

Predicting the distribution of potential natural vegetation based on species functional groups in fragmented and species-rich forests

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Background and aims – Potential natural vegetation (PNV) can provide a basic reference in guiding the restoration activities for damaged landscapes. Our aim was to find a practicable approach of reconstructing PNV based on functional groups (FGs) in species rich and fragmented forest region.

Methods – A total of 149 sample plots (20 × 20 m) were laid and investigated systematically by 1 × 1 km or 1 × 2 km grids across the 482 km² forest region in Bawangling nature reserve, Hainan Island, China. The 579 woody plant species found were aggregated into eight functional groups (FGs) according to successional status and potential maximum height. The ecological niche model (MaxEnt) was adopted in predicting the potential distribution of the FGs. The relationship between occurrence probability of FGs and environmental factors was determined as a function of the predicted response curves. The PNV was produced by the overlay of maps for the potential distribution of the FGs, while referring the FGs interactions.

Key results – The predicted pioneer FGs scattered widely in the whole landscape, while climax FGs mainly distributed in the central and south part of the study region. Pioneer FGs could better withstand environmental change and occurred in warmer and drier sites, while climax FGs are distributed in cooler and wetter conditions. The PNV could be reconstructed by considering interactions among the FGs. Sixteen main functional patch types were reconstructed in the tropical forest landscape, among which twelve were dominated by climax FGs, accounting for 72.7% of the area, and only four were dominated by pioneer FGs, and accounting for 18.8% of the area.

Conclusion – We produced successful prediction of the observed PNV by applying a niche-based model (MaxEnt) based on FGs in fragmented and species rich forest region. This is helpful for predicting how PNV will change to natural and anthropic stressors.

Key words – Functional groups, MaxEnt, niche modeling, potential natural vegetation, tropical forests.

INTRODUCTION

Potential natural vegetation (PNV) is the vegetation developed in a given habitat in absence of human interferences (Zerbe 1998), which is usually the climax vegetation of the habitat. The PNV has been used in many aspects, such as in the assessment of landscape structure on ecosystem processes (Ricotta et al. 2002), in landscape planning and management (Chytrý 1998, Zerbe 1998), in evaluating the effects of climate change on forest vegetation (Hickler et al. 2012), and in selecting sites and species for restoration (del Arco Aguilar et al. 2010). Theories and applications related to simulating the distribution of PNV at different scales (e.g. land-

scape, region and globe) has become one of the main study field in ecology and biogeography in recent years (Chytrý 1998, Loidi & Fernández-González 2012).

There are two alternatives methods for constructing PNV under given habitat conditions. The first method relies on qualitative approaches, which are mainly based on expert knowledge and experience (Liu et al. 2009). The second method relies on quantitative modeling approaches, which are based on the modeled relationships between vegetation survey data and mapped environmental information. Because predictive spatial modeling can overcome the weaknesses (a low degree of objectivity, reproducibility, and high

costs) of traditional qualitative approaches, it has become an increasingly important tool to study PNV (Chytrý 1998, Liu et al. 2009).

Predicted species distribution from spatial modeling is commonly used for conservation planning (Andelman & Willig 2002). The PNV-maps can be produced by overlay the potential distributions of two or more different species in a study region (Manies & Mladenoff 2000, Franklin 2002, Hemsing & Bryn 2012). However, this kind of approach of predicting PNV was usually applied to few species (Ferrier et al. 2002), which is feasible in regions where species richness is low. It is therefore difficult to apply this approach in regions where the species are diverse or the indicator species is not easy to determine. Spatial predictions for individual species could be analyzed at higher levels of ecological complexity, i.e. reconstructing species assemblages and biological communities in a bottom-up approach (Ferrier et al. 2002, Guisan & Thuiller 2005). Models at the community level have two apparent advantages: (i) they can make full use of the field investigation records, break the limitations of sample points for each individual species (Guisan et al. 1999); (ii) they aggregate the species with similar distribution patterns or common ecological requirements into species groups, which is more convenient for ecologists to explore and explain the complex ecological features (Ferrier & Guisan 2006). At present, the procedure for predicting PNV by the models at community level is as follows: firstly, quantitatively classifying the species with similar distribution patterns or similar characteristics into different species groups, and then predicting the potential distribution of each species group (Ferrier et al. 2002), finally the PNV-map is produced by overlay of the potential distribution maps of different species groups (Manies & Mladenoff 2000).

In tropical regions, the forest landscape pattern has changed dramatically due to anthropogenic activities and climate change. Most of the primary forest landscapes have been fragmented into mosaics composed of secondary forest patches of different recovery stages, or even no forest patches (Wright 2005). Fragmentation and corresponding changes in forest structure and composition could have dramatic impacts on the functions of forest ecosystems. Preventing further anthropogenic disturbances and restoring the fragmented tropical forest landscape has become one of the most important challenges faced by human being in the 21st century. In carrying out the process of restoration for these damaged ecosystems, the first step is to set the objectives of restoration, i.e. to discern what kinds of vegetation should be restored in different habitat or site conditions. Prediction of PNV can provide the reference potential vegetation patch for each site, guiding the restoration activities for damaged tropical forest landscapes (Zerbe 1998).

Functional groups (FGs) are defined as groups of species either exhibiting similar responses to an environment or having similar effects on major ecosystem processes (Kelly & Bowler 2002). By making an analogy with plant FGs, Chabrierie et al. (2007) thought that a heterogeneous forest landscape is composed of different patch mosaic FGs, which are groups of landscape cells showing similar function and or respond similarly to environment. Establishing a habitat clas-

sification system based on FGs co-occurrence may help the drawing up of conservation plans (Hérault & Honnay 2007).

Tropical forest landscape is characterized by high species richness and non-apparent dominant species (Zang et al. 2004). Predicting the distribution of PNV could be carried out more precisely based on the potential distribution of major FGs in the species rich tropical forest landscapes. In this study, we conducted an intensive field survey with 149 systematic-grid sampling plots across the landscapes in the Bawangling forest area, a typical fragmented tropical forest region on Hainan Island. The objective of this study was to test a niche model approach to predict the distribution of PNV based on FGs, so that the approach used in this study might be refereed in the restoration of other species rich and damaged forest landscapes.

MATERIALS AND METHODS

Study area

The study site is located in the Bawangling Nature Reserve (BNR) (18°53'–19°20'N 109°05'–109°53'E), Hainan island, China, which covers an area of 482 km² (fig. 1). The elevation of the region ranges from 50 m to 1654 m a.s.l. The region is characterized by a tropical monsoon climate with a distinct wet season from May to October and a dry season from November to April. The average annual precipitation is 1,750 mm and the average air temperature is 23.6°C. Soils at higher elevations are mixtures of red loam and yellow loam, while latosol developed from granite dominates soils at lower elevations.

The landscape in BNR is a mosaic of natural vegetation and plantations, in which natural tropical forests occupy a greater area. Five major vegetation types are found in this region: the tropical lowland rainforest, the tropical montane rainforest, the montane evergreen forest, the montane dwarf forest and the tropical coniferous forest. Prior to 1957, most part of the BNR was covered by the above-mentioned types of old growth tropical forests. Before the 1960s, deforestation occurred mainly due to natural disturbances, such as fire, strong monsoon wind, insects, and the traditional low intensity shifting cultivation by the indigenous people. From the 1960s onwards commercial timber harvesting became the major mode of deforestation (Zang et al. 2004). In the 1980s, because of decreased tropical forest resources, timber harvest changed from clear cutting to selective logging. Since 1994, timber harvest has been banned in order to protect and restore the degraded forests. Because of the severe and repeated anthropogenic disturbances over the past forty years, forest landscapes in BNR had become increasingly fragmented, and the old-growth forests were displaced by secondary forests of various recovery stages, shrub/grass land and agricultural lands. Some bare or shrub/grasslands have been converted to forest plantations.

Data preparation

A total of 149 sample plots (20 × 20 m) were placed and investigated systematically by 1 × 1 km or 1 × 2 km grids across the 482 km² forest region (BNR) (fig. 1). At each

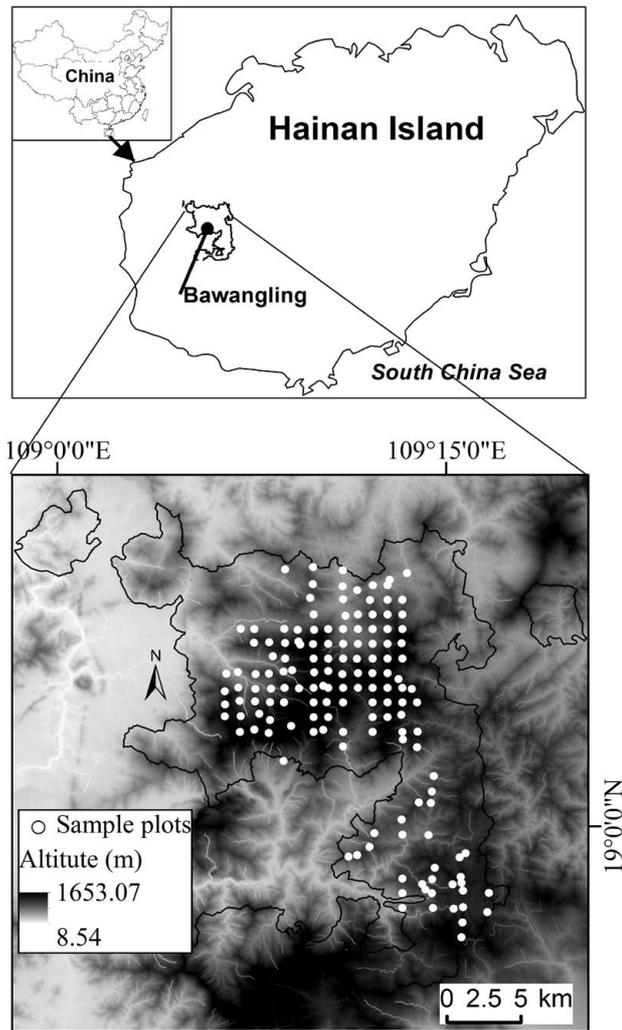


Figure 1 – The study area and design of field survey sample plots in the tropical forest region of Bawangling, Hainan Island, China.

line intersection of the grid, a plot was established and positioned by GPS for vegetation survey. Within each sample plot all free standing woody stems with diameter at breast height (DBH) ≥ 1 cm were counted, measured and identified to the species level. Through this survey, we counted a total of 58,225 woody stems belonging to 579 species, 247 genera and 82 families.

Nine environmental (including climatic and topographical) factors were used in this study. The climatic data were collected from eighteen long-term meteorological stations on Hainan Island and three ecological observation points in BNR. The thin plate smoothing spline was used to produce the climatic layers in the software of ANUSPLIN 4.1 (Hutchinson 2000). The ANUSPLIN procedure fits interpolation surfaces to rainfall and temperature data as a function of position and elevation (i.e. the longitudinal and latitudinal position and elevation of the meteorological stations). The climatic parameters are annual mean precipitation (MeanP), annual mean temperature (MeanT), minimum temperature of coldest month (MinT), maximum temperature of warmest month (MaxT), mean temperature of

driest quarter (MeanDT), and mean temperature of wettest quarter (MeanWT). The topographical factors (including slope, elevation, and topographic wetness index) were estimated for each cell in the DEM produced by running ANUDEM 4.6 (Hutchinson 1999) combined with ArcGIS (9.3.1 by ESRI). The topographic wetness index (TWI) has been used as a relative index of long-term soil water content for the purpose of predicting vegetation response (Bickford & Mackey 2004). The TWI is calculated as the ratio of the area upslope from any given point on the landscape to the local slope at that point, and thus represents the amount of water that should enter a given spatial unit divided by the rate at which the water should flow out of that unit. We equalized the cell sizes to one arc-second resolution (approximately 30×30 m). To avoid potential redundancy between environmental variables, the Pearson correlation coefficients for all pairs of predictors were calculated. It appeared that the predictors used were not highly correlated ($|r| < 0.80$).

Assignment of the functional groups

We adopted the FGs classification methods of Köhler et al. (2000). The species were grouped into pioneer or climax according to their successional status, and were divided into four height classes (2–5 m, 5–15 m, 15–30 m and > 30 m) according to potential maximum height (PMH). Successional status was determined by wood density and seed size. Details of determined methods of successional status are found in Zhang et al. (2008). These traits (PMH, wood density and seed size) were selected since they provide coarse indicators of plant functional strategy and it exists strong linkages with the abiotic environment (Moles et al. 2009, Laughlin et al. 2011). The species with small seeds and light wood density were grouped together as pioneers and species with heavy wood and large seeds as climax species. PMH was determined based on field data and information from published literature such as Flora of China. The identification of the height class limits was based on observations of typical canopy heights and mean maximum tree heights of different species in BNR's forests. The height classes could be named according to their canopy positions as emergent (> 30 m), canopy (15–30 m), sub-canopy (5–15 m) and shrub (2–5 m). Thus the free standing woody plants were aggregated into eight FGs according to the combination of the two criteria: pioneer shrub (P1), pioneer sub-canopy tree (P2), pioneer canopy tree (P3), pioneer emergent tree (P4), climax shrub (C1), climax sub-canopy tree (C2), climax canopy tree (C3) and climax emergent tree (C4).

Predicting distributions of the functional groups

We adopted the community-based spatial modeling (Ferrier et al. 2002, Ferrier & Guisan 2006), predicting the potential distributions of the eight FGs in a multi-dimensional environmental space. We used MaxEnt (Phillips et al. 2006, Phillips & Dudík 2008) ecological niche model that is characterized by a very high predicting power of potential species distributions compared to other methods (Elith et al. 2006). MaxEnt is a machine learning method, estimating species distribution by finding the probability distribution of maximum entropy subject to the constraints of represent-

ing the incomplete information about the distribution of the observed occurrences. The constraints are that the expected value of the environmental variables should match its average over sampling locations (Phillips et al. 2006). In recent comparisons, MaxEnt has been shown to be robust for modeling presence-only occurrence data with good performance using both small and large datasets (Elith et al. 2006). Convertino et al. (2011) showed also its scale and resolution invariance properties until a threshold related to the average home range or geographical range of the species considered. In this analysis, we used a logistic output of MaxEnt, with suitability values ranging from 0 (fully unsuitable habitat) to 1 (optimal habitat) (Phillips & Dudík 2008). Following Pearson et al. (2007), we used the 10th percentile training presence as a suitability threshold, i.e. we assumed that a cell is suitable if its suitability score is greater than the 10th percentile of training presence points. We used linear, quadratic and hinge features with default convergence threshold (10^{-5}) and maximum number of iterations (500). We considered only one presence record per grid cell (30×30 m).

The accuracy of the ecological niche model was evaluated by constructing the model using only 75% of the available records, with the remaining 25% used for testing purposes as the validation dataset. We applied several techniques to evaluate the MaxEnt model. First, we used a jackknife test (Pearson et al. 2007) of variable importance to compare models with all combinations of the environmental variables. This procedure quantifies the explanatory information in each variable when used in isolation and also the unique information lost when omitted from a given model. Second, Model accuracy was determined using a receiver operating characteristic (ROC) analysis (Phillips et al. 2006). By calculating the sensitivity and specificity of model at all possible thresholds, a ROC curve was produced with sensitivity plotted on the y-axis and (1-specificity) plotted on the x-axis. The area under the curve (AUC) of the resulting plot provides a measure of model performance. The higher the value of AUC, the better the model set. The prediction is perfect when AUC equal to one, while the prediction accuracy is lowest when AUC equal to 0.5. Following the recommendations of Pawar et al. (2007), niche models possessing an AUC > 0.75 and a p-value of < 0.05 (for the sensitivity and specificity test) were retained for this analysis. In this process, we put both the environmental data and the presence data of FGs into ArcGIS. These data were transformed into the ASCII format to meet the requirement of the MaxEnt model. We also used response curves to illustrate the relationship of probability of occurrence to environmental variables (Phillips & Dudík 2008).

Reconstruction of the potential natural vegetation

Most of the studies concerning the PNV prediction use the method of setting numerical thresholds for reclassifying the presence probability surfaces of the species or species group to overlay them and reconstruct the PNV (Batek et al. 1999, Manies & Mladenoff 2000). In this study, we used the 10th percentile training presence as a suitability threshold and reclassified the MaxEnt output to a binary grid (1 = above the threshold; 0 = below), and selected the 'suitable' areas of each FG to overlay.

In the process of natural recovery, the successional sere is generally like the following steps: grass → pioneer shrub → pioneer tree → climax tree (Finegan 1996). Although a large pioneer tree is able to coexist with a smaller climax tree over successional process, it is rarely found in mature primary forests. Study indicated that large pioneers refer to species which are dominant in late secondary forest, later than small pioneers but before climax species become dominant (Budowski 1965). So the pioneer FGs will be finally replaced by the climax ones except in extreme stress conditions or additional disturbances (Rees et al. 2001). For example, in BNR, pioneer tree species are seldom found in mature primary forests, but are most dominant in secondary forest following regrowth of abandoned land or in highly disturbed forests after logging or catastrophic events. In addition, the species within C1 are characterized by shade-tolerance and can only survive under a closed forest canopy. Therefore, the species within C1 will probably disappear in full sun. According to successional theory and FGs interactions, we set the following decision rules in reconstructing the PNV in our study region: (1) the pioneer FGs and the climax FGs can't coexist in the same PNV unit; (2) a PNV unit could be occupied by one pioneer FG, P1, P2, P3, P4 respectively; (3) a PNV unit could be jointly occupied by different combinations of pioneer FGs; (4) a PNV unit could be occupied by one climax FG C2, C3, C4 respectively; (5) a PNV unit could not be occupied solely by C1; (6) a PNV unit could be jointly occupied by different combinations of climax FGs.

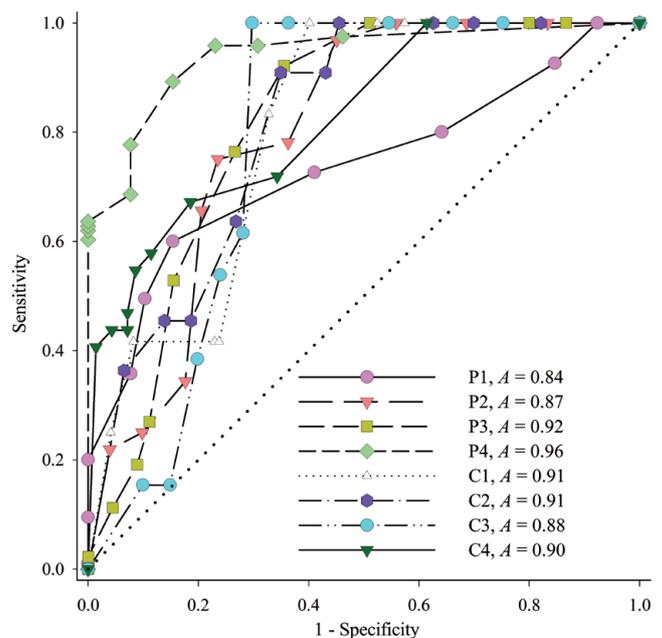


Figure 2 – The Receiver Operating Characteristics (ROC) curves of test for the MaxEnt models of the eight functional groups in the tropical forest region of Bawangling, Hainan Island, China. P1=Pioneer shrub, P2=Pioneer sub-canopy tree, P3= Pioneer canopy tree, P4= Pioneer emergent tree, C1= Climax shrub, C2=Climax sub-canopy tree, C3= Climax canopy tree, C4= Climax emergent tree.

RESULTS

The functional groups

Among the species investigated, 89.5% were climax and 10.5% were pioneers. The numbers of species belong to the four pioneer FGs (from P1 to P4) were: 18, 29, 12 and 8, and belonged to the four climax FGs (from C1 to C4) were: 69, 270, 157 and 16 respectively.

Distribution of the functional groups

Evaluation on the models for the eight FGs showed that the predictive accuracies of the MaxEnt models were acceptable and superior to the random predictions. The ROC analysis indicated that the asymptotic significant tests for AUC values were all extremely significant ($p < 0.001$). The AUC values for the eight FGs were all more than 0.8, in which five of them were more than 0.9 (fig. 2). This meant that all the predictions performed well.

The jackknife analysis of variable importance showed that slope was important for determining suitable habitat for all FGs (table 1). MaxT and MeanDT were the primary determinants in characterizing the habitat suitability for FGs except P4. MeanP was an important factor in controlling the suitable distribution of the climax FGs C2 and C4. Elevation was important for determining suitable habitat for pioneer FG P4, this factor accounts for 24.5% of the variations (table 1). TWI was important for determining suitable habitat for pioneer FGs except P3.

Considering the response curves of most important factors in controlling the suitable distribution of the FGs (fig. 3), P1 had a strong response to TWI occurring in areas with a TWI over 0.6 (relatively arid soil conditions), and the likelihood of occurrence declining rapidly above this threshold (fig. 3E). In addition, it could tolerate a wide range of MeanDT, slope and MaxT (fig. 3A & C). Similarly, P2 and P3 could also tolerate a wide range of MeanDT, slope and MaxT, but the extent of tolerance was weaker than P1 (fig. 3A & C). Still, higher suitability for P2 was associated with drier soil conditions (fig. 3E). For P4, a negative relationship was observed with slope: a high contribution occurred at around 0–20 degree, with a sharp drop above this

slope degree (fig. 3B). A similar pattern was observed for elevation: higher suitability for P4 was associated with low elevation (0–450 m), and the habitat suitability began to decrease with increasing elevation (fig. 3F). Still, P4 responded passively to TWI (fig. 3E), indicating it preferred drier conditions. In comparison with most of the pioneer FGs, which could tolerate much wider range of MeanDT and MaxT, the climax FGs could tolerate relatively narrower range of MeanDT and MaxT (fig. 3A & C). For the most climax FGs, the likelihood of occurrence declined rapidly with increasing MeanDT and declined slowly with increasing MaxT up to the range of 33–34°C. C1 and C2, however, showed a lower suitability in areas with high MeanDT and MaxT than C3 and C4 (fig. 3A & C). The climax FGs except C4, could tolerate a wide range of slope degrees (fig. 3B). The suitability for C1, C2 and C4 increased steeply in areas having MeanP below 1800 mm. However, they responded differently when MeanP was above 1,800 mm (fig. 3D).

The predicted distribution patterns for the pioneer and the climax FGs showed significant differences in the study area (fig. 4). The pioneer FGs P1 and P2 had similar predicted distribution patterns, their areas of higher presence probabilities were patchily distributed in the whole landscape, and having lower probabilities in the west, north edge and central portion of the study region. P3 and P4 had a more scattered distribution in the study area and P4 showed medium probability of occurring in the north and northwest section of the study area. For P1-P4, the 10th percentile training presence logistic threshold was 0.46, 0.43, 0.41 and 0.39 respectively. According to these thresholds, 59.16%, 62.50%, 53.26%, and 55.28% of the land considered were suitable for the pioneer FGs P1-P4.

For the climax FGs, The predicted distribution patterns were very similar. They had high probability of occurring in the mid and south section of the study area. The geographical areas with the highest suitability for C4 were wider than the areas for the three other climax FGs. For C1-C4, the 10th percentile training presence logistic threshold was 0.33, 0.32, 0.33 and 0.39 respectively. According to these thresholds, 57.13%, 60.52%, 60.12%, and 61.13% of the land considered were suitable for the climax FGs C1-C4.

Table 1 – Individual variable contribution to the MaxEnt models in the tropical forest region of Bawangling, Hainan Island, China (%).

See fig. 2 for functional groups abbreviations.

Variables	Functional groups							
	P1	P2	P3	P4	C1	C2	C3	C4
MeanP	5.4	1.3	2.4	2.6	4.3	7.6	4.6	16.8
MeanT	0.6	1.1	1.6	0.4	1.8	2.4	6.8	4.2
MinT	0.8	2.4	0.4	0.8	2.8	4.8	2.9	4.5
MaxT	30.8	14.4	32.2	5.1	10.2	28.9	51.8	12.7
MeanDT	12.4	47.8	19	3.8	54.1	23.9	7.3	37
MeanWT	0.4	2.5	1.5	0.2	2.1	2.7	2.9	6.1
Slope	40.2	18.3	37.4	51.4	21.1	20.1	18.7	9.9
Elevation	0.2	2.7	0.9	24.5	2.7	2.5	1.9	1.5
TWI	9.3	9.4	4.6	11.1	0.8	7.2	3.1	7.3

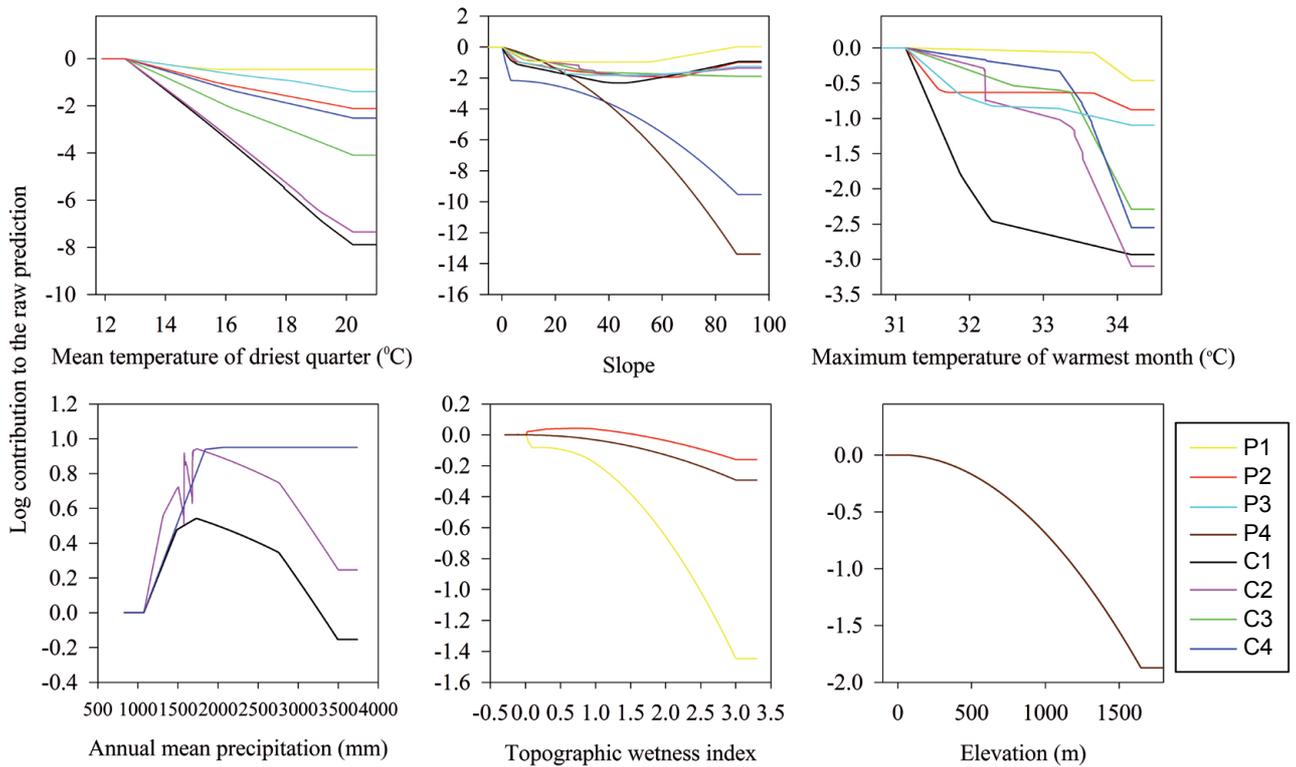


Figure 3 – Response curves (log contribution to prediction) for the predictor variables as generated by the MaxEnt models run for the eight functional groups in the tropical forest region of Bawangling, Hainan Island, China. See fig. 2 for functional groups abbreviations.

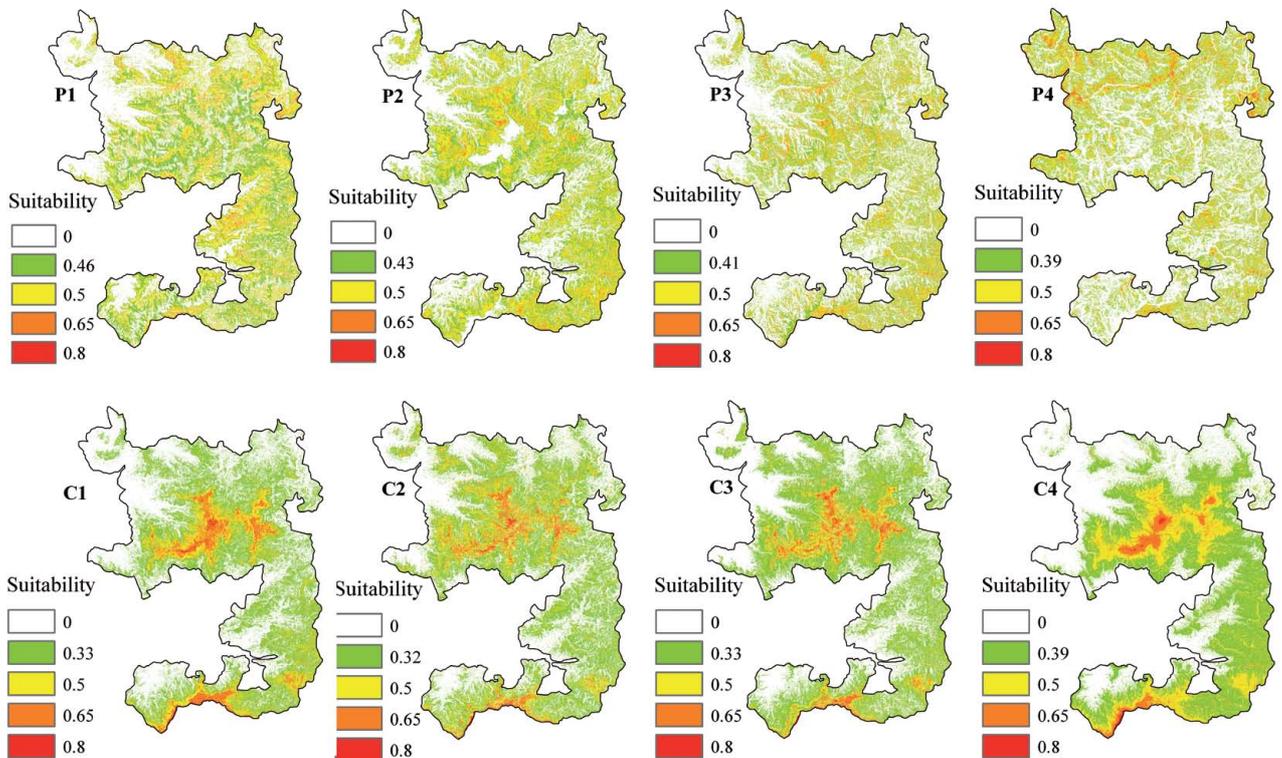
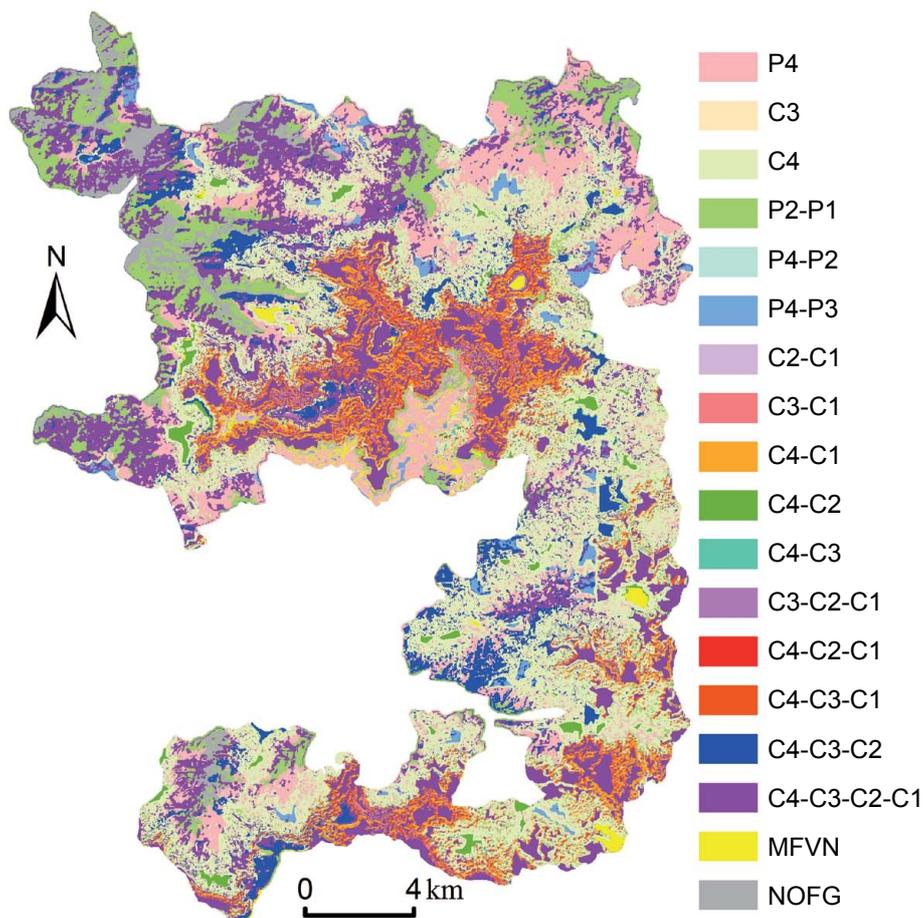


Figure 4 – Maps of the predicted probability of occurrences of the eight woody plant functional groups (FGs) in the tropical forest region of Bawangling, Hainan Island, China. The different suitability thresholds (0.46, 0.43, 0.41, 0.39, 0.33, 0.32, 0.33 and 0.39) correspond to the 10th percentile training presence thresholds of the FGs P1-P4 and C1-C4 suitability models, respectively. See fig. 2 for functional groups abbreviations.

Table 2 – Area of main functional-vegetation units in the tropical forest region of Bawangling, Hainan Island, China.

Potential natural vegetation types	Code	Area (km ²) (%)
Climax emergent tree-climax canopy tree-climax subcanopy tree- climax shrub	C4-C3-C2-C1	69.78 (14.5)
Climax emergent tree	C4	58.87 (12.2)
Climax emergent tree-climax canopy tree-climax shrub	C4-C3-C1	42.05 (8.7)
Climax emergent tree- climax shrub	C4-C1	40.97 (8.5)
Pioneer emergent tree	P4	40.35 (8.4)
Pioneer subcanopy tree- pioneer shrub	P2-P1	35.88 (7.4)
Climax emergent tree- climax canopy tree- climax subcanopy tree	C4-C3-C2	27.06 (5.6)
Climax emergent tree- climax subcanopy tree- climax shrub	C4-C2-C1	22.45 (4.6)
Climax canopy tree- climax shrub	C3-C1	22.02 (4.7)
Climax emergent tree- climax canopy tree	C4-C3	20.63 (4.3)
Climax canopy tree-climax subcanopy tree- climax shrub	C3-C2-C1	15.05 (3.1)
Climax emergent tree- climax subcanopy tree	C4-C2	13.74 (2.9)
Climax canopy tree	C3	9.35 (1.9)
Climax subcanopy tree- climax shrub	C2-C1	8.14 (1.7)
Pioneer emergent tree- pioneer subcanopy tree	P4-P2	7.30 (1.5)
Pioneer emergent tree-pioneer canopy tree	P4-P3	7.08 (1.5)
Minor functional-vegetation units (each <2% of the study area)	MFVU	33.35 (6.9)
Vegetation units unsuitable to functional groups presence	NOFG	7.93 (1.6)
Total		482.00 (100.0)

**Figure 5** – The predicted potential natural vegetation based on functional groups in the tropical forest region of Bawangling, Hainan Island, China. See fig. 2 for functional groups abbreviations.

Reconstruction of the potential natural vegetation

Twenty-nine PNV functional patch types were reconstructed in the tropical forest landscape, among which twelve patches (accounting for 72.7% of the area) were dominated by climax FGs, four patches (accounting for 18.8% of the area) were dominated by pioneer FGs, while the remaining 8.5% of the landscape were occupied by thirteen small patches (each < 1.5% of the study area) composed by varied combinations of different FGs or by non-forest lands (table 2).

The PNV types with the largest areas (such as C4-C3-C2-C1 and C4) had wide spatial ranges and varied patterns (fig. 5). The patch types of C4-C3-C2-C1 were relatively clumped distributions in the central part of the region, while they were relatively patchy distributed in the northwest and southeast part of the region. The patch type of C4 was dominant and formed distribution mosaics with P4, C4-C3-C2 and so on in the central to north and south part of the region. The other functional patch types with small areas were randomly dispersed among the larger patch types in the landscape.

DISCUSSION

Distributions patterns of functional groups and their determinants

Our analyses showed that the predicted distribution patterns for the pioneer and the climax FGs had differences in the study area. The pioneer FGs had a wider and more scattered distribution in the whole landscape, while climax FGs had a relatively narrower and more concentrated distribution in the central and south part of the study region. Thus, the larger range seems consistent with broader ecological niche of pioneer as opposed to climax species (Zangerl & Bazzaz 1983). As expected, pioneer FGs, could better withstand environmental change than the climax FGs (fig. 3A & C). Species experiencing wider abiotic variation would be more stress tolerant and could grow and survive under harsher conditions (Morin & Chuine 2006). This idea proposed by Morin & Chuine (2006) might justify that pioneer FGs (stress-tolerant species) could occur in more xeric regions than climax FGs, which were usually found in study regions where soil water availability was higher.

Plant functional traits could be used to explain community composition across a strong environmental filter (Laughlin et al. 2011). Distinct distribution patterns of pioneer vs. climax FGs are a reflection of the quite different life-history strategies of the two groups of species. In the present study, two traits (seed size and wood density) were used to classify species into pioneer vs. climax FGs (see Materials and methods). Seed size has a profound effect on fecundity, establishment success, seedling survival, seedling growth rate, competitive ability, and persistence in the seed bank (Rees et al. 2001). Small-seeded species have high fecundity, long dispersal capacity and can deploy roots and leaves rapidly to become autotrophic. This advantage allows for rapid growth in size in an open, disturbed environment where competition is minimal (Turnbull et al. 2012). This might provide an explanation for our findings that pioneer FGs with smaller seeds could occur in hot and xeric regions (fig. 3A, C & E). Wood density represents the biomass invested per unit wood

volume (Poorter et al. 2008). High wood density provides a stronger defense against physical damage and pathogens (Meinzer 2003). Trees with higher wood density are often found in habitats with lower disturbance rates, lower light and moist condition (Wiemann & Williamson 1989, Osunkoya 1996). The similar pattern was found in our study. The frequency of occurrence of climax FGs with higher wood density reached a maximum for locations with cooler (low levels of MeanDT and MaxT) (fig. 3A & C) and more humid (high levels of MeanP) (fig. 3D) conditions. Although likelihood of occurrence was lower than that of pioneer FGs, some climax FGs (e.g. C3 and C4) with high wood density could also occur in hot and relatively dry habitats. These species of the climax FGs might be the remnants of the original communities experienced the most recent disturbances. On the other hand, this might be due to the fact that species with higher wood density found in drier habitats are better able to resist drought-induced embolism (Hacke et al. 2001).

There were important differences in responses to environment changes across different PMH groups. In this study, tallest species regardless of their successional status showed a lower suitability in habitats with steep slope (fig. 3B). Meanwhile, tallest species preferred lower altitude and more humid areas (fig. 3D & F). Our results were consistent with the results of a number of other investigations. For instance, Koch et al. (2004) proposed that large species are usually greater in valleys than on ridges due to hydraulic constraints. Similar results have been observed for an Ecuadorian rain forest (Wilcke et al. 2008). Moles et al. (2009) found that shorter species are often associated with the drier, hotter and more unproductive sites. However, the results of Moles et al. (2009) are opposite to findings of climax FGs in the present study, in which shorter species (C1 and C2) preferred lower temperature than taller ones (C3 and C4). Overall, our results could be understood in terms of the different strategic trade-offs (e.g. growth-survival tradeoff and life-history tradeoff) that allowed coexistence of different FGs along environmental gradient. Distribution patterns of FGs in the study added further evidence to stress tolerance hypothesis (Cornwell et al. 2006), energy availability hypothesis (Morin & Chuine 2006) and niche differentiation theory (Kraft et al. 2008).

Reconstruction of the potential natural vegetation

In the present study, we adopted the ecological niche model (MaxEnt) to predict the presence probabilities of different FGs, while considering the FGs interactions in producing the PNV distribution map. The model evaluations indicated that our results were satisfactory. In future, many work should be considered in further improving the simulations, such as to set up sample points (Araújo & Guisan 2006, Hemsing & Bryn 2012), to select more appropriate environmental factors used in the models (Liu et al. 2009), and to develop more accurate simulation models (Thuiller et al. 2006).

Our results showed that climax FGs-dominated patch types have larger area and wider spatial ranges than pioneer FGs-occupied patch types in the study region (fig. 5, table 2). This was inconsistent with predictions from single FG modeling (fig. 4). This means that distribution patterns of FGs-based patch types are not only influenced by abiotic

environmental predictors, but also by interactions among the FGs. According to the niche and competition tradeoff and successional niche theory (Rees et al. 2001), pioneer FGs are good colonists in recently disturbed and stressful environments because of their lower migration limitation, and have rapid growth rates under resource-rich conditions. However, in absence of disturbances in high-resource environments, climax FGs generally competitively exclude pioneer FGs due to better resource use efficiency (Rees et al. 2001). Only when disturbance is greater or more frequent, climax FGs will be extinct and pioneer FGs will finally prevail. Consequently, the distribution patterns of pioneer FGs-based patch types, to a large extent, depend on the degree of range filling of climax FGs (Guisan et al. 2007). That is to say, pioneer FGs-based patch types, should rarely dominate in the landscape and tended to scatter in the areas that were characterized by barren soils, open, hot and xeric conditions, permanently. Besides FGs interactions, dispersal limitation may constrain FGs-based patch type's distributions. Guisan & Thuiller (2005) indicated that the absence of some species in certain habitats at large ecological scales is mainly caused by dispersal limitations, not by interspecific competitions. The pioneers FGs mainly expand their space by way of wind dispersals. The climax FGs mainly influences dispersals by animal, water or gravity. Thus, the dispersal limitation is more prevalent in climax than in the pioneer FGs. Dispersal limitation might be the main constraint in the formation of FGs-based vegetation mosaic patterns at larger spatial scales.

Conclusions and perspectives for applications

With the present study, we find a practicable approach of reconstructing PNV based on FGs in species rich and fragmented tropical forest landscapes. The results of this study are expected to form a valuable baseline for decision making related to both maintenance and restoration of forest biodiversity in the area. More generally the methodology can be applied to any other forest of the reconstruction of PNV and this can elucidate differences in PNVs by doing forest inter-comparisons across geographical areas. In BNR, forest management has a long tradition of planting trees in abandoned agricultural lands or heavily degraded forest sites. Through this study we showed that, if deforested agricultural lands (or heavily degraded forest sites) are located in the pioneer FGs-dominated patches, managers should introduce pioneer tree species to provide seed sources for near-natural regeneration. Otherwise, if they are located in the climax FGs-dominated patches, managers should first plant pioneer tree species to act as shelter trees permitting climax species saplings to grow, and then pioneer trees are harvested, paying for the restoration effort. This might be a profitable and feasible mechanism to restore degraded habitats in BNR and possibly in other similar areas worldwide. Based on FGs-based PNV, we can also identify potential priority areas for biodiversity conservation in BNR. For example, important conservation areas in BNR are located in the central, north and south parts of the study area, which are dominated by climax FGs-based patch types. Overall, FGs-based PNV allow us to obtain valuable information that could prove useful when designating protected areas or performing functional zoning in the region. The approach used in this study might be extended

into other species rich and damaged forest regions such as the Amazon, so that the FGs-based PNV mosaic maps could be used as basic references in activities concerning biodiversity conservation and vegetation restoration. The dynamical application of the model for the determination of PNVs in time is also very useful for land use planning of future developments, zoning of emerging pathogens related to specific vegetation types, and detection of exotic species introduced from outside the ecosystem.

ACKNOWLEDGMENTS

This work was supported by the National Public Benefit Forest Research Foundation (201104029-01), the National Natural Science Foundation of China (30430570), and Ministry of Science and Technology of China (2008BADB0B02). We thank many local staffs in the BNR, who helped us in conducting the laborious and hard field grid plot investigations. M.C. acknowledges the funding from the NSF award #1114924 (Division of Environmental Biology) Coupled Natural-Human Systems (CNH): "Global Sensitivity and Uncertainty Analysis in the Evaluation of Social-Ecological Resilience: Theoretical Debates Over Infrastructure Impacts on Livelihoods and Forest Change".

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Manuscript received 5 Aug. 2012; accepted in revised version 23 May 2013.

Communicating Editor: Tariq Stévant.