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Authors: Long, Cheng, Yang, Xiaobo, Long, Wenxing, Li, Donghai, Zhou, Wei, et al.

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Research Article

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**Cheng Long[1], Xiaobo Yang[1], Wenxing Long[1], Donghai Li[1], Wei Zhou[1], and Hui Zhang[1]**

## Abstract

Understanding the responses of species diversity and dominant species to soil nutrient dynamics can enhance our knowledge of species coexistence and the recovery of secondary forests. Here, we assessed how species diversity and the abundance of dominant species varied as a function of soil nutrients at early- and mid-successional stages in two tropical monsoon coastal secondary forests in southern China. Results showed that species diversity was higher in the mid-successional stage. Species diversity was significantly correlated with organic matter and available P in both stages. The abundance of dominant species was significantly associated with organic matter, K, P, and N. Soil nutrients are therefore likely to play vitally important roles in the successional trajectory and restoration of these tropical coastal secondary forests.

## Keywords

dominant species, forest recovery, plant diversity, species turnover, soil nutrients, tropical coastal forest

## Introduction

Large areas of primary tropical forest have been changed by human activity, including urbanization (Brown & Lugo, 1990; Crk, Uriarte, Corsi, & Flynn, 2009; Sloan & Sayer, 2015). Currently, tropical forests are disappearing at a rate of 6 million ha per year (Keenan et al., 2015). Secondary forest has now become the dominant forest type across much of the tropics (Chazdon et al., 2007), resulting from the relatively quick recovery and succession after abandonment of arable land (Asner, Rudel, Aide, Defries, & Emerson, 2009; Houghton, 1994; Wright, 2006). Forest structure appears to recover relatively rapidly in secondary forests (Chazdon et al., 2007), but species composition remains quite different from old-growth forests for an extended time (Aide, Zimmermann, Pascarella, Rivera, & Marcano-Vega, 2000). Despite this discrepancy, tropical secondary forests continue to supply a number of ecosystem goods and services such as timber and nontimber products, food and fuel (Trumbore, Brando, & Hartmann, 2015). In addition, secondary forests also play an important roles in climate stabilization, protection from erosion, carbon sequestration, nutrient cycling, and water retention (Guariguata & Ostertag, 2001; Montagnini & Jordan, 2005). Hence, understanding the drivers of community assembly during tropical forest succession remains of both fundamental and applied importance in ecology and conservation biology (Bhaskar, Dawson, & Balvanera, 2014; Buzzard, Hulshof, Birt, Violle, & Enquist, 2015; Lin et al., 2016).

Plant community attributes, such as plant biomass, vegetation cover, and species composition, can be impacted by variation in soil nutrients (Perroni-Ventura, Montaña, & García-Olova, 2006). Especially, in the early stages of reforestation, tree communities and the rate of forest recovery can be limited by a lack of soil nutrients, especially nitrogen (N; Cárate-Tandalla, Camenzind, Leuschner, & Homeier, 2018; Nagy, Rastetter, Neill, & Porder, 2016; Zhang et al., 2015). However, at the late phase of secondary forest recovery,

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[1] Institute of Tropical Agriculture and Forestry, Hainan University, Haikou, P. R. China

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**Corresponding Author:**
Wenxing Long, Institute of Tropical Agriculture and Forestry, Hainan University, Haikou 570228, P. R. China.
Email: oklong@hainu.edu.cn
Donghai Li, Institute of Tropical Agriculture and Forestry, Hainan University, Haikou 570228, P. R. China.
Email: dhlye@163.com

aboveground litter dynamics are often regulated and influenced by both net primary production and the availability of the limiting soil phosphorus (P; Cleveland et al., 2011; Read & Lawrence, 2003; Wright et al., 2011; Zhang et al., 2015). The presence and abundance of dominant species in secondary forest are also determined by soil quality via previous land use (Jakovac, Bongers, Kuyper, Mesquita, & Peña-Claros, 2016). Thus, studying how species diversity and dominant species respond to soil nutrients can reveal species coexistence mechanisms and potential management options during secondary forest recovery.

Tropical coastal forests are characteristic of the northeastern coast of Hainan Island in south China but have suffered severe anthropogenic (slash and burn) and natural (typhoon) disturbances. The tropical coastal forest in Tongguling Nature Reserve (TNR) is a unique natural forest vegetation, with few comparable ecosystems in southern China (Wu, 1995). It is therefore of vital importance in biodiversity conservation, counteracting typhoons, and environmental protection in this region. Secondary forests are now regenerating, and we used this system to test how species diversity and composition respond to soil nutrients during forest recovery. Our successional communities were an early-successional shrub forest and a mid-successional evergreen forest. In these two forests, we collected an extensive data set consisting of (a) species incidence and abundance and (b) soil nutrients. Based on this data set, our study addressed the following questions: (a) How do species diversity, dominant species abundance, and soil nutrients vary from early- to mid-succession? and (b) Do soil nutrients play important roles in species diversity and dominant species abundance?

## Methods

### Study Sites

This study was conducted in the TNR (19°36′–19°41′ N, 110°58′–111°03′ E), in the northeast of Hainan Island, South China. TNR covers 44 $km^2$ at 338 m.a.s.l. and has a tropical monsoon climate, with a distinct wet season from May to October and a dry season from November to April. The mean annual temperature is 23.9°C, and the mean annual precipitation is 1,721.6 mm. The primary forest type throughout TNR was tropical evergreen monsoon forest. All of these forests were deforested prior to 1980 and degraded to grassland, shrub, or, secondary forest. After the TNR was established in 1983, deforestation was banned and forests have been well protected. The history of each plot was reconstructed based on official records from forest faculty or from interviews with the administration of TNR. Each plot was investigated to determine whether human logging or grazing occurred. Representative sites were selected using the following criteria: (a) existence of sufficiently large, spontaneously successional sites; (b) known age of vegetation; (c) general similarity of soils, topography, and primitive vegetation of the sites; and (d) no evident additional disturbance. It thus could be inferred that these study communities for all successional stages could likely develop into the same climax community.

We chose two different successional stages within TNR. One was 30-year-old shrub forest (*Shrub*: 19°38′26.0″ N, 111°01′59.0″ E), and the other was 50-year-old secondary tropical evergreen monsoon forest (*Forest*: 19°40′11.3″ N, 110°01′06.4″ E; Figure 1). Shrub was regarded as the early stage of Forest during community succession. The litter fall in Shrub and Forest is 4.15 to 8.63 t $hm^2$ and 2.96 to 10.60 t $hm^2$, respectively. Both types of vegetation are mainly distributed between 150 and 330 m elevation.

### Data Collection

Nine $50 \times 50$ m plots were established randomly within each vegetation type (Shrub and Forest) using an electronic total station (Leica TSP1200+; Heerbrugg, Switzerland). All plots were located on southeastern slopes with inclination ranging from 30° to 45°. Each plot was divided into twenty-five $10 \times 10$ m subplots and one hundred $5 \times 5$ m quadrats for precisely measuring the tree coordinates. All free-standing trees with diameter at breast height $\geq 1.0$ cm were mapped and were identified to species according to the nomenclature in Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China, 2004).

Soil organic matter (OM), pH, total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen, available phosphorus (AP), and available potassium (AK) were measured during the wet season. Five soil profiles in each plot were chosen randomly and sampled. For each profile, the litter or grass layer above the soil were carefully removed, and a top-soil sample (0–20 cm) was obtained (Jobbágy & Jackson, 2001). Soil samples were mixed evenly, air-dried, and then ground to a fine powder using a mill. Finally, the samples were hand-sieved and analyzed.

Soil for OM ($g \cdot kg^{-1}$) analysis was ground to $\sim 2.00$ mm. First, 0.5 g of soil were mixed with 5 ml of 1 N $K_2Cr_2O_7$ solution and 5 ml 98% $H_2SO_4$ and left for 30 min. Second, deionized water and concentrated $H_3PO_4$ were added, and the mixture was titrated with 0.5 $mol \cdot L^{-1}$ ferrous ammonium sulfate solution until the color changed from violet-blue to green, indicating the end point of titration.

Soil for pH analysis was ground to $\sim 2.00$ mm. First, 25 g of soil were added to deionized water and stirred.

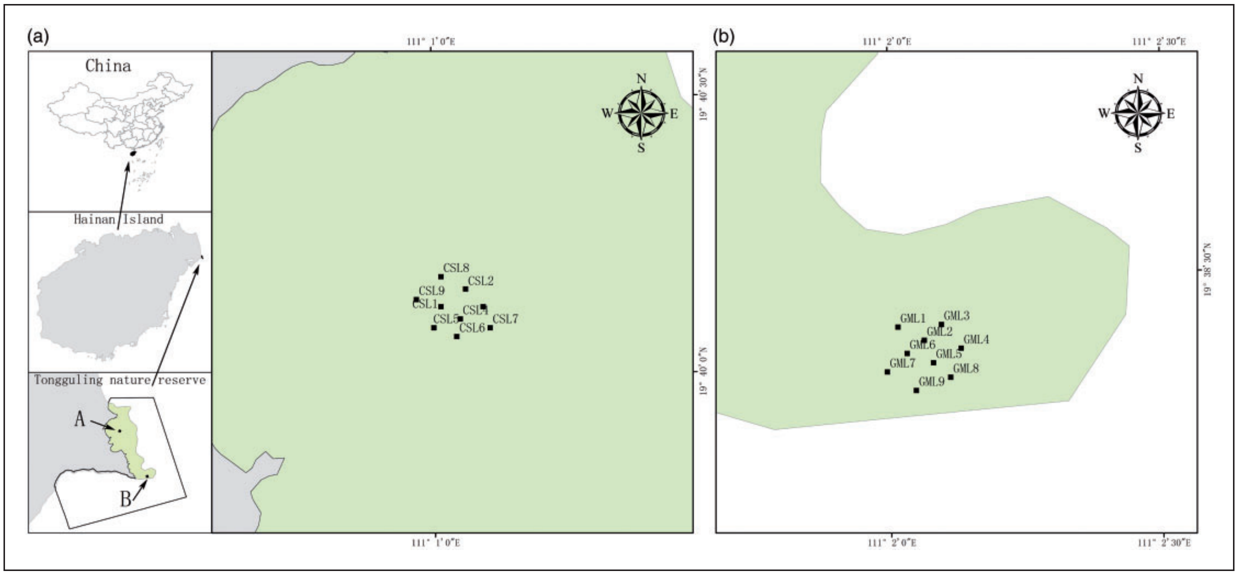

**Figure 1.** Locations of the study plots in secondary tropical evergreen monsoon forest (Panel (a)) and shrub forests (Panel (b)).

Second, pH of the suspension was measured using a pH electrode at 20°C to 25°C.

Soil for TN ($g \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 1 g of soil was digested in 98% $H_2SO_4$ with $K_2SO_4$–$CuSO_4 \times 5$ $H_2O$–Se. Second, ammonium-N from the digest was obtained by steam distillation using 0.1 $mol \cdot L^{-1}$ NaOH in excess to raise the pH. Third, the distillate was collected in 2% $H_3BO_3$ and titrated with 0.05 M $H_2SO_4$ to pH 5.0. Finally, the concentration of TN was calculated according to changes in the volume of the 0.05 M $H_2SO_4$ solution.

Soil for TP ($g \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 0.25 g of soil were digested with 60% $HClO_4$ solution. Second, the digest was diluted with ammonium-vanadomolybdate reagent, standards, and samples at 700 nm wavelength. Third, TP was calculated from the calibration curve.

Soil for TK ($g \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 0.25 g of soil were melted using 2 g solid NaOH for 15 min at 720°C. Second, the solution was collected and dissolved in deionized water. Third, a calibration curve as plotted using a series of appropriate potassium standards, and TK was measured using a flame photometer (Shanghai Precision Instruments Co., Ltd. 6400 A).

Soil for available nitrogen ($mg \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 2.0 g of soil were added to 0.2 g Devarda's alloy, and the sample was digested with 2 ml 0.01 $mol \cdot L^{-1}$ boric acid solution and 11.5 ml 1.8 $mol \cdot L^{-1}$ NaOH. Second, the solution was diluted with 0.01 M HCl.

Soil for AP ($mg \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 3.0 g of soil were digested with 50 ml 0.03 N $NH_4F$–0.025 N HCl solution. Second, the solution was then diluted with 2 ml of 0.06 M boric acid solution, deionized water, and ammonium-vanadomolybdate reagent, and 0.25% p-nitrophenol indicator was added. Third, a standard curve was arranged by reading the absorbance of blank with an ammonium-vanadomolybdate reagent, standards, and samples at 700 nm wave length. Finally, AP concentrations were calculated according to the calibration curve.

Soil for AK ($mg \cdot kg^{-1}$) analysis was ground to ~2.00 mm. First, 5.0 g of soil were digested with 50 ml 1 $mol \cdot L^{-1}$ ammonium acetate solution. Second, the supernatant was collected, and the combined ammonium acetate extract was diluted with 1 N ammonium acetate solution. Third, a calibration curve was plotted by a series of suitable potassium standard, and the extract was measured with a flame photometer at 767 nm wavelength (Anderson & Ingram, 1989).

## Data Analysis

The species diversity of each plot was estimated as species richness, the Shannon–Wiener index ($H$), and Pielou's evenness index ($E$). Species richness was calculated as the number of species, while the $H$ and $E$ were calculated according to the following equations

Shannon–Wiener index ($H$):

$$H = -\sum_{i=1}^{s} P_i \mathrm{In} P_i$$

Pielou index ($E$):

$$E = \frac{H}{\mathrm{In} S}$$

where $S$ is the total number of species in all plots per study vegetation, and $P_i$ is the proportional abundance of species $i$ in total species.

Dominant species were defined as the plant species with importance value more than 1.00.

Sørensen's dissimilarity coefficient were used to estimate species turnover in each 50 m × 50 m plot, and its detail equation is given as below:

$$\mathrm{CD} = 1\text{–}[2C/(S_1 + S_2)]$$

where $C$ is the number of common species between two adjacent subplots, and $S_1$ and $S_2$ are the numbers of unique species for Subplot 1 and Subplot 2, respectively.

Differences in species diversity, species evenness, species turnover, and soil nutrients between two vegetation types were assessed by Wilcoxon's rank tests. Relationships between plant diversity and soil conditions were evaluated using multiple stepwise linear regression. Selection of the best model depended on statistical methods for model comparisons, namely, on $R^2$ and the difference between the models' Akaike Information Criterion values. The effects of soil nutrients on dominant species in each recovery stage were assessed using linear regression. Analyses were conducted using SAS (SAS Institute, Cary, NC, USA). Critical soil nutrients for different dominant species were evaluated by canonical correspondence analysis using CANOCO version 4.5 for Windows. In addition, a Monte Carlo permutation test was conducted with 499 permutations for the significant tests of variables and ordination axes.

**Table 1.** Comparisons of Species Richness, Shannon–Wiener Index, Species Evenness, and Species Turnover Between the Shrub and Forest.

| | | | Wilcoxon's rank | |
|---|---|---|---|---|
| Parameters | Forest | Shrub | *W* | *p* |
| Species richness | 91.7 ± 7.9 | 73.8 ± 5.2 | 45 | .03 |
| Shannon–Wiener index | 3.7 ± 0.1 | 3.2 ± 0.2 | 45 | .03 |
| Species evenness | 0.8 ± 0.0 | 0.8 ± 0.0 | 44 | .04 |
| Species turnover | 0.2 ± 0.0 | 0.2 ± 0.0 | 763 | .20 |

*Note.* Values are mean ± standard deviation, $n = 9$.

## Results

### Patterns of Species Diversity Between Shrubs and Forests

In the Shrub, we found a total of 26,926 trees of 132 species in 48 families. The dominant species were *Maclurodendron oligophlebium*, *Hydnocarpus hainanensis*, *Mischocarpus sundaicus*, *Aporosa yunnanensis*, and *Ardisia crassinervosa*. In the Forest, we recorded a total of 16,354 trees of 148 species in 52 families. The dominant species were *Schefflera heptaphylla*, *Syzygium acuminatissimum*, *Xantolis longispinosa*, and *Koilodepas hainanense* (Supporting information, Appendix 1).

All three measures of diversity (species richness, Shannon–Wiener index, and species evenness) were significantly different between the two vegetation types. Shrub plots had lower species diversity than Forest plots (Table 1). Species turnover, however, was not significantly different between the two vegetation types (Table 1).

### Patterns of Soil Nutrients Between Shrubs and Forests

Soil nutrients varied between Shrub and Forest: pH, total P, and total K were all significantly higher in Shrub than Forest, whereas OM and available N were significantly higher in Forest than Shrub (Table 2). Other soil nutrients, including total N, available P, and available K, did not differ between the two vegetation types.

**Table 2.** Comparisons of Soil Conditions Between Shrub and Forest Sites: OM, TN, TP, TK, AN, AP, and AK.

| | | | Wilcoxon's rank | |
|---|---|---|---|---|
| Soil nutrient | Forest | Shrub | *W* | *p* |
| pH | 4.66 ± 0.33 | 5.60 ± 0.44 | 1,021 | .001 |
| OM ($g \cdot kg^{-1}$) | 393.3 ± 103.4 | 304.9 ± 43.8 | 128 | .001 |
| TN ($g \cdot kg^{-1}$) | 39.1 ± 7.6 | 38.0 ± 9.6 | 457 | .49 |
| TP ($g \cdot kg^{-1}$) | 1.7 ± 0.7 | 3.4 ± 0.7 | 780 | .01 |
| TK ($g \cdot kg^{-1}$) | 143.5 ± 61.9 | 310.4 ± 75.7 | 1,000 | <.001 |
| AN ($mg \cdot kg^{-1}$) | 177.7 ± 28.8 | 153.2 ± 30.6 | 206 | .01 |
| AP ($mg \cdot kg^{-1}$) | 0.5 ± 0.3 | 0.5 ± 0.3 | 501 | .86 |
| AK ($mg \cdot kg^{-1}$) | 394.5 ± 145.3 | 343.50 ± 84.0 | 371 | .10 |

*Note.* Differences in each soil nutrient were compared with Wilcoxon's rank tests. Values are mean ± standard deviation, n = 9. OM = organic matter; TN = total nitrogen; TP = total phosphorus; TK= total potassium; AN = available nitrogen; AP = available phosphorus; AK = available potassium.

### *Effects of Soil Nutrients on Plant Diversity*

Species diversity was significantly correlated with OM, total N, total K, total P, and available K using multiple regression (Table 3); while species evenness, however, was significantly correlated with OM and available P in both vegetation types.

### *Effects of Soil Nutrients on Dominant Species*

Canonical correspondence analysis revealed a significant correlation between soil nutrients and ordination axes (Monte Carlo permutation test, $p = .002$). In total, OM, soil K, P, and N contributed largest effects for dominant species in Forest and Shrub (Figure 2; Supporting Information, Appendix 2). In Shrub, the abundance of the dominant species *Arytera littoralis*, *Canthium horridum*, *Litsea glutinosa*, *Ficus hispida,* and *Sapindus saponaria* declined, while the abundance of *Sterculia lanceolata*, *Cryptocarya chinensis,* and *Garcinia oblongifolia* increased, with changes in soil nutrients (Supporting Information, Appendix 3). Similarly, in Forest, the abundance of *Syzygium tephrodes*, *Syzygium buxifolioideum*, *Xantolis longispinosa,* and *Psychotria asiatica* declined, while the abundance of *Maclurodendron oligophlebium*, *Drypetes arcuatinervia*, *Camellia furfuracea,* and *Hydnocarpus hainanensis* increased along the soil nutrient gradient (Supporting Information, Appendix 4).

## Discussion

### *Patterns of Soil Nutrients in Forests and Shrubs*

Soil nutrients are considered as one of the main factors limiting tropical forest structure, primary productivity, and other biological processes such as plant root allocation, growth, and litter production (Vitousek, Porder, Houlton, & Chadwick, 2010; Wright et al., 2011; Zhang et al., 2015). As we expected, we found differences in soil nutrients between the early- (Shrub) and mid- (Forest) successional sites. For example, soil OM was greater, but pH was lower in Forest compared with Shrub. Similar trends were also observed by Sparrius and Kooijman (2013) in inland dunes.

Total *p* values were significantly higher in Shrub than Forest. Soil P is an important nutrient regulating plant growth and development in forest ecosystems (Chen,

**Table 3.** Multiple Regression Analyses Between Soil Nutrients and Species Richness, Shannon–Wiener Index (H), and Species Evenness (E) in Shrub and Forest: pH, OM, TN, TP, TK, AN, AP, and AK.

| Parameters | pH | OM | TN | TP | TK | AN | AP | AK | AIC values | $R^2$ | *p* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species richness | – | 0.07 | 0.02 | 0.003 | 0.003 | 0.21 | – | 0.04 | −126.25 | 0.87 | <.001 |
| Shannon–Wiener index | – | 0.03 | – | 0.06 | – | – | – | 0.14 | −137.62 | 0.72 | <.001 |
| Species evenness | – | 0.01 | – | – | 0.22 | 0.22 | 0.03 | – | −140.23 | 0.60 | .01 |

*Note.* The AIC values, $R^2$ values, and *p* values of regression models were shown. OM = organic matter; TN = total nitrogen; TP = total phosphorus; TK = total potassium; AN = available nitrogen; AP = available phosphorus; AK = available potassium; AIC = Akaike Information Criterion.

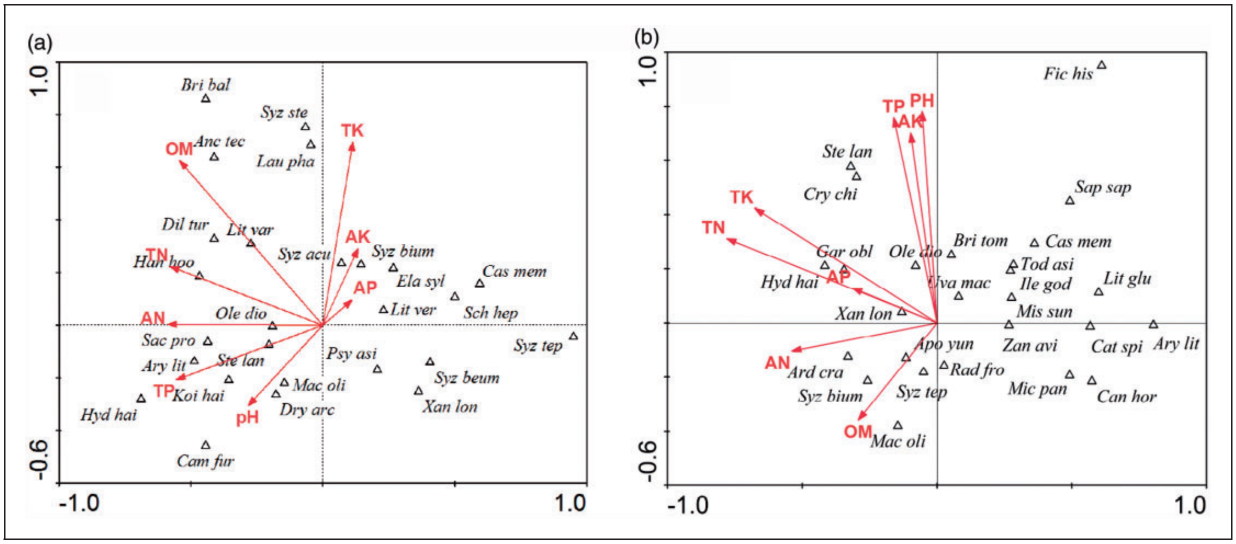

**Figure 2.** Canonical correspondence analysis between dominant species abundance (black species abbreviations) and soil nutrients (red nutrient abbreviations) in secondary tropical evergreen monsoon forest (Panel (a)) and shrubs (Panel (b)).

Chondron, Davis, & Sherlock, 2000; Paul & Clark, 1997). Moreover, forest productivity at the late recovery stages has been found to be limited by P (Cuevas & Medina, 1988; Gehring, Denich, Kanashiro, & Vlek, 1999), particularly in tropical forest ecosystems (Asner, Townsend, & Bustamante, 1999; Porder, Vitousek, Chadwick, Chamberlain, & Hilley, 2007). A previous study has shown that as an inducible enzyme, phosphatase can enhance the demand for P during forest recovery (Chen, Chondron, & Xu, 2008), which may explain the increased available P concentrations in forests in our study.

There was no significant difference in total N between the two vegetation types, but there was in available N. Increases in nitrogen availability during forest recovery are also reported in other studies (Erickson, Keller, & Davidson, 2001; Lamb, 1980; Maloney, Garten, & Ashwood, 2008; Robertson, 1984). This increase in N may be because uptake of soil N by aboveground vegetation in shrubs is higher than forests. In Forest, however, the N uptake could be compensated by the available N from litter mineralization and by inputs from N-fixing species. In addition, as a relatively young ecosystem, shrubs generally lack atmospherically derived elements, especially N, but is rich in rock-derived elements such as P (Broadbent et al., 1999). It is reasonable to assume that in shrubs, primary production accumulation is constrained by N supply (Zhang et al., 2015). It is also expected that high total P in shrubs could partly compensate for the low N availability, which has also been observed in previous studies (Du, Pan, Li, Hu, & Wang, 2011; Huang et al., 2013).

Although K is usually abundant in the environment (Zheng & Shangguan, 2007), it can be more easily leached than N or P, and up to 70% of all studied terrestrial ecosystems are K limited (Sardans & Peñuelas, 2015). Furthermore, a significant decline of total K and nonsignificant increase in available K during forest recovery implies that processes such as translocation or nutrient uplift allow maintenance of higher available K levels in the topsoil (Table 2; Barré, Berger, & Velde, 2009). A previous study showed that soil available K concentrations can be lower than available P and available N concentrations (Sardans, Peñuelas, Prieto, & Estiarte, 2008), which contrasts with our findings. Changes in total K and available K, therefore, may be caused by drought during forest recovery (Table 2; Sardans & Peñuelas, 2007).

## Correlations of Soil Nutrients With Species Diversity and Dominating Species Abundance in Forests and Shrubs

In global biomes, the broad-scale variation in patterns of species richness is often controlled by contemporaneous climate (Vázquez-Rivera & Currie, 2015) and the water–energy balance over ecological time (Kreft & Jetz, 2007). However, our study was performed at the local scale in sites with similar climate, topography (such as aspect and inclination of slope), and soil parent materials. We therefore assumed that soil nutrient availability is a critical factor influencing species distributions. Indeed, we found that species richness in both successional stages was significantly associated with nutrients such as OM, total N, and total P (Table 3). Nevertheless, OM and total N may be the main limiting resources associated with the changes in species diversity during forest recovery. Indeed, studies show that that community species compositions even within successional forests are likely influenced by the availability of soil nutrients (Guariguata & Ostertag, 2001). One possible reason why OM and total N are the main soil elements responsible for the changes in species diversity is that, as forest recovery proceeds, forest net primary productivity increases, which may cause a loss of N in soils. Higher OM and total N content can balance this loss of soil N, increasing species diversity, and dominant species abundance (Schmidt, Veldkamp, & Corre, 2015). This is especially the case for OM, which contains considerable amounts of N (Long, Yang, & Li, 2012). Thus, an increase in OM may compensate for the nonsignificant change in total N, ultimately resulting in an increase in available N during recovery, thereby increasing species diversity and dominant species abundance from early to late succession.

## Dominant Plant Species and Their Responses to Soil Nutrients

Species composition of local communities is often affected by environmental gradients (Mason, de Bello, Mouillot, Pavoine, & Dray, 2013). In our local-scale study, a gradient in soil nutrient concentration played a large role in species coexistence and replacement. A previous study showed that as forest succession proceeded, the main soil nutrients limiting dominant species changed (Zhang et al., 2015). Although in our study, this phenomenon might have been caused by soil conditions in the two stands, it also reflects that the requirements of plant species for soil nutrients in different successional stages differ (Huang et al., 2013).

The two forest successional stages had different dominant species (Supporting Information, Appendixes 1, 3, and 4), which might have been caused by differential responses of dominant species to soil nutrients (Perroni-Ventura et al., 2013). In shrubs, the early-successional stage, the abundance of species such as *Arytera littoralis*, *Litsea glutinosa*, and so on, declined, while the other species increased. In contrast, in Forest, which represents a mid-successional stage, the abundance of species, for example, *Syzygium buxifolioideum*, *Litsea glutinosa*, and so on, declined, while the other species increased. These results suggest that late recovery species are more able to adapt to the changing understory environment (Huang et al., 2013). The response of dominant species to limiting soil nutrients could predict the destiny of dominant species in late-successional or climax forest. Thus, in shrubs, we would predict the following species to be dominant: *Syzygium tephrodes*, *Maclurodendron oligophlebium*, *Syzygium buxifolium*, *Aporosa yunnanensis*, *Hydnocarpus hainanensis*, *Xantolis longispinosa*, and *Ardisia crassinervosa;* whereas in forest, we would predict *Syzygium buxifolium*, *Elaeocarpus sylvestris*, *Litsea variabilis*, *Dillenia turbinata*, *Ancistrocladus tectorius*, *Bridelia balansae*, *Hancea hookeriana*, *Litsea verticillata*, *Schefflera heptaphylla*, *Casearia membranacea*, and *Olea dioica*. Decline of different dominant species in each successional stage differed (Supporting Information, Appendices 3 and 4). The species with higher decline rates may be eliminated rapidly in the future forest recovery, whereas the species with lower decline rates might persist for a longer time. This phenomenon may be caused by transient adaption to the appearance of a more heterogeneous environment in later successional stages (Bartels & Chen, 2010). However, these species will likely eventually make space for mature-phase dominant species. As forest ecosystems are highly complex, the factors influencing species coexistence and replacement during recovery may be extremely diverse (Lin et al., 2016). Thus, further studies are required to fully explore the species coexistence mechanisms in secondary forest recovery processes.

## Implications for Conservation

The high species richness (more than 70 species in each 2,500 $m^2$ plot) in both the shrub and the secondary forests helps us understand the effectiveness of protection since the TNR was established in 1983. The species diversity in the shrub and secondary forests suggests that vegetation in this region is recovering in a progressive successional process, in large part due to its protection. In addition, the evidence that soil nutrients are associated with this succession suggests that management or restoration of soil nutrients should be a priority in the management strategies of these protected areas. Finally, the turnover of dominant species in both the shrub forest and the secondary forest can help inform tree species selection for the restoration of coastal windbreak forests in this region.

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