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Differences in mixed-species bird flocks across forest succession: Combining network analysis and trait-based ecology related to the fast-slow continuum

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Conflict of interest

There is no conflict of interest.

Authors' contributions

Y.S., E.G. and Q.Z. conceived the idea and designed methodology; Q.Z. and Q.Q. collected the data; Y.S. analysed the data; Y.S. and E.G. led the writing of the manuscript. S.E., M.U. and S.R. contributed critically to the drafts and revision. All authors gave final approval for publication.

Data availability statement

Data available from the figshare: https://figshare.com/s/e14928b06414c19518a5

Abstract

1. Secondary forests are increasingly important for biodiversity conservation and ecosystem functioning. Yet, we know little on how species interactions shift across the

wide range of life history strategies in the context of forest succession, especially for non-trophic animal social systems.

2. Using data from mixed-species flocks (hereafter MSFs) and life history and morphological traits from the "fast-slow" continuum, we utilized a novel combination of network theory and trait-based ecology to examine the assembly of associations of MSFs among species with different fast-slow strategies across stages of forest succession that exhibit different degrees of forest complexity.

3. MSFs formed the most connected and cohesive network in the intermediate successional stage. In contrast, we observed the least connected and cohesive network in the early stage, and a strongly connected but intermediately cohesive network in the late stage. Fast species with smaller body size and mass, and larger clutch size, were gradually replaced by slow species during succession. Interspecific associations generally shifted from those among similarly fast species (early stage) to associations between fast and slow species (intermediate stage), and finally to those among similarly slow species (late stage).

4. We suggest that vegetation complexity (e.g., tree size, height, diversity and canopy cover), related to the availability of resources and number of niches, shaped the network structure and functional composition of MSFs. Although the late successional forests play an irreplaceable role in protecting forest specialists (i.e., slow species), intermediate stage forests should be also protected, because the large-sized networks formed by MSFs at intermediate stages can simultaneously conserve more species with varying ecological strategies.

KEYWORDS: ecological networks, fast-slow trait continuum, forest succession, interspecific interactions, mixed-species bird flocks

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INTRODUCTION

Understanding how communities respond to shifts in environmental conditions originated by forest succession is a key objectives of community ecology (Gonzalez & Loreau 2008; Grilli et al., 2017). This knowledge is relevant for predicting the composition of communities, and hence the functioning of ecosystems, as they respond to anthropogenic disturbance (Weiskopf et al., 2020). Classic theory on succession focuses on understanding and predicting species interactions during the successional sequence, by examining whether dominant species at one stage of succession facilitate or inhibit those species that follow (Connell & Slatyer 1977; Pulsford et al., 2016). This theory has been foundational for multiple studies examining species interactions in food webs, plant animal interactions and mutualisms as they go through the process of succession (Velho et al., 2012; Yang et al., 2018). Yet understanding how other kinds of mutualisms, such as intraguild mutualisms (Crowley & Cox 2011), are affected by succession remains relatively unexplored. More generally, it is important to understand how species interactions are affected by anthropogenic disturbance for predicting future environments and conservation planning (Tylianakis et al., 2010; Valiente-Banuet et al., 2015).

An important model system for intraguild mutualisms and their response to anthropogenic disturbance are mixed-species flocks of birds (hereafter, MSFs). MSFs, are defined as moving groups of multiple species of birds that form through interspecific attraction. MSFs are a well-studied and globally-distributed phenomenon in forest habitats (Zou et al., 2018) and have a major impact on how efficiently birds forage and their risk of predation (Goodale et al., 2017). MSFs generally degrade as the intensity of anthropogenic disturbance increases, especially as forest gives way to

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open habitats or fragmented landscapes (Maldonado-Coelho & Marini 2004; Sridhar & Sankar 2008; Zou et al., 2018). However, participating in MSFs has been reported to buffer the response of birds to some kinds of disturbances such as selective logging (Borah et al., 2018; Srinivasan 2019) and to natural environmental stress such as elevation (Zhang et al., 2020). Researchers have used social network analyses (Farine & Whitehead 2015) to explore how species interactions in MSFs change due to anthropogenic disturbance, measuring the connectedness (the strength and connectedness of associations) and the cohesion of the system (whether species all interact together or rather break into different subgroups or "modules") (Mokross et al., 2014; Borah et al., 2018; Zhou et al., 2022). Yet despite our understanding of how MSFs degrade with deforestation, how MSFs regain structure during forest succession, if they do at all, is relatively unknown.

Predicting changes to MSFs in response to anthropogenic disturbance requires the consideration of two steps in the process: first, how the composition of the general bird community is affected, and second, how MSFs themselves are directly shaped by the new environment (Sridhar & Sankar 2008; Zou et al., 2018). To start with the whole community, forest succession generates a variety of environmental changes, due to simultaneous alterations in microhabitats (i.e., temperature) and plant composition (i.e., food availability) (Quesada et al., 2009; Lohbeck et al., 2013) that consequently affects animal community re-assembly (Velho et al., 2012; Acevedo-Charry & Aide 2019). A key transition occurs from species with "fast" life histories and associated functional traits that allow them to colonize early successional environments, reproduce quickly and then disperse as the habitat begins to change, to species with "slow" life histories better adapted to competition in more stable environments (Salguero-Gómez et al., 2016; Dent & Estrada-Villegas 2021). For

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birds, fast species are characterized by smaller body size, larger clutch size, shorter nestling period and shorter longevity, and are expected to thrive in early successional habitats, gradually giving way to slower species as the forest matures (Salguero-Gómez et al., 2018; Dent & Estrada-Villegas 2021). Therefore, during the course of forest succession, we would expect a shift in the functional traits of the overall bird community from fast to slow species, altering the community from which MSF-participating species are drawn.

As MSFs are an adaptation to reduce predation and simultaneously increase foraging efficiency, predicting how their structure changes across succession will require an understanding of how vegetation alters predation risk and resource availability (Thiollay 1999; Sridhar & Sankar 2008). MSF participants are not a randomly drawn subgroup of the avian community, but rather they predictably include those species most vulnerable to predation (e.g., small species) that have an insectivorous diet for which resources are relatively evenly distributed (Sridhar et al., 2012; Sainz-Borgo et al., 2018). Further, species have been shown to prefer to join MSFs that match them in major aspects of their ecology such as their size and diet (Sridhar et al., 2012; Sridhar & Guttal 2018), which may ensure that they are vulnerable to the same suite of predators and move at similar speeds through the forest, while at the same time partitioning other finer aspects of their foraging niches, such as microhabitat choice and foraging technique, in order to avoid competition (Goodale et al., 2020; Jones et al., 2020). It would seem essential therefore to combine trait-based ecology with network analyses to fully explore MSFs' response to forest succession.

In this study, we combined monitoring of MSFs, and data on fast-slow traits of MSF participants in the Dinghushan Mountains in southern China, to investigate how

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associations in MSFs re-assemble during forest succession. Our hypotheses, summarized in Figure 1, were that (1) early successional forest would be characterized by low vegetation complexity and few resources for insectivores (Montaño-Centellas & Jones 2021), so only a limited number of species with fast life history strategies and functional traits that allow them to be tolerant of disturbance would survive in the overall community (Schieck & Song 2006; Carlo & Morales 2016). Further, we predicted that a relatively low number of MSFs would be drawn from this whole community, producing networks with low connectivity and cohesion, and associations concentrated among a few fast species. (2) In intermediate successional forests, the combination of pioneer and old growth forest plants may offer more diverse resources and foraging niches, therefore fostering higher species richness (Molino & Sabatier 2001) and harboring a bird community with mixed life history strategies. We expected both fast and slow species to participate together in MSFs, leading to a network with high connectivity and cohesion, and associations between random and/or dissimilar species-pairs (Montaño-Centellas & Jones 2021; Shen et al., 2022). (3) In old-growth forest, the vegetation complexity increases significantly, and sufficient resources foster slower species that are better competitors (Huang et al., 2018; Schuldt et al., 2018). At this successional stage we expected finer microhabitat partitioning (Pigot et al., 2016), and species to join MSFs that match their microhabitat, producing separate canopy/midstorey and understorey MSF sub-types (Montaño-Centellas & Jones 2021; Shen et al., 2022). These processes would generate a network with high connectivity but low cohesion, with interactions concentrated among slow species.

MATERIALS AND METHODS

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Study site

This study was conducted in the Dinghushan Nature Reserve in Guangdong Province, southern China (23˚09'21"-23˚11'30"N, 112˚30'39”-112˚33'41"E). The Dinghushan Nature Reserve in well known as an “Important Bird Area” in China (BirdLife International, https://www.birdlife.org/). The climate is subtropical, with mean annual temperature and humidity are 20.9 °C and 85%, respectively, and mean annual precipitation is 1927 mm (Shen et al., 2014).

The main source of anthropogenic disturbance in this forest has been logging. The successional process of the forest in the reserve has been classified by plant ecologists based on the community structure and species composition: needle-leaved forest replaced by needle and broad-leaved mixed forest, and then replaced by evergreen broad-leaved forest (Peng & Wang, 1995). According to this successional process, we divided our study site into three successional stages. The early successional forest (EF) is mostly made up of conifers, dominated by the pioneer tree *Pinus massoniana*; we estimate its age over 40 years at the time of the fieldwork, following Zhou et al. (2006), but emphasize that this forest has also been under continuous human pressure (e.g., tapping pine trees for resin, understory removal), different than the older forests. The intermediate successional forest (IF), about 80 years old, is a mixed coniferous and broadleaved forest co-dominated by coniferous (*P. massoniana*) and broadleaved species (e.g., *Castanopsis chinensis* and *Schima superba*). The late successional forest is an old-growth broadleaved forest (OF, over 400 years old) dominated completely by native broadleaved species, such as *Castanopsis chinensis*, *Schima superba*, *Machilus chinensis* and *Cryptocarya chinensis*. Plant data taken at the same time as the bird surveys showed that vegetation complexity increases across the forest successional stages (i.e., increasing tree size,

height, species diversity and canopy cover), confirming the classification of vegetation complexity in EF, IF and OF as low, moderate and high, respectively (Zhang et al. 2013). As we are interested in changes over time, but compare different habitats at different stages of succession, we acknowledge that we are using a space-for-time substitution approach to study forest succession.

Avian community and mixed-species flocks survey

Permit to carry out fieldwork was provided by the Administration of Dinghushan Nature Reserve. We established two transects of 2.5-3 km in each successional stage, monitoring six transects in total (Zhang et al., 2013), as Dinghushan is not a very large reserve (1155 ha). We covered a good amount of the area and the habitats of the more accessible eastern half of the reserve (Figure S1). Bird surveys were conducted monthly from March 2008 to February 2009. We set 10 sampling points within each transect, separated by > 200 m, where all birds including intraspecific and interspecific flocks, or solitary individuals, were recorded by timed point counts (10 min). An MSF was defined as a roving group of birds composed of more than one species of foraging individuals staying within 25 m of each other for at least 5 min (Hutto 1987). Bird surveys were conducted at sunrise and ended before 11:00 AM in clear weather. Each transect was observed once a month to avoid recording the same MSFs or individuals repeatedly. The 10 points per transect were surveyed in the same day; all birds seen and heard were counted by two observers simultaneously during the timed point counts within a 25 m radius plot. When an MSF was visually detected, we noted the species composition and the abundance of each species.

Avian traits collection

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We used 12 bird traits per species to represent their life history characteristics and other functional traits (see Table 1). Life span and nestling period were obtained from Myhrvold et al. (2015) and the Birds of the World (the Cornell Lab of Ornithology, https://birdsoftheworld.org/bow/home). The other 10 traits were obtained from Wang et al. (2018).

Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	2.5-3 km transects in different successional stages	4 replicates (two transects, each with two seasons for each successional stage)

Data analysis

Our objective was to use the variability between the two transects and monthly surveys in each successional stage to provide statistical inference about how the successional stages differed from each other. However, when we subdivided the survey data in one successional stage into more than six replicates, many replicates were left with little or no data (i.e., two or fewer MSFs, Table S1). We therefore explored analyses with n = 3 replicates (two transects combined, three seasons: winter, breeding [spring and summer combined], and autumn), n = 4 (two seasons, winter combined with spring, and summer combined with autumn for each transect), and n = 6 (three seasons for each transect). Because the number of MSFs in spring and summer were fewer, the most balanced segmentation of the data was n = 4

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replicates, and we show these analyses in the main text, with the qualitatively similar analyses for n = 3 and n = 6 included in the supplemental.

Trait-base ecological strategies of the whole bird community and MSF-participants

To determine whether life history strategies of bird species are consistent with the fast-slow trait continuum, we first performed a principal component analysis (PCA) on all 12 traits for all 40 MSF-participating species (see Table S2 for list of species). We later used this same approach for all species to determine whether the "whole community" (that is, all bird species seen during the fieldwork, inside and outside MSFs) has a similar fast-slow trait continuum as do MSFs. This PCA defines main multivariate axes of highly correlated traits (Shen et al., 2019).

To identify the strategies of bird species at different successional stages, we calculated community-weighted mean trait (CWM) values per replicate and per trait. We used bird species abundance in each successional stage to calculate CWM values as follows: $CWM = \sum_{i=1}^{n} P_i \times trait_i$, where n is the species number found in a given dataset; P_i is the relative abundance of species i, and $trait_i$ is the trait value of species i (Garnier et al., 2004). In the CWM calculations, we focused on seven traits related to the fast-slow continuum, including body length, wing length, tail length, body mass, clutch size, nestling period and longevity. CWM was calculated with the package "FD" (Laliberté et al., 2014) in the R statistical environment (www.r-project.org; version 3.5.0). CWM values were calculated for both the whole community and for MSF participants. Because we expected linear change in this analysis (EF < IF < OF), we examined how CWM of traits changed along successional stages using linear

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mixed-effects regression models using the R package "lme4" (Bates et al., 2015). The independent variable was the age of the successional stage (log-transformed); season and transect were incorporated as intercept-specific random effects, and separate models were conducted for each of the traits. We also compared traits between MSF-participating species and the whole community for each successional stage, to understand what types of traits MSF participants have.

Network construction and evaluation of their structure

We compared network structures across successional stages using network analysis. Our analysis assumed that any species occurring in a given MSF was connected with the rest of the species in the MSF (Mokross et al., 2014; Borah et al., 2018). We first calculated the simple ratio index (SRI) for species-pairs using the data on species co-occurrences, and then constructed four weighted networks using SRI for each successional stage to measure interspecific association strength (Farine & Whitehead 2015). The weighted networks also incorporate a metric for the strength of the associations (i.e., edge weights) between the connected species. We used SRI to assign these weights (Zhou et al., 2022), calculated as: SRI = AB/(AB+A+B), where AB is the number of times both species A and B were present in each MSF, A is the number of times only species A was present, and B is the number of times only species B was present. The networks were constructed with the R package "igraph" (Csardi, G. & Nepusz, T., 2006).

We calculated five network-level metrics to represent network structure (see the detailed descriptions and their biological interpretations in Table S3). Higher weighted degree and normalized degree are related to higher average association strength. Higher density and lower skewness are related to higher network connectivity.

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Density is equal to normalized degree when we use SRI to construct a weighted network, so we only reported the result of normalized degree. Higher clustering coefficient and lower modularity (which describes the degree to which MSFs are partitioned into modules, defined via random walks in package "igraph") represent higher network cohesion. To determine whether these metrics differed among successional stages, we conducted linear mixed-effects ANOVA models, also using the "lme4" package, with successional stage as the independent variable, and season and transect again as random effects; pairwise multiple comparisons were conducted using the R package "emmeans". To place unimodal curves and confidence intervals through the three points on the graphs, we used smoothed conditional means in "ggplot2" package (Wickham, 2016). We also calculated some species-level network metrics, which we used in describing the composition of the modules (see Supplemental Methods).

As social data is inherently non-independent, it is necessary to use null models to test whether the structure of a network is non-random. We implemented null models (specifically pre-network permutation models) to determine whether observed networks (n = 4 per successional stage) were likely caused by social interactions among flocking species, rather than by co-occurrences driven by the same habitat preferences (Montaño-Centellas 2020). See Supplemental Methods for more details.

Network assortativity

To measure whether species associations occur typically between functionally similar or dissimilar species, we evaluated network assortativity by calculating the assortativity coefficient (r) for each weighted network (Farine 2014; n = 4 per successional stage). The assortativity coefficient is a Pearson's correlation coefficient

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suitable for networks, ranging from -1 (perfect disassortment) to 1 (perfect assortment). An r = 0 refers to a random association. To examine if assortment of the networks was significant, we performed a randomization. We randomly re-allocated the trait values (trait by trait) across the nodes in a given network (9,999 times) and calculated the assortativity coefficient for each permutated network. The p-value equals the proportion of assortativity coefficients that were larger than the observed coefficient (Wang et al., 2022). Assortativity coefficients were calculated with the "assortnet" package (Farine 2014). Differences in assortativity coefficients among successional stages were also tested by linear mixed-effects ANOVA, followed by pairwise post hoc multiple comparisons.

Relationships between interspecific associations and traits

In order to understand how interspecific associations shift among species with different traits across the three forest types, we analysed the relationships between life history (PC1) and normalized and weighted degree, using linear regression models for each successional stage separately. In this analysis, normalized and weighted degree were calculated by combining all the data collected in that successional stage.

RESULTS

The fast-slow trait continuum of the whole community and MSF participants

The first and second principal components (PC1 and PC2) explained 47.2% and 16.8% of the variations in trait space of 40 MSF-participating species, respectively (Figure 2; see Table S4 for the factor loadings). Species on the left side of the first component represent the fast strategy, including species with smaller body size (i.e. body, wing, tail length) and mass, shorter nestling period and longevity, and larger

clutch size. The PCA on the whole community showed a very similar pattern (Figure S2).

Traits of the whole community and MSFs

In total, we recorded 82 species across all six transects and all three successional stages. Intermediate forest (IF) had the largest number of species (60 species), and 50 species were recorded in both EF and OF. Of all the 82 species, 40 were recorded as MSF-participating species across all the successional stages. For the number of species and individuals in all MSFs observed on a transect, the different successional stages were statistically different from each other, with EF having the lowest numbers, IF having the highest numbers, and OF being intermediate (Figure S3).

Compared to the whole community, MSF participants were mostly insectivores and smaller species. Thirty one out of 40 (77.50%) MSF-participating species were insectivores, compared to only 23 species (54.76%) that did not join MSFs. In each successional stage, MSF-participating species had lower body mass and size, shorter nestling period, but larger clutch size than species that did not join MSFs (Figure S4).

Network structures of MSFs across successional stages

The network metrics tended to be unimodally distributed, with IF having the lowest or highest mean value (Figure 3). Weighted degree and normalized degree metrics were significantly higher in IF than in EF, with OF similar to IF. For skewness, IF was significantly lower than EF, related to higher median normalized degree values (Figure S5), while OF was intermediate and not distinguishable (i.e. significantly different) from either IF or EF. Modularity had the same pattern as skewness with IF being low, EF being high, and OF being intermediate. Compared to the null model,

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we found that most of observed network metrics significantly differed from null expectations (45 out of 60; Table S5), indicating that these not random associations.

Patterns in module topology

MSF participants formed small modules in EF (see Figure S6 for illustrations of the networks and modules). In EF, seven modules had two species, and two modules had more than five species), without any interactions between modules, resulting in high modularity. In comparison, in IF, there were larger modules (three modules of two species; five modules with greater than five species) and they were extensively connected. The OF networks were intermediate in size (six modules of two species, five modules with greater than five species) and connectivity (Figure S6). For a detailed description of the module composition, and species-level network metrics, see Supplemental Results.

Community-weighted means of fast-slow traits of MSF-participating species across successional stages

CWM of body size (body, wing, tail length) and mass significantly increased, while clutch size significantly declined with successional stage (Figure 4). However, CWM of nesting period and longevity were not significantly related with successional stage. The CWM analysis for the whole community was similar, showing linear relationships across successional age, although which exact traits showed significance differed from the MSF analysis (Supplemental Results, Figure S7).

Network assortativity between traits and interspecific associations

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Assortativity coefficients (r) were evaluated to examine the relationship between species association and functional similarity, with the curves tending to be unimodal. More significant positive assortativity coefficients of body, wing, tail length, body mass and clutch size were found in EF's (19) and/or OF's networks (16) than in IF networks (13, Table S6). Assortativity coefficients of body size measurements and clutch size in EF were significantly higher than in IF and OF (Figure 5).

Relationships between fast-slow traits and interspecific associations

Network degree, assessed from one network per successional stage significantly increased across the fast-slow continuum (PC1) in OF (Figure 6). In comparison, there were no clear relationships between degree and the fast-slow continuum in EF and IF.

DISCUSSION

In this study, we combined network theory and trait-based ecology to examine how interspecific interactions of MSFs shift during forest succession among species with different traits that exemplify different positions on the fast-slow life history continuum. Our PCA analysis of trait variation showed a clear difference between species in early succession (EF) and those in late succession (OF) for both the whole community and the MSFs. This result is consistent with the idea that to predict how disturbance (and recovery from disturbance) affects species interactions, one must first understand what it does to the whole community (Zou et al. 2018). Our permutation analysis indicated that the patterns we found in the network analysis were not produced by random associations among species, or by changes in species

occurrences in MSFs in particular habitats, but represent changes in how species associate together across the successional gradient.

Our results showed that MSFs had the most connected (high weighted and normalized degree, low skewness) and cohesive network (low modularity) in the intermediate successional stage (IF). Early in succession (EF), species in the fast end of the life history spectrum tended to compose the community and form MSFs, whereas in late succession (OF stage) species in the slow end of the life history spectrum were involved. We believe these results provide valuable insights into the mechanisms that drive community re-assembly of MSFs during forest succession.

Resource limitations and vegetative simplicity may drive a poorly connected MSF network in early forests

Our results suggest that network-level metrics of MSFs responded to the potential gradual change in vegetation complexity that occurs over succession at our study site. The vegetation in the early stages of succession at Dinghushan is structurally quite simple, with low species richness, and the forest is dominated by short-stature trees (Zhang et al., 2013). These young forests offer a limited number of resources and habitats for birds (Leach et al., 2018; Hořák et al., 2019), such as fewer invertebrates, seeds, fruits and nest sites, and hence few available foraging niches (Zhang et al., 2013; Montaño-Centellas & Jones 2021). The low species richness and abundance of birds in this environment seems likely to underlie the low strength of associations (lowest weighted and normalized degree) and poor connectivity (highest skewness) of MSF networks.

At the same time, the small networks in the EF were divided into several separate modules that were unconnected (Figure S6), leading to high modularity. The

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most common associations in EF were microhabitat-specific. For example, some transient MSFs found in three of four networks were composed of Light-vented Bulbul (*Pycnonotus sinensis*, PYSI) and Red-whiskered Bulbul (*Pycnonotus jocosus*, PYJO), omnivorous birds that foraged on fruit-bearing trees. The most central species in EF, the Swinhoe's White-eye (*Zosterops simplex*, ZOSI), which is a weak leading species, prefered foraging in open shrubs. Occasionally, a patch of thicker understory allowed the presence of the stronger leader Huet's Fulvetta (*Alcippe hueti*, ALHU). As MSFs had such a small number of species and individuals, there were no species that linked together these different modules.

At the same time, MSFs in the EF were dominated by fast species with smaller body size and body mass, but larger clutch size (Figure 4), following the pattern set by the whole community (Figure S7). These traits represent disturbance-tolerant species (Schieck & Song 2006; Carlo & Morales 2016; Li et al., 2021) with a higher recovery rate if disturbed (Brose et al., 2006; Bird et al., 2020). Combining the trait results with the significant positive assortativity coefficient (Figure 5), interactions among fast species dominated MSFs in EF.

The structure of intermediate forest supports the most connected and cohesive network

MSFs in IF showed a completely different network structure. The networks of MSFs in this successional stage had the greatest mean interspecific association strength, network connectivity and cohesion compared to the other two stages (Figure 3). In other words, these were large and speciose networks with little structure-species that had different characteristics mixed together, and there was little evidence of distinctive modules.

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One aspect that might be important contributor to these patterns is that the moderate vegetation complexity in IF, less complex than that in OF, does not allow fine partitioning of foraging strata and microhabitats among MSF participants (Montaño-Centellas & Jones 2021). There was no clear distinction between a subcanopy/canopy and an understorey sub-type of MSFs and birds of all strata mixed together freely (Montaño-Centellas & Jones 2021). The lowest mean network modularity across successional stages (Figure 3), and the presence of large subgroups (Figure S6), supports this interpretation. These large subgroups contained both understorey species, such as the Huet's Fulvetta (ALHU) and tits, minivets and sunbirds typical of the upper parts of the forest strata.

MSFs in IF also tended to include species with both fast and slow life history strategies. This is evidenced by intermediate values across CWMs (Figure 4), random network assortativity (Table S6), and no significant relationship between the fast-slow continuum and weighted or normalized degree (Figure 6). These patterns are consistent with intermediate disturbance hypothesis (IDH). IDH predicts that competitive exclusion reduces species richness at low levels of disturbance, whereas a few tolerant species dominate areas that experience high levels of disturbance; in intermediate conditions, species with both kinds of life histories can coexist (Connell 1978; Molino & Sabatier 2001).

Interactions of MSFs in old-growth forests tend to be more modular and concentrated among slow species

In OF, most species that preferred open habitats, such as the Light-vented Bulbul (PYSI), Red-whiskered Bulbul (PYJO), White-rumped Munia (*Lonchura striata*, LOST) and prinias, disappeared and were replaced with species with slow life history

characteristics. Associations between species in MSFs were therefore concentrated among slower species. This is shown best by the relationship between the fast-slow continuum (measured by PC1 scores) and the strength of associations (weighted and normalized degree, Figure 6): species with slower traits had stronger connections in this successional stage.

MSF networks in OF also showed some indications of being more modular than IF, although admittedly this was not significant in the network calculations (Figure 3). Whereas all four networks in IF included connections between the understorey leader Huet's Fulvetta (ALHU) and species of the canopy and subcanopy, in two of the four networks in OF such connections were missing (see Supplemental Results). As we have argued in earlier sections of the Discussion, we see these patterns shaped by high resource and habitat availability allowing a speciose community of slower species (Huang et al., 2018; Schuldt et al., 2018), and increased vegetational complexity providing the opportunity for greater vertical strata partitionin, which may be linked to a tendency for more assortment by the birds. Given that other studies have proposed that elevational change produces similar shifts in MSFs (Montaño-Centellas 2020; Shen et al., 2022; Montaño-Centellas et al., 2023), we suggest the vegetation complexity may be the underlying factor influencing both the elevational and disturbance gradients.

Implications for conservation

We propose three approaches for conserving MSFs in different successional stages. First, conserving MSFs provides an efficient mechanism to ensure the protection of many species simultaneously (Zou et al., 2018). Therefore, protecting MSFs in IF, where the MSF network is most connected and cohesive (Figure 3), can be a cost-

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effective way to preserve bird diversity, particularly in the tropics where MSFs are frequent year-round, and especially in areas where old-growth forests have been lost (Poorter et al., 2016; Rozendaal et al., 2019). This could be accomplished by targeting "nuclear species", those species that are important to MSF formation or cohesion (Moynihan, 1962; Goodale & Beauchamp, 2010), as measured by centrality and their connectivity within and between modules, such as Huet's Fulvetta (ALHU). Second, protecting old-growth forest is still critical. Even though forests at an intermediate stage of succession can harbor high species richness, the recovery of forest specialists (which may include most species in the slow end of the life-history continuum) requires more time (Acevedo-Charry & Aide, 2019). Given that MSFs in our older forests were mainly dominated by slow species (Figure 6), it is paramount that large tracts of old-growth and late successional forests are protected across a landscape. Third, a range of secondary forests should be better protected to promote succession towards old-growth forests. Trait composition of MSFs (from fast to slow) matches the progression of forests complexity from early to late successional stages (Figure 4). Therefore, protecting a mosaic of forests of different ages across the landscape also preserves the variability of trait diversity in bird communities. Providing habitat to both forest specialists (i.e., slow species) and disturbance-tolerant species makes communities more resilient to further changes in land use (Brawn et al., 2001). Including early successional forest in landscapes also allows a variety of human land-uses in the area, therefore making conservation more compatible with the needs of the local human communities (Lehn & Bahrs, 2018; He & Jiao, 2023).

Caveats

Our results have some limitations that should be discussed. First, vegetation

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complexity is only a proxy of resources, such as food resources and habitats of bird communities. A previous study by Zhang et al. (2013) has quantified vegetational complexity at Dinghushan Nature Reserve, and here we use that earlier work as a foundation to define the successional gradient. But we cannot ourselves closely connect our findings to the vegetational characteristics the birds require or their ecological niches. Second, the number of replicates is limited (n = 4 replicates representing two seasons for two transects per successional stage). Analyses with three or six replicates (Supplemental Information Part II and III) gave qualitatively similar results, yet further segmentation of the data lead to too few MSFs per replicate, and it would be better to gather multiple-year data in the future. A limitation specific to the transects, which, although few in number, were long (2.5-3 km) and covered much of the small reserve, is that we did not incorporate their position at a landscape level into the analyses. However, like most national nature reserves in China (Xu et al., 2016), habitat disturbance and landscape integration in Dinghushan Nature Reserve are linked, with more disturbed habitat types along the periphery of a central core of mature forest. Finally, we are ultimately interested in processes that occur over time, but we infer such processes by comparing different habitats at different successional stages. A longitudinal study that surveys the same locations repeatedly and evaluates successional progress over time could strengthen our conclusions.

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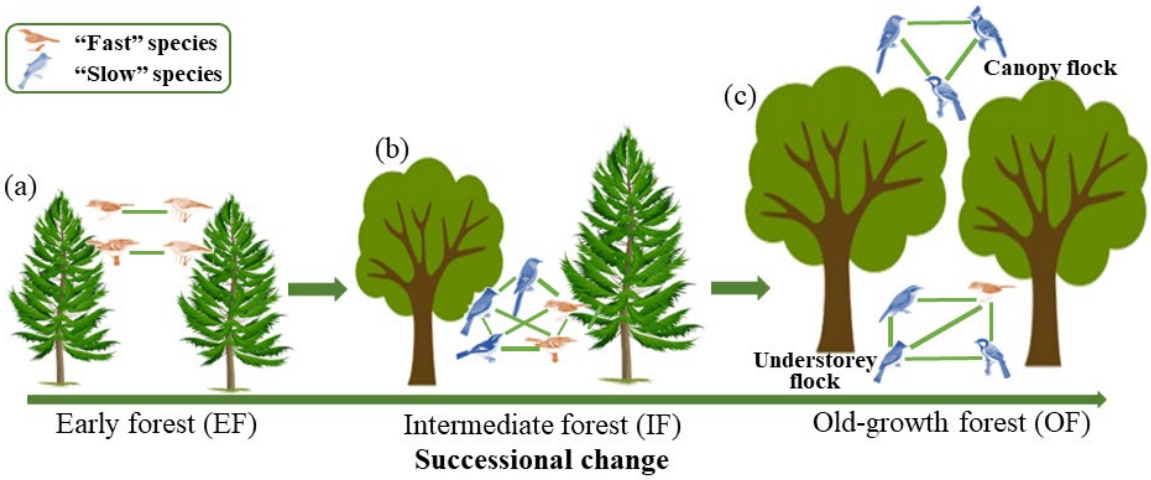


FIGURE 1 Conceptual illustration of hypothesized changes of avian mixed-species flock (MSF) networks with forest succession. Based on contemporary succession theories, "fast" species should be replaced by "slow" species during forest succession. The early stages of succession were expected to be inhabited by a few disturbance-tolerant species (i.e., fast species), and a poorly connected and less cohesive MSF network might be established (a). MSFs in the intermediate stages of succession may include a combination of species from both young and old-growth forests. A highly connected and more cohesive network is predicted occur at intermediate stages of succession due to moderate vegetation complexity (b). The vegetation complexity may be highest in the late successional stages. MSFs' partitioning of foraging microhabitats there were expected to be finer, with the costs of "activity matching" resulting in more segregated canopy and understorey MSFs, and a highly connected but less cohesive network (c).

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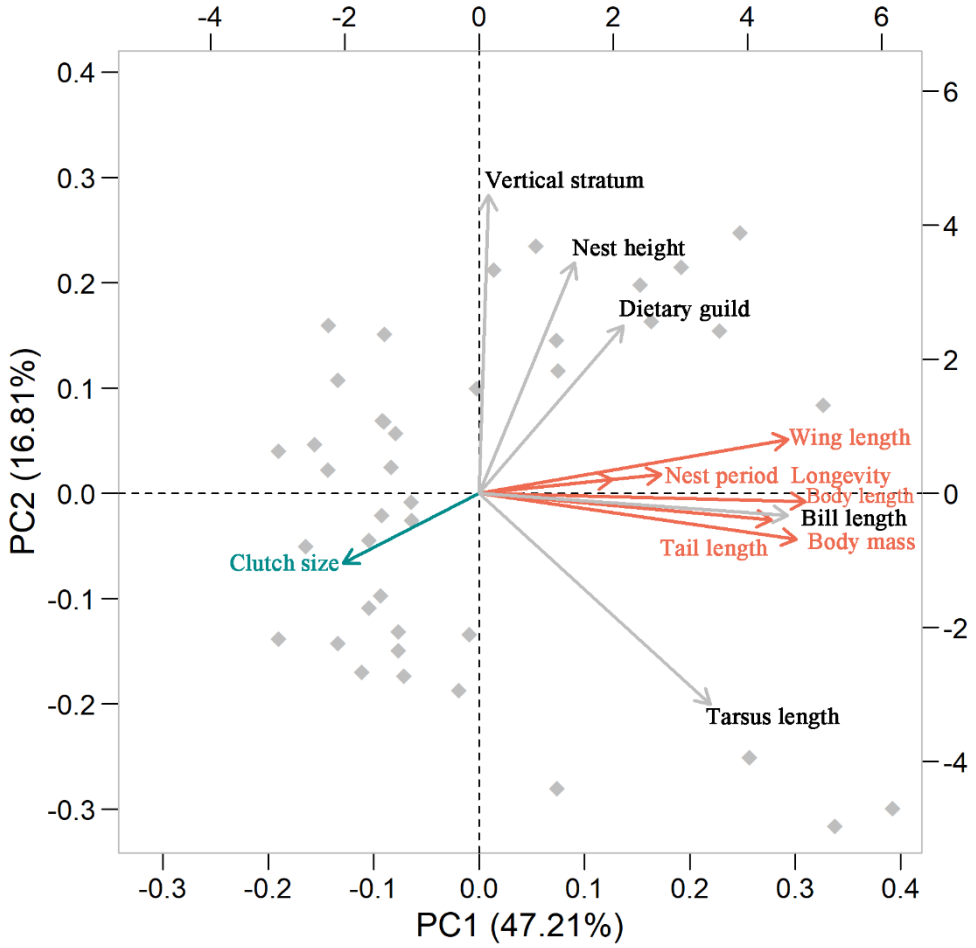


FIGURE 2 Functional trait loadings biplot illustrating the "fast" and "slow" strategies of 40 MSF-participating species, derived from principal components analysis (PCA) in the Dinghushan mountains. Grey points represent species. Green and red and arrows indicated traits expected to be positively associated with fast or slow strategies, respectively. Species at the right side tended to have traits associated with the slow strategy; species at the left side tended to have traits associated with the fast strategy. Grey lines are not included in "fast-slow" traits. The top and the right-side axes represent PCA-scores of the samples (datapoints), whereas the bottom and the left-side axes represent PCA-loadings of the vectors (arrows).

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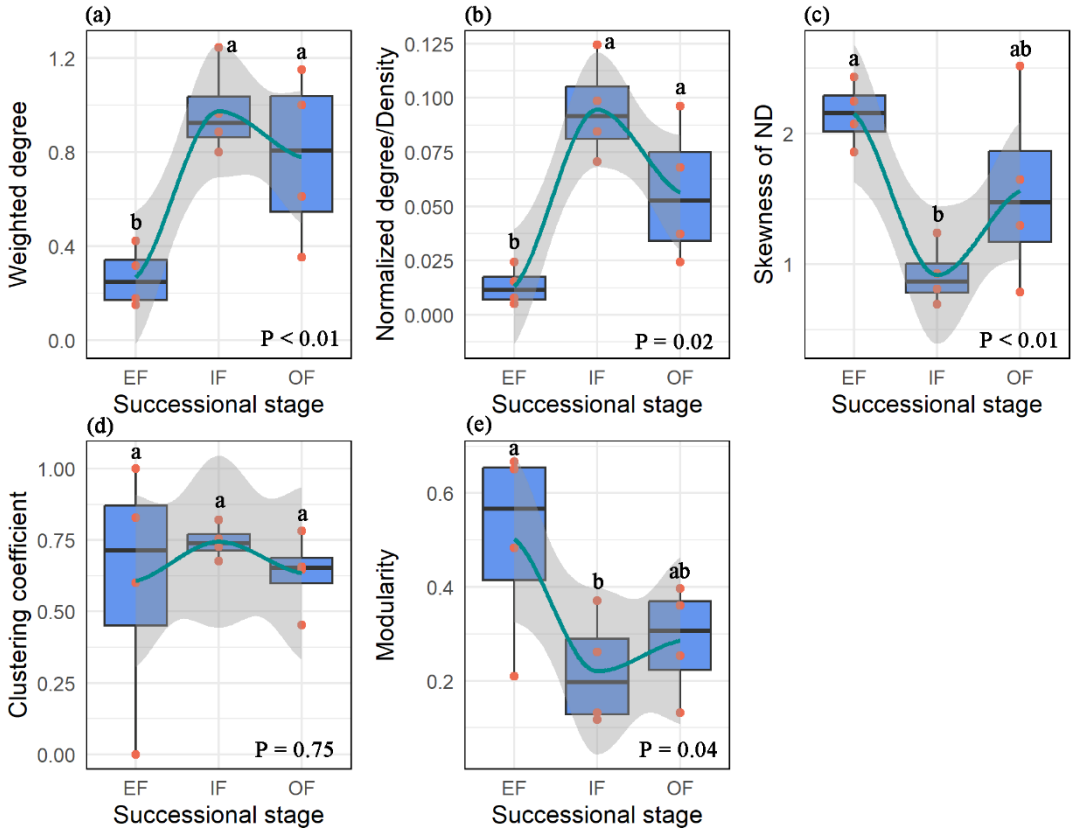


FIGURE 3 The network-level metrics across successional stages at the Dinghushan mountains, including weighted degree (a), normalized degree or density (b), skewness of normalized degree (c), clustering coefficient (d) and modularity (e). The red points indicate network-level metrics from four networks at each stage. The boxplots represent median ± standard deviation. The curves were fitted by smoothed conditional means, including 95% confidence intervals (grey shade area). P values were obtained by linear mixed-effects ANOVA models (season and transect as random effects), followed by pairwise post hoc multiple comparisons. Successional stage abbreviations follow Figure 1.

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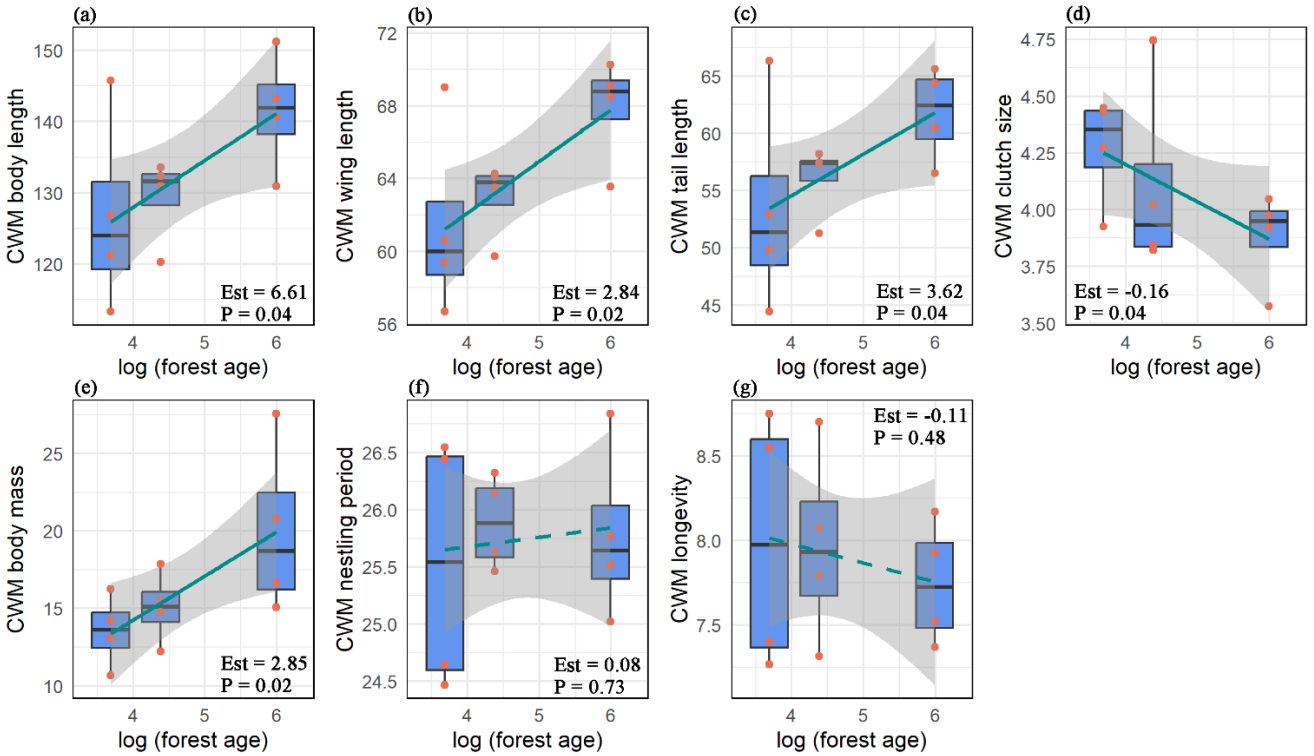


FIGURE 4 Community weighted mean (CWM) trait values for "fast-slow" traits of MSF-participating species across successional stages at the Dinghushan mountains. The boxplots represent median ± standard deviation. Significance was tested by linear mixed-effects regression models (season and transect as random effects). Estimates (Est) and P-values are shown. Solid and dashed lines represent significant and insignificant relationships, respectively. See Table 1 for trait definitions.

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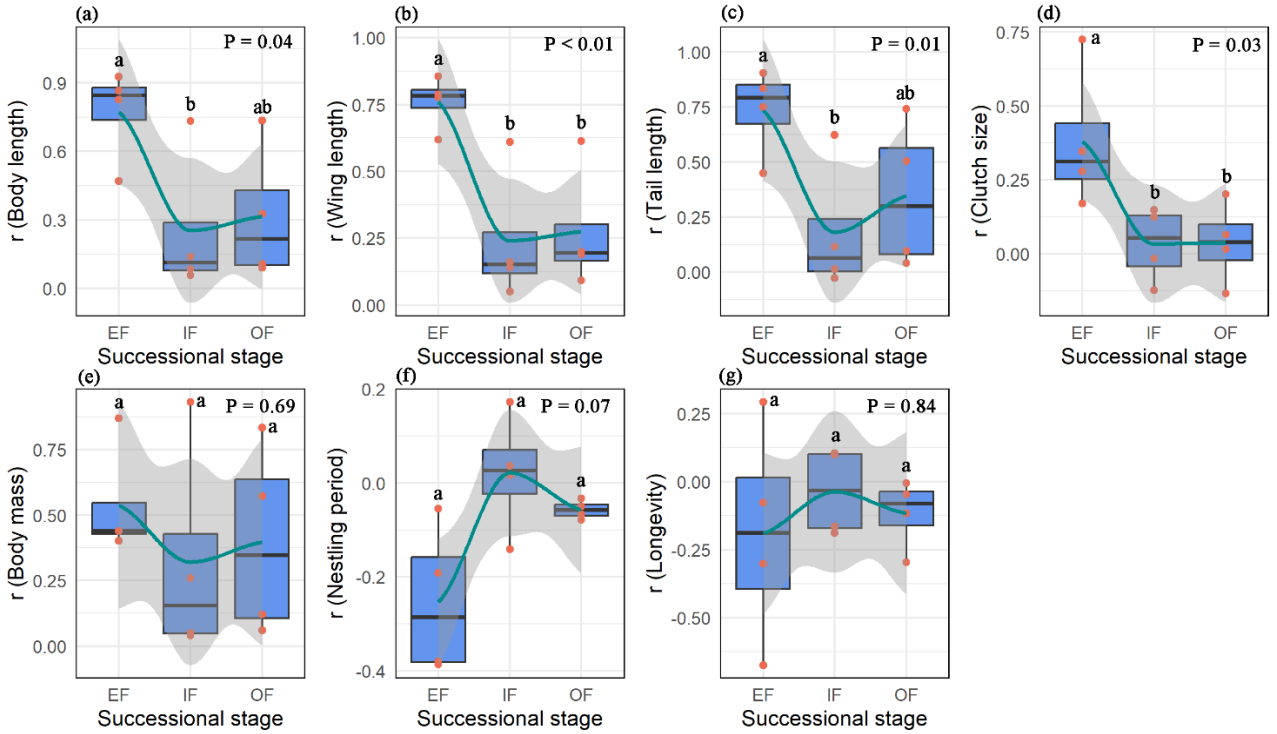


FIGURE 5 Assortativity coefficients (r) for "fast-slow" traits of weighted networks across successional stages in the Dinghushan mountains. The boxplots represent median ± standard deviation. The curves were fitted by smoothed conditional means and their confidence intervals (grey shade area). P values were obtained by linear mixed-effects ANOVA models (season and transect as random effects), followed by pairwise post hoc multiple comparisons. See Table 1 for trait definitions, and Figure 1 for successional stage abbreviations.

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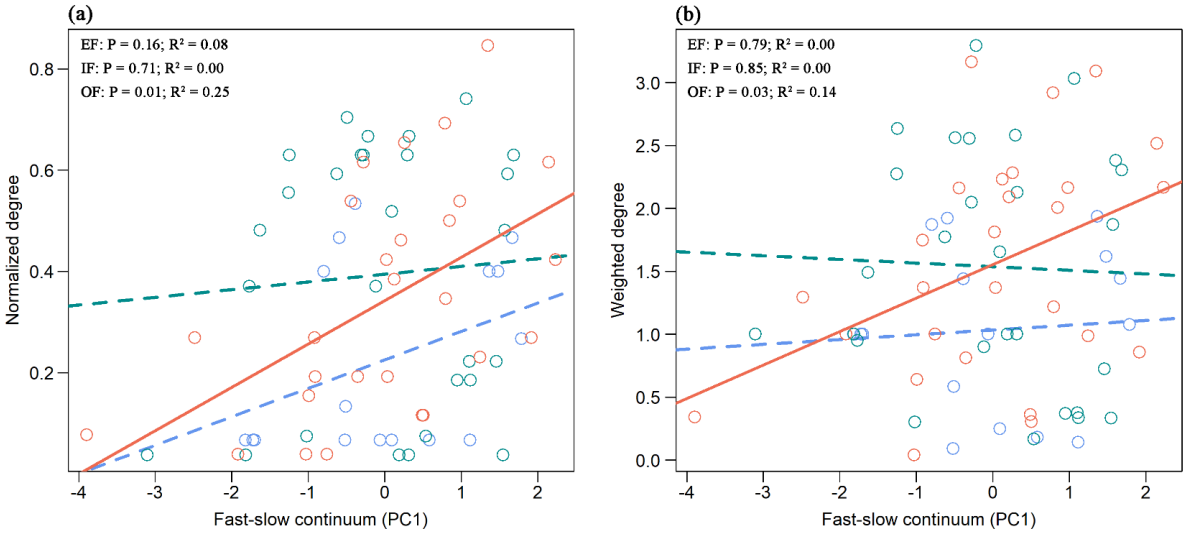


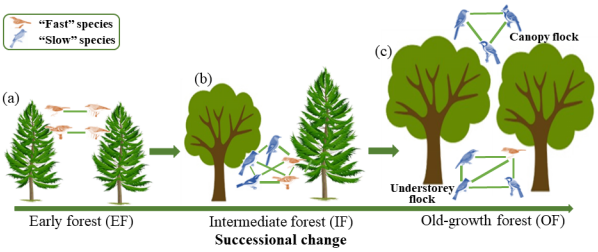
FIGURE 6 Linear regression between species' scores on the fast (low PC1 scores) and slow (high PC1 scores) continuum (from principal component analysis, see Figure 2) and normalized (a), and weighted degree (b) of each node (species) in each forest successional stage, including early forest (EF, blue), intermediate forest (IF, green) and old-growth forest (OF, red). Dotted lines indicate an insignificant relationship, while a solid line is used to present a significant relationship. P values and R^2 are shown. Since the PCAs were conducted for each successional stage separately, the PCA scores are slightly different from those in Figure 2.

TABLE 1 The summary of 12 bird species traits related to life-history and the relationship with fast-slow continuum in this study, from early to late successional habitats.

Trait	Unit	Description	Expected relationship with fast-slow continuum
Body length	mm	The length from bill to tail	Increasing with succession
Wing length	mm	Total wing length	Increasing with succession
Tail length	mm	Total tail length	Increasing with succession
Body mass	g	The body weight of a bird	Increasing with succession
Bill length	mm	The upper margin of the beak or bill	/
Tarsus length	mm	The tibiotarsal articulation to the toes	/
Clutch size	/	Number of eggs per clutch	Decreasing with succession
Nest height	m	The height of nest from the base	/
Dietary guild	/	Insectivore, frugivore or omnivore	/
Vertical stratum	/	Canopy, midstorey, understorey or ground	/
Nestling period	d	Period of egg incubation and young bird fledging	Increasing with succession
Longevity	y	The lifespan of an individual in years	Increasing with succession

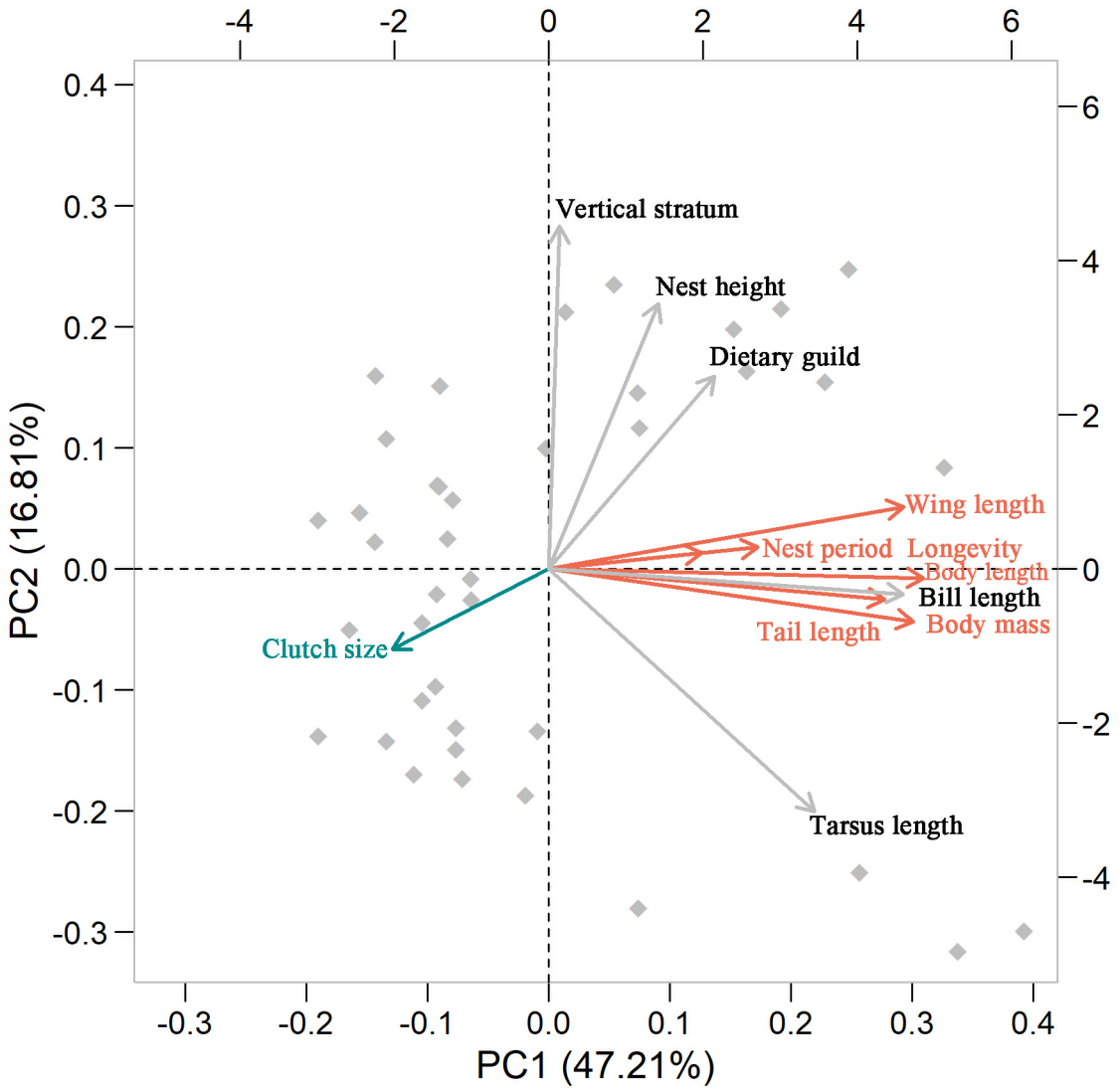
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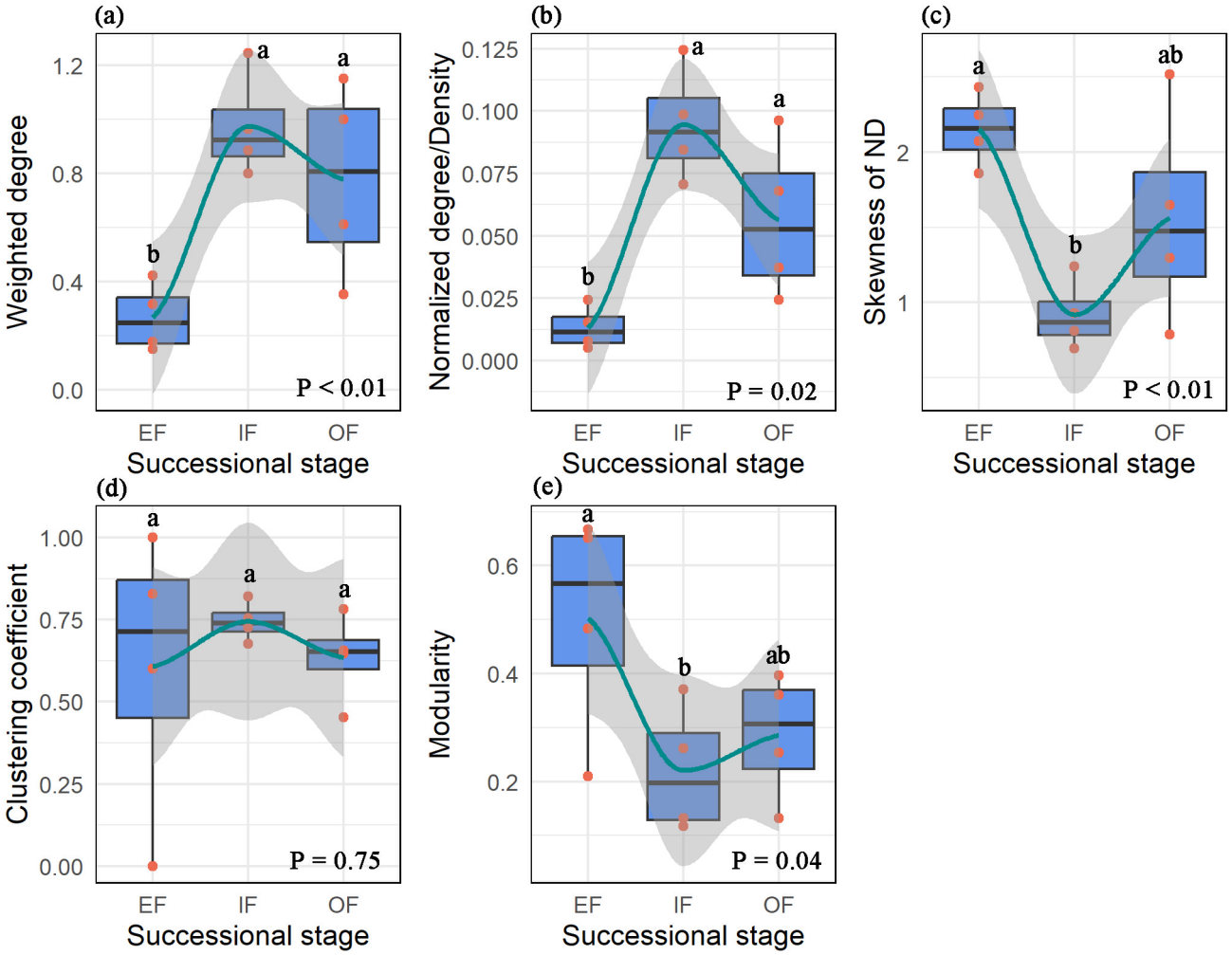
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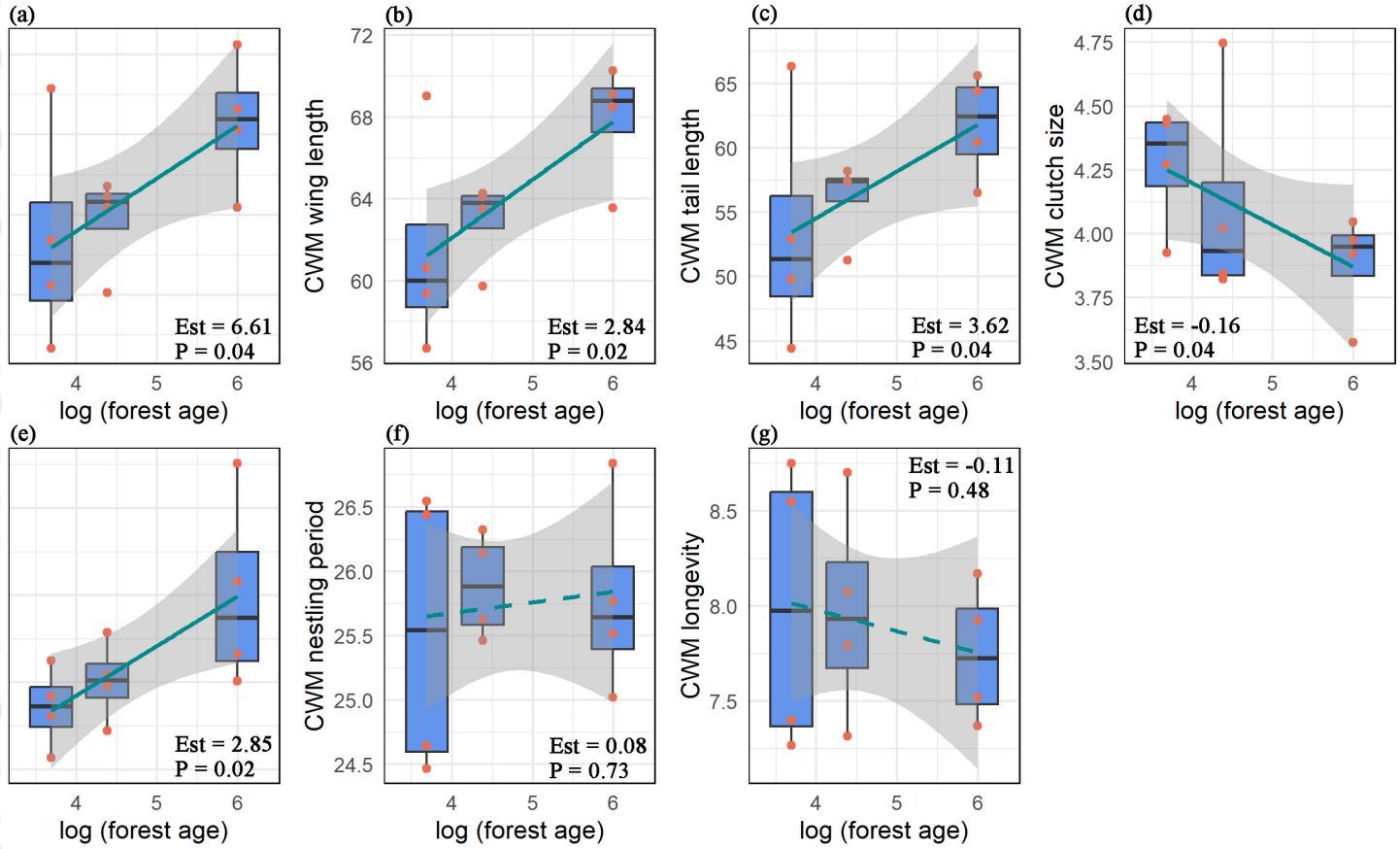
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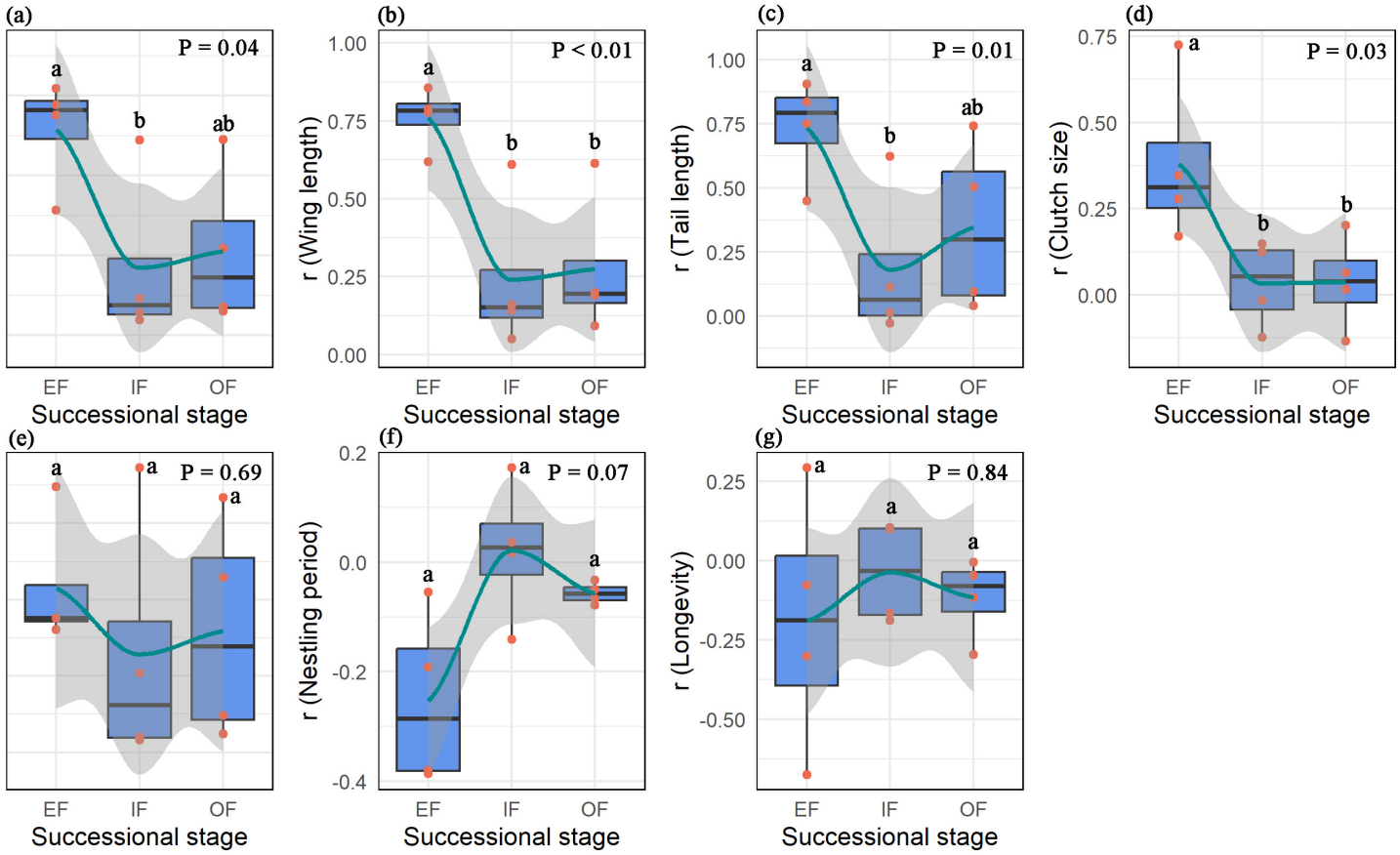
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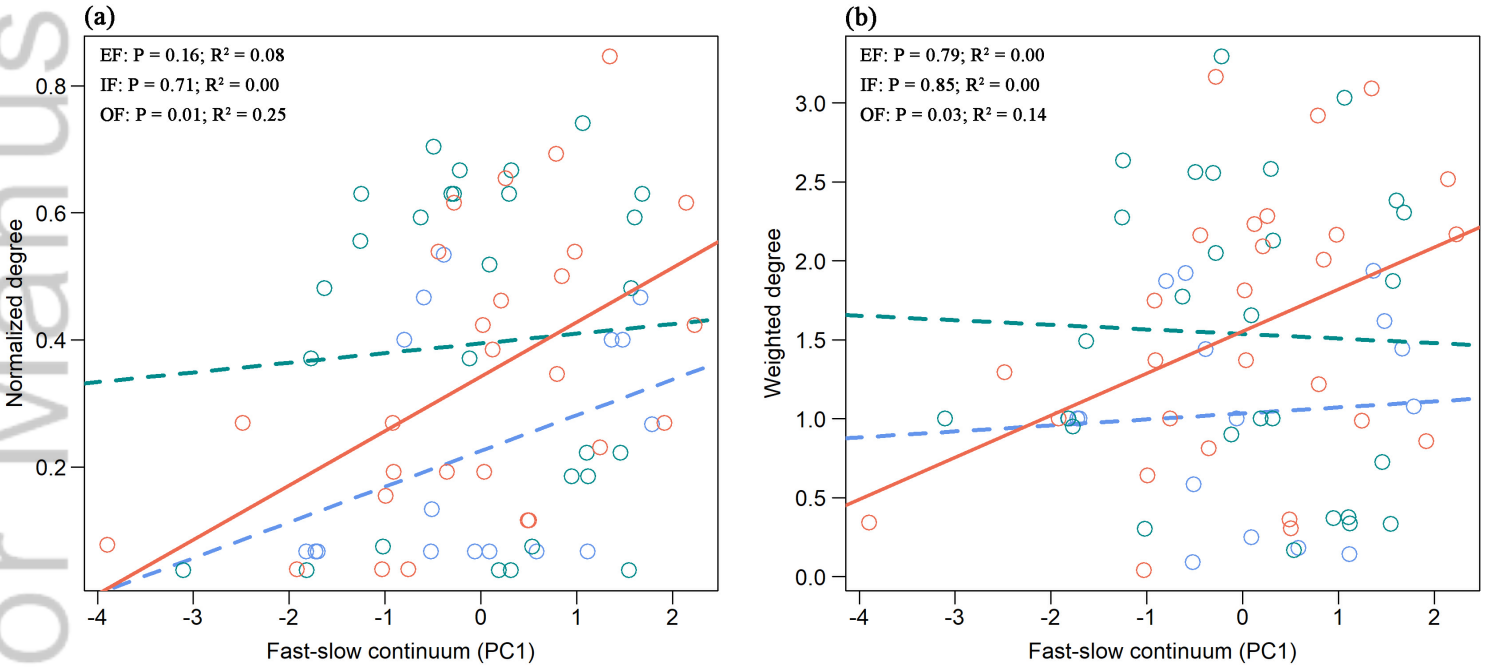
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