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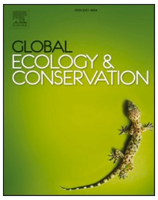

Original research article

Phylogenetic structure and turnover between lowland and montane subtropical forests indicate differential community assembly processes, affected by successional stage and spatial gradients

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ABSTRACT

Secondary forests represent an increasing proportion of global forest cover and offer a range of ecosystem services that are integral to environmental policy targets. Highly disturbed landscapes with temporal records of forest plant community composition offer key insights into the processes that shape plant communities as forests undergo secondary succession. We investigated patterns of plant community phylogenetic structure and phylogenetic beta diversity. Mean pairwise distance (MPD) and Mean Nearest Taxon Distance (MNTD) metrics were determined between co-occurring species within plant communities, in addition to phylogenetic beta diversity metrics relative to null models of random phylogenetic assembly. MPD and MNTD were compared between elevational and successional classes and modelled as products of intercommunity distance (metres) and forest community age (years). Phylogenetic nonmetric multidimensional scaling explored phylogenetic community structure between lowland and montane forest type in Hong Kong. We found that plant communities in secondary forests in Hong Kong exhibited patterns of increased basal phylogenetic clustering with increasing community elevation, while phylogenetic turnover was influenced by spatial and successional factors in lowland and montane forest. Our findings indicate differential community assembly in lowland compared to montane forest type in Hong Kong, as well as evidence for barriers to plant dispersal in secondary forest communities due to patterns of spatial phylogenetic clustering. Plant communities in montane forests were found to be phylogenetically distinct from lowland forest plant communities. Patterns of spatial phylogenetic clustering may suggest significant dispersal or post-dispersal processes causing the clustering of related species at fine spatial scales, while phylogenetic turnover with increasing successional age may indicate compositional changes during the process of passive forest regeneration. Collectively, these results emphasize the need to investigate active pathways for rewilding dispersal limited late successional forest tree species in Hong Kong.

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1. Introduction

Secondary forests represent an increasing proportion of global forest cover. In East-Asia over 70 % of forests are non-primary, while land abandonment and rural-urban migration are expected to lead to further expansions of secondary forests during the 21st century (GFO, 2020). Forest regeneration may facilitate the resumption of numerous ecosystem functions and services, such as water provisioning, soil stabilization and flood mediation (Bonner, Schmidt and Shoo, 2013; Arroyo-Rodríguez et al., 2017; Edwards et al., 2019; Shi et al., 2021). However, secondary forest plant communities regenerating after significant historical anthropogenic disturbances may exhibit idiosyncratic patterns of community assembly, particularly if spatial, biotic and abiotic filters restrict the range of species which can colonize regenerating forest communities (Chokkalingam and De Jong, 2001). For instance, passive rewilding has been shown to be an effective means of forest restoration when primary forests grow adjacently to secondary patches and seed dispersal networks are intact, while the absence of adjacent primary forests may restrict dispersal opportunities during regeneration (Mayhew et al., 2019). Assessment of tropical forest regeneration indicates that once forest clearance has surpassed a 60 % threshold, active replanting is needed to restore highly degraded landscapes (Ewers et al., 2024). Characterizing community assembly in regenerating secondary forests can provide an opportunity to identify such barriers to secondary succession, which can guide conservationists to optimize forest restoration in response to localized contexts and regional land use histories (Meli et al., 2017).

Determining patterns of plant community assembly during secondary succession requires delineation of the eco-evolutionary processes shaping regional and local forest plant species pools. Community assembly may be evaluated through several methodologies, ranging from assessing patterns of taxonomic alpha and beta diversity, to exploring the distribution of traits and relative abundances of functional groups (Baselga, 2010; Liu et al., 2022). Plant functional traits such as seed and fruit dispersal strategies, individual and species environmental physiological tolerances, and facilitative-competitive intra-specific and inter-specific interactions collectively determine which species can co-occur at local and regional scales through deterministic (niche) and stochastic (neutral) processes of community assembly (Vellend, 2016; Li et al., 2020; Rosbakh et al., 2022). The influence of community assembly filters upon regenerating secondary forests are dependent upon the distribution of intra- and inter-specific traits within regional plant species pools and local communities, which situates community assembly within broader evolutionary contexts, and makes measuring traits and trait proxies such as phylogenetic relationships meaningful for understanding regeneration in forest secondary succession (Maherali and Klironomos, 2007; Cadotte et al., 2013). Studying the distribution of species traits at the local and landscape level may refine our understanding of spatio-temporal and environmental processes driving community assembly in regenerating forest systems, as the relative change in trait distributions from regional to local scales can indicate whether species sharing common traits or species

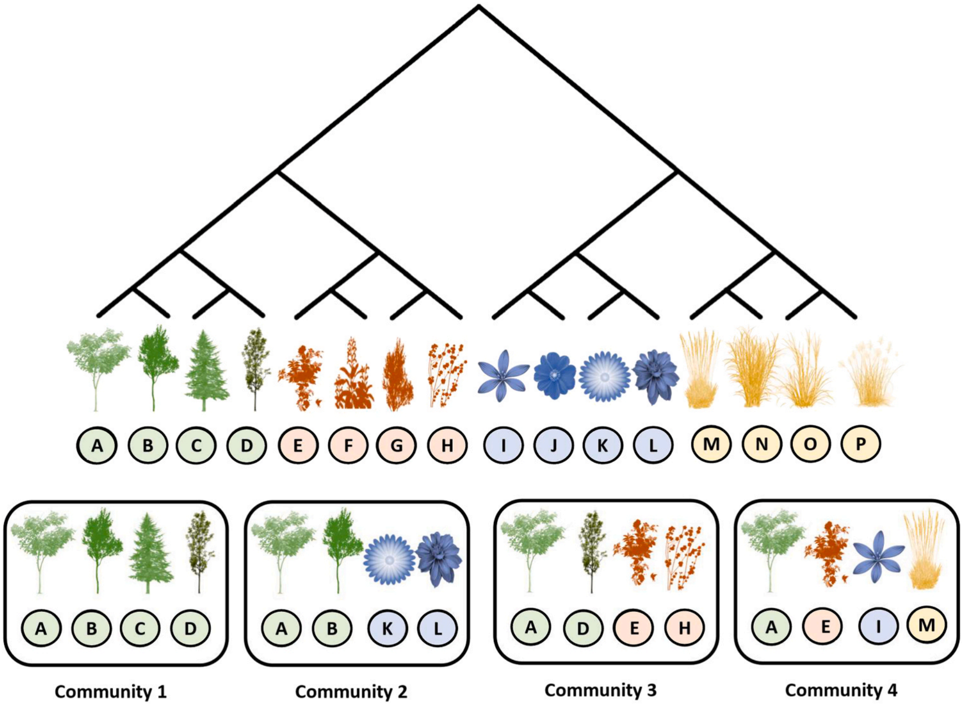

Fig. 1. Four prevailing scenarios for plant community phylogenetic structure are represented by these hypothetical species communities (1–4) which are situated within the above phylogeny of species A-P; I) In Community 1 the community is clustered at basal and terminal levels i.e., it shows close relatedness at basal and terminal branches of the phylogeny; II) Community 2 is overdispersed at the basal level as it includes species from across divergent branches, but clustered at the terminal level, where more recently diverged species from within branches are present; III) Community 3 shows clustering at the basal level but overdispersion at the terminal level (i.e., clustering of overdispersion); IV) Community 4 is overdispersed at both basal and terminal levels. This figure was adapted from (Padullés Cubino et al., 2021).

with diverse strategies co-occur in communities (Letcher et al., 2012; Enquist et al., 2017; Funk et al., 2016; Maitner et al., 2023). Measuring plant functional traits and trait proxies are critical to assigning appropriate conservation policies in cases where major determinants of community assembly have become fundamentally altered, such as seed dispersal in highly degraded forests in East-Asia (Corlett, 2011), or soil conditions impacting post-dispersal processes during plant recruitment (Rosbakh et al., 2022).

1.1. Phylogenetic community structure

Phylogenetic niche conservatism asserts that species traits are associated with phylogeny, and phylogenetic relationships can serve as proxies for direct trait measurements within ecological communities in the absence of trait data (Rocha, 2018; Sólymos et al., 2018; Li et al., 2020). In instances where only a narrow subset of traits can be measured or resources for trait data collection are insufficient and trait data is unavailable, assessing phylogenetic relationships within and between regenerating secondary forest plant communities can serve as an alternative but relevant approach to ascertaining the drivers of regional and local community assembly (Purschke et al., 2017). Studying community phylogenetic relationships can deepen insights into the drivers of community assembly in secondary forests and identify areas with distinct compositions, where phylogenetic relationships reflect the degree of evolutionary relatedness amongst co-occurring species in a regional species pool, and accordingly, act as a proxy measure of the traits they share, although this is not always the case in practice (Webb et al., 2002; Morales-Castilla et al., 2017). Comprehensive understandings of plant assemblages undergoing secondary succession thus require consideration of the evolutionary relationships between coexisting species, termed the phylogenetic structure of communities, in addition to taxonomic and trait-oriented approaches (Cadotte et al., 2013; Tucker et al., 2019).

Communities may exhibit phylogenetic overdispersion, where co-occurring species have diverged farther in the past, or phylogenetic clustering, where co-occurring species are more recently diverged (Letcher et al., 2012). These relationships can be drawn between basal (anciently diverged), and terminal (recently diverged), branches in phylogenetic trees (Mazel et al., 2016), and communities can simultaneously exhibit patterns of basal or terminal clustering and over-dispersion, which indicate differential community assembly processes (Fig. 1) (Padullés Cubino et al., 2021). Abiotic filtering is expected to lead to phylogenetic clustering as species with similar traits are selected for, while competitive and facilitative biotic filtering may cause overdispersion and the selection of diverse survival strategies (Letcher et al., 2012). Patterns of clustering and over-dispersion may subsequently reveal the community assembly mechanisms shaping regenerating secondary forest plant communities.

Patterns of community phylogenetic overdispersion and clustering at basal and terminal levels of phylogenies can be broken down into four generalized cases. Firstly, plant communities in high-stress environments may exhibit basal and terminal phylogenetic clustering, wherein strong environmental filtering, and phylogenetic niche conservatism leads to a high proportion of closely related species with similar traits, and thus tolerances to environmental stressors (Fig. 1; Community 1) (Lososová et al., 2015; Lososová et al., 2020; Qian et al., 2019). Second, basal overdispersion, and terminal clustering may be observed where more distantly related species co-occur in a community (Fig. 1; Community 2) (Padullés Cubino et al., 2021), which may reflect long-term environmental filtering and recent niche differentiation of clades of species in a community (Kooyman et al., 2011). Third, basal clustering and terminal overdispersion may occur where closely related species undergo niche differentiation (Fig. 1; Community 3)(Hardy and Senterre, 2007). In the fourth case, basal and terminal overdispersion may indicate environmental stability and recent niche differentiation among species (Fig. 1; Community 4).

1.2. Community phylogenetic structure during secondary succession

Assessing community phylogenetic structure can indicate mechanisms driving community assembly during secondary forest succession and reveal selective regimes shaping forest plant communities. Such phylogenetic relationships can implicate long term evolutionary patterns, yet in secondary forests which have only been regenerating for several decades these measures can indicate the influence of recent environmental and ecological processes (Letcher et al., 2012; Jin, Qian and Yu, 2015; Comita et al., 2018). During the process of secondary forest succession, distinct compositional and functional transitions are hypothesized to take place which, if occurring in practice, may be detectable through within- and between-community phylogenetic structural analyses (Odum,1969; Horn, 1974; Prach and Walker, 2019).

For instance, in secondary forests undergoing regeneration, phylogenetic clustering of plant species at early phases of succession may be expected (Chai et al., 2016). At this early stage of succession, environmental filtering from high light intensity, desiccation pressure and poor soil quality is hypothesized to select for fast growing shrubby species sharing traits that enable survival in harsh abiotic conditions, leading to clustering of phylogenetically closely related species which share similar traits (Letcher et al., 2012). Conversely, as fast-growing early successional shrub and small tree species alter the local abiotic conditions and a canopy forms with a moist understorey and increased leaf litter input, early successional patches are expected to become increasingly dominated by shade-tolerant, slow-growing, canopy tree species, with a shift away from strong abiotic filtering towards intensified biotic competition for light and nutrients (Letcher et al., 2012; Chai et al., 2016). This gradual closure of the canopy may lead to phylogenetic overdispersion over time with competing species exhibiting a broader range of competitive strategies as intra-specific competition for light and nutritive resources, as well as the development of mutualisms, intensifies.

Observing the phylogenetic structure of secondary forest chrono-sequences is significant for the ecological characterization and description of the phenomenon of secondary forest succession and can offer important insights for conservation practitioners. The heightened availability of phylogenetic and phylogenomic resources within the early 21st century has been driven by the proliferation of mega-phylogenies constructed from pre-existing taxonomies, and molecular phylogenies utilizing open source genetic and genomic sequence data in repositories such as the NCBI GenBank and Tree of Life databases (Smith and Brown, 2018; Jin and Qian, 2019). This availability of phylogenetic resources for the study of vascular plants at the family, genus and species level can facilitate assessment of previously difficult to test community assembly hypotheses in secondary forests regarding phylogenetic structural change. Understanding whether secondary succession leads to phylogenetic structural changes situates the study of forest regeneration and conservation within broader eco-evolutionary theoretical frameworks and may allow for enhancement of conservation policies by indicating whether secondary forest communities diverge from these expected patterns of community assembly, and those found in primary and conservation plantation forests (Letcher et al., 2012).

The majority of early phylogenetic structural studies focussed upon intact ecosystems and broader biogeographical and evolutionary hypotheses, while less attention has been paid to regenerating ecosystems such as secondary forests, where phylogenetic community assembly may occur over decades rather than centuries or millennia (Letcher et al., 2012). Additionally, the majority of phylogenetic structural analyses of regenerating forests have largely been conducted within European forest systems, while phylogenetic structural changes in the regenerating forests of tropical and subtropical East Asia remain understudied (Lososová et al., 2020; Padullés Cubino et al., 2021). This bears direct relevance for conservation, as an understanding of the phylogenetic relationships within secondary forest plant communities during the successional continuum may allow for targeted species reintroductions and restoration where human disturbances have significantly altered regional plant species pools (Kusumoto et al., 2016; Morel et al., 2019). For instance, if the phylogenetic structure of secondary forest remains clustered over time and does not resolve to match that of comparable primary forest, this may indicate barriers to secondary succession and highlight the need for species reintroductions through active replanting.

Crucially, a consensus regarding the pattern of basal and terminal phylogenetic structural change during succession is necessary before phylogenetic structural analyses during secondary succession can be applied to conservation practices. Previous works investigating community phylogenetic structure in regenerating tropical and subtropical forests indicated opposing trends, with some exhibiting increasing phylogenetic overdispersion over time following the onset of secondary succession (Lososová et al., 2020; Padullés Cubino et al., 2021), while in other instances secondary succession was found to lead to increased levels of plant phylogenetic community clustering in young growth and even 200-year-old subtropical forests in Xishuangbanna, China (Mo et al., 2013). Further investigations of phylogenetic structural responses during secondary succession may help in consensus building, while regional investigations can help to evaluate the status of passive ecological restoration and indicate whether active conservation forestry is necessary (Ewers et al., 2024).

1.3. Phylogenetic beta diversity

In addition to assessing basal and terminal phylogenetic structural change during secondary succession, investigating phylogenetic community differentiation (phylogenetic beta diversity), and how phylogenetic dissimilarity between communities changes with spatial, temporal and environmental gradients may offer insights into the processes shaping ecological communities during secondary succession (Graham and Fine, 2008). While species beta diversity integrates information on community species dissimilarity, phylogenetic beta diversity incorporates the degree of phylogenetic distances between communities and allows for assessment of community assembly mechanisms from spatial perspectives (Purschke et al., 2017). Phylogenetic beta diversity can be decomposed into subcomponents of phylogenetic turnover and nestedness, which can confer important information regarding mechanisms driving community assembly during secondary forest succession (Baselga, 2010; Leprieur et al., 2012; Purschke et al., 2017).

Phylogenetic turnover may be high or low between different communities, which may reflect differential community assembly mechanisms in action. Communities may exhibit i) spatial phylogenetic clustering or ii) spatial phylogenetic overdispersion. If species are more recently evolutionarily diverged within a community and thus more closely related and less closely related to species in other communities, phylogenetic turnover between sites will be high - termed spatial phylogenetic clustering (Purschke et al., 2017). High phylogenetic turnover may indicate abiotic filtering, where distinct groups of related and physiologically similar species are favoured in sites with specific patterns of abiotic filtering (Baraloto et al., 2012; Purschke et al., 2017). Spatial phylogenetic clustering may also indicate competitive exclusion of species within competitive hierarchies if traits conferring dominance are phylogenetically conserved, in addition to dispersal constraints (Mayfield and Levine, 2010; Eiserhardt et al., 2013; Purschke et al., 2017). Conversely, if co-occuring species within a community are phylogenetically less related than species from other communities, phylogenetic turnover between sites will be lower; this is termed spatial phylogenetic overdispersion (Purschke et al., 2017). This can indicate biotic filtering where negative interactions limit similarity competition between closely related species, but may also indicate abiotic filtering in cases of convergent evolution of important niche traits (Cavender-Bares et al., 2004).

1.4. Questions & hypotheses

In Hong Kong, the majority of forests are secondary and have been subject to historical disturbances (Zhuang and Corlett, 1997; Xing, Corlett and Chau, 1999). Dispersal networks are severely degraded, with key dispersing species such as Edwards's Long Tailed Rat and Flying Squirrel extirpated following mass deforestation during the second world war (Corlett, 2011). Deforestation and alterations to the primary forests once found in Hong Kong has taken place over several centuries. Fossilized fruits and seeds from Penny's Bay, Lantau island, indicate that tree species belonging to the Fagaceae and Laraceae families such as genera *Castanopsis*, *Lithocarpus* and *Quercus*, formed major components of Hong Kong's ancient forest ecosystems but are now limited in their distribution (Dudgeon and Corlett, 1994, 2011; Atha and Yip, 2016). Of these, oaks and chestnuts, which bear large dry fruits with no outer layer, are thought to be particularly limited by dispersal agent extirpation. Other plant species found in preserved samples include

Choerospondias axillaris, *Gnetum luofuense*, *Pinus massoniana* and *Schima superba*, which are still found in contemporary forest plant communities in Hong Kong. Archaeological evidence indicates that the earliest forms of deforestation of contemporary relevance commenced and endured throughout the Song (960–1278), Ming (1368–1644) and Qing (1644–1912) dynasties, when *Aquilaria sinensis* was exported, as well as extensive farming of tea terraces and rice paddies cultivated by Hakka communities in the uplands, and Cantonese Punti communities in the lowlands (Dudgeon and Corlett, 1994; Zhu et al., 2024). These agricultural and forestry activities would have resulted in the small-scale clearance of Montane and Lowland forests across Hong Kong, with records of tea plantations dating back to 1688 attesting to a history of deforestation spanning multiple centuries. The subsequent introduction of exotic species by the colonial British administration from 1841 onwards, and the near-total clearance of forest during the second world war particularly between 1941 and 45 mark the most recent and significant alteration to regional forest cover (Corlett, 1999). This long history of deforestation in the region has resulted in the complete clearance of primary forest beyond small remnant patches, and contemporary forests are secondary. Land-use patterns have changed significantly over the 20th century, with the abandonment of agriculture from the 1955 maximum of 23,000 acres of land cultivated for rice and tea in the New Territories alone falling to the current 852 acres in 2024 still thought to be actively farmed (Hayes, 2012; Lo, 2024). Significant rural to urban migration has also occurred in this time, and forests have been undergoing spontaneous secondary succession in these contexts. Assessing the phylogenetic structure of secondary forests in Hong Kong offers an opportunity to evaluate the phylogenetic community structure of secondary forests undergoing passive regeneration following extensive disturbance in the absence of neighbouring primary forest patches. The present study addressed the following questions and hypotheses concerning the phylogenetic structure of forest communities in the regenerating forests of Hong Kong:

i) Do recovering forest in Hong Kong exhibit phylogenetic clustering at early stages in succession and over-dispersion in later stages? It is hypothesized that phylogenetic overdispersion will increase in older forest communities due to increasing levels of intra-specific competition with the altered structure of forest abiotic conditions caused by the development of canopy cover and alterations to soil nutritive conditions.
ii) Do forests exhibit phylogenetic clustering at higher elevations and overdispersion at lower elevations due to changes in abiotic filtering regimes? It is hypothesized that at higher elevations secondary forests will exhibit phylogenetic clustering due to changes in selective regimes driven by temperature niche, which are thought to cause damage to some plants species found in lowland but not montane forests in Hong Kong.
iii) Does Forest succession lead to increased phylogenetic turnover and decreased nestedness with succession? It is hypothesized that transitions between early to middle and later successional communities will lead to phylogenetic turnover matching the turnover of shrub species to small and canopy tree species during the process of secondary succession.

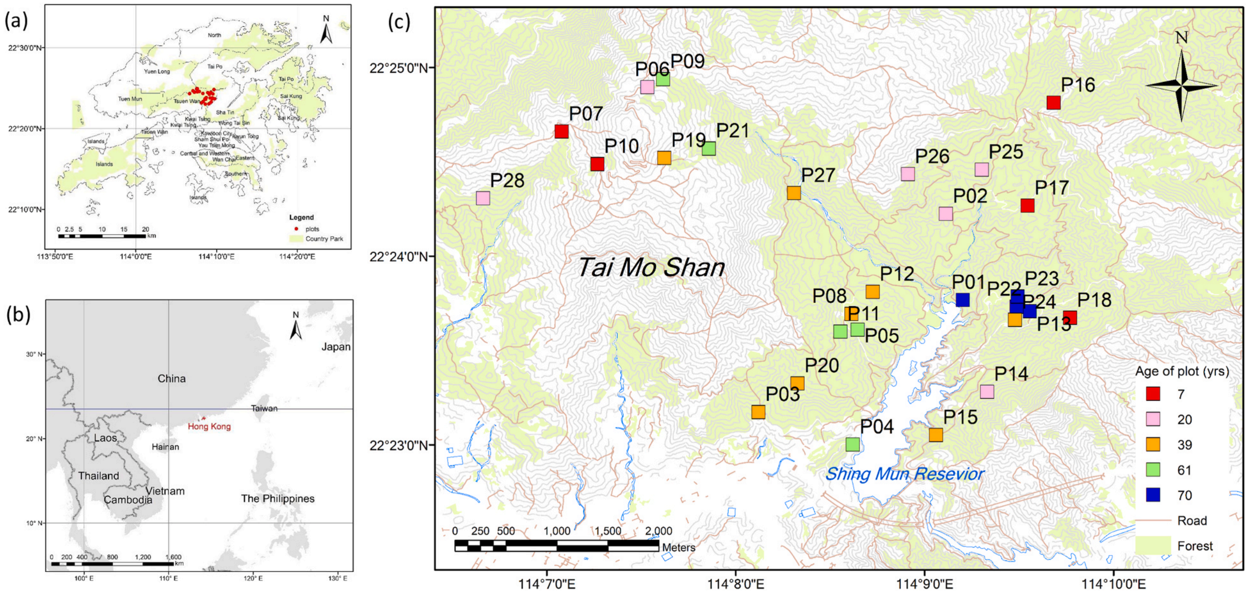

Fig. 2. Study sites located within the Tai Mo Shan and Shing Mun Country Parks in the New Territories of Hong Kong SAR with ages of plots in years following the onset of secondary succession from open grassland.

2. Methods

2.1. Forest vegetation species data

Plant community composition data was surveyed along a secondary forest successional gradient in the Tai Mo Shan and Shing Mun Country Parks in Hong Kong (Abbas et al., 2019)(Fig. 2). Hong Kong is located east of the Pearl River estuary in south China at 22°09′–23°37′ N and 113°52′–114°30′ E (Fig. 2), with a land area of 1106 km^2. Hong Kong has distinctive wet, hot summers in May to October with mean daily temperatures of 24–33°C and dry, cool winters in November to April with mean daily temperatures of 9–22°C. The mean annual rainfall is approximately 1800–2100mm (Dudgeon and Corlett, 2011; Abbas et al., 2019). The secondary forests in the present study developed through spontaneous succession following extensive deforestation in World War II (Corlett, 1999, Hau, Dudgeon and Corlett, 2005). A series of 28 plots within these regenerating areas were characterized by (Abbas et al., 2019) (Fig. 2). The age of vegetation was estimated via sequential analysis of vegetation cover over time and observation of vegetation development from aerial photographs which were collected annually by the Hong Kong government from the mid-20th century until the present day. Ages of plots represented time in years since the onset of secondary succession from open grasslands as characterized by these archival aerial records. Sites were selected based upon representation of forest age classes, lowland and montane forest type, and consistent archival record availability and quality. Sites had uniform land use history, with all plots having been subject to the same clearance events in the 1940s prior to re-establishment of shrub and tree species, while having only regenerated through secondary succession with no instances of active replanting initiatives. Study sites were located within the Tai Mo Shan and Shing Mun Country Parks in the Northern New Territories of Hong Kong. The terrain in the region comprises rugged, convex slopes which rise to the highest peak in Hong Kong, Tai Mo Shan (957 m), as well as the steep slopes surrounding the Shing Mun Reservoir. Analyses by (Abbas et al., 2016) noted that the landscape has undergone transformation from the mid-1940s until the present from being grassland-dominated to being forest-dominated, with forest cover increasing from 0.17 % in 1945 to 36.50 % in 2014. Woody species with a DBH >1 cm were surveyed from March 2015 to May 2016 across the plots and species presence, abundance and location within plot data was recorded. The names of plant species were standardized in accordance with The Plant List (Version 1.1) in (Abbas et al., 2019). Species were classified into one of four growth forms, being classed as either 1) canopy trees; 2) small trees; 3) shrubs or; 4) scandent shrubs or lianas. Elevation data were extracted from a 2 m resolution Digital Elevation Model (DEM), and slope, aspect and curvature were calculated using SAGA software (Abbas et al., 2019). Soil samples were collected in May to June 2016, for measurement of texture (sand, silt or clay), pH, organic matter, carbon content, nitrogen content and moisture. Each soil sample was collected from the centre of the 20 m × 20 m plot at a depth of 20 cm after the surface litter was removed (Abbas et al., 2019).

2.2. Community phylogenetic data

Phylogenetic community structure was determined by assessment of phylogenetic relationship between co-occuring species in 20 m x 20 m plots. A community phylogeny for species occurring at all forest plots was determined by extraction of a phylogeny using the R package V.Phylomaker, which extracts species phylogenetic relationships from a mega-phylogeny of all extant described families of vascular plants, encompassing 74,533 species which are held in a Newick Tree format constructed from Genbank molecular and Open Tree of Life project data, which includes age estimates for all 479 families of extant vascular plants (Jin and Qian, 2019). A full description of the construction of the molecular phylogeny can be found in (Smith and Brown, 2018). Survey data were collected for 50 plant species as these were the species which passed the minimum DBH requirement and were subsequently used to extract a community phylogeny across all 28 plots of the successional gradient. Predictions of phylogenetic relationships between co-occuring species was based on branch lengths from this tree. A phylogenetic tree of plants occurring in the study sites was constructed from the V.Phylomaker megaphylogeny, and in cases where representation of species was only available at the genus level, branch length indices were generated from these node points rather than species level termini. Although this decreases the accuracy of phylogenetic metric calculation, it still facilitates an exploration of community phylogenetic relationships which is relevant to the exploration of community assembly during secondary succession. The constructed phylogenetic tree was then assessed to assure that it was i) ultrametric and ii) binary, which would facilitate the calculation of basal and terminal phylogenetic diversity metrics. Ultrametric trees must fulfil key preliminary assumptions; each tip must be uniquely labelled; each internal node must be dichotomous and; the number of nodes must decrease from root to tip. These assumptions were fulfilled, and the constructed tree was prepared for downstream metric extraction.

2.3. Mean Pairwise Distance (MPD) & Mean Nearest Taxon Distance (MNTD)

To determine whether communities are phylogenetically overdispersed or clustered, the metrics of mean pairwise distance (MPD) and Mean Nearest Taxon Distance (MNTD) were calculated using the R Packages Phylomeasures and GGtree. MPD is the mean branch length distance between all pairs of species in a plot, while MNTD is the mean branch length distance between each species and its most closely related neighbouring species in a vegetation plot. MPD shows the degree of relatedness between basal branches of the phylogeny, while MNTD shows relationships at the terminal branches of the tree.

2.4. Phylogenetic beta diversity, turnover & nestedness

Phylogenetic beta diversity analysis was chosen to assess phylogenetic distinction between communities undergoing succession. To assess patterns of phylogenetic beta diversity, the R package picante was used to generate metrics of phylogenetic Sorensen's dissimilarity, as well as the sub-components of phylogenetic turnover and nestedness. Phylogenetic beta diversity components were generated against null models of community dissimilarity.

2.5. Phylogenetic non- metric multidimensional scaling

Phylogenetic non-metric multidimensional scaling (NMDS) was conducted using vegan. A phylogenetic distance matrix was generated and standardized effect size of mean pairwise distance and mean nearest taxon distance (SES MPD and SES MNTD) were generated. Standardized effect size measures of MPD and MNTD were generated by comparing observed values for these metrics with values expected under null communities with randomized phylogenetic differences. This calculation is summarized as follows:

$$\text{SES}_{\text{metric}} = (\text{Metric}_{\text{observed}} - \text{mean}(\text{Metric}_{\text{null}})) / \text{sd}(\text{Metric}_{\text{null}})$$

Where metric refers to either MPD or MNTD, and sd refers to the standard deviation of metrics generated in the null models. Multidimensional scaling (MDS) was conducted against phylogenetic distance matrices of SES MPD. Ordinations were plotted between phylogenetic dissimilarity matrices and environmental variable matrices. MANOVA was used to assess for the relative contribution of elevation, age and distance to phylogenetic dissimilarity.

2.6. Data analysis

Community phylogenetic metrics MPD and MNTD were assessed for dissimilarity between age classes via Welches t-test and non-metric multidimensional scaling (NMDS). Boxplots of MPD and MNTD were plotted across successional and elevational groups. Plots were classified into lowland (<500 m.a.s.l) and montane (>500 m.a.s.l) forest type, as well as early (7–20 years), mid (39 years) and late-stage (61–70 years) successional stages. Plots were split into age classes in line with literature regarding succession in tropical forests suggesting that up to 20 years of successional time may be necessary to observe associated biotic and community compositional changes from grass and shrubland (Dunn, 2004; Bowen et al., 2007; Abbas et al., 2019). The justification of choosing 39 years as a mid-succession phase and 61–70 as late succession phase mirrored previous works investigating secondary succession in neotropical secondary forest succession (Finegan, 1996). Plots were split into elevational categories in line with previous investigations of elevational thresholds between lowland and montane forests in Hong Kong (Zhuang and Corlett, 1997). While lowland forests are typically found below 500 m, montane forest in Hong Kong in the Tai Mo Shan and Tai Po Kau area were previously found to occur at elevations above 500 m (Zhuang and Corlett, 1997; Corlett, 2011). MPD and MNTD responses along elevational and successional gradients were analysed via linear regression. MPD and MNTD were assessed for normality via Shapiro Wilkes test, and models were subsequently constructed with a p value of < 0.05 indicative of significant influence of predictors upon observed variations in each phylogenetic diversity metric. In each model, continuous variables of community elevation (metres) and community age (years) and their interactions were used to predict MPD and MNTD. To assess the response of phylogenetic community dissimilarity to succession, the metrics of phylogenetic turnover and nestedness were modelled using generalized dissimilarity modelling (GDM), which employs an I-spline function in order to identify curvilinear responses of biodiversity to spatial and environmental gradients (Ferrier et al., 2007). Phylogenetic turnover and nestedness were modelled as products of geographic distance (metres) and age dissimilarity (years). Welches t-tests and ANOVA tests were used to test for differences between lowland and montane forest, and successional age groups in

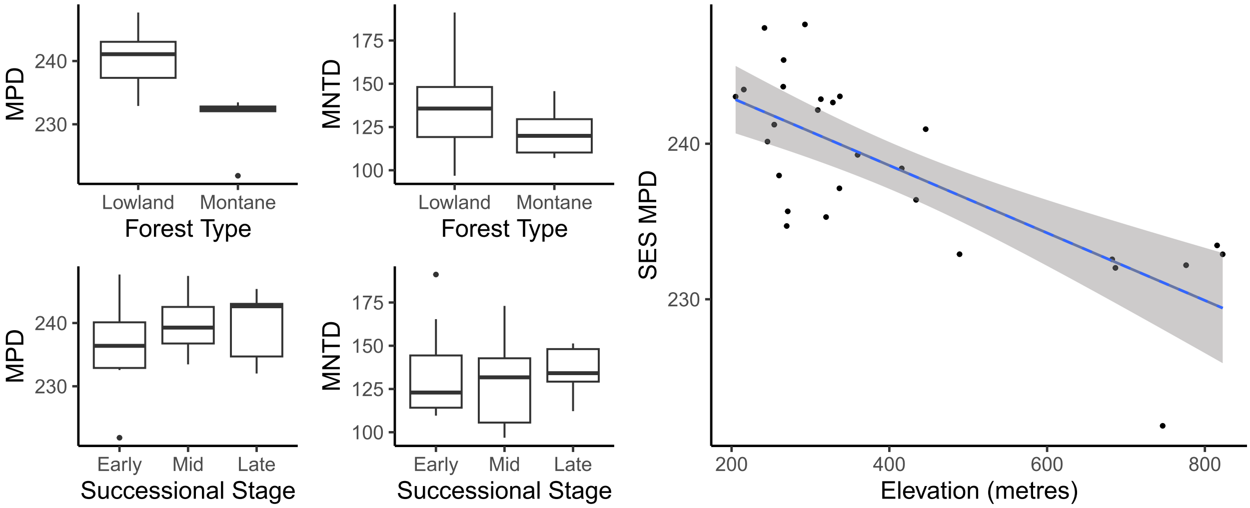

Fig. 3. a) Analysis of variance of MPD and MNTD between successional and elevational classes, and b) linear regression of SES MPD as a function of community Elevation.

beta diversity subcomponents of turnover and nestedness to determine differences between classes as well as responses to geographic and temporal gradients. ANOSIM was used to assess plant community species dissimilarity, while MANOVA was used to test for plant community species dissimilarity.

3. Results

3.1. MPD & MNTD, and phylogenetic NMDS

Two-way ANOVA found that MPD did not differ significantly between successional classes ($p > 0.05$)(Fig. 3a). Welches t-test testing found that MPD was significantly higher in lowland (mean = 240.52) communities than montane (mean = 230.83) communities, showing significantly higher means in lowland forest compared to montane forest ($p < 0.05$)(Fig. 3a). Linear models of MPD with continuous predictor variables of community age (years), and elevation (metres), found that elevation was the sole significant predictor with a negative relationship between MPD and elevation ($t = -3.554$; $p < 0.05$)(Fig. 3b). Welches t-testing found that MNTD did not significantly differ between lowland and montane forest type and ANOVA found that MNTD did not significantly differ between successional classes ($p > 0.05$), while linear models found that neither elevation nor successional age significantly predicted variation in models of MNTD (Fig. 3a). ANOSIM found that plant species community composition differed significantly between age groups. MANOVA found that elevation ($p < 0.05$, $F = 59.06$) and forest age ($p < 0.05$, $F = 5.56$) significantly predicted phylogenetic dissimilarity and exhibited a significant positive interaction. Distance did not significantly predict phylogenetic community structure. NMDS analysis found that phylogenetic community composition showed distinct communities in montane forests compared to

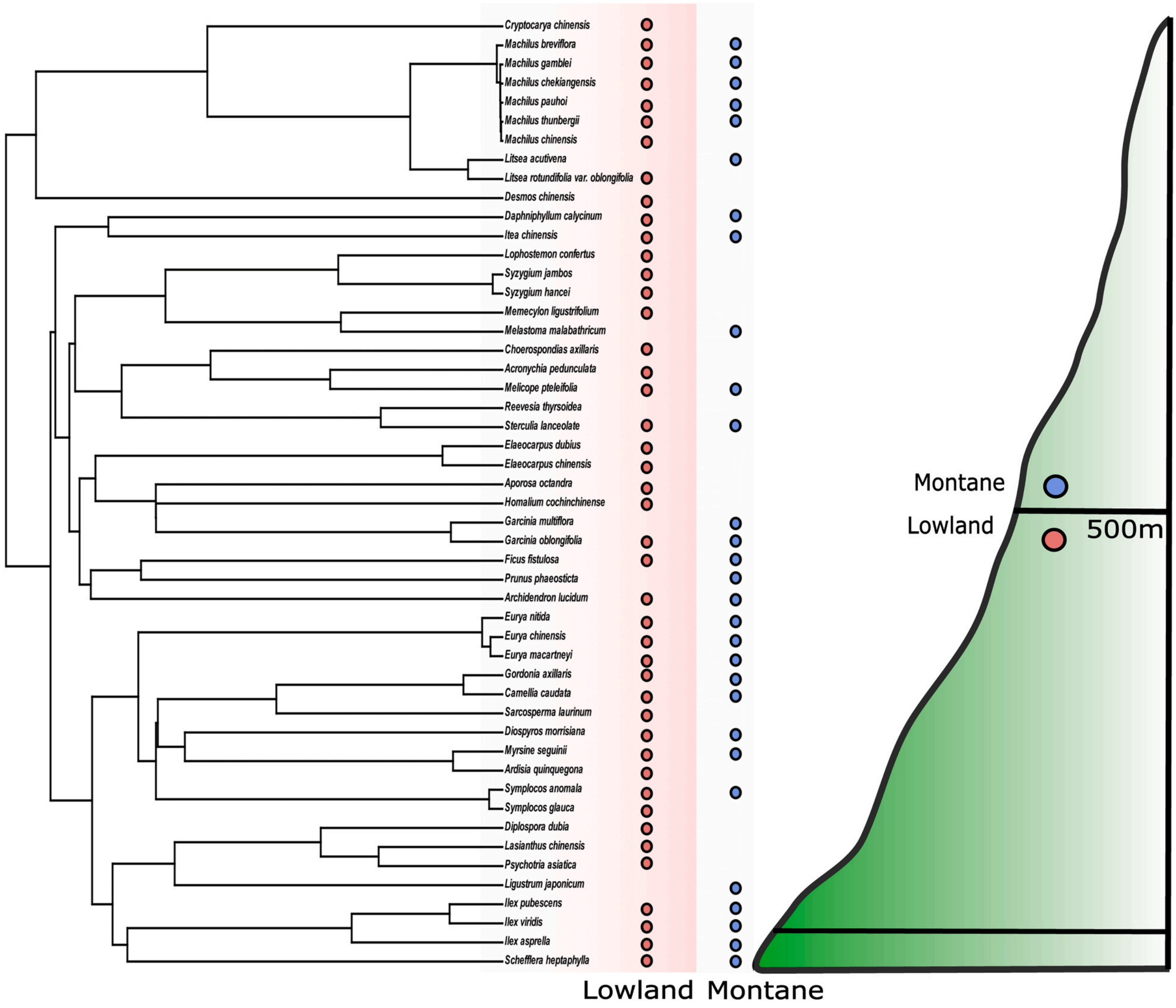

Fig. 4. Phylogenies at lowland (red) and montane (blue) elevational bands exhibit phylogenetic community structural differentiation.

lowland forests (Fig. 4; Fig. 5).

3.2. Phylogenetic turnover & nestedness

Generalized dissimilarity modelling (GDM) of phylogenetic turnover explained 20.266 % of deviation in lowland forest and 52.844 % of deviation in montane forest (Fig. 6) (Table 1). GDM models found that in lowland forests phylogenetic turnover was influenced primarily by inter-community distance (Sum of coefficients: 0.278), and secondarily by age dissimilarity (Sum of coefficients: 0.204) (Fig. 6) (Table 1). GDM models of phylogenetic turnover found that in montane forest phylogenetic turnover was influenced primarily by inter-community distance (Sum of coefficients: 0.343), and secondarily by age dissimilarity (Sum of coefficients: 0.213) (figure 6bii) (Table 1). GDM analysis of phylogenetic nestedness responses to geographic distance and age dissimilarity explained <1 % of deviance and models were subsequently discarded due to their weak explanatory power. Unpaired two-sample t-testing and Welches testing found that phylogenetic turnover ($p<0.05$) and nestedness ($p<0.05$) significantly differed between lowland and montane forest type but not successional groups ($p>0.05$) (Fig. 7). There was higher phylogenetic turnover within montane forest compared to lowland forest, and lower nestedness within montane forest compared to lowland forest (Fig. 7).

We identified 50 morphotypes across 8575 woody individuals of DBH≥1 which were identified to species level. Additional morphotypes were identified to courser taxonomic resolutions including two species of *Symplocos* and one species of *Machilus* which were identified to genus level, and one species from *Lauraceae* which was identified to family level, which were not included within phylogenetic analyses. Additionally, three gymnosperm species were recorded, including: *Cunninghamia lanceolata*, *Gnetum luofuense* and *Pinus elliottii*. *Acacia confusa*, *Duranta erecta*, *Eucalyptus exserta*, *Lantana camara*, *Lophostemon confertus* and *Pinus elliottii* which are exotic, were recorded. *Cunninghamia lanceolata* and *Dimocarpus longan*, species native to China and historically cultivated in the region. The number of species recorded increased sharply in the first 20 years of succession. It reached a steady rate following 20 years and dropped after 70 years. One-Way ANOVA showed non-significant difference in species richness and Shannon's species diversity between different forest age classes (F1, 26=0.535, p=0.471). One-Way ANOVA also showed no variation between density of individuals and between age classes. However, the median of density in 7-year-old forests was 170/400m2 (4250/ha), while it ranged from 201 to 328/400m2 (8200/ha) for other ages.

4. Discussion

4.1. Community assembly & phylogenetic structure of secondary forests in Hong Kong

The present study sought to characterize the processes shaping plant community assembly within secondary regenerating forests in Hong Kong through describing the phylogenetic structure and dissimilarity of plant communities (Abbas, Nichol and Fischer, 2016). Significantly, assessment of phylogenetic clustering and overdispersion within and between plant communities has previously been

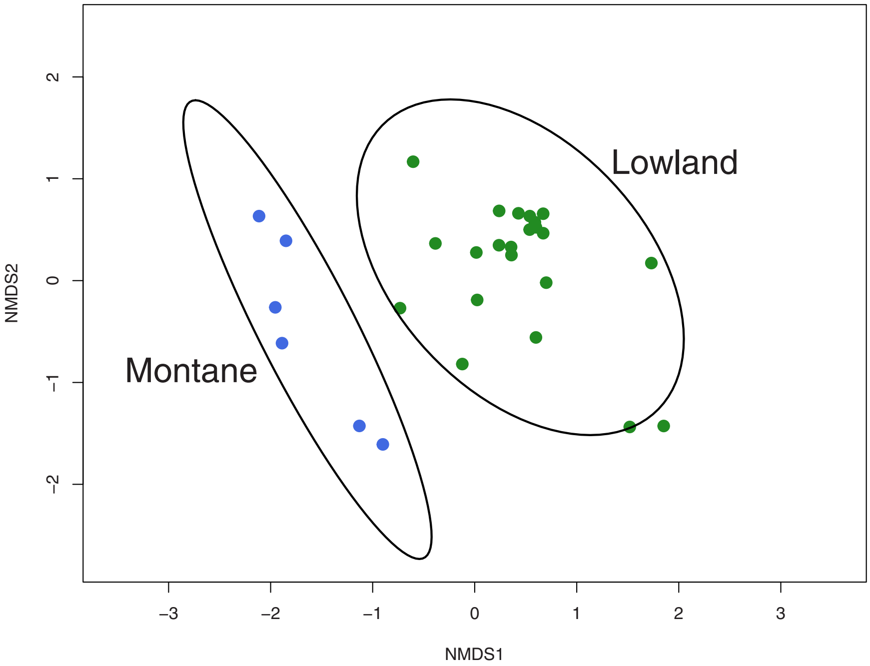

Fig. 5. Phylogenetic Non-Metric Multidimensional Scaling constructed upon distance matrices of mean pairwise distance and environmental distances, with ordination ellipses, including ellipse 1 (lowland forest below 500 m) and ellipse 2 (montane forest above 500 m)($R^2=0.937$).

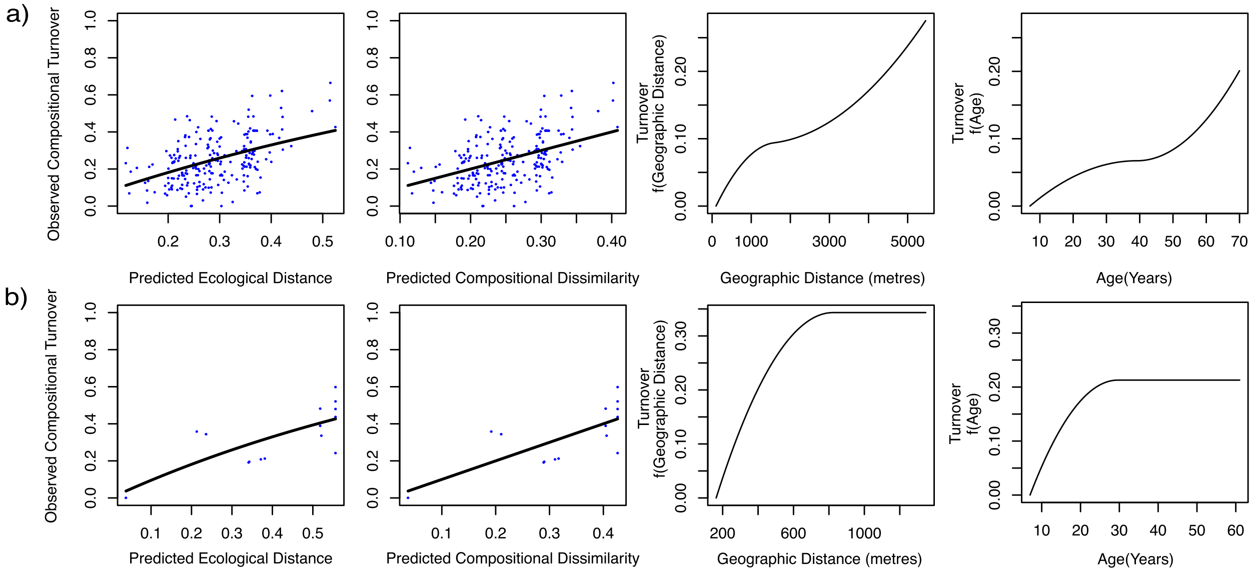

Fig. 6. GDM models of phylogenetic turnover in a) lowland and b) montane forest displaying i) fitted relationships between predicted ecological distance (summed transformed pairwise environmental dissimilarities of study sites) and observed compositional dissimilarity (pairwise phylogenetic turnover) and; predicted versus observed biological distance and;) I-spline function plots of plant species phylogenetic turnover explained by transformed predictor variables including; ii) Geographic Distance between communities (metres); iii) Age dissimilarity between communities (years).

Table 1
Summary of generalized dissimilarity models with significant variables presented in lowland and montane forest. Relative importance of variables is determined by summing I-spline coefficients from GDMs.

Model	Null Deviance	GDM Deviance	%Deviance Explained	Variables	Coefficients
Lowland					
β_{Sim}	21.156	16.869	20.266	Geographic Distance	0.278
				Age	0.204
Montane					
β_{Sim}	1.873	0.882	52.844	Geographic Distance	0.343
				Age	0.213

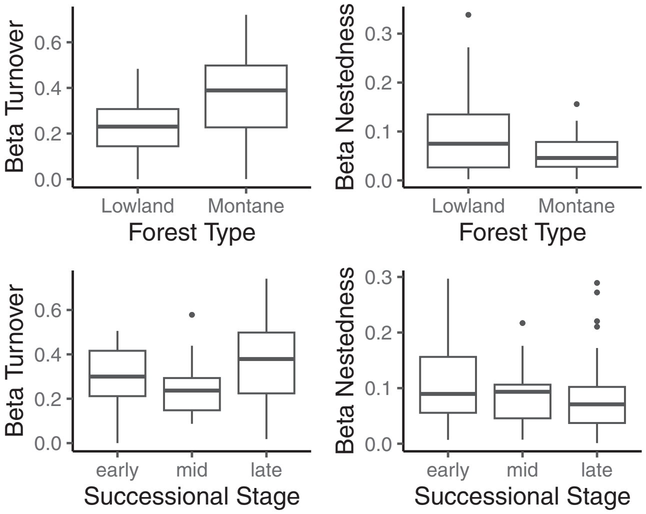

Fig. 7. Pairwise turnover and nestedness boxplots of phylogenetic turnover and nestedness responses at different successional and lowland and montane forest type.

shown to reflect environmental filtering and niche differentiation in regenerating forests (Padullés Cubino et al., 2021). Additionally, phylogenetic beta diversity, turnover and nestedness can help to contextualize community responses to spatial and environmental gradients and indicate the nature of competitive and selective regimes (Purschke et al., 2017). These metrics integrate ecological and evolutionary components of community assembly, implicating plant traits and niche space in the study of plant community formation. The response of plant phylogenetic community structure and phylogenetic beta diversity during secondary succession may prove highly informative to conservationists in evaluating the process of passive secondary succession and indicate potential barriers or modifications to succession in highly degraded landscapes.

4.2. Secondary forests basal clustering with increasing elevation

We found that regenerating tropical forests in Hong Kong exhibited increased basal phylogenetic clustering in montane compared to lowland forest type. Additionally, lowland and montane forests exhibited high degrees of phylogenetic turnover at basal, and thus ancient, branches of the phylogeny. Elevation primarily determined basal phylogenetic community structure, while forest successional age was insignificant in shaping MPD or MNTD metrics, although increasing forest age drove phylogenetic turnover in lowland and montane forest communities. This contrasts with investigations in secondary tropical forests in Puerto Rico (Muscarella et al., 2016) and Costa Rica (Letcher, 2010), which found that plant communities became more phylogenetically overdispersed with age, with a greater degree of less recently diverged species co-occurring within communities. However, the forest plots used in these studies were situated along different successional gradients (4–91 years and 1–44 years) than the present study (7–70 years) and neither study accounted for elevational differences amongst sites. The absence of primary forest in Hong Kong may be limiting the introduction of later successional plant species, while the persistence of some understorey species from early succession through to later succession such as *Psychotria asiatica* and shrub species may lead to similar phylogenetic community structural patterns across successional age groups in our findings (Mayhew et al., 2019). Investigations comparing lowland secondary and primary tropical rainforest chrono-sequences in New Guinea found that while primary forests become overdispersed as they aged, secondary forests became increasingly phylogenetically clustered through secondary succession, demonstrating that forest type can influence observations of phylogenetic community structural change during secondary succession (Whitfeld et al., 2012). Our findings may reflect the lack of opportunity for recolonization by larger tree species capable of growing above 30 m due to the clearance of forest throughout Hong Kong during the second world war (Abbas, Nichol and Fischer, 2016). Plant species within the Fagaceae family are known to be poorly dispersed in Hong Kong, and their absence from the sites upon which the present study was conducted may further influence the phylogenetic structural characteristics we observed during secondary succession (Corlett, 2011). These findings may support assisted regeneration through conservation planting of genera such as *Quercus*, which may facilitate phylogenetic structural change with time by increasing the number of families and life history strategies, as these genera do not currently appear to be facilitated by existing dispersal processes.

The present study included temporal and spatial variables within its design, and emphasized abiotic filtering driven by elevational changes leading to different selective regimes between lowland and montane forests rather than those brought on by secondary succession with respect to basal and terminal phylogenetic structural characteristics (Zhuang and Corlett, 1997). Abiotic conditions can significantly change along elevational gradients, with temperature, soil moisture and hydrological regimes shifting between lowland and montane systems (McCain and Grytnes, 2010). Research into plant communities in Broadleaf forests in Zhejiang, China, found that communities became phylogenetically clustered at elevations of 500m-1000m, while showing overdispersion both below and above this elevational band (Zhang et al., 2021). The 500–1000 m elevational band of this study is within the same elevational range at which the forest communities in the present study exhibited similar patterns of basal clustering. The finding that plant communities were phylogenetically clustered in montane forests and compositionally distinct from lowland forest supports the role that elevation plays in shaping patterns of community structure in Hong Kong secondary forests. This may be due to differential abiotic filtering in montane relative to lowland forests, as the former forest type experiences lower temperatures during the coldest months of the year and have even been found to experience frosts periodically (Dudgeon and Corlett, 2011).

Investigations of montane and secondary seasonal tropical forest in Oudomxay, Lao, and Xishuangbanna, China, along elevation gradients between 600m-1500m also found that elevation significantly influenced community phylogenetic structure, due to the integrative nature of elevation for the abiotic changes that occurred with the transition from lower to higher elevations in these forest communities (Satdichanh et al., 2019). Integrating elevational gradients within investigations of plant community phylogenetic structure may facilitate accurate partitioning of the influence of secondary succession upon plant community assembly dynamics by recognizing that lowland and montane forest types are subject to distinct community assembly processes. While plant communities may exhibit responses to successional age, correcting for elevational change demonstrates the importance of abiotic conditions in driving niche-based community assembly through environmental filtering (Vellend, 2016).

4.3. Phylogenetic turnover was consistent between lowland and montane forest

We found that phylogenetic turnover increased primarily with inter-community distance and secondarily with successional age dissimilarity in both lowland and montane forest. These patterns of phylogenetic turnover in Hong Kong forests suggest spatial phylogenetic clustering (Purschke et al., 2017), while the turnover between lowland and montane forest type conforms with the regional forest type zonation described by (Zhuang and Corlett, 1997), wherein lowland forests are found below 500 m and montane forests are found above 500 m in Hong Kong. Conversely, phylogenetic nestedness did not appear to respond to temporal, spatial or environmental gradients in either lowland or montane forest type.

Global analysis of phylogenetic turnover in plant communities in tropical forests in Panama, Thailand, Cameroon, Colombia, Malaysia, Sri Lanka and Ecuador found that environmental dissimilarity drove phylogenetic turnover (Baldeck et al., 2016). However, the analyses across these regions did not take succession or elevational gradients into account, potentially overlooking the influence of temporal and environmental factors upon phylogenetic dissimilarity between communities. An assessment of subtropical broadleaf forests in Zhejiang, China, found that phylogenetic turnover varied with environmental differentiation more significantly than between successional stages (Purschke et al., 2017). These investigations in Zhejiang were conducted over a similar successional gradient (20–80 years) but used a broader elevational gradient (250 m - 1258 m) and were based upon metrics of transformed environmental dissimilarity rather than using direct measures of elevation. Notwithstanding, while phylogenetic turnover may be deterministically driven by elevational gradients, our own findings indicate that phylogenetic turnover occurs during succession within both lowland and montane forest. This may reflect compositional taxonomic changes which have previously been shown to occur in the same communities upon which the present analyses were conducted (Abbas et al., 2019; Guclu et al., 2024). Meanwhile, our finding that intercommunity distance played the most significant role in shaping phylogenetic turnover suggests that plant communities in lowland and montane forests may be exhibiting spatial phylogenetic clustering.

Spatial phylogenetic clustering implies that communities of plants are assembling in ways that violate null models of spatial dissimilarity and implicate a broad array of potential ecological processes (Morlon et al., 2011). Communities typically exhibit patterns of spatial phylogenetic overdispersion in contexts where dispersal is not limited, or where inter-community distances are relatively small, whereas clustering is more typically associated with larger scale patterns where dispersal is inhibited (Chave, Chust and Thébaud, 2012; Forest et al., 2007; Cavender-Bares et al., 2009; Kraft and Ackerly, 2010). Our finding that Hong Kong plant communities in secondary forests exhibited spatial phylogenetic clustering suggests that dispersal may be compromised. Having undergone significant deforestation and the concomitant extirpation of several frugivorous seed dispersing and scatter hoarding species, Hong Kong seed and fruit dispersal networks have been previously classified as highly degraded (Chung and Corlett, 2006; Corlett, 2011). Recent investigations suggest that larger gaped bird species have become re-established, while scatter hoarding rodents remain underrepresented within regional dispersal networks (Leven and Corlett, 2004). Notwithstanding, our findings suggest that despite select dispersing fauna having been found to have returned to the region, the legacies of historical dispersal network degradation may still be influencing spatial phylogenetic turnover within the forest plant communities we investigated. Notably, even in the presence of intact dispersal networks, the lack of adjacent and widespread primary forest from which later successional tree species can disperse to secondary patches and the significantly low coverage of forest in Hong Kong following 1946 may continue to limit the scope for passive restoration without active planting (Corlett, 2011; Dudgeon and Corlett, 2011; Mayhew et al., 2019; Ewers et al., 2024).

The influence of dispersal limitation upon spatial phylogenetic clustering has been recorded in tropical forests in Madagascar, wherein plant communities assembled in non-random patterns that varied between clustered and over-dispersed communities depending upon the dispersing fauna present (Razafindratsima and Dunham, 2016). Assessment of tropical forest in Pasoh, Malaysia found that spatial patterns of phylogenetic clustering were driven by seed dispersal syndrome, which may also be reflected in the patterns observed in Hong Kong secondary forests (Seidler and Plotkin, 2006). An assessment of fruit and seed morphology, dispersal syndrome and dispersing fauna associated with the plant species within the regenerating secondary forest communities we studied may help to determine the contribution of dispersal to the observed pattern of spatial phylogenetic clustering outside of these speculations. Notwithstanding, it can be drawn that spatial phylogenetic clustering and successional driven phylogenetic turnover is apparent within lowland and montane forests in Hong Kong, while this turnover does not appear to significantly alter the basal or terminal phylogenetic structure of plant communities during secondary succession.

4.4. *Conclusions & considerations for regional conservation*

The present study found evidence of basal phylogenetic clustering in montane forest relative to lowland forest, and evidence of phylogenetic compositional change and differentiated community assembly processes between these forest types in Hong Kong. Additionally, patterns of phylogenetic turnover suggested spatial phylogenetic clustering and turnover between successional classes. These findings emphasize the importance of conserving plant communities at large spatial scales which can capture the full range of species found between unique forest communities in the region, with the differential community assembly within and phylogenetic turnover between lowland and montane forests in the region is testament to the differentiation of these forest types (Devictor et al., 2010; Morlon et al., 2011). The lack of basal or terminal phylogenetic differentiation between successional classes may be driven by numerous extraneous factors with differential conservation implications for landscape restoration in Hong Kong.

If passively regenerating secondary forests exhibit no differentiation in basal or terminal phylogenetic structure during the process of secondary succession, this may suggest either that; i) in later stages of succession plant community assembly is still being driven by similar processes to those at play during early succession, or that; ii) other extraneous processes which have not been accounted for are strongly influencing phylogenetic community structure including dispersal limitation, or post-dispersal processes impacting recruitment such as seed predation. The dispersal restriction of late-successional stage tree species, which are not evenly regionally distributed, and the lack of primary forest in the region, may place concrete restrictions upon the presence of genera such as *Quercus, Castanopsis,* and *Lithocarpus* in forest patches assessed. Our findings also suggest that seed dispersal or post-dispersal processes in lowland and montane forests in Hong Kong are leading to spatial phylogenetic clustering and emphasize the necessity for determining the precise drivers of these observations through future investigation of plant trait distributions, post-dispersal recruitment, and the presence and abundance of dispersing fauna (Corlett, 2011). While plant species dependent upon frugivores to traverse large spatial gradients may grow in the presence of dispersing fauna, the lack of nearby source populations for several tree species due to absence of primary forest in Hong Kong suggest that active forest restoration with planting of native plant species in the region is necessary at a large scale. Hong Kong experienced severe deforestation during the second world war, and while plantation forestry and restoration initiatives have been initiated, governmental programmes have used a combination of native and non-native species, while the post-war vegetation cover was below 4 % of the total land cover (Corlett, 1999, 2011). Non-governmental projects restoring post-fire hillsides in Hong Kong have used many Fagaceae species and set a precedent for future conservation activities needed elsewhere in Hong Kong (Fischer and Zhang, 2016).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability

Data will be made available on request.

Appendix I. . A list of the 50 species recorded in the present study found across the 28 study sites

Genus	species	Genus	species
Acronychia	*pedunculata*	*Lasianthus*	*chinensis*
Aporosa	*octandra*	*Ligustrum*	*japonicum*
Archidendron	*lucidum*	*Litsea*	*acutivena*
Ardisia	*quinquegona*	*Litsea*	*rotundifolia*
Camellia	*caudata*	*Lophostemon*	*confertus*
Choerospondias	*axillaris*	*Machilus*	*breviflora*
Cryptocarya	*chinensis*	*Machilus*	*chekiangensis*
Daphniphyllum	*calycinum*	*Machilus*	*chinensis*
Desmos	*chinensis*	*Machilus*	*gamblei*
Diospyros	*morrisiana*	*Machilus*	*pauhoi*
Diplospora	*dubia*	*Machilus*	*thunbergii*
Elaeocarpus	*chinensis*	*Melastoma*	*malabathricum*
Elaeocarpus	*dubius*	*Melicope*	*pteleifolia*
Eurya	*chinensis*	*Memecylon*	*ligustrifolium*
Eurya	*macartneyi*	*Myrsine*	*seguinii*
Eurya	*nitida*	*Prunus*	*phaeosticta*
Ficus	*fistulosa*	*Psychotria*	*asiatica*
Garcinia	*multiflora*	*Reevesia*	*thyrsoidea*
Garcinia	*oblongifolia*	*Sarcosperma*	*laurinum*
Gordonia	*axillaris*	*Schefflera*	*heptaphylla*
Homalium	*cochinchinense*	*Sterculia*	*lanceolate*
Ilex	*asprella*	*Symplocos*	*anomala*
Ilex	*pubescens*	*Symplocos*	*glauca*
Ilex	*viridis*	*Syzygium*	*hancei*
Itea	*chinensis*	*Syzygium*	*jambos*

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