we simulated the number of individuals that died for each species as a binomial process, as in a lottery model. The resultant community was then calculated by updating n_s values for each species s at each site.

After this mortality event, we calculated the total number of dead individuals, g_i, at each site. We replaced any dead individuals using a combination of *in situ* recruitment and immigration from the mainland, continuing to maintain abundances. We defined the probability of a mortality gap being filled by recruitment or dispersal using an immigration factor, m, constant across sites. For a defined value m and number dead g_i at site i, $(1 - m)g_i$ gaps were filled by random sampling of species already at the site (recruitment) while mN gaps were filled by new propagules from the mainland following the same dispersal processes. Specifically, for each species s in the local pool with abundance n_s, the number of new recruits in the next time step is

$$recruits = (1 - m)\frac{n_s}{\sum n_s}$$

This is based on the simple population growth equation, assuming relative growth rate = 1 for all species. The number of dispersed individuals to the site for each species s in the regional pool is given by the dispersal probability outlined in the equation in the previous section. We repeated these processes of competition mortality and subsequent recruitment for 5000 iterations as illustrated in Fig 2.1.

Analyzing the BEF relationship

The primary production of the community is a sum of the production values across all individuals in the site. The productivity trait, p_s represents the production value of species s per unit biomass. Assuming individuals of equal biomass, we computed the expected primary production at each site by

$$B = \sum_{s\ in\ i} p_s n_s$$

where B is the production per unit area, p_s is the per capita productivity trait of a species s and n_s is the abundance of the species at each time step.

We also calculated the species richness at each site, S_i, as the number of species at the site with non-zero abundance. We also compute the functional diversity of each community, F_i, (functional dispersion, (Laliberte & Legendre, 2010)) as the mean of abundance-weighted sum of squares of the three traits in the local community.

$$F_i = \frac{1}{3}\sum x_s - \bar{x}$$

where x_s is any of the traits d_s, b_s or p_s. Using species richness and functional diversity as two distinct measured of diversity, we analyzed the BEF relationship by fitting the function

$$B = c\, S^{\theta}$$

or

$$\log(B) = C + \theta \log{(S)}$$

Where $C = \log(c)$. The log-log fit allows for various relationships – positive concave-down, negative concave-up, and linear - to be described using the same equation, depending on the value of θ. For each time step, we calculated value of θ as the slope of the linear model of *log(B)* as a function of *log(S)*. We tracked the change of θ across timesteps in our simulations.

Sensitivity to parameters

We tested the sensitivity of the final values of θ to correlations between traits at the regional species pool and to the role of dispersal in replacement. For trait correlations, we analyzed three different conditions - a negative correlation between dispersal and productivity ("disp:prod -ve"), a positive correlation between dispersal and productivity ("disp:prod +ve") and no correlation between dispersal and productivity ("random") as in Fig 2.1. We assembled these three regional species pool types by first sorting the dispersal trait and either sorting the productivity trait in the same direction (disp:prod +ve), in the opposite direction (disp:prod -ve) or not sorting the traits.

To test the sensitivity of the θ to the immigration factor m, we ran simulations using three different values of m=0.1, 0.5 and 0.9, to simulate communities that have large amount of continued dispersal over time, equal contribution by recruitment and dispersal and low dispersal leading to large contribution by *in situ* recruitment.

All R code is provided on GitHub.

2.3 Results

Colonization of ten empty sites with equal-abundance communities along a distance gradient from a regional species pool resulted in a gradient of biodiversity and production values (Fig S2.1 a, b). From a regional species pool of 300 species, dispersed communities in the first time-step spanned an order of magnitude in species richness and in functional diversity (Fig S2.1 a, b, c, d). However, the range of production values was lower; maximum values were only three times the minimum (Fig S2.1 e, f). Among the different sets of regional species pool conditions varying in trait correlations, highest species richness was attained by communities with a trade-off between the dispersal trait and the productivity trait (disp:prod -ve), whereas highest values of functional diversity and production were by consistently in communities where all traits were uncorrelated (random). Communities with positive correlation between the dispersal trait and the productivity trait (disp:prod +ve) had intermediate values of maximum species richness, functional diversity and production.

Strength of the BEF relationship

The nature of the curve and the fit differed across correlation structures among dispersal and productivity trait in the regional species pool (Fig 2.2 a, b). Specifically, a regional species pool with trade-offs between dispersal trait and productivity trait resulted in a positive, concave-down curve of production with species richness (exponent θ= 0.2, adjusted R^2=0.85) and functional diversity (θ = 0.5). However, both when dispersal and productivity were positively correlated and when traits were uncorrelated, production had a negative exponential relationship with species richness (disp-prod +ve: theta = -0.07, adjusted R^2=0.69, random: theta = -0.01, adjusted R^2=0.28). The random treatment had a low negative value, very close to zero. Moreover, the fit of the BEF curve was better with the trade-offs between dispersal and productivity, while the log relationship was a poorer fit for the random treatment. On the other hand, the relationship of production with functional diversity was always positive and concave-down with an exponent of 0.5.

After 5000 model runs, with competition-driven mortality and abundance compensation by both *in situ* reproduction and dispersal from the pool (each with probability m=0.5), the qualitative nature of the biodiversity-production relationship for all four cases remained unchanged from the original relationship at the first step post colonization (Fig 2.2 c, d). However, the values of the exponent, θ changed significantly through this process. Dynamics from the regional species pool in communities with a dispersal-productivity trade-off (disp:prod -ve) resulted in production continuing to have a positive concave-down relationship with species richness (exponent $\theta = 0.16$, adjusted $R^2 = 0.66$) and functional diversity ($\theta = 0.5$, adjusted $R^2=1$). Moreover, this condition resulted in high variation in the production of low diversity communities (Fig 2.2 c). Dynamics in communities with dispersal-productivity trait synergy and uncorrelated traits continued to result in production having a negative relationship with species richness (disp-prod +ve: $\theta= -0.09$, adjusted $R^2 = 0.70$; random: $\theta = -0.05$, adjusted $R^2=0.72$). In all cases, production had a positive and concave-down relationship with functional diversity (theta = 0.5, adjusted $R^2=1$). Moreover, although the relationships between the trends between the treatments remained fairly consistent in the final communities compared to the initial colonization step, there was a marginal gain in the maximum production in the random case despite a decrease in the species richness (Fig S2.1).

Trait correlations modify the influence of biodiversity on production; regional species pools with random trait correlations show overall low influence of biodiversity on production compared to the other treatments at all timepoints (Fig 2.3, Fig 2.2). The absolute value of the exponent (θ) of the log-linear fit of production with biodiversity at the first timepoint was an order of magnitude lower than the biodiversity effect in communities with correlated traits. In comparison, in the random treatment, communities showed almost no biodiversity-production relationship. These differences were consistent with time; with the last time point showing similar variation among treatments as the initial.

Change in the BEF relationship over time under trait-based assembly

As community assembly progresses from colonization to the end of the simulation, biodiversity-production relationships changed across the correlation structures we explored (Fig 2.3). Overall, the biodiversity effect and its change over time (final θ – initial θ) were greatest when dispersal and productivity traits traded off (disp-prod -ve) than when they were positively correlated or when traits were uncorrelated (Fig 2.3a, c, e). However, we report a decrease in the biodiversity effect, theta, in two out of three cases; for disp:prod -ve and random (Fig 2.3 a, e). On the other hand, communities assembled from regional species pools with a positive correlation between dispersal and productivity trait showed an increase in biodiversity effect, θ, with time. Across the ten replicate communities assessed, these qualitative changes in the relationship were similar within each correlation structure, although there was considerable variability among the communities in the slopes with time. In all three scenarios, the functional diversity effect increased across time to a small degree.

The immigration factor, the proportion of gaps filled by immigration from the regional species pool, did not significantly affect the final value of the biodiversity effect in the range of possibilities explored (Fig 2.4). The final values of the exponent, theta, did not differ significantly between runs with immigration factor m = 0.1, 0.5 and 0.9, irrespective of the correlation structure within the communities. The difference in θ was indicative of differences in correlation structures, and these differences stayed consistent across values of *m* both within and across correlation structures.

2.4 Discussion

We show that the processes of community assembly can strongly influence biodiversity-ecosystem functioning relationships at the regional scale. Across a set of sites along a gradient of distance from a mainland, cycles of dispersal from the regional species pool, competition-driven mortality and abundance compensation, mediated through species traits, can affect the biodiversity-production relationship. Community assembly processes affect both the magnitude of the biodiversity effect on production as well as the trajectory of the biodiversity-production effect over time in communities post-colonization. Modelling a limited set of assembly processes, we show that considerable variation in BEF relationships can be predictable, furthering basic understanding of spatiotemporal variation in EFs.

Biodiversity-production relationships in realistic systems vary over time with community assembly. Depending on the correlation structure between relevant dispersal, competition and productivity traits, we show that the biodiversity effect on production can predictably intensify or diminish over time even in the absence of other contributing factors than community assembly processes (Fig 2.3). Specifically, in our simulations of dispersal-limited communities where dispersal trait and productivity trait trade-off or are uncorrelated, the biodiversity effect on production decreased over time; in the uncorrelated case, it shifted from a small positive effect to a small negative effect (Fig 2.3 a, c). On the other hand, when dispersal trait and productivity trait were positively correlated, the biodiversity effect increased over time (Fig 2.3 b). In all cases, the effect of functional diversity on production increased with time (Fig 2.3 d, e, f). Our results support prevailing understanding from empirical systems that ecosystem age is an important factor affecting observed biodiversity-production relationships (Guerrero-Ramírez et al., 2017; Lasky et al., 2014; Meyer et al., 2016; Ravenek et al., 2014; Reich et al., 2012). Although studies on restoration ecology deals with change in these relationships over time, most studies of biodiversity and ecosystem function are focused on static variables and single timepoint measures to infer the effect of biodiversity on ecosystem functioning (Laughlin, 2014; Zirbel et al., 2017). Our results show that temporal effects might be important to consider while managing ecosystems for biodiversity and functioning co-benefits.

Eco-evolutionary processes that create linkages and covariation between traits of relevance can have lasting consequences on the biodiversity effect on production. The effects of community assembly processes on the biodiversity-production relationship, both in the initial colonization event and in the final community, are mediated by correlations between dispersal, competition and productivity traits in the regional species pool (Fig 2.2, 2.4). Biodiversity-production relationships vary in their nature and strength with changes in the correlations between filtered traits, i.e. dispersal and competition traits, and the effect trait for productivity. Trait correlations have significant impact on the biodiversity effect, altering it from positive to negative depending on the correlation structure in the regional species pool. In fixed-abundance communities, we find that relationships between biodiversity and production are mediated largely by the correlation between traits and less by dispersal limitation (Fig 2.4). Studies have earlier demonstrated the effect of trait correlations in the number of functions maintained above critical thresholds, but we show that even the shape and nature of individual biodiversity-function relationships can be affected by correlation structures (Heilpern et al., 2020). Our results suggest that predictions for empirical relationships between biodiversity and production at the regional scale can be improved with knowledge of traits that influence context-specific dispersal and competition as well as their correlation with a productivity trait.

In the absence of other processes, communities with high values of production immediately after colonization continue to maintain high values and vice versa, concurrent with empirical understanding at shorter timescales (Fig S2.1, Vellend et al., 2013). The range of values seen in species richness, functional diversity and production at the end of the simulation closely track the first colonization event (Fig S2.1, 2.2). The maximum and minimum values of measured community parameters – species richness, functional diversity and biomass production – at the final community after 5000 cycles of assembly, track the same patterns as the initial community post-colonization independent of differences in trait correlations (Fig S2.1). In these simulations, we show that in the absence of other structuring processes dispersal has strong persistent effects on species richness, functional diversity, biomass production and their relationships, an idea less explored in literature (Wandrag et al., 2017; Zobel et al., 2006). Although changes in plant-soil feedbacks, positive biotic interactions, and simultaneous evolutionary processes are proposed mechanisms for shifts in biodiversity effect (Thakur et al., 2021; van Moorsel et al., 2018; Zuppinger-Dingley et al., 2016), our study was able to recreate the range of observed relationships without invoking complex processes, and focusing only on dispersal, competition and abundance compensation. A critical direction would be to extend this framework into analyzing multiple ecosystem functions as well as ecosystem multifunctionality.

Adding to the critical examination of the utility of biodiversity-ecosystem functioning theory, our study provides a predictive framework for BEF relationships across sites linked by landscape processes, expanding the scale of relevance from coarser global scales to finer regional scales. Despite simplifying assumptions, our simulations at the regional scale, for sites assembled from the same regional species pool, recreate some of the common biodiversity-production relationships observed with global data in realistic magnitudes (Fig S2.2). In congruence with empirical studies, the range of regional species pool characteristics and community assembly processes simulated in our study led to both positive, saturating and negative relationships between species richness and diversity (Duffy et al., 2017; Liang et al., 2016). Moreover, the magnitude of the exponent of the biodiversity effect in our simulations closely matched the range observed in an empirical study across global forests, both in the positive and negative realm (Fig 2.2). The biodiversity effect on production in global forest plots resampled across unrelated geographies, regional species pools and climatic variability, and bootstrapped in Liang et al. 2016, had a mean biodiversity effect of θ=0.26 (SD = 0.09), closely matching communities assembled from a regional species pool with a negative correlation between dispersal distance and productivity trait (Fig 2.4). Further, across all scenarios, functional diversity had a consistent, strong, positive, saturating effect on production, concurrent with prevalent understanding (Wolf & Zavaleta, 2015; but see Finegan et al., 2015). Although our simulations explored only the extremes of trait correlations and interactions observed in nature, it is likely that examining the spectrum of possibilities in between can result in a more expanded range of magnitudes of the biodiversity effect, more similar to natural variability.

Our study explores three discrete possibilities in the range of trait correlations observed in nature and also ignores biotic interactions other than competition. We explored the influence of a positive, negative or no correlation between dispersal and productivity traits. Seed dispersal in trees is strongly linked to seed size and dispersal mode and productivity is linked to wood density, maximum adult size and leaf photosynthetic rates (Chave et al., 2009; J. A. Myers et al., 2004; Perez-Harguindeguy et al., 2013; Tackenberg et al., 2003). Although established correlations exist between growth and mortality in trees, the correlation between dispersal ability and growth or productivity is less clear and can potentially take different forms (but see Terborgh et al., 2020). Besides more realistic correlations and interactions, other relevant traits like species relative growth rate, mortality rate, environmental optimum (e.g., light-demanding vs shade-tolerant species) as well as environmental correlates of the different sites are likely to strongly influence observed biodiversity and production from these expectations. However, our study also ignores critical species interactions like facilitation, seed dispersal and negative density dependence that affect dispersal, growth and mortality uniquely across species (Bagchi et al., 2018; Camargo et al., 2020; Fricke et al., 2018; Wandrag et al., 2017). Since several studies have examined realistic trait correlations and species interactions, combining these within the community assembly framework can further inquiry into the influence of biodiversity on ecosystem functioning.

Conclusion

We show how trait-based assembly processes shape the relationship between biodiversity and ecosystem functioning at landscape scales. Specifically, we compared a gradient of biodiversity generated by varying key factors that influence assembly in a trait-based framework focusing on production as a core function important to most ecosystem functions and the services they provide. We found that the relationship between diversity and production can assume many different forms over the time course of assembly and is strongly influenced by correlations among the key traits of diversity, competition and production. This framework can help provide a predictive framework for variation in BEF relationships, as proposed by recent reviews (Mori, Lertzman, et al., 2017). By focusing on factors and processes at the landscape scale, our study provides a richer set of expectations for biodiversity-production relationships at spatial scales relevant for restoration and management, across a range of scenarios in the absence of other factors.

2.6 Figures and Tables

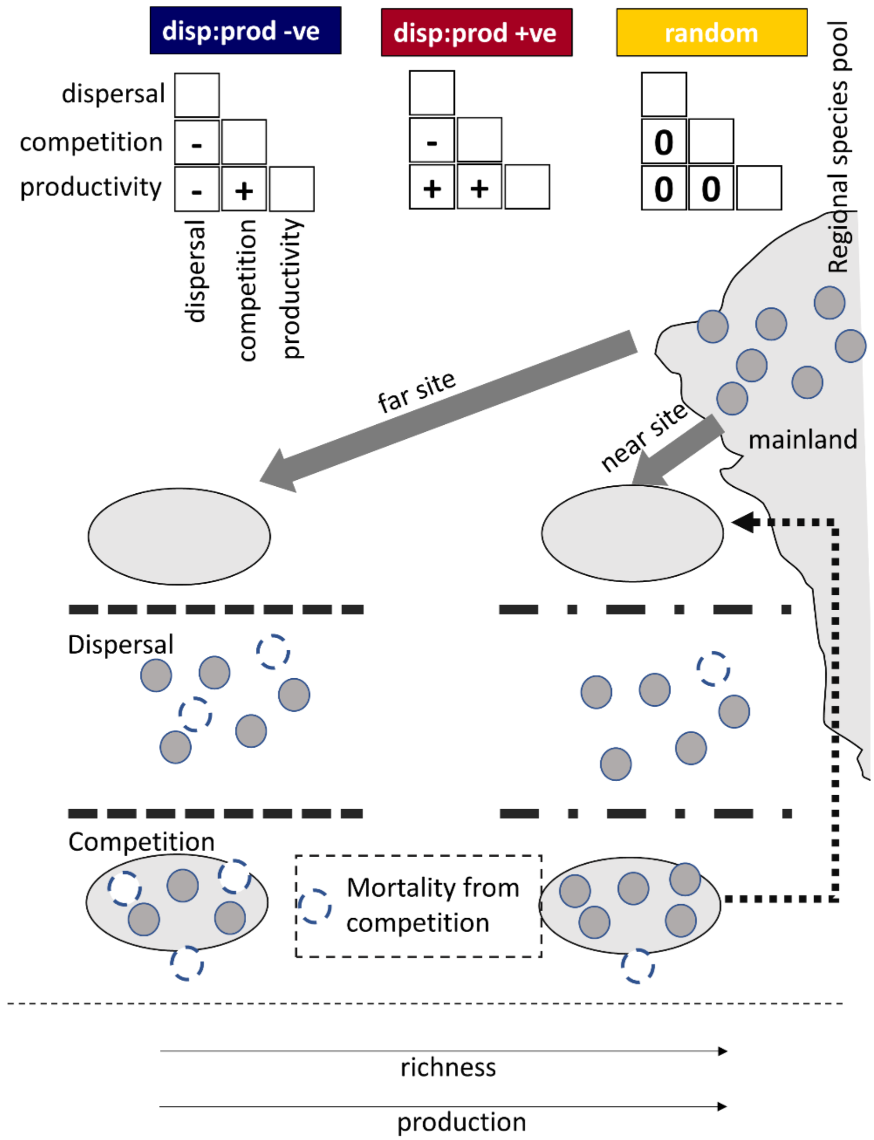

Figure 2. 1 Conceptual diagram of simulation framework. We consider three traits within a species and three correlation structures between them, namely “disp:prod -ve” (a negative correlation between dispersal and productivity), “disp:prod +ve” (a positive correlation between dispersal and productivity) and “random” (no correlation between dispersal and productivity) and build regional species pools. From the regional species pool, a set of sites are colonized based on species traits and distance of the site from a mainland. Trait-based competition among

dispersed species leads to mortality, which are compensated in the next time-step through a combination of *in situ* reproduction and further dispersal. These processes occur in cycles, allowing the examination of BEF relationships across time.

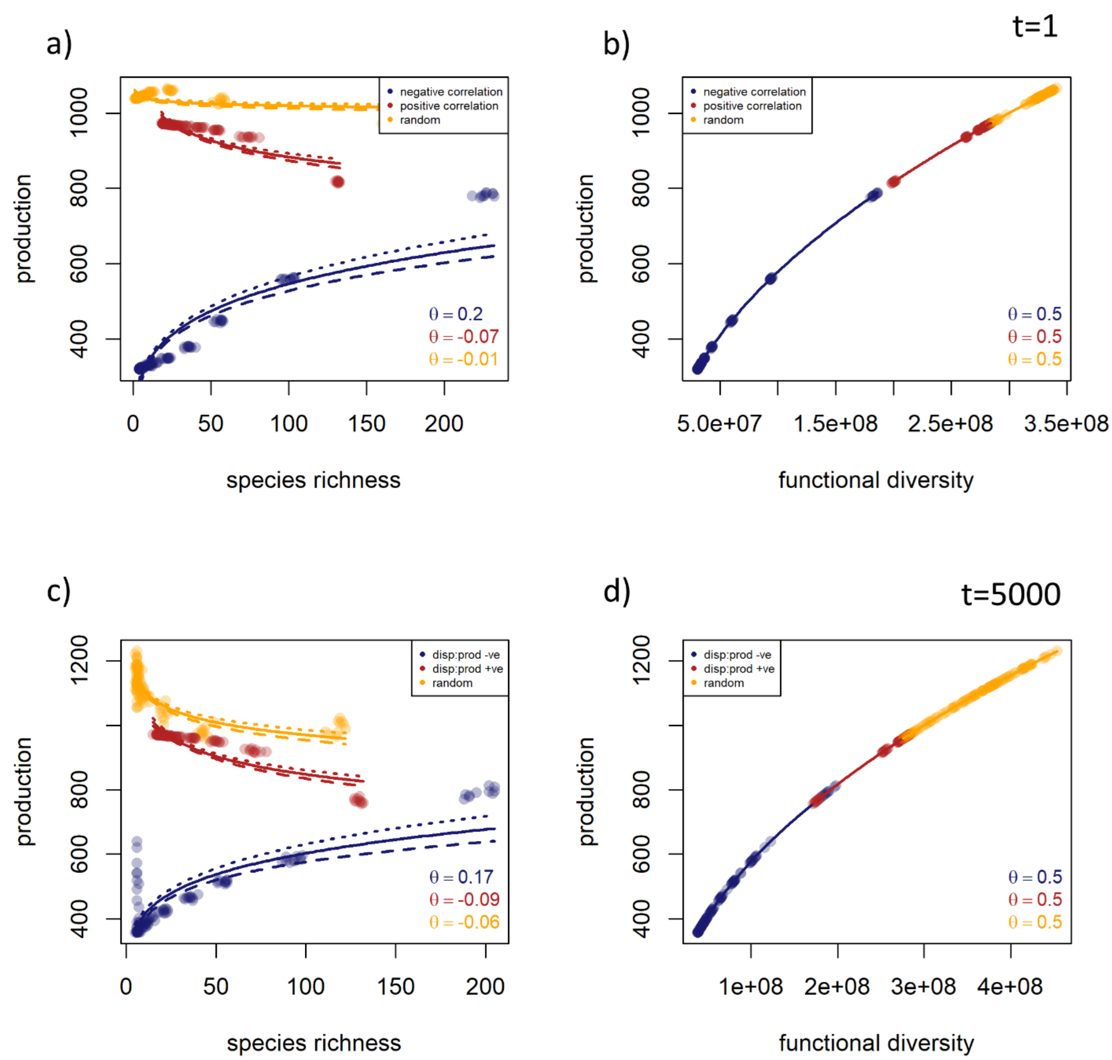

Figure 2. 2 BEF relationships in a), b) the first time step post colonization and c), d) final communities after 5000 time steps in a series of sites along a distance gradient for different trait correlation structures at the regional species pool. θ values represent the slope of the fit of a model log(B) = θ*log(S) + c, where B is production and S is species richness (a, c) or functional diversity (b, d).

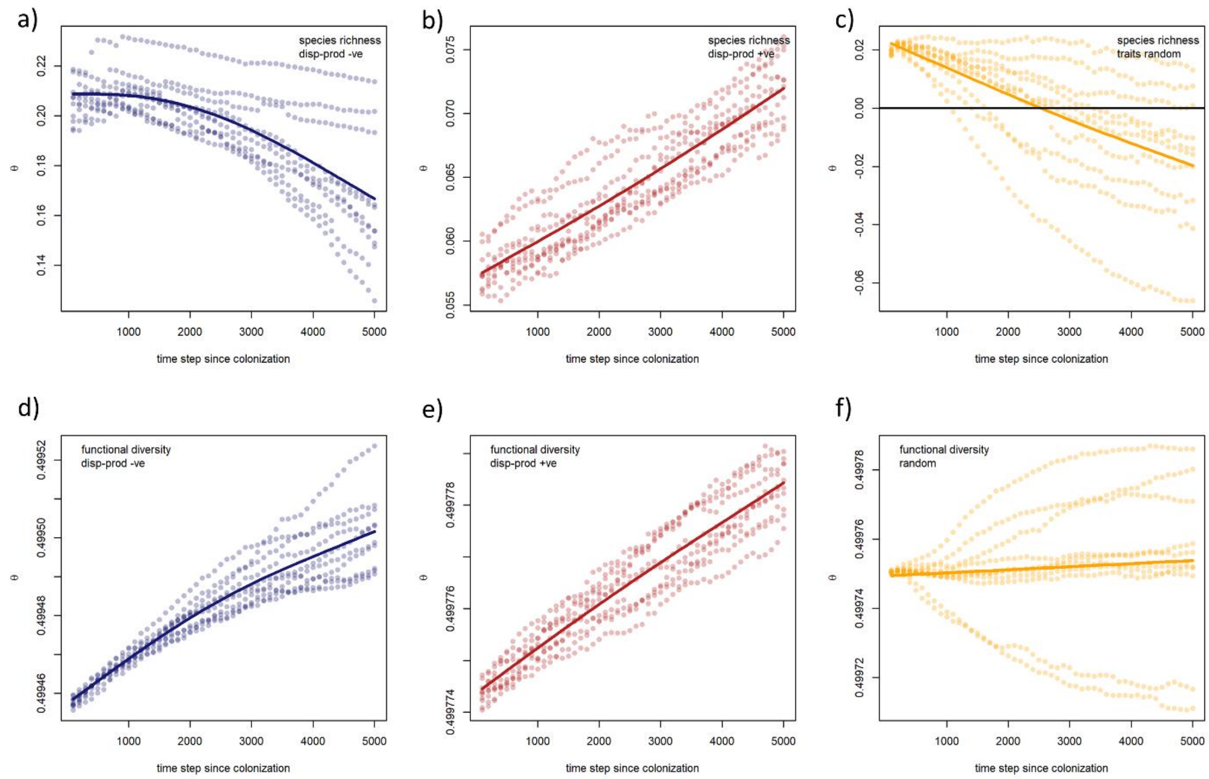

Figure 2. 3 BEF relationships over time. Biodiversity effect, the slope of the log-log relationship between biodiversity and production, across cycles of mortality and dispersal for different correlation structures. a) and d) dispersal-productivity trait negative correlation, b) and e) dispersal-productivity trait positive correlation, c) and f) traits uncorrelated. Immigration factor, m=0.5, i.e. 50% abundance compensation through immigration and 50% through *in situ* reproduction. Lines are smooth spline interpolation fits over the points.

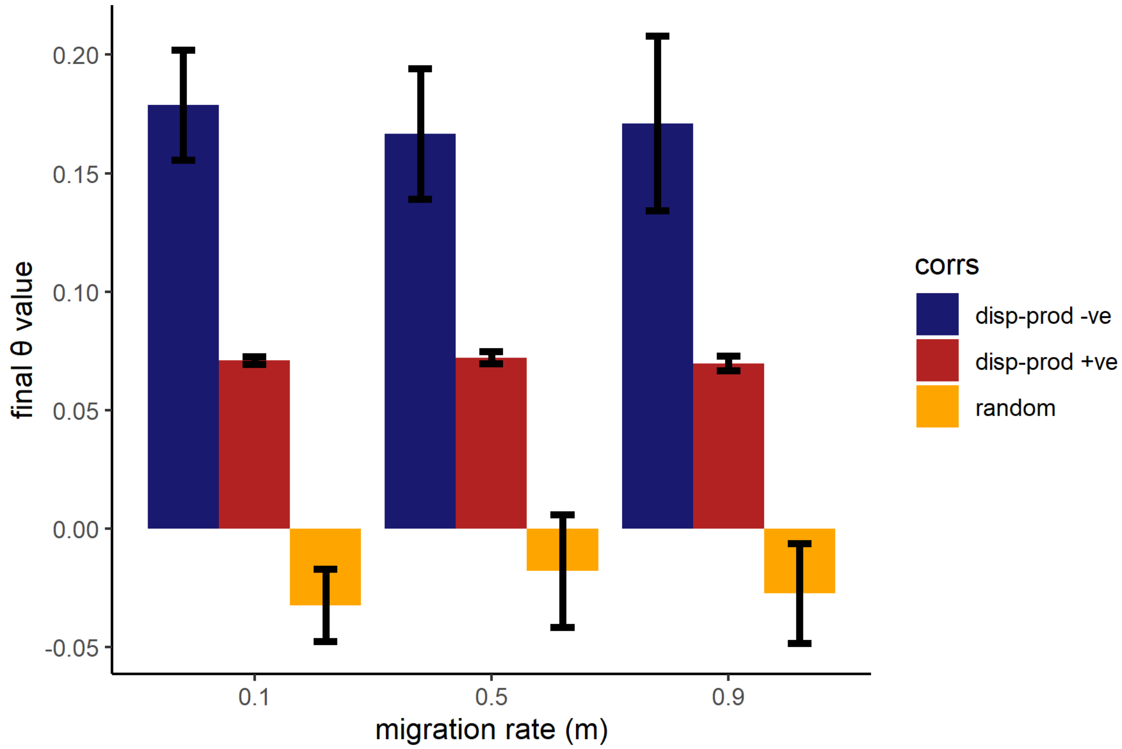

Figure 2. 4 Sensitivity to migration rate. Sensitivity of the final value of θ (the biodiversity effect) to the immigration factor, *m*. The factor, *m* defines the proportion of gaps from competition-associated mortality that will be filled by immigration from the regional species pool. Error bars represent standard deviation values from 10 replicate runs.

Tables

Table 2. 1 Variables used in the model and their definitions

Variable	Definition
Subscript s	Species
Subscript i	Location
d_s	Dispersal trait value for species s
b_s	Biotic competition trait value for species s
k_s	Abundance of species *s*
p_s	Productivity trait of species *s*
L	Local species pool
l_i	Distance of location *i* from the mainland
M	Number of sites
a_i	Area of location *i*
w	Relative niche width
m	Immigration factor; proportion of gaps filled through immigration
B	Biomass production

Chapter 3: Effectiveness of protection in maintaining net primary productivity in a tropical forest landscape is contingent on environmental factors

Krishna Anujan, Jazlynn Hall, María Uriarte, Ruth DeFries, Shahid Naeem

3.1 Introduction

Tropical forests have the highest net primary productivity (NPP) among terrestrial ecosystems, but this ecosystem function is vulnerable to local and global stressors (Giam, 2017; Malhi et al., 2014; Wilcove et al., 2013). Anthropogenic stressors acting at the local scale, like land-use change, have been a major threat to tropical forests (Tabor et al., 2018). In addition, the last two decades have seen large-scale changes in tropical climate; global climate change has altered mean annual precipitation and the frequency of extreme events across the tropics (IPCC 2021). Combined climate and anthropogenic stresses on tropical forests are projected into the future, rendering large carbon stocks potentially irrecoverable in the event of loss (Noon et al., 2021). Ensuring the stability of NPP is important not only for securing these stocks but being correlated with several ecosystem functions and services at local and regional scales, its stability is a crucial foundation of human well-being (Costanza et al., 2017). While interventions like forest protection have largely been effective in preventing forest loss, their effectiveness in maintaining NPP for ensuring the persistence of these carbon stocks under climate threats remains unresolved.

At the global scale, protected areas (PAs) have proven effective in preventing both biodiversity loss and forest loss within their boundaries, despite ethical controversy (Andam et al., 2008; Gray et al., 2016; Krishnadas et al., 2018). However, most analyses assessing PA effectiveness at the global scale are biased towards countries and regions with robust documentation of PA boundaries, with several tropical regions being incompletely assessed (see De La Fuente et al., 2020). Tropical forests are located predominantly in lower income countries with limited documentation of protection strategies, and data from these are not often available in large global databases like the World Database of Protected Areas. For example, as of 2021, this database reports boundaries of 41 PAs in India, whereas the National Wildlife Database Cell reports a network of 987 PAs. At the regional scale, the Andaman and Nicobar Islands, an archipelago in the Indo-Burma biodiversity hotspot, with over 50% of the forest under protection, has none of its over 100 PAs represented in the database. In these tropical biodiversity hotspots with high carbon density, global findings about PA effectiveness are not necessarily informative about meeting their intended objectives on a local level, nor do they address the range of threats currently impacting these ecosystems.

PAs around the world, and especially in the humid tropics, are facing considerable threats from climate variability, threatening NPP, a function that is closely linked to environmental conditions (Noon et al., 2021; Tabor et al., 2018). Extreme events like hurricanes, extreme droughts, floods or fires that significantly exceed long term averages, can lead to losses in tree biomass, reduction in photosynthetic vegetation (Hall et al., 2020; Schwartz et al., 2017), potentially lowering NPP stability. NPP is also influenced by spatial and temporal heterogeneity in environmental factors that affect photosynthesis like light, temperature, precipitation and soil nutrients (Chu et al., 2016; Linger et al., 2020; Murray-Tortarolo et al., 2016; Peng et al., 2016; Šímová & Storch, 2017). Spatial patterns in environmental variables can also lead to high spatial heterogeneity in forest types; tropical evergreen patches, deciduous patches and mixed patches co-exist in a forested landscape, each with distinct species associations (González-M et al., 2018;

Roy et al., 2015). Differences across these forest types, in species composition, traits and biomass can significantly impact spatial heterogeneity in NPP as well as its temporal stability (Rajashekar et al., 2018). Even in the face of multiple co-occurring threats to their stability, PA strategies predominantly involve regulating access to and extraction of forest resources, often with the intent of mitigating the adverse impacts of anthropogenic stressors (Government of India, 1972). PAs, however, are often not directly designed for or explicitly managed to sustain ecosystem functioning, such as NPP. In spite of this omission, PA management, and its interaction with environmental factors, can indirectly impact NPP stability (Koulgi et al., 2019).

Beyond forest loss, evaluating the effectiveness of *status quo* PAs in ensuring NPP stability is crucial to secure vulnerable, and potentially irrecoverable, carbon stocks. Since 2010, agriculture, wildfire and logging have released 4 Gt of carbon (Noon et al., 2021). An estimated 139.1±443.6 Gt of carbon stocks in natural spaces remains potentially irrecoverable by mid-century if lost, and about 23% of this is within PAs (Noon et al., 2021). Tree biomass loss through anthropogenic action like deforestation and selective logging threatens tropical NPP (Giam, 2017; Wilcove et al., 2013). A spatially explicit approach to NPP stability within PAs is also important because threats to tropical forests are spatially heterogenous within the landscape. This biomass vulnerability of tree communities to extreme events is heterogenous within a landscape; smaller forest patches, with irregular boundaries are more vulnerable, as are locations closer to the edge in such habitats (Schwartz et al., 2017). Consequently, NPP is also likely to be less stable along these variables. Moreover, current climatic trends in the humid tropics involve lower total rainfall, increased seasonality and increasing unpredictability, all of which have unique and varied effects on tree functional types (Allen et al., 2017; O’Brien et al., 2017; Uriarte et al., 2018). To effectively manage a tropical forest landscape, the relative importance of environmental variables to stability, their sensitivity across forest types, and the effects of PAs across existing axes of variability need to be assessed.

PAs are often delineated in remote and marginal land in a landscape, rendering their effectiveness contingent on their location and the environment. Tropical NPP is largely driven by tree photosynthesis and respiration, which depends on tree biomass, diversity and the physiological interactions of trees with the environment (Chu et al., 2016). PAs, by supporting high tree cover and high diversity can potentially enhance NPP stability when compared to controls. Diversity can increase the temporal stability of NPP through insurance and portfolio effects (Isbell et al., 2018; Loreau et al., 2021). Species differ in their environmental optima, leading to stable functioning on average in diverse communities, over some temporal environmental variation (Osuri et al., 2020; Schnabel et al., 2019). Current protection measures being effective in reducing forest loss and maintaining diversity, PAs could have increased NPP and stability in locations compared to unprotected areas. On the other hand, PAs are often delineated in poor and remote land, with low productivity and low conversion risk (Defries et al., 2005; Nolte et al., 2013). Due to poor environmental conditions like poor soils, low rainfall or high edge effects peculiar to their location, PAs could be associated with low NPP and/or low stability. To accurately assess the effectiveness of tropical PAs on NPP stability, the effects and specificities of their location must be explicitly addressed.

Here we test the interactions between environmental factors and protection in determining the temporal (inter-annual) stability of NPP in a tropical forest landscape with high density of irrecoverable carbon and high climate risks (Noon et al., 2021). We use a mix of remote sensing, landscape analysis and machine learning to answer this question. We ask the following questions:

1) Within the landscape, what is the likelihood of protection of a site across spatial and environmental covariates? Specifically, we ask what the likelihood of protection is across elevation, slope, precipitation, island size and distance from the sea.
2) How effective are PAs in maintaining NPP mean and stability across environmental conditions relative to unprotected forests? Does effectiveness increase or decrease across the range of precipitation, island area, distance to sea, slope and elevation observed in this landscape?

We use annual mean Enhanced Vegetation Index, a proxy for NPP, derived from MODIS satellite imagery spanning the years 2000 to 2021, and compute inter-annual mean and stability (mean/standard deviation or 1/CV) at each pixel. These two decades represent large-scale environmental change, including the Indian Ocean tsunami, several cyclonic storms and a large ENSO-associated drought event. Within this timeframe of environmental variability, we sample across static spatial and environmental covariates.

3.2 Methods

Study area

We analyzed data from the tropical forest landscape in the Andaman Islands, India, part of the Indo-Burma biodiversity hotspot (Myers et al., 2000). This archipelago of more than 70 islands of varying sizes, has over 80% forest cover and hosts at least three naturally occurring inland forest associations or types; evergreen forests (growing on low, moist alluvial soils or moist loamy fertile hills), deciduous forests (growing on undulating land and poor or comparatively dry soils) and hilltop forests (growing on parches and shallow-soiled slopes of high hills) (Parkinson, 1922). These three forest types are distinguished by different dominant species associations in their canopy; evergreen forests are often dominated by species like *Dipterocarpus griffithii*, *Dipterocarpus turbinatus*, *Hopea odorata*, deciduous forests by *Pterocarpus dalbergioides*, *Terminalia procera*, *Artocarpus chaplasha* and *Canarium euphyllum*, and the uncommon hilltop forests by *Dipterocarpus costatus, Mesua ferrea* and *Canarium manii* (Parkinson, 1922). Moreover, these types can blend in space or be altered over time with logging history, lending to more nuanced recent land cover classifications (Roy et al., 2015). For this study, we considered all areas classified as "forest" - either "Semi-evergreen", "Andaman evergreen", "Moist deciduous", "Secondary evergreen", "Evergreen", "Degraded forest" or "Southern Hilltop" and other classifications that are either settlements, agriculture, monoculture plantations, water body, mangrove or littoral forest were excluded from the study.

Nearly 50% of inland forest is legally protected as Wildlife Sanctuaries, National Parks or Tribal Area Reserves (Fig 3.2, Table S3.1). These PAs are distributed along different forest types, islands of varying sizes as well as other environmental factors like precipitation, elevation and slope, exposing them to varied environmental pressures. Remotely-sensed vegetation indices vary at short spatial scales in this landscape. Although this has been attributed to introduced mammalian herbivores, recent studies show that adult tree communities are not strongly structured by this top-down mechanism (Ali & Pelkey, 2013; Anujan et al., in review). On the other hand, the past two decades have seen large ecological and anthropogenic change in these islands (Oommen & Ramesh, 2019; Srivastava, 2012). The Indian Ocean tsunami of 2004 and the ENSO drought of 2016, as well as several large tropical cyclones in this landscape have affected the structure and functioning of the natural vegetation in this area (Prasad et al., 2010; Rama Chandra Prasad et al., 2009). Moreover, forest that falls outside of the three PA types is either Reserve Forest or Revenue Forest, associated with low or no protection and high human use (Table S1). Parts of reserve forest had been under selective logging cycles and a change in legislation in 2002 has led to halting of the expansion, but intensification in the logging frequency in some of the logged locations, leading to altered biomass and C stocks (Surendra et al., 2021).

Data acquisition and processing

Mean EVI and 1/CV of EVI: To measure the mean and temporal stability of NPP in this landscape, we derived response variables from Enhanced Vegetation Index (EVI), a reliable measure of NPP in forests (Jay et al., 2016; Potter et al., 2012; Turner et al., 2006). EVI is an index that measures the greenness of vegetation, and is less prone to saturation than comparable metrics like the Normalized Difference Vegetation Index (NDVI) in high biomass landscapes like tropical forests (Maeda et al., 2014). We used a pre-calculated EVI from Moderate Resolution Imaging Spectroradiometer (MODIS) Terra Daily EVI on Google Earth Engine, MODIS/MOD09GA_006_EVI, for the time period 2000-2021. EVI was calculated as $EVI = 2.5\ \frac{(NIR-RED)}{(NIR+6*RED-7.5*BLUE+1)}$, with constants specific to MODIS imagery used in previous studies (Rahman et al., 2005; Sims et al., 2006). Annual mean EVI from MODIS was calculated in Google Earth Engine by collating all images across the time period collected every two weeks across the landscape, applying a cloud mask over each image and removing pixels with high cloud cover values. Across cloud-corrected images for each year in the study period, for each pixel, we calculated mean annual EVI, EVIa. We then calculated final response variables, inter-annual mean EVI and 1/CV for each pixel across the timeseries as the mean of EVIa and as the mean divided by the standard deviation of EVIa respectively.

Spatial autocorrelation: We then calculated a spatial autocorrelation layer for each of the response variables, mean EVI and 1/CV of EVI, as the simple mean of all 80 pixels in the 9x9 square surrounding the focal pixel.

PA status and PA type: GIS layers of most protected area boundaries from this landscape are not publicly available through databases such as the World Database on Protected Areas. For this study, we collated published maps of different protected areas from the grey literature. We accessed maps of Wildlife Sanctuaries from the ENVIS Centre on Wildlife and Protected Areas. We accessed physical copies of management plans for forest divisions in the landscape for National Parks and the Tribal Area Reserve. We then georeferenced and hand-digitized these using the software QGIS. We inferred strictness of protection in different management types from the Wildlife Protection Act (1972). Based on these, we classified Tribal Area Reserve as very high protection, National Park as high protection, Wildlife Sanctuary as medium protection and the rest of the forest as low or no protection (Table S3.1). Some part of the forest in the landscape is Reserve Forest, the management type with the least protection under the Department of Environment and Forest. This is a low protection management type, with slightly higher protection than Revenue Forests, controlled by the Revenue Department. Although controlled by different governing bodies and used for different purposes, these represent the higher intensity human-use types in this landscape. For the purposes of this study, these two management types were classified and analyzed together.

Precipitation, elevation and slope: Environmental predictors considered were mean annual precipitation, slope and elevation. A digital elevation model from the Shuttle Radio Topography Mission (SRTM) at 1 arc-second and the slope derived from this layer using the function “terrain” in R and aggregated at the 0.5 km x 0.5 km spatial scale, were used for elevation and slope. Mean annual precipitation was derived from WorldClim/BioClim layer 12. At 1 km x 1 km, this was the only predictor at a coarser spatial resolution. However, since variation in precipitation occurs at a coarser spatial scale, to match the spatial scale, it was resampled to the 0.5 km x 0.5 km spatial resolution. We excluded pixels with precipitation values <2750 mm because of a discrete break in values (n=14).

Island size, %edge and distance to sea: Spatial predictors considered were island size, the percentage of edge habitat within the island and distance to the sea. Island size was calculated by projecting the boundary shapefile of the archipelago into the Projected Coordinate Reference System WGS84/UTM46 (corresponding to the location), and calculating areas of individual features. Percentage of edge habitat was calculated by defining a core habitat 100 m inward from the edge of each island using *gBuffer*, calculating percentage of core habitat in the total island area, and edge percent as 100 - %core area. All pixels were assigned %edge value of the island in which they are present. All islands with 100% edge area thus defined (all pixels 100 m or less from the sea) were excluded from the analysis, because of putative lack of inland forest habitat and potential inaccuracies in environmental layers. For the same reasons, we also excluded all islands with area less than $1km^2$. Distance of each pixel to the sea as calculated by assigning all values on land as NA and calculating the distance to the nearest non-NA pixel using the *distance* function.

Forest type: Finally, a pre-classified land cover layer was used to classify forested pixels into distinct forest types (Roy et al., 2015). This dataset at the 30 m x 30 m resolution was down sampled to the analysis resolution using the “neighborhood” method. This was then reclassified as “Semi-evergreen”, “Andaman evergreen”, “Moist deciduous”, “Secondary evergreen”, “Evergreen”, “Degraded forest” and “Southern Hilltop”.

All analysis was conducted at the pixel level with a 0.5 km x 0.5 km spatial resolution to match the spatial resolution of the response variable. A boundary map of the Andaman Islands (cropped from https://geodata.lib.utexas.edu/catalog/stanford-jm149wc6691) was used to limit the extent of these layers. Pixel level data was analyzed using generalized linear models and random forest classification.

Statistical analysis

All statistical analyses were conducted at the pixel level using R version 4.1.3 (R Core Team, 2022). For statistical analyses, we considered all forest pixels with complete information, n=9308.

Distribution of PAs across covariates: To model the probability of a pixel to be protected in one of the categories, we scaled the values of all predictors between 0 and 1 and modelled

$$PA\ status \sim elevation + precipitation + slope + island\ area + \%edge \\ + spatial\ autocorrelation + \varepsilon$$

as a generalized linear model with a binomial family of errors using the package *lme4* (Bates et al., 2022). We tested the goodness of fit of this model with the R^2, RMSE and using a Hosmer-Lemeshow test of goodness-of-fit with the hoslem.test function in the *ResourceSelection* package (Lele et al., 2019).

Relative effects of covariates on EVI mean and 1/CV: To evaluate the relative effects of environmental and management factors on EVI mean and 1/CV, we ran random forest models with 70% of the unmatched data (total n=9308). The random forest model was specified as

$$EVI\ mean\ or\ \frac{1}{CV} \sim elevation + precipitation + slope + island\ area + \%edge \\ + forest\ type + PA\ status + PA\ type + spatial\ autocorrelation$$

Random forest models were run using the package *randomForest* with 500 trees (Breiman et al., 2022). We calculated importance values of each variable in the model. We also used the *Boruta* package with the same model specification to bootstrap importance values and derive the confidence around the estimates (Kursa & Rudnicki, 2020). We then used the package *pdp* on the main *randomForest* model to calculate partial dependence of the response variable on multiple predictors (Greenwell, 2017). As partial dependence is calculated as a point estimate without an error, we calculated the confidence around this estimate by iteratively calculating partial dependence over 10 repeated random forest runs of the same model. We calculated the mean predicted value for each variable, the standard deviation of the estimates and the 95% confidence interval as 1.6 times the standard deviation. All plots were visualized using *ggplot2* and associated packages *sf*, *scales* and *ggspatial* (Pebesma, 2022; Wickham et al., 2021; Wickham & Seidel, 2020).

Interactions between PA status and environmental predictors: Random forest models are not directly useful for testing interactions between variables and therefore we tested the interactions between PA status and environmental predictors on mean EVI and 1/CV using generalized linear models. To reduce biases in analysis due to unbalanced covariates across protected and unprotected areas, we performed the analysis on a reduced subset in which pixels within and outside PAs were picked using propensity score matching (Butsic et al., 2017). We used packages *MatchIt* and *optmatch*, and discarded points with unmatched covariates from outside PA based on the distance between them using the function *matchit* (Hansen et al., 2022; Ho et al., 2022). This matching resulted in a reduced sample size of 7850 pixels, with equal numbers within and outside PAs (3925 each), distributed more evenly across forest type, precipitation, elevation, slope, distance to sea and island area and slope. Further details and heuristics of matching are provided in the supplementary material.

Using the matched dataset, we tested the effect of environmental and management factors on mean EVI and 1/CV of EVI by modelling these responses using generalized linear models,

$$EVI\ mean\ or\ \frac{1}{CV} \sim elevation + precipitation + slope + island\ area + \%edge + forest\ type + PA\ status + spatial\ autocorrelation + \varepsilon$$

the model with interactions,

$$EVI\ mean\ or\ \frac{1}{CV} \sim elevation + precipitation + slope + island\ area + \%edge + forest\ type + PA\ status + PA\ status * elevation + PA\ status * precipitation + PA\ status * slope + PA\ status * island\ area + PA\ status * \%edge + PA\ status * forest\ type + spatial\ autocorrelation + \varepsilon$$

the model without forest type

$$EVI\ mean\ or\ \frac{1}{CV} \sim elevation + precipitation + slope + island\ area + \%edge + PA\ status + PA\ status * elevation + PA\ status * precipitation + PA\ status * slope + PA\ status * island\ area + PA\ status * \%edge + spatial\ autocorrelation + \varepsilon$$

and the null model with only spatial autocorrelation

$$EVI\ mean\ or\ \frac{1}{CV} \sim spatial\ autocorrelation + \varepsilon$$

We evaluated the best fit model using AIC, with a criterion of $\Delta AIC \geq 6$ and by calculating R^2 for individual models using functions from the *modelsummary* package (Arel-Bundock, 2022). Predictions and plots from these models were created using the package *sjPlot* (Lüdecke, 2021).

3.3 Results

What is the likelihood of protection of a site across spatial and environmental covariates?

Protected areas across the landscape are not randomly distributed across environmental variables (RMSE=1.09, Hosmer-Lemeshow goodness of fit X^2 = 442.43, df=8, p<0.001***). Pixels in larger islands and islands with more edge habitat are more likely to be protected than smaller islands or more regularly shaped islands (Fig 3.3). Moreover, locations with lower mean annual precipitation, lower elevation and gentler slopes are likely to be protected than high precipitation, high elevation or steep sloped regions. However, these environmental factors are also correlated with each other, with slope and elevation having the strongest correlation (Pearson's correlation coefficient, r=0.54), followed by precipitation and %edge (r=0.51) (Fig S3.3).

How effective are PAs effective in maintaining NPP mean and stability across environmental conditions?

Environmental factors rank higher than protection status in predicting the mean and stability of EVI across the landscape (Fig 3.4). Random forest models of mean EVI and EVI stability explained substantial variance (R^2 mean = 0.84, stability = 79.63). Aside from spatial autocorrelation, both spatial and environmental variables ranked high in predicting both mean and stability of EVI. Distance to sea (mean importance = 33.87), precipitation (12.47) and %edge (11.01) were the top three predictors for mean EVI while precipitation (20.48), %edge (18.01) and island area (14.84) were top three for EVI stability. Although confirmed as an important variable, PA type and PA status had low importance in explaining variation for both mean EVI (mean importance value PA type = 5.27, PA status = 4.83) and stability of EVI (PA type = 7.53, PA status = 4.92).

Spatial and environmental drivers of EVI mean and stability are different (Table 2). EVI mean and stability are correlated (Pearson's coefficient $r=0.57$) and stable EVI is predicted by high mean (estimate=12.42, $p<0.001$). Distance to sea decreases both mean and stability of EVI. Mean annual precipitation significantly increases mean EVI, while island area and %edge decrease it significantly. On the other hand, besides distance to sea, elevation is the only environmental variable that significantly decreases EVI stability; no other variable has significant effects irrespective of management type. While most of these factors match the results of the random forest model, precipitation was the second most important variable in the random forest to predict EVI stability but was not significant in the GLM analysis, when PA status was not considered (Table 2).

Does effectiveness increase or decrease across the range of precipitation, island area, distance to sea, slope and elevation observed in this landscape?

Environmental factors and protection status interact to predict mean EVI and stability (Table 2, Fig 3.5). Protection significantly increases mean EVI but decreases its stability (Table 2). The full generalized linear model with all predictors and interaction of protection status with every environmental variable was the best candidate model for both stability and mean EVI (R^2=0.76 and 0.63 respectively); it performed better than the model without forest type (ΔAIC mean = 14.19, stability = 44.98), the model without interactions (ΔAIC mean = 89.48, stability = 29.83) and the null model (ΔAIC mean = 389.32, stability = 466.74). The models also improved the goodness of fit compared to the null model (R^2 null of mean = 0.60, stability = 0.74).

Protection increased stability at low EVI but decreased it at high mean EVI (Fig 3.5). In the full model for mean EVI, interaction of protection status with all environmental variables except slope was significant (Table 2). Protection and precipitation interacted negatively; at low precipitation pixels, protection increased mean EVI while the effect decreased with precipitation. Similarly, protection increased mean EVI in smaller islands and in islands with higher edge. Finally, although precipitation itself did not significantly alter the stability of EVI, it interacted significantly with protection. EVI stability had a positive association with precipitation under protection while they were negatively associated in unprotected pixels.

Forest type affects the stability of EVI and the mean (Fig 3.6). Random forest models and GLM predictions agreed on the overall low effect of PA on EVI mean and stability across forest types. In both models, degraded forests had the lowest mean EVI across the years. Although GLMs predict overlaps in the estimates for most forest types, random forest models show that semi-evergreen and moist deciduous forests have lower mean than other types while moist deciduous forests have significantly higher stability than other types. Random forest models do not account for interactions between the forest type and protection status and predicts a decrease in both EVI mean and EVI stability with protection across all forest types (Fig 3.6 c, d). On the other hand, in GLMs, where interactions have been accounted for, protection increases the stability of evergreen and secondary evergreen forests (Fig 3.6 a, b). Protection also increases mean EVI for Andaman evergreen and other evergreen forests.

3.4 Discussion

We show that NPP and its stability within a tropical forest landscape can be predicted interactively by environmental factors and protection status. The temporal mean and stability of remotely-sensed EVI across two decades in a heterogenous tropical forest landscape was predicted by environmental factors, protection status and their interactions. We show that pixels under protection can have higher mean NPP in areas where some environmental factors are unfavorable for supporting high values. Our results build on existing understanding of spatiotemporal dynamics in tropical forests by combining the effects of environmental and management factors and extend the framework of PA effectiveness into the measurements of ecosystem functioning.

Across a period of high environmental variability in a tropical forest landscape in the Andaman Islands, the mean and temporal stability of NPP was predicted largely by environmental factors. The highest ranked predictors for mean EVI were distance to sea, precipitation and the percent edge in the island, while for stability, it was precipitation, edge percent and island area (Fig 3.4). The dominant land cover type in the landscape is evergreen forest, requiring high rainfall and potentially explaining this pattern (Roy et al., 2015). Moreover, habitats with high edge percent are usually smaller islands with irregular boundaries which makes for exposed habitats and vulnerability to wind and rainfall and our results align with this understanding (Schwartz et al., 2017). Regardless of protection, areas with higher rainfall and in islands with lower edge percent had higher mean EVI across the years (Table 3.2). Further, inland areas had lower mean EVI and removing the confounding effect of high EVI leading to higher stability, areas further inland also had higher stability. In an island landscape, habitats along the edge are more exposed and therefore more likely to experience mortality and biomass loss, this is an unexpected result. This could be related to structural protection from disturbance by coastal mangroves and littoral forests that were excluded from this study (Dahdouh-Guebas et al., 2005). Another potential explanation is changes in forest composition from coast to inward in terms of species composition and diversity (Franklin et al., 2006; Gutiérrez et al., 2009).

We find evidence that PAs can rescue NPP in locations where environmental factors predict low baselines. A critique of PAs is that they are often located in remote and marginal land that is unsuitable for agriculture or settlements (Defries et al., 2005; Nolte et al., 2013). We find evidence in our landscape for that as well – areas with low precipitation, low elevation and in islands with higher edge habitat are more likely to be protected, biasing the potential for PAs to affect NPP (Fig 3.3). Within this high rainfall region, with a range from 2750 to 3200 mm mean annual rainfall, mean EVI increased along the precipitation gradient (Fig 3.5). At low rainfall, predictions for PAs were higher than for unprotected pixels. Similarly, although edge habitats decreased mean EVI, protection buffered against this decrease (Fig 3.5). Precipitation although was not a significant predictor of EVI stability, it had a significant interaction. Although stability of unprotected areas decreased with precipitation, it increased for PAs. Moreover, protection significantly improved functioning in the two most vulnerable forest classes – it increased the mean EVI of degraded forests and the EVI stability of secondary evergreen forest (Fig 3.6d).

Forest types had significantly different mean and stability of NPP, providing a start point to understand ecosystem resilience in such landscapes. While tropical forests continue to respond to changing precipitation regimes, whether one type of forest assemblage can endure over the other is an open question (Zuidema et al., 2013). Among the forest types in the landscape, Andaman evergreen was the most dominant and had some of the highest values of mean NPP (Fig 3.6a). On the contrary, some evidence from our study suggests that moist deciduous forests, although less abundant had comparable mean and higher EVI stability than the dominant

Andaman evergreen forests (Table 3.2, Fig 3.6d). We show that unprotected evergreen forests continue to be stable against environmental variability, aligning with some forecasts of other Asian tropics (Scheiter et al., 2020). While our study was not balanced in our design across forest types, our results pose open questions for future inquiry. Although we report relative values of EVI stability across forest types, baseline variability and how present-day values of stability predict long-term stability in the face of altered climate need further exploration.

Controlling for environmental variables, we show that while protection status increased mean NPP, it decreased NPP stability when compared to low protection forests or unprotected areas. Our results show that protection interacts with environmental factors to predict both mean and stability of EVI (Table 3.2, Fig 3.5). While our study does not have accurate measurements of anthropogenic impacts across this landscape, in this landscape with low population density, PA status could be a reliable proxy for on-ground anthropogenic disturbance. Although our result for mean follows the expectations for PAs from published studies at the global scale, our observations on stability contradicts conclusions from analyses of PA effects on reducing forest loss (Andam et al., 2008; De La Fuente et al., 2020). This is also an effect of a landscape with low population density, low anthropogenic impact on the environment and high biomass. This indicates that PAs in their status quo may not have positive impacts on temporal stability of NPP in a forest landscape under low anthropogenic, but high climate stress (Noon et al., 2021).

Although these patterns may be different at the global scale, planning is a regional problem and the effectiveness of PAs needs to be understood at the landscape scale where priorities can be assessed. Global studies that have examined the effectiveness of PAs often measure local effects, within and outside the PA and combine many such cases (De La Fuente et al., 2020; Gray et al., 2016). Knowing that PAs are not randomly located, disentangling effectiveness from artefacts of location becomes difficult in the absence of appropriate controls. Our study provides assessments of environmental and management factors that affect stability at the landscape scale, where decisions can be made to prioritize conservation. We also analyze a hitherto incomplete dataset of PAs in the landscape, filling information gaps on boundaries and allowing a full landscape approach. Our results from examining stability of NPP in PAs in the context of their ecology, suggests that for managing landscapes for ecosystem services, we need to identify locations most vulnerable to change under ongoing and predicted threats.

Our study modelled NPP as predicted by static environmental variables, while environments in these regions are currently highly dynamic. By the end of the twenty-first century, average temperature over India is projected to rise by approximately 4.4C and there have been shifts in rainfall with more frequent dry spells (Krishnan et al., 2020). More gravely, our study shows that in this landscape, low elevation and nearness to coast predict high mean and stability of EVI (Fig 3.5). Sea level rise in the next few decades affecting coastal and small island ecosystems highly vulnerable is therefore likely to threaten habitats with high NPP in this landscape (IPCC, 2022). These ecosystems also are routinely ignored even in country-specific climate conversation, while it is known that small island economies are most vulnerable (IPCC, 2022; Krishnan et al., 2020). To combat these, management plans and State Action Plans for climate change have been implemented but are revised only at decadal timescales. Moreover, current management strategies within these plans are limited to protection against anthropogenic stressors, while long-term resilience strategies that account for species physiology in novel climate have been implemented in natural resource management elsewhere with some success (Chmura et al., 2011; Williams & Brown, 2016). To effectively manage ecosystems under a volatile climate, threats and effectiveness in the context of ecology needs to be assessed routinely and management plans updated iteratively at timescales that match change (Bergstrom et al., 2021; Tompkins & Adger, 2004).

Our findings have implications for understanding the role of forest protection, designed to prevent forest loss, in maintain forest functioning tropical landscapes under climate threat. Our framework integrating environmental and management drivers reveals interactions between them in maintaining NPP stability. With global climate change affecting tropical systems through changing coastlines, rainfall and extreme events, securing the future of forest-associated ecosystem functions and services is paramount. We suggest that similar frameworks be implemented across tropical forest landscapes to identify priority locations where protection can be effective in buffering forest functioning in the face of altered climate.

3.5 Figures and Tables

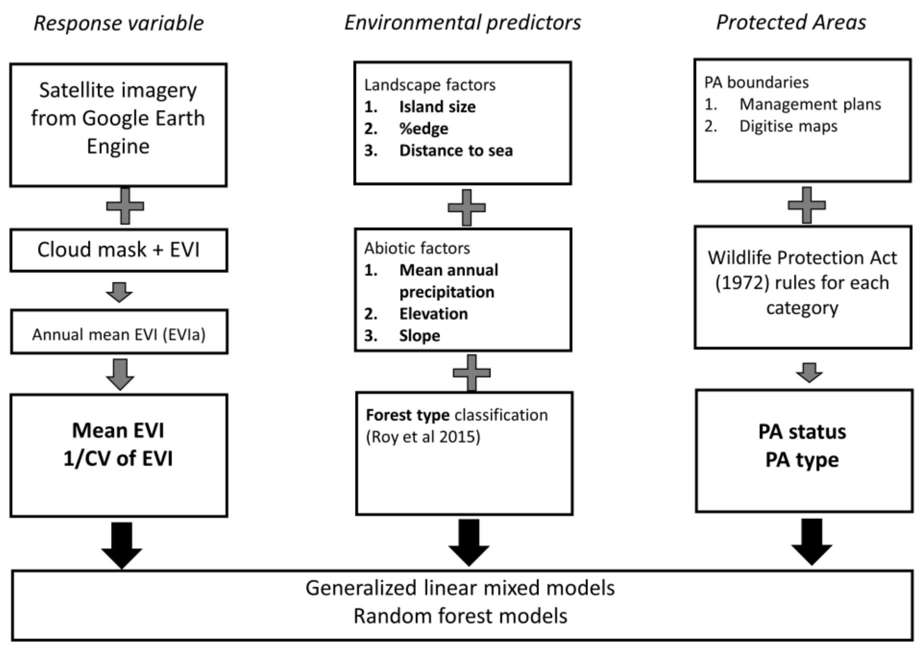

Figure 3. 1 Schematic of analysis. Schematic of the predictor and response variables and analytical models. The study combines spatial, environmental and management predictors to explain temporal mean and stability of EVI at the pixel level. Final variables used in models shown in bold.

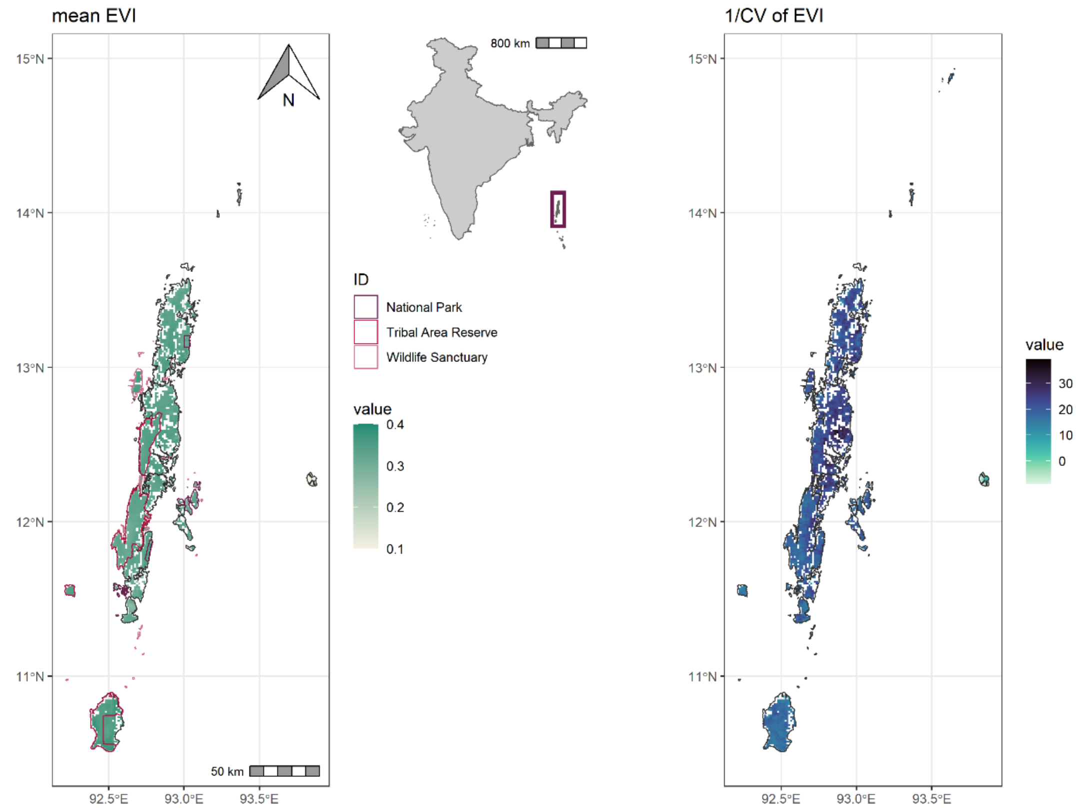

Figure 3. 2 Maps of study areas. Study location, response variables and protected area boundaries digitized from grey literature for this study. Response variables a) mean EVI and b) EVI stability (1/CV), summarized from mean annual EVI from MODIS imagery from 2000-2021 for forested pixels, processed using Google Earth Engine. Pink, red and purple boundaries in a) represent boundaries of all Wildlife Sanctuaries, National Parks and Tribal Area Reserve in the Andaman Islands, digitized for this study. Pixel values shown for all forested pixels derived from land cover classification published in Roy et al., 2015.

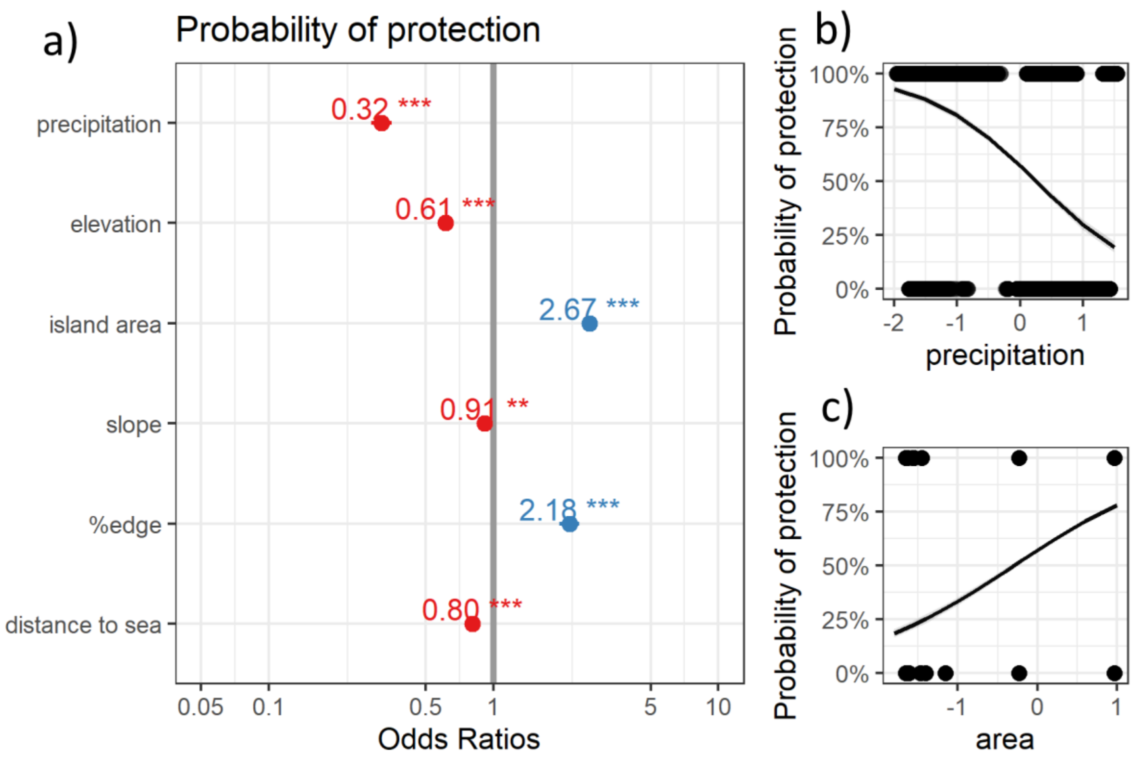

Figure 3. 3 : Factors influencing the probability of a pixel to be protected using a logistic regression (generalized linear model with binomial family of errors) and standardized predictor variables. a) parameter estimates for spatial and environmental factors; predicted probabilities of protection as a function of b) precipitation and c) island area.

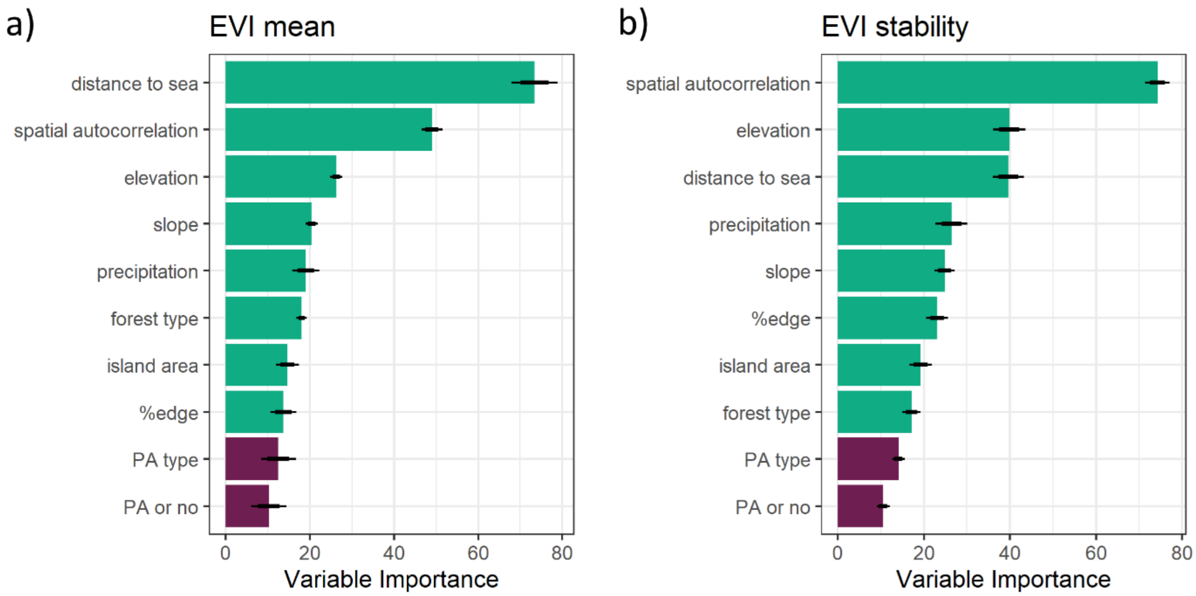

Figure 3. 4 Relative importance of environmental and management factors in explaining the variance of a) EVI mean and b) EVI stability over pixels of mean annual EVI from 2000-2021. Bars represent mean importance value of each variable over 10 and 14 Boruta (bootstrap) runs, thick black lines show standard deviation of importance value and thinner black lines show 1.6 x standard deviation. Variables are ordered in the decreasing order of mean importance value. Purple values indicate variables related to protection.

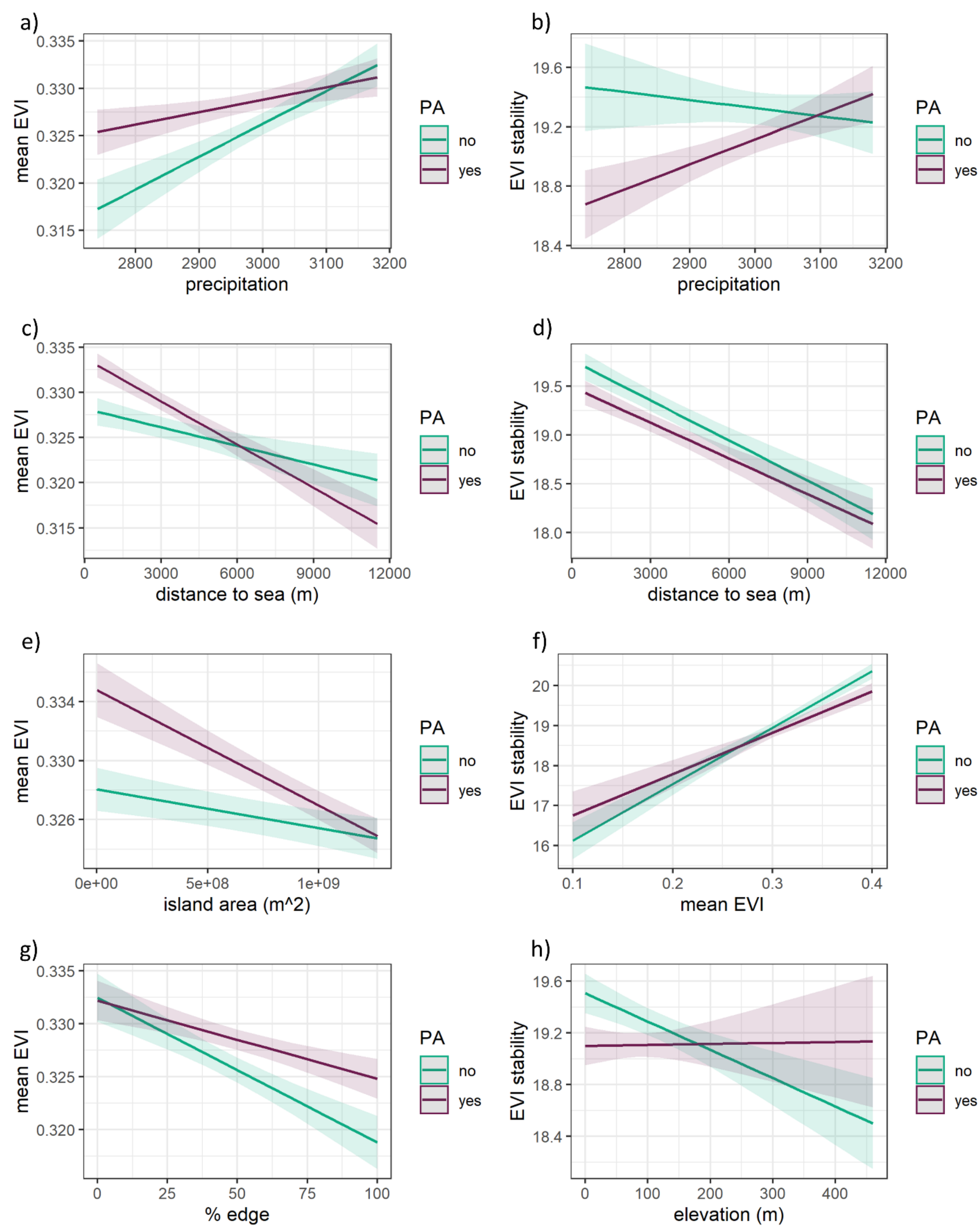
a)
mean EVI
precipitation
PA
no
yes
b)
EVI stability
precipitation
PA
no
yes
c)
mean EVI
distance to sea (m)
PA
no
yes
d)
EVI stability
distance to sea (m)
PA
no
yes
e)
mean EVI
island area (m^2)
PA
no
yes
f)
EVI stability
mean EVI
PA
no
yes
g)
mean EVI
% edge
PA
no
yes
h)
EVI stability
elevation (m)
PA
no
yes

Figure 3. 5 Generalized linear model predictions for interactions between protection status and environmental factors on mean EVI and EVI stability. EVI mean at the pixel level as predicted by an interaction between protection status and a) precipitation, c) distance to sea e) island area and e) %edge in the habitat. EVI stability at the pixel level as predicted by protection and its interaction with b) precipitation d) distance to sea e) mean EVI and d) elevation. Green represents low/no protection forests, purple represents PAs. Lines represent mean prediction and polygons 95% confidence interval over the prediction.

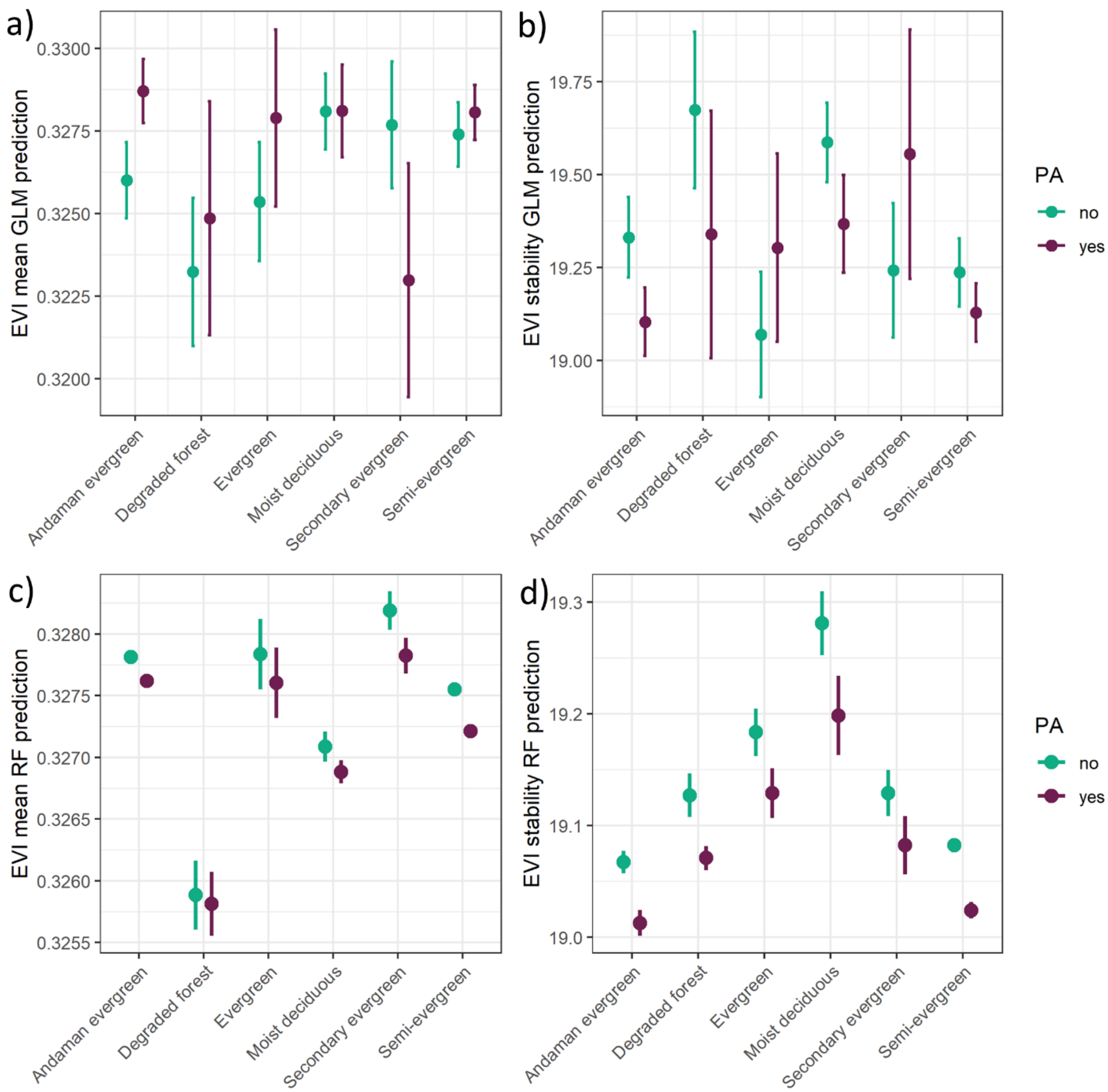

Figure 3. 6 Effect of forest type on mean EVI and EVI stability. Predictions from the full generalized linear model for a) EVI mean and b) EVI stability and from the random forest model for c) EVI mean and d) EVI stability. For a) and b), dots represent mean effects and error bars are 95% CI of estimates; c) and d) are partial dependence plots bootstrapped over 10 random effect models where dots represent the mean effect across runs and error bars represent 1.6 x standard deviation of the estimate across runs.

Tables

Table 3. 1 Data acquisition and processing. Variables used in the model, data source, processing methods and specific transformation procedures used where applicable.

Variable	Data source	Processing	Transformation
Response variable			
Annual EVI at 0.5 km x 0.5 km resolution	MODIS	Google Earth Engine cloud mask	Mean, 1/CV
Predictor variables			
Protected areas			
Wildlife Sanctuaries	Wildlife Institute of India maps	Georeferencing, digitizing	Rasterize
National Parks	Forest Department ANI management plan, published map	Georeferencing, digitizing	Rasterize
Tribal Area Reserve	Forest Department ANI management plan, published map	Georeferencing, digitizing	Rasterize
Environmental predictors			
Forest type	Roy et al., 2015	*projectRaster*, *neighbour*	
Island size, %edge, distance to sea	Shapefile	Processing in R using *rgdal* and *rgeos*	Rasterize
Mean annual precipitation	BioClim layer 12	*projectRaster*, *bilinear*	
Elevation, slope	SRTM	*terrain*, *projectRaster*, *bilinear*	

Table 3. 2 Model estimates and fit from generalized linear model of EVI mean and EVI stability across environmental predictors, protection status and their interactions. Significant effects at p<0.05 shown in bold.

	Mean EVI			**1/CV of EVI**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*P*
(Intercept)	-0.05	-0.08 – -0.02	**0.004**	-3.32	-6.39 – -0.26	**0.034**
EVI mean				14.09	12.09 – 16.10	**<0.001**
slope	-0.01	-0.02 – -0.00	**0.010**	0.51	-0.31 – 1.34	0.222
precipitation	0.00	0.00 – 0.00	**<0.001**	-0.00	-0.00 – 0.00	0.306
elevation	0.00	0.00 – 0.00	**0.018**	-0.00	-0.00 – -0.00	**<0.001**
island area	-0.00	-0.00 – -0.00	**<0.001**	-0.00	-0.00 – 0.00	0.677
%edge	-0.00	-0.00 – -0.00	**<0.001**	-0.00	-0.00 – 0.00	0.976
distance to sea	-0.00	-0.00 – -0.00	**<0.001**	-0.00	-0.00 – -0.00	**<0.001**
PA	0.07	0.03 – 0.11	**0.001**	-5.30	-9.49 – -1.11	**0.013**
Spatial autocorrelation	0.89	0.87 – 0.91	**<0.001**	1.08	1.06 – 1.10	**<0.001**
forest type [Degraded forest]	-0.00	-0.01 – -0.00	**0.033**	0.34	0.10 – 0.58	**0.005**
forest type [Evergreen]	-0.00	-0.00 – 0.00	0.536	-0.26	-0.45 – -0.07	**0.008**
forest type [Moist deciduous]	0.00	0.00 – 0.00	**0.013**	0.26	0.10 – 0.41	**0.001**
forest type [Secondary evergreen]	0.00	-0.00 – 0.00	0.146	-0.09	-0.30 – 0.12	0.414

forest type [Semi-evergreen]	0.00	-0.00 – 0.00	0.071	-0.09	-0.24 – 0.05	0.195
precipitation * PA	-0.00	-0.00 – -0.00	**0.002**	0.00	0.00 – 0.00	**0.001**
Island area * PA	-0.00	-0.00 – -0.00	**<0.001**	-0.00	-0.00 – -0.00	**0.002**
elevation * PA	0.00	0.00 – 0.00	**<0.001**	0.00	0.00 – 0.00	**0.007**
distance to sea * PA	-0.00	-0.00 – -0.00	**<0.001**	0.00	-0.00 – 0.00	0.481
slope * PA	-0.01	-0.02 – 0.01	0.279	-0.56	-1.76 – 0.64	0.360
%edge * PA	0.00	0.00 – 0.00	**0.018**	-0.01	-0.01 – -0.00	**0.012**
PA * forest type [Degraded forest]	-0.00	-0.01 – 0.00	0.638	-0.11	-0.53 – 0.31	0.615
PA * forest type [Evergreen]	-0.00	-0.00 – 0.00	0.927	0.46	0.13 – 0.79	**0.006**
PA * forest type [Moist deciduous]	-0.00	-0.01 – -0.00	**0.026**	0.01	-0.21 – 0.23	0.947
PA * forest type [Secondary evergreen]	-0.01	-0.01 – -0.00	**0.001**	0.54	0.13 – 0.95	**0.009**
PA * forest type [Semi-evergreen]	-0.00	-0.00 – -0.00	**0.045**	0.12	-0.07 – 0.30	0.213
EVI mean * PA				-3.77	-7.00 – -0.54	**0.022**
Observations	7850			7850		
R^2	0.627			0.755		

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Appendix A: Supplementary Information for Chapter 1

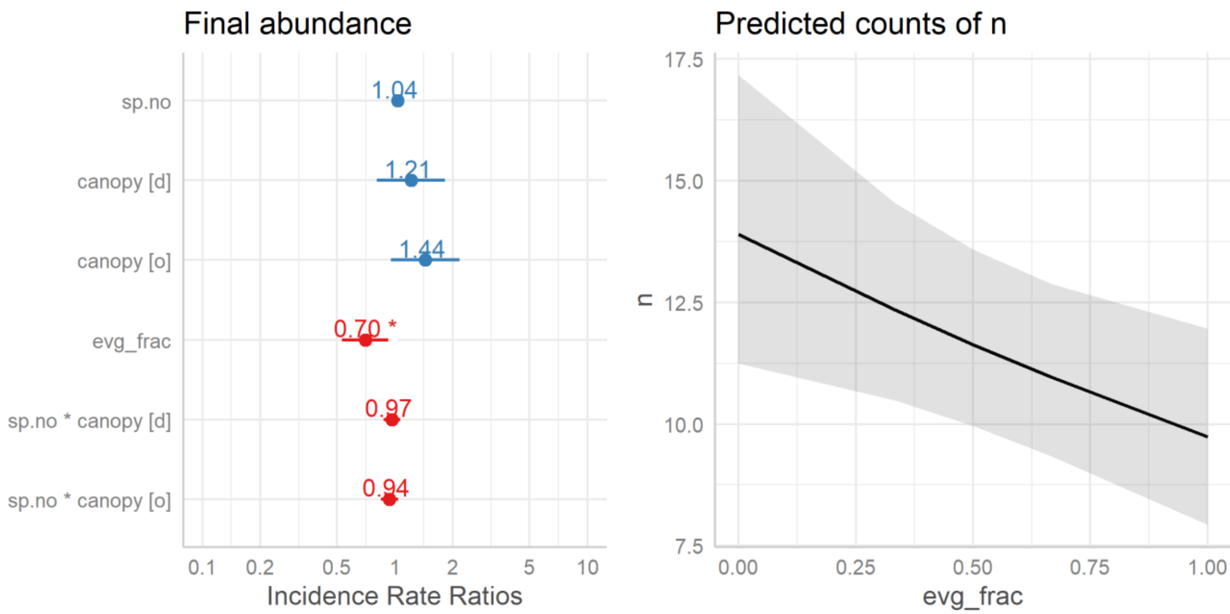

Figure S1. 1 Generalized linear model with negative binomial family of errors modelling the number of individuals surviving at the end of 12 months of the experiment starting from equal abundance communities with 18 individuals each. Model deviance = 50.354, df=46, p=0.305.

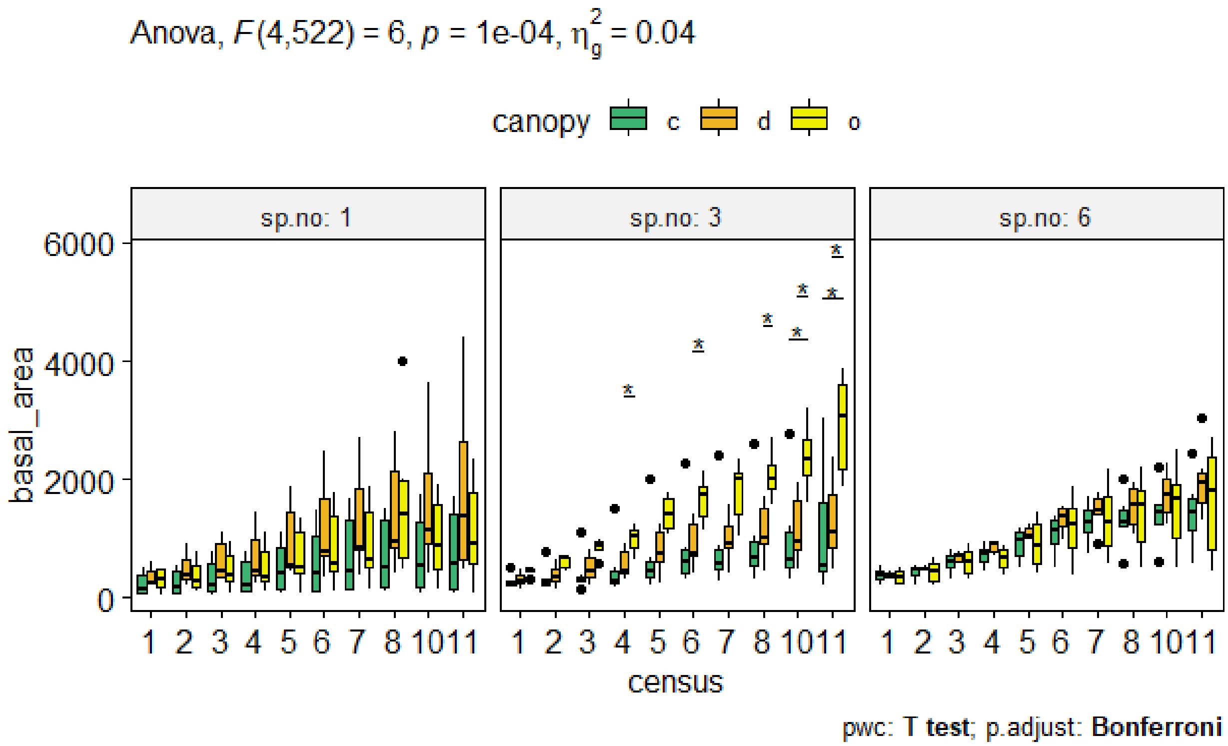

Figure S1. 2 Repeated measures three-way ANOVA of mean basal area in a plot across monthly censuses during the experiment. Both species richness and canopy treatment are significant as is their interaction. F statistic = 6, p<0.001. Significantly different groups marked.

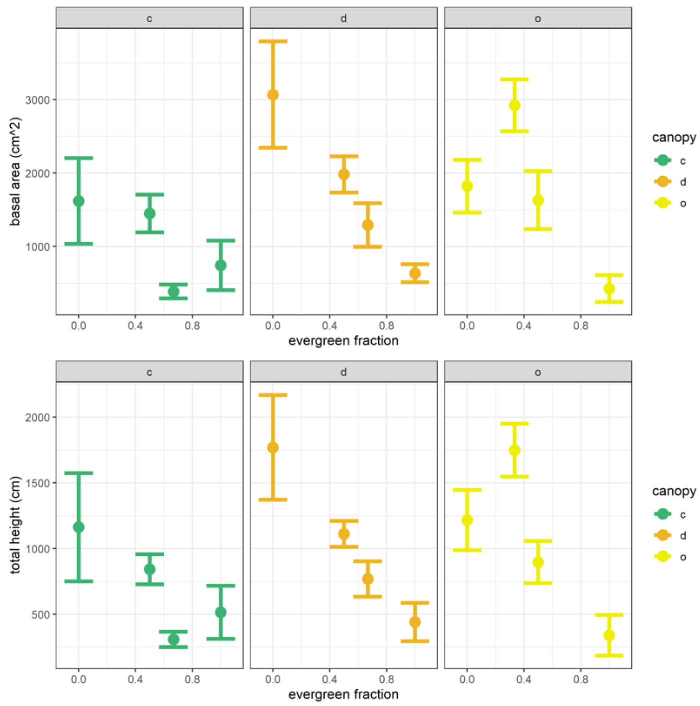

Figure S1. 3 Final community properties as a function of functional composition. Evergreen fraction was calculated as the proportion of planted individuals from evergreen species in each community. Dots represent mean values at the end of the experiment across communities with similar functional composition. Error bars represent standard errors.

Table S1.1. Model selection for basal area and height in observed long-term dynamics plots. Generalized linear model coefficients of total basal area and height in each plot as linear and quadratic functions of species richness and canopy openness with year of observation as a random effect. Estimates, random effect and AIC values reported. Significant slopes at p<0.05 marked with * and significantly different AIC values at ΔAIC=2 marked in bold.

			Estimates				
			Intercept	Linear term	Quadratic term	Random effect variance	AIC
Basal area	species richness	Linear	118***	18.02		1.50E-06	858.6
		Quadratic	60.38	82.60*	-13.43*	0	**856.7**
	canopy openness	Linear	150.10***	9.13		1.79E-13	862.2
		Quadratic	116.21***	363.55*	-538.12**	46.03	**858.6**
Height	species richness	Linear	181.27	23.71		1.76E-11	917.8
		Quadratic	125.93	86.93	-13.4	0	918.2
	canopy openness	Linear	233.21	-43.69		0	920.8
		Quadratic	164.39***	641.40***	-970.11***	69.15	**913.9**

Appendix B: Supplementary Information for Chapter 2

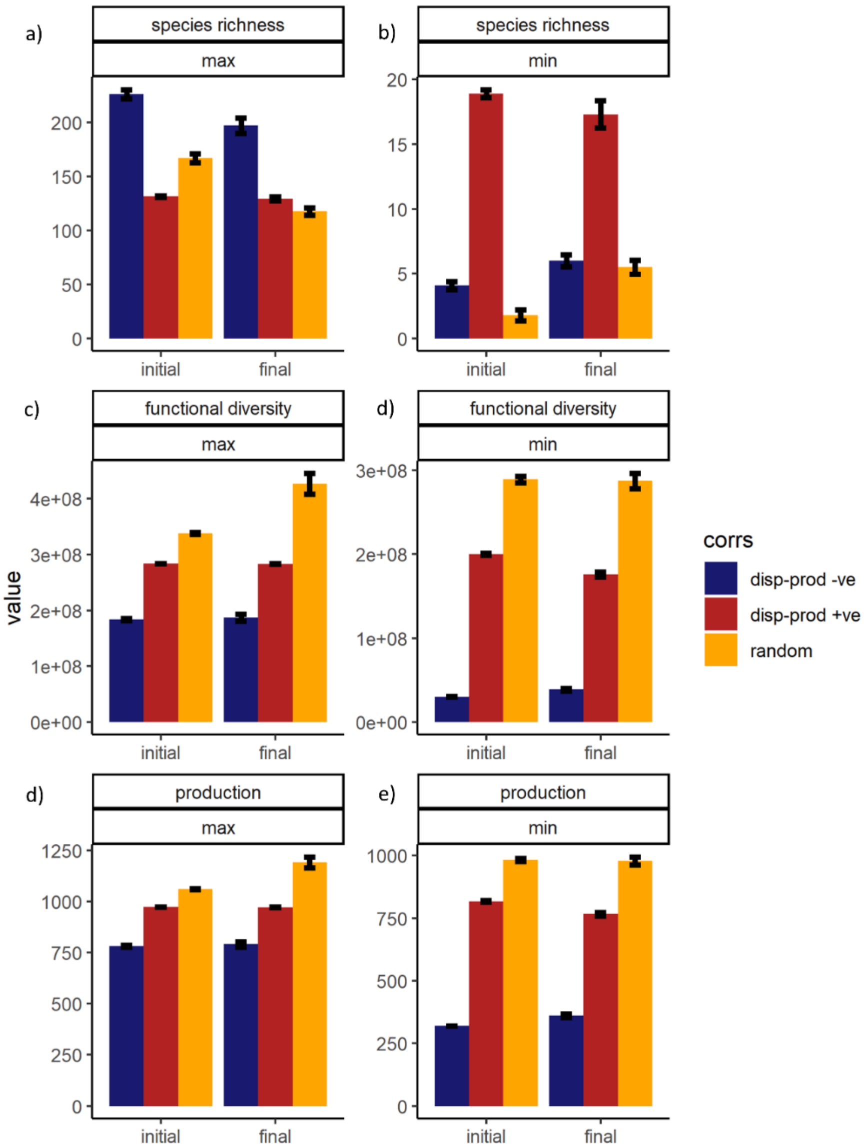

Figure S2. 1 Summary characteristics of initial and final communities in the simulation experiment. Panels a, c, and e represent maximum values across communities for species richness, functional diversity and production respectively while panels b, d and f represent minimum values. Black lines represent standard deviation values from 10 replicate runs. The three colors represent the three correlation structures detailed in Fig 2.1.

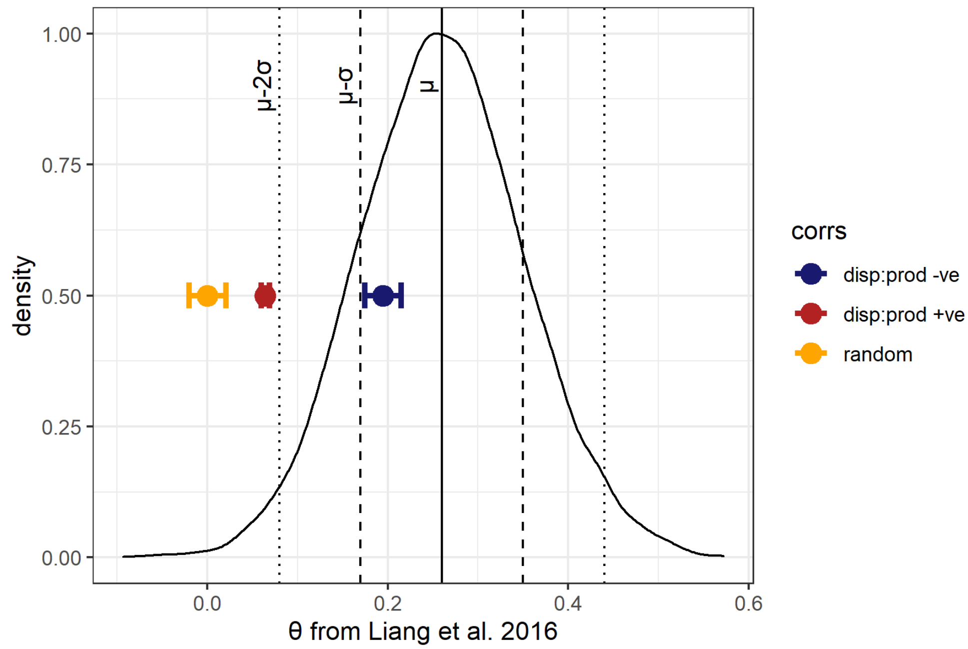

Figure S2. 2 Comparing coefficients from this study at the regional scale to bootstrapped coefficients from global forests plots reported in Liang et al. 2016. The black line is the distribution of θ with $\mu = 0.26$ and $\sigma = 0.09$. The dots represent the mean θ values across all communities assessed for each trait correlation and errors bars represent standard deviation from the mean. Dots are represented at density at 0.5 for visual comparison.

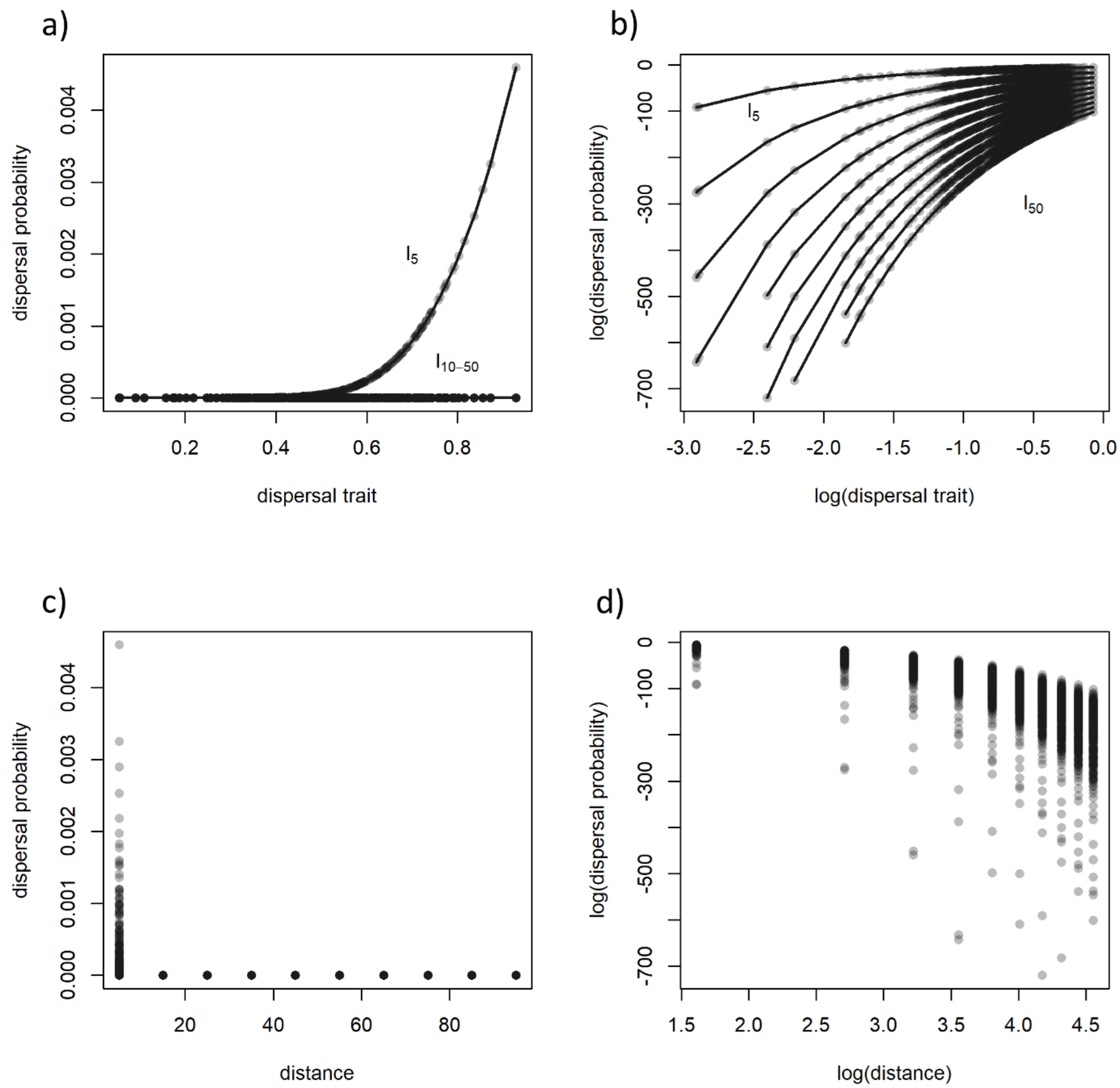

Figure S2. 3 Dispersal probability by distance and dispersal trait. a) Dispersal probability as a function of dispersal trait value for sites at different distances – dispersal increases exponentially with trait value; b) log-log curves of dispersal probability as a function of dispersal distance; c) dispersal probability across all species with distance; d) log-log curves of dispersal probability with distance. Dispersal decreases exponentially with distance.

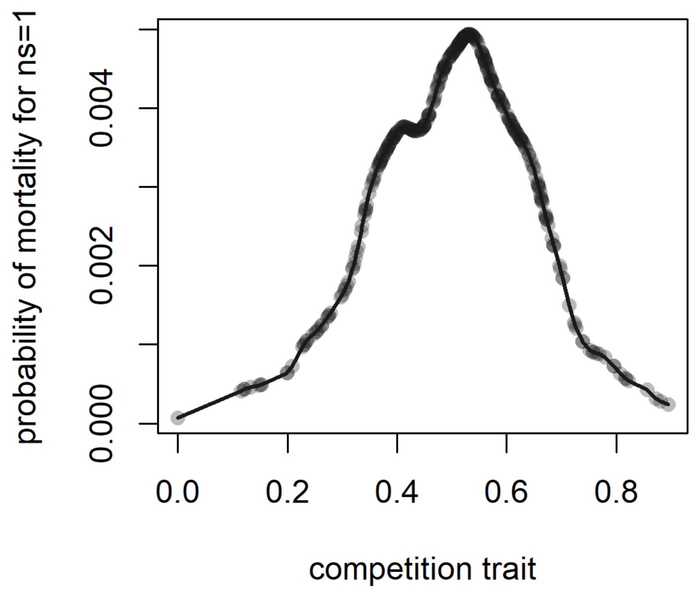

Figure S2. 4 Biotic competition trait and probability of mortality at w=0.05. Calculated mortality from competition in a community consisting of one individual of each species with the specific value of the trait (n_s =1 for all s). Highest probability of mortality is for moderate values of the trait.

Appendix C: Supplementary Information for Chapter 3

Supplementary methods for propensity score matching

To reduce biases in analysis due to unbalanced covariates across protected and unprotected areas, we performed the analysis on a reduced subset in which pixels within and outside PAs were picked using propensity score matching. We performed matching using packages “MatchIt” and “optmatch”, discarding unmatched points based on the distance between them using the function matchit.

The function used for matching was:

matching<-matchit(PA_yes~precip+elev+area+slope+edgepc+dist_sea+veg_ID,

method="optimal", data=sample_for,

distance="glm", link = "probit", discard = "both")

This matching resulted in a reduced n of 7850 pixels, with equal numbers within and outside PAs (3925 each), distributed more evenly across forest type, precipitation, elevation, slope, distance to sea and island area and slope. In this dataset, the balance in the variables was substantially improved.

<u>Propensity score diagnostics:</u>

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.4574	-0.9116	0.5289	0.8103	2.9381

Table of coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.462e+01	7.171e-01	20.386	< 2e-16 ***
precipitation	-4.936e-03	2.561e-04	-19.275	< 2e-16 ***

elevation	-6.211e-03	3.472e-04	-17.888	< 2e-16 ***
island area	1.167e-09	4.277e-11	27.284	< 2e-16 ***
slope	-1.056e+00	2.635e-01	-4.008	6.17e-05 ***
%edge	1.109e-02	9.991e-04	11.097	< 2e-16 ***
distance to sea	-6.767e-05	8.565e-06	-7.901	3.08e-15 ***
forest type [Andaman evergreen]	-1.574e+00	8.602e-02	-18.303	< 2e-16 ***
forest type [Degraded forest]	-7.077e-01	7.018e-02	-10.084	< 2e-16 ***
forest type [Evergreen]	-8.912e-01	4.577e-02	-19.472	< 2e-16 ***
forest type [Moist deciduous]	-1.059e+00	8.033e-02	-13.187	< 2e-16 ***
forest type [Secondary evergreen]	-1.646e-01	3.736e-02	-4.405	1.07e-05 ***
forest type [Semi-evergreen]	-4.626e+00	2.692e+01	-0.172	0.864
forest type [Southern Hilltop]				

(Dispersion parameter for quasibinomial family taken to be 1.072702)

Null deviance: 12715 on 9307 degrees of freedom

Residual deviance: 10156 on 9295 degrees of freedom

Number of Fisher Scoring iterations: 13

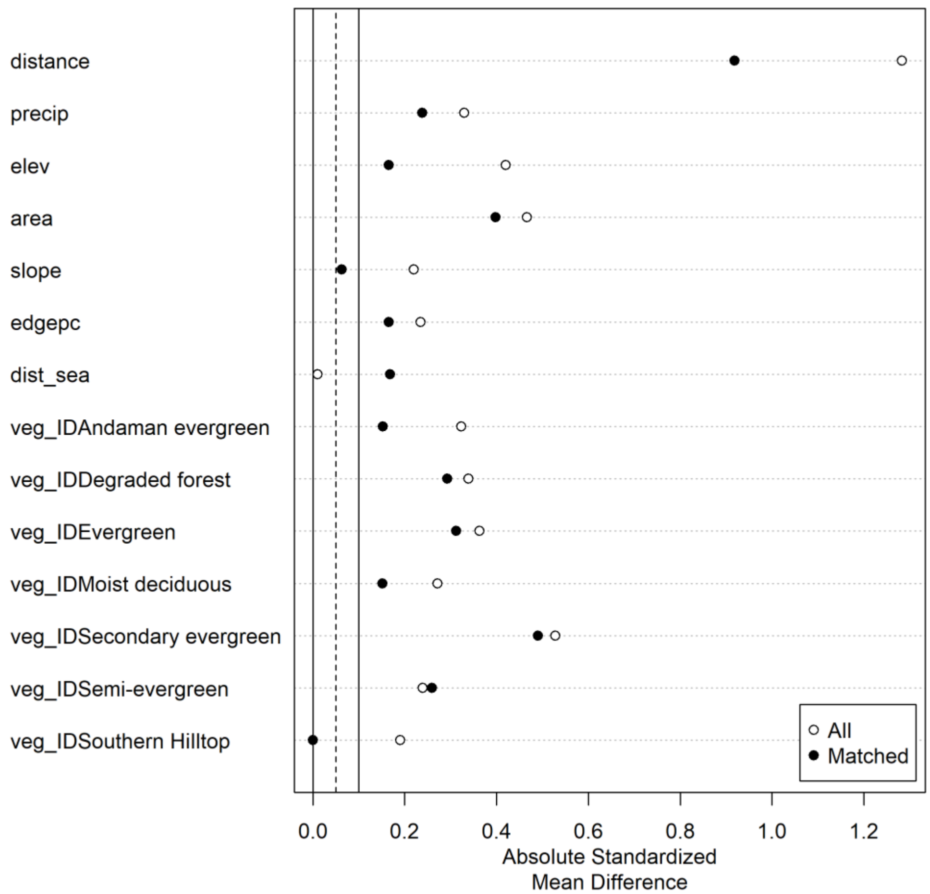

Figure S3. 1 Heuristics for matching and improvement of balance

Heuristics for the matching

Call:

matchit(formula = PA_yes ~ precip + elev + area + slope + edgepc +

dist_sea + veg_ID, data = sample_for, method = "optimal",

distance = "probit", discard = "both")

Summary of Balance for All Data:

	Means Treated	**Means Control**	**Std. Mean Diff.**	**Var. Ratio**	**eCDF Mean**	**eCDF Max**
distance	0.6822	0.4291	1.2831	0.7364	0.2991	0.4713
precipitation	2967.5530	3006.9450	-0.3294	1.0664	0.1031	0.2260
elevation	67.2068	85.7550	-0.4202	0.4209	0.0748	0.1379
island area	888340680.1106	678163385.0152	0.4668	0.8394	0.0264	0.2450
slope	0.0881	0.1043	-0.2202	0.8327	0.0662	0.0975
%edge	42.7561	49.9513	-0.2347	1.0598	0.0770	0.2241
distance to sea	3023.8778	3003.0530	0.0110	0.7247	0.0345	0.0547
forest type [Andaman evergreen]	0.4045	0.2459	0.3231	.	0.1586	0.1586
forest type [Degraded forest]	0.0164	0.0594	-0.3388	.	0.0430	0.0430
forest type [Evergreen]	0.0286	0.0892	-0.3633	.	0.0606	0.0606
forest type [Moist deciduous]	0.1206	0.2091	-0.2718	.	0.0885	0.0885
forest type [Secondary evergreen]	0.0173	0.0862	-0.5278	.	0.0688	0.0688
forest type [Semi-evergreen]	0.4126	0.2948	0.2394	.	0.1178	0.1178
forest type [Southern Hilltop]	0.0000	0.0155	-0.1909	.	0.0155	0.0155

Summary of Balance for Matched Data:

	Means Treated	Means Control	Std. Mean Diff.	Var. Ratio	eCDF Mean	eCDF Max	Std. Pair Dist.
distance	0.6176	0.4365	0.9181	0.7193	0.1950	0.3633	0.9184
precipitation	2978.3780	3006.9372	-0.2388	1.0682	0.0746	0.2074	1.0745
elevation	76.5121	83.8254	-0.1657	0.5042	0.0405	0.0706	1.2992
island area	866906495.9806	687824941.8983	0.3977	0.9284	0.0262	0.2048	1.1622
slope	0.0975	0.1022	-0.0633	1.0005	0.0262	0.0604	1.1297
%edge	44.7397	49.8166	-0.1656	1.0605	0.0616	0.1896	1.0519
distance to sea	3343.5314	3023.6914	0.1683	0.7997	0.0710	0.1294	1.2299
forest type [Andaman evergreen]	0.3248	0.2499	0.1526	.	0.0749	0.0749	0.8088
forest type [Degraded forest]	0.0222	0.0594	-0.2931	.	0.0372	0.0372	0.6184
forest type [Evergreen]	0.0387	0.0907	-0.3118	.	0.0520	0.0520	0.7215
forest type [Moist deciduous]	0.1633	0.2127	-0.1518	.	0.0494	0.0494	0.8856
forest type [Secondary evergreen]	0.0234	0.0874	-0.4903	.	0.0639	0.0639	0.7951

forest type [Semi-evergreen]	0.4275	0.2999	0.2593	.	0.1276	0.1276	0.9217
forest type [Southern Hilltop]	0.0000	0.0000	0.0000	.	0.0000	0.0000	0.0000

<u>Percent Balance Improvement:</u>

	Std. Mean Diff.	**Var. Ratio**	**eCDF Mean**	**eCDF Max**
distance	28.4	-7.7	34.8	22.9
precipitation	27.5	-2.7	27.6	8.2
elevation	60.6	20.9	45.8	48.8
island area	14.8	57.6	0.5	16.4
slope	71.2	99.7	60.5	38.1
%edge	29.4	-1.1	20.0	15.4
distance to sea	-1435.9	30.6	-105.6	-136.8
forest type [Andaman evergreen]	52.8	.	52.8	52.8
forest type [Degraded forest]	13.5	.	13.5	13.5
forest type [Evergreen]	14.2	.	14.2	14.2
forest type [Moist deciduous]	44.2	.	44.2	44.2
forest type [Secondary evergreen]	7.1	.	7.1	7.1
forest type [Semi-evergreen]	-8.3	.	-8.3	-8.3

forest type [Southern Hilltop]	100.0	.	100.0	100.0

Sample Sizes:

	Control	**Treated**
All	3995	5315
Matched	3925	3925
Unmatched	0	1388
Discarded	68	2

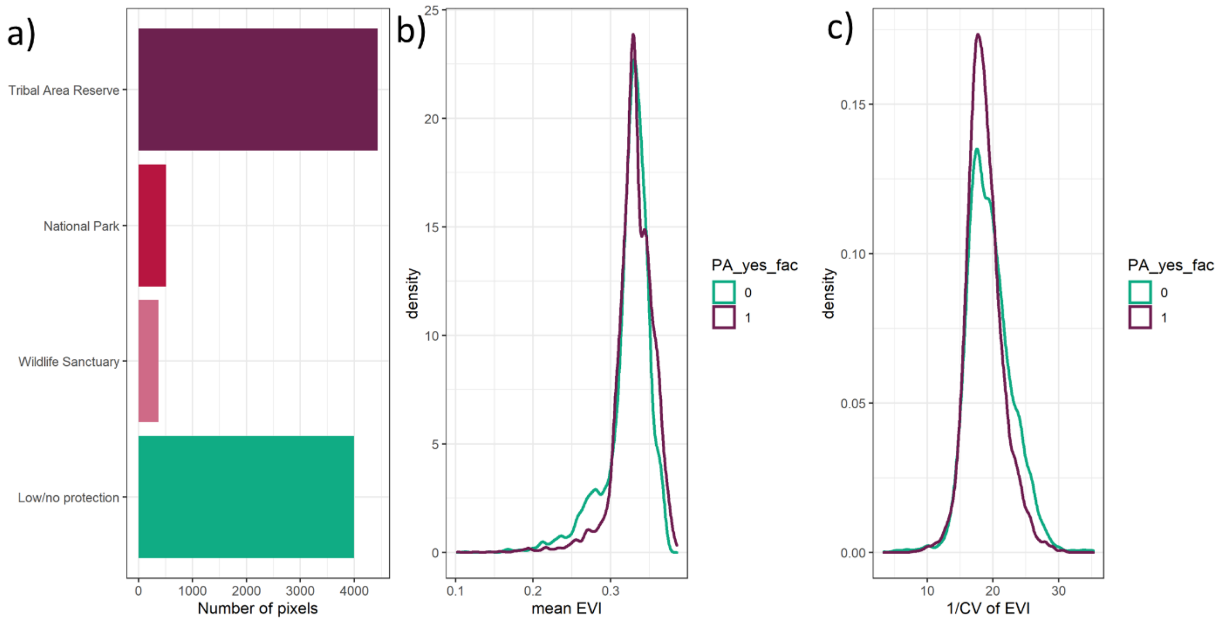

Figure S3. 2 Distribution of variables. A) the number of pixels under different types of protection, b) distribution of mean EVI and c) distribution of 1/CV of EVI across protected and unprotected pixels.

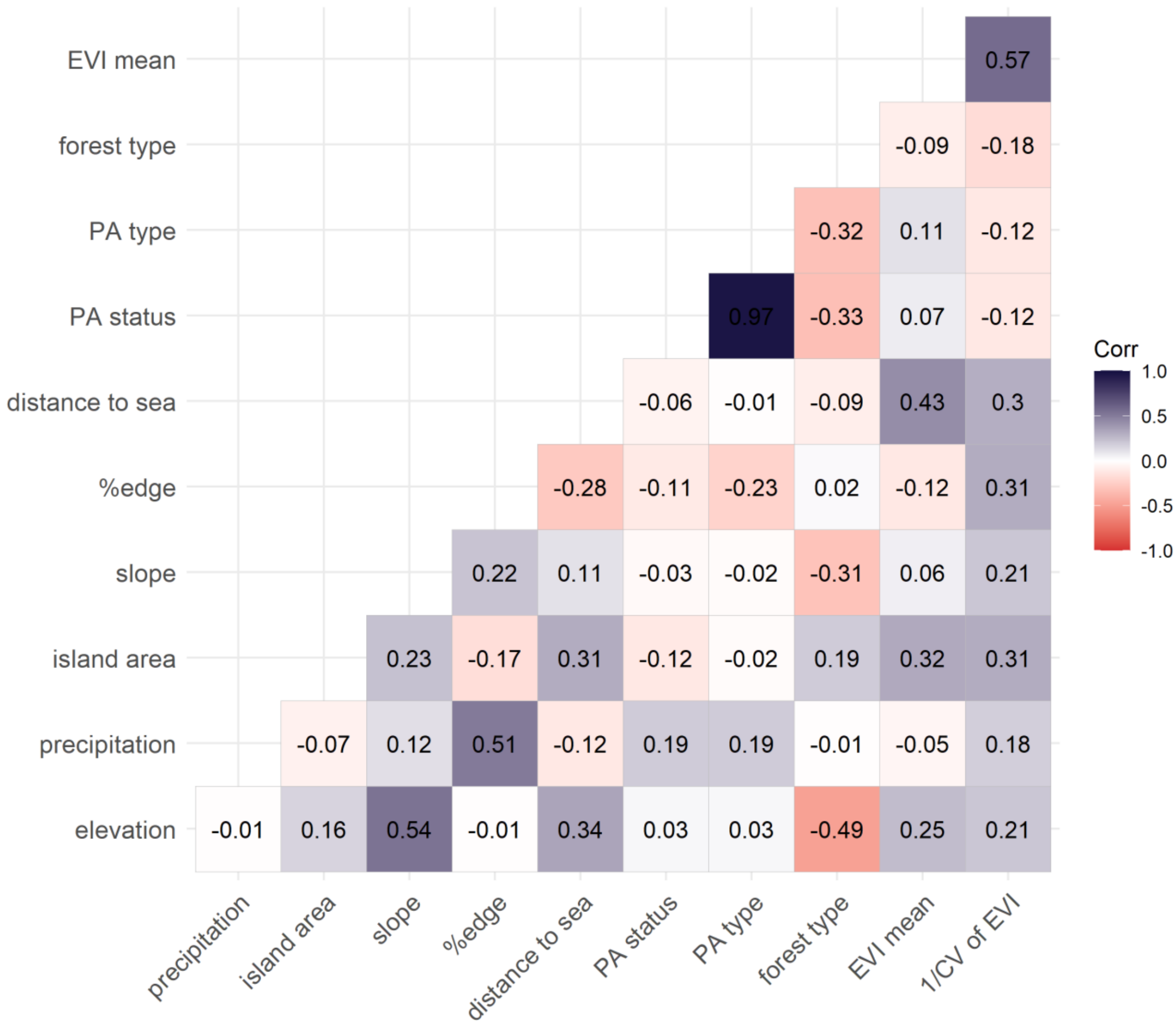

Figure S3. 3 Correlations between all variables of interest used in the models. The highest correlations are between EVI mean and 1/CV of EVI which are not used in the same model. Moreover, correlations between PA type and PA status are not used other than in random forest models. All other correlations are less than 55%, which makes it suitable for analysis using random forests.

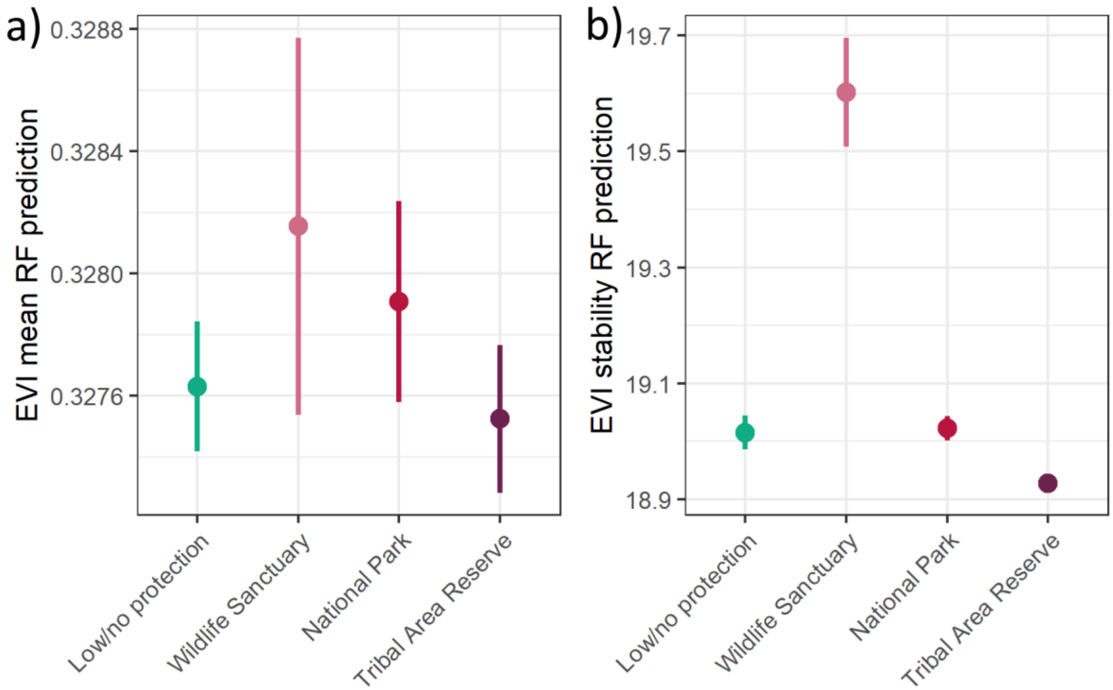

Figure S3. 4 Mean EVI and EVI stability across different protection types. Partial dependence plots from random forest models bootstrapped 10 times, detailing predictions of a) EVI mean and b) EVI stability across the time period 2000-2021 in the Andaman Islands. Dots represent mean effects across the bootstrap runs and error bars represent 1.6 times the standard deviation of the estimate.

Table S3. 1 Protected Area types and strictness of protection. Specific regulations from the Wildlife (Protection) Act 1972 were used to derive the strictness of protection based on allowed types of entry and extraction. Areas in the Andaman Islands that are protected under specific type also detailed.

Type of PA	**Wildlife Protection Act**	**Areas in the region**	**Strictness of protection**
Tribal Area Reserve		Jarawa Reserve, Onge Reserve, North Sentinel Island	Very High
National Park	"no entry" "forest produce only to meet the bona fide needs of people in and around" "no entry or grazing of livestock"	Saddle Peak, Mt Harriet NP, Mahatma Gandhi Marine National Park, Rani Jhansi National Park	High
Wildlife Sanctuary	"restriction on entry" "no removal of wildlife or forest produce or destroy/damage habitat" "forest produce to meet the needs of people living in and around the sanctuary is permitted, grazing, livestock movement also permitted" "no fire, no weapon"	53 areas	Medium
Reserve Forest	Not protected under any of the above – owned by the central govt		Low
Revenue Forest	Unprotected forest not under the forest department purview, multiple use		No