Journal of Vegetation Science **25** (2014) 1257–1266

Transition patterns across an evergreen–deciduous broad-leaved forest ecotone: the effect of topographies

Kun Song, Takashi S. Kohyama & Liang Jun Da

Keywords
Biome boundary; Climate change; Eastern China; Functional traits; Variation partitioning

Abbreviations
CI = Coldness index; DBT = Deciduous broad-leaved species; EBT = Evergreen broad-leaved species; EDF ecotone = Evergreen–deciduous broad-leaved forest ecotone; IV = Relative importance value; WI = Warmth index.

Nomenclature
Catalogue of Life China 2012 Annual Checklist

Received 25 June 2013
Accepted 14 December 2013
Co-ordinating Editor: Otto Wildi

Da, L.J. (corresponding author, (ljda@des.ecnu.edu.cn) &
Song, K. (seceek@ gmail.com): Department of Environmental Science, East China Normal University, Shanghai, 200241, China
Song, K. & **Kohyama, T.S.** (kohyama@ees.hokudai.ac.jp): Faculty of Environmental Earth Science, Hokkaido University, Sapporo, 0600810, Japan
Da, L.J. : Tiantong National Station of Forest Ecosystem, Shanghai, 200241, China

Abstract

Question: Topography has distinct effects on local-scale vegetation distribution by creating heterogeneous habitats. In ecotones, which are sensitive to environmental variation, this effect on vegetation differentiation may be magnified at a regional scale. Here, we evaluate vegetation transition patterns across an evergreen–deciduous broad-leaved forest ecotone (EDF ecotone) in eastern China, to investigate whether the transition pattern differs between two topographic positions with different habitats, and identify underlying environmental mechanisms driving variation in species- and trait-based community structure.

Location: Anhui Province, China.

Methods: Across an EDF ecotone, community data were collected in 47 20 × 20-m plots situated on upper and lower hill slopes. Trait-based community structure was constructed based on seven functional traits and weighted by species abundance. Environmental variables were grouped into three categories: thermal conditions, water availability and edaphic variables. Trends in species richness and dominance along latitude were evaluated for both evergreen broad-leaved species (EBT) and deciduous broad-leaved species (DBT). Variation partitioning analysis was used to distinguish the roles of the three environmental variables in determining transition patterns within the two topographies.

Results: For both EBT and DBT, species richness showed similar transition patterns along the latitudinal gradient on both the upper and the lower slope. However, species dominance changed more abruptly on the upper than on the lower slope. Compared with edaphic variables, both thermal conditions and water availability had a larger impact on transitions across the EDF ecotone, but their relative roles differed between the upper and the lower slopes. Thermal conditions primarily explained the variation in species- and trait-based community structure on the upper slope, while water availability primarily explained variation on the lower slope.

Conclusions: Our results suggest different roles of thermal conditions and water availability in determining transition patterns between the two topographies. Evergreen *Castanopsis* trees, having less cold tolerance, make transitions on the upper slope more sensitive to thermal conditions. *Cyclobalanopsis* trees, which prefer wet habitats, make the transition on the lower slope more sensitive to water availability. Based on the present findings, we predict that the EDF ecotone will become narrower and there will be a sharper boundary between the evergreen and deciduous broad-leaved forests of eastern China under warmer and drier climate conditions.

Doi: 10.1111/jvs.12156

Introduction

A major challenge in plant community ecology is to understand processes determining species composition. It has been widely documented that vegetation types and species composition can be predicted using broad-scale climate-related variables, especially temperature and water availability (Stephenson 1990; Wang et al. 2011). But topography and edaphic conditions control community structure at fine to moderate scales and can predict species distributions more accurately than climatic variables alone (Danz et al. 2011; Piedallu et al. 2012). Ecotones are known as transition areas between two adjacent ecosystems, and are usually narrow relative to their adjacent ecosystems and sensitive to environmental variation, resulting in abrupt spatial transitions in species composition (Danz et al. 2012). Ecotones between forested zones, e.g. deciduous–boreal forest ecotones, are usually controlled via climatic and historical legacies at coarse scales, and topography, soil and disturbance at finer scales (Goldblum & Rigg 2010).

In eastern China, as latitude increases, forests are in gradual transition from rain and monsoon forest to evergreen broad-leaved forest, then to deciduous broad-leaved and finally to coniferous forest. The distributions of these forest types are closely coupled with climate (Hou 1983; Song 1999; Fang et al. 2002). However, controversies over these boundaries between forest zones remain, especially concerning the ecotone between evergreen broad-leaved and deciduous broad-leaved forest (EDF ecotone) (Song 1999; Fang et al. 2002). Previous studies suggest that evergreen broad-leaved forests are limited by temperature in subtropical and warm temperature regions of East Asia, with their northern (upper) boundary defined by three thermal conditions: a warmth index (WI) of 85 °C·mo (sum of monthly mean temperatures above 5 °C), a coldness index (CI) of −10 °C·mo (sum of monthly mean temperatures below 5 °C) and a coldest monthly mean temperature of −1 °C (Ohsawa 1990). But in China the northern boundary of evergreen broad-leaved forest has a CI of nearly −2 °C·mo and 135 °C·mo of WI (Song 1999) and so does not reach the cold temperature limit. Accordingly, it has been suggested that moisture conditions primarily restrict northward distribution of evergreen broad-leaved forests in China (Fang & Yoda 1991; Fang et al. 2002).

Topography is one of the most important factors affecting vegetation patterns within a climatic region. In subtropical or temperate regions of East Asia, hill slopes can usually can be divided into two topographies distinguished by the erosion front and termed upper and the lower slope (Kikuchi & Miura 1993; Hara et al. 1996; Nagamatsu & Miura 1997). The lower slope is formed through dissection and fluvial processes, whereas within the upper slope, denudation is more influential (Nagamatsu & Miura 1997). It is suggested that the erosion front is the line demarcating these two habitats within a slope, from the ridge to the valley bottom (Hara et al. 1996). The lower slope is the water sink of a catchment, and thus usually has higher soil moisture content and nutrient availability (Enoki et al. 1996; Hara et al. 1996; Zhang et al. 2006) with more frequent disturbances (Nagamatsu & Miura 1997) compared to the upper slope. Due to the differing characteristics of the upper and the lower slopes, species composition and forest structure differ, with some species restricted to specific hill slopes (Kikuchi & Miura 1993; Hara et al. 1996; Nagamatsu & Miura 1997; Yang et al. 2005). Near the northern limits of evergreen broad-leaved forests there is a tendency towards increasing dominance of deciduous species, spreading from the upper to the lower slope (Sakai & Ohsawa 1994; Yang et al. 2005).

The EDF ecotone region in this study is dominated by hills and low mountains. Temperature and precipitation gradually decrease with increasing latitude across this ecotone, co-varying with soil properties (e.g. pH, phosphorus; Han et al. 2005; Wang et al. 2011). Because of the pronounced difference in water and soil nutrients between the upper and the lower slopes, we hypothesize that environmental gradients across this ecotone may differ between the two topographies and therefore, as responses, forests on the upper slopes may present distinct transition patterns from those on the lower slopes. Based on well-documented relationships between traits and climate for Chinese woody plants (Han et al. 2005; Zhang et al. 2010, 2011, 2012), we also predict that trait- and species-based community structure will respond similarly to environmental gradients across this ecotone.

To assess these hypotheses, we collected community data, including plant functional trait data, in natural forests at the basal vegetation zone of mountains across the EDF ecotone in eastern China. These data were related to environmental variables, which were grouped into three categories: thermal conditions, water availability and edaphic variables, in order to: (i) test whether the abundance of evergreen and deciduous species differs with increasing latitude between the upper and the lower slopes; and (ii) determine the degree to which species composition and plant functional traits are explained by thermal conditions, water availability and edaphic variables on the upper and the lower slopes.

Methods

Study region

The study was performed in Anhui province (29°22′–34°40′ N, 114°53′–119°30′ E) in eastern China (Appendix S1).

Journal of Vegetation Science
Doi: 10.1111/jvs.12156

Within the study region, climate ranges from warm-temperate to subtropical monsoon, with mean temperature varying from 14 °C to 16 °C and mean annual precipitation from 750 mm to 1700 mm. Most precipitation falls from June to August. Natural forests in this region are restricted to mountainous areas, with zonal vegetation transitioning from evergreen broad-leaved forest in the south to deciduous broad-leaved forest in the north. Therefore, we collected data in three mountain regions: Guniujiang, Dabieshan and Huangcangyu mountains, which are within the evergreen broad-leaved forest, EDF ecotone and deciduous broad-leaved forest, respectively (Editorial Committee for Vegetation of Anhui 1981).

Guniujiang Mountain (30°00′–30°14′ N, 117°20′–117°37′ E) is in the south of Anhui, where the climate is subtropical monsoon; mean temperature is 14.9 °C and mean annual precipitation is 1700 mm at the base of the mountain. The surface soil is yellow-red earth at low altitude and zonal vegetation is evergreen broad-leaved forest (Han 1990; Shen et al. 2007).

Dabieshan Mountain (30°02′–31°55′ N, 114°30′–117°05′ E) is at the junction of Anhui, Hubei and Henan provinces. The mean temperature ranges from 13 °C to 17 °C and annual precipitation is from 1000 mm to 1600 mm (Liu 1993). The surface soil is yellow-brown earth below 800 m a.s.l. (Liu 1993). Zonal vegetation is mixed evergreen and deciduous broad-leaved forest (Editorial Committee for Vegetation of China 1980).

Huangcangyu Mountain (34°00′–34°06′ N, 117°03′–117°06′ E) is the only well-preserved forest area in the north of Anhui. The climate is warm-temperate monsoon, with a mean temperature of 14.5 °C and mean annual precipitation of 800 mm. The surface soil is brown earth, and zonal vegetation is deciduous broad-leaved forest (Xie et al. 1995).

Species composition data

The mountain forests of the study region are structurally and floristically heterogeneous due to micro-topographic variability and human activities. We selected 47 plots, each 20 m × 20 m, on two distinct topographies, upper and lower hill slopes, according to the micro-landform classification of Nagamatsu & Miura (1997), which is relevant to hilly areas of Eastern Asia. Eighteen plots were located on Guniujiang Mountain, 17 on Dabieshan Mountain and 12 on Huangcangyu Mountain. At each site, general information, e.g. altitude, exposure and inclination, was noted for each plot.

Each plot was divided into four subplots. All trees > 1.5-m high were identified and recorded; the DBH (1.5 m above the ground) and height were measured. Cover and maximum height of herb layer species were recorded. Each tree seedling was identified, measured for height and counted for further analyses. The fieldwork was carried out in late April to early November 2010 and 2011.

Relative importance value (IV) was used to measure the species abundance (Curtis & McIntosh 1951), which is the average of relative density, relative frequency and relative basal area at 1.5-m height. The IV of evergreen broad-leaved species (EBT) and deciduous broad-leaved species (DBT) was calculated for each plot. For variation partitioning analysis of species composition and functional traits (see below), rare species were excluded. Rarity was determined using two criteria: (1) species with maximum IV <5% for all plots; (2) species with frequency <5%.

Functional traits data

We included seven functional traits in the analysis: wood density ($g{\cdot}cm^{-3}$), leaf life span (years), leaf N content per dry mass ($mg{\cdot}g^{-1}$), leaf phosphorus content per dry mass ($mg{\cdot}g^{-1}$), leaf area (cm^2), specific leaf area ($cm^2{\cdot}g^{-1}$) and leaf dry matter content (%). The variation with latitude in the first four traits, as well as their correlation with climate in China, has been documented (Han et al. 2005; Zhang et al. 2010, 2011, 2012). Leaf area and specific leaf area correlate with soil fertility and water availability in many cases (Cornelissen et al. 2003). Additionally, leaves with higher leaf dry matter content tend to have thicker and more rigid cell walls, which enables the maintenance of turgor at lower leaf water potentials and thus they can resist cavitation caused by drought or freezing (Markesteijn et al. 2011).

Leaf traits of 42 species were measured during the 2010 and 2011 growing seasons. For each species, three to seven mature individuals were sampled by collecting three to five branches from the upper canopy. For evergreen species, according to bud scales, leaves were divided into different ages and counted to establish a static life table for each branch, and leaf life span was calculated as average life expectancy based on the static life table (Kikuzawa & Lechowicz 2011). Branch data for leaf life span were averaged for each individual and then for each species. For deciduous species, leaf life span was determined from leafing and defoliation times according to local records.

On average, 20 (range: 5–107) intact leaves were selected from each individual tree for leaf area and fresh weight measurements. Leaf area was determined by scanning leaves using a flatbed scanner and analysing the pictures with ImageJ software (Schneider et al. 2012). Samples were oven-dried at 70 °C for 48–72 h to constant weight, and dry weights recorded. The dried leaves were ground and digested with H_2SO_4–$HClO_4$. Leaf N/P concentration was determined using a flow-injection auto-analyser (Skalar, NL). Wood density of 25 species was measured in autumn 2011. For each species, three to five individuals were cored at the stem base. Fresh volume was measured as water displacement. After oven-drying at 60 °C for 4 d, wood density was calculated as oven dry mass/fresh volume. Individual data for each functional trait of each species were averaged.

Because only 60% of species used for variation partitioning analysis were measured in the field, we also collected functional trait data for those species not measured. Data measured in the same climate region and in the same forest types as in our study were selected from published papers (Han et al. 2005; Zhang et al. 2010, 2011, 2012). We also used functional trait data measured in Mt. Tianmu (30°18′–30°21′ N, 119°24′–119°27′ E; Shang KK, Da LJ, unpublished data), which is close to the EDF ecotone. In order to identify systematic differences between variables measured in the field and those taken from the literature, we also collected the functional trait data of measured species from the same data sources and correlated their mean values with our measured data. The results showed high positive correlations between our measured data and the mean value of collected data, with linear slopes ranging from 0.54 to 1.46 (Appendix S2). Hence, mean value for collected data was transformed using the above linear correlations to represent species values for unmeasured species.

For each trait in each plot, we calculated the abundance-weighted mean trait value using the species mean values. These weighted mean values were necessary for redundancy analysis of variation partitioning, to detect community-level relationships between traits and environmental influences (Kleyer et al. 2012). Plot-based values of traits were standardized from 0 to 1 in order to control for differences in variance and units of measurement among traits.

Environmental data

Four edaphic variables were measured: pH, soil organic matter content (%), total N ($mg{\cdot}g^{-1}$), total P ($mg{\cdot}g^{-1}$). Soil samples were collected from the upper mineral layer (0–20 cm depth) of four subplots per plot. These samples were then air-dried and divided into two subsamples. One subsample was sieved to 2 mm for soil organic matter content, which was determined following the oil bath–K_2CrO_7 titration method, and pH was determined using a Mettler-143 Toledo pH meter (1:2, H_2O). The other subsample was sieved to 0.25 mm to measure total N (Kjeldahl), and total P concentration (chloro-molybdophosphonic blue colour method). Total N and total P concentrations were determined using a flow-injection auto-analyser (Skalar, NL). Additionally, slope was included in edaphic variables for variation partitioning analysis.

Fifteen climate variables, which have previously been shown to correlate with forest or woody plant distribution in East Asia, were used in the analysis (Ohsawa 1990; Fang & Yoda 1991; Wang et al. 2011). All climatic variables were grouped into two categories: (1) thermal conditions, including mean annual temperature (°C), mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), annual range of temperature (°C), seasonality of temperature (SD of mean monthly temperature), potential evapotranspiration (mm), minimum monthly potential evapotranspiration (mm), warmth index (°C), coldness index (°C); and (2) water availability, including mean annual precipitation (mm), precipitation of the driest quarter (mm), seasonality of precipitation (coefficient of variation of mean monthly precipitation), annual evapotranspiration (mm), moisture index, annual water deficit (mm). The first five variables of thermal conditions and the first three variables of water availability were extracted for each plot from the WorldClim database, with a spatial resolution of 30 arc-sec (Hijmans et al. 2005). The other variables were calculated based on monthly data extracted from WorldClim, following the methods described in Wang et al. (2011).

Data analysis

To examine transition patterns across the EDF ecotone on the two topographies, we conducted regression analyses, in which richness and IV of EBT and DBT were response variables and latitude was explanatory variable, by fitting ordinary linear regression, second-order polynomial regression and exponential regression models. Akaike's information criterion (AIC) was calculated to select best-fit models.

Variation partitioning (Borcard et al. 1992) was used to determine the degree to which species-based and functional trait-based community structure were explained by thermal conditions, water availability and edaphic variables. First, PCA were used to reduce the dimensionality of the three environmental matrices, as well as to avoid multicollinearity among variable suites (Legendre & Legendre 1998). Then, we used forward selection (Blanchet et al. 2008) to generate more parsimonious sets of explanatory variables generated by PCA. We ran separate models of forward selection and variance partitioning for IV of EBT and DBT, species composition and plot-based functional traits. The amount of variance explained by each component was estimated using adjusted R^2 values, and the significance of components was determined using permutation tests (Peres-Neto et al. 2006). Species composition data and functional trait data were Hellinger-transformed prior to the variation partitioning analysis (Legendre & Gallagher 2001). Variance partitioning analysis of thermal

Doi: 10.1111/jvs.12156

conditions, water availability and edaphic variables showed that the latter variables explained much less variation than climate, but a similar proportion of variation at the upper and lower slopes (Appendix S3). Therefore, we focused on variance partitioning results for thermal conditions and water availability as explanatory variables. The results of these permutation tests are shown in Appendix S4.

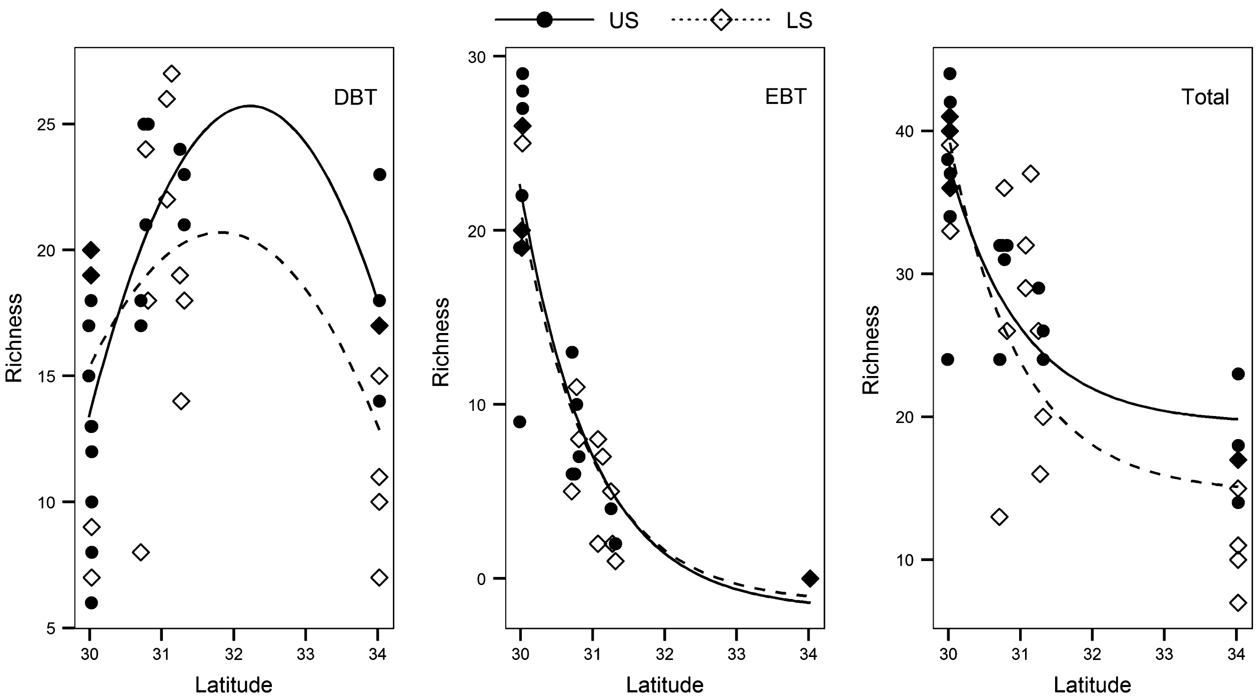
All analyses were performed in R (R Foundation for Statistical Computing, Vienna, AT). The variance partitioning and tests of significance of components were conducted using the 'vegan' package and forward selection was conducted using the 'packfor' package.

Results

Transition patterns

In total, 198 species of woody plant, of which 68 species (34.3%) were EBT, 127 species (64.1%) were DBT and three species (1.6%) were evergreen conifer, were recorded in this study. EBT richness decreased dramatically with increasing latitude on both the upper and lower hill slopes. On the other hand, DBT richness showed bell-shaped latitudinal gradients on both topographies but was larger on the upper slope at progressively higher latitudes. Therefore, the decrease in rate of total richness with increasing latitude was larger on the lower slope than on the upper slope (Fig. 1). The relative importance value of EBT decreased strongly on the upper but not the lower slope near 31° N, which is near the southern boundary of the EDF ecotone. On the other hand, the relative importance value of DBT increased strongly on the upper but not the lower slope near 31° N (Fig. 2).

Variations in community species composition with increasing latitude were also different on the two topographies, especially for the dominant species (Fig. 3). On the upper slope, the dominant *Castanopsis* species (*C. eyrei*, *C. sclerophylla*) were replaced by the deciduous species *Quercus variabilis*. On the lower slope, the dominant *Castanopsis* species were replaced by *Cyclobalanopsis* species *(C. glauca*, *C. myrsinifolia*) and then replaced by deciduous species such as *Pteroceltis tatarinowii* and *Tilia miqueliana.* The

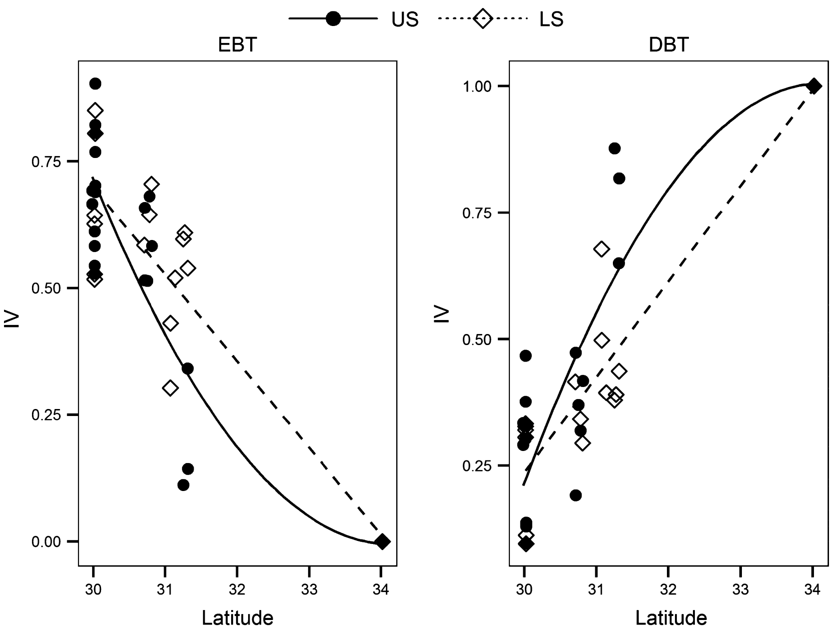


Topography:model	AIC	R squared
US:Linear model	156.2	0.07
US:Exponential model	150.0	0.28
US:Quadratic model	142.9	0.50
LS:Linear model	143.0	0.10
LS:Exponential model	140.7	0.01
LS:Quadratic model	140.2	0.26

Topography:model	AIC	R squared
US:Linear model	170.2	0.61
US:Exponential model	149.2	0.85
US:Quadratic model	149.2	0.83
LS:Linear model	142.2	0.63
LS:Exponential model	106.9	0.93
LS:Quadratic model	108.1	0.92

Topography:model	AIC	R squared
US:Linear model	151.6	0.72
US:Exponential model	149.6	0.76
US:Quadratic model	151.1	0.73
LS:Linear model	148.4	0.70
LS:Exponential model	147.1	0.74
LS:Quadratic model	148.1	0.70

Fig. 1. Variation in woody species richness with latitude on the upper slope (US) and the lower slope (LS) for deciduous (DBT), evergreen (EBT) and all broad-leaved species. Exponential regression models best describe the richness–latitude relationship for the EBT and all broad-leaved species, except for DBT, which was best described with a quadratic model.



Topography:model	AIC	R squared
US:Linear model	−21.0	0.80
US:Exponential model	−17.3	0.78
US:Quadratic model	−24.5	0.85
LS:Linear model	−39.9	0.93
LS:Exponential model	−8.7	0.71
LS:Quadratic model	−38.2	0.93

Topography:model	AIC	R squared
US:Linear model	−25.4	0.81
US:Exponential model	−21.7	0.78
US:Quadratic model	−28.8	0.85
LS:Linear model	−33.0	0.89
LS:Exponential model	−6.9	0.63
LS:Quadratic model	−32.5	0.90

Fig. 2. Variation in relative importance value (IV) with latitude on the upper slope (US) and the lower slope (LS) for evergreen (EBT) and deciduous (DBT) broad-leaved species. For both EBT and DBT, second-order polynomial regression models best describe the IV–latitude relationship for US and ordinary linear regression models were best for LS.

evergreen–deciduous replacement of dominant species among sites >300 m a.s.l. exceeded the rate among sites <300 m a.s.l., with a south to north tendency (Fig. 3).

Variation partitioning

The total variation explained by the model that included thermal conditions and water availability ranged from 57.0% to 96.8% in all cases. The shared contributions of thermal conditions and water availability (fraction c in Fig. 4) were smaller than contributions independently explained by thermal conditions or water availability.

For species composition, the relative importance value of EBT and DBT, and plot-based functional traits, thermal conditions independently explained 50.9%, 86.0%, 86.7% and 57.3% on the upper slope, respectively (fraction a in Fig. 4), which were all higher than the respective proportions explained on the lower slope. On the lower slope, however, water availability independently explained 27.5%, 76.3%, 91.2% and 42.4%, respectively, all values being higher than proportions explained on the upper slope (fraction b in Fig. 4). On the upper slope, thermal conditions explained more than water availability in all cases. Conversely, water availability explained more than thermal conditions on the lower slope, except for species composition, for which both explained ca. 28%. These results indicate that thermal conditions predominantly explained the transition pattern on the upper slope, whether assessed according to species- or functional trait-based community structure. In contrast, water availability explained more on the lower slope.

Discussion

Topography affects local-scale vegetation distribution by creating heterogeneous habitats (Kikuchi & Miura 1993; Hara et al. 1996; Nagamatsu & Miura 1997; Yang et al. 2005; Broll et al. 2007; Martin et al. 2007). Ecotones, where vegetation is usually sensitive to environmental change (Martin et al. 2007; Danz et al. 2012), may increase the effect of topography on regional-scale vegetation distribution. However, few studies have evaluated the effect of topography on transition patterns across eco-regions. We tested the hypothesis that transition patterns across the EDF ecotone would differ between upper and lower hill slope topography in eastern China. Our results

Journal of Vegetation Science
Doi: 10.1111/jvs.12156

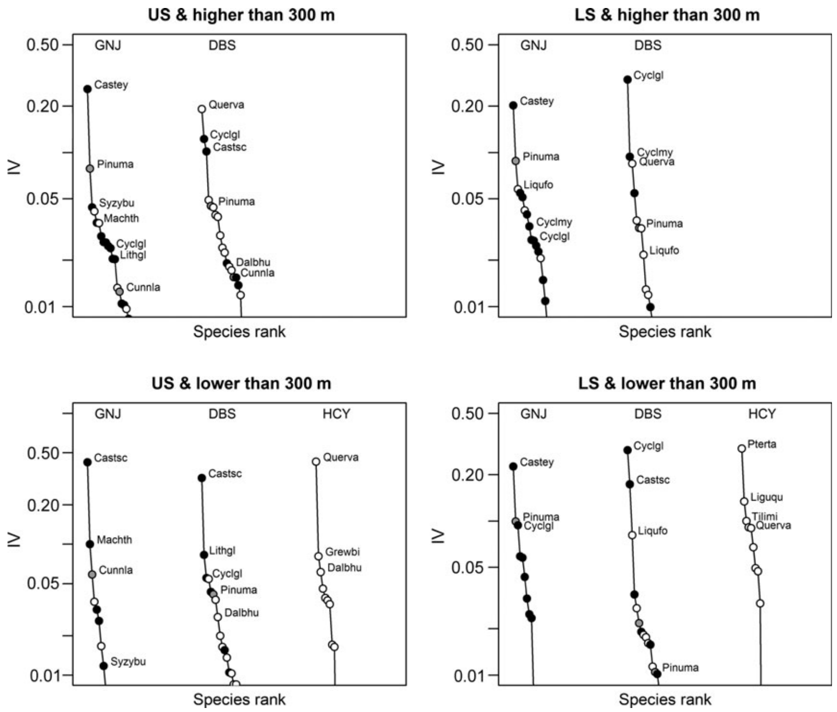


Fig. 3. Rank–IV diagram of common species (IV > 0.01) for different topographies and altitudes in Guniujiang (GNJ), Dabieshan (DBS) and Huangcangyu (HCY) mountains. All plots in HCY are <300 m a.s.l. Evergreen broad-leaved species (EBT): black circles, deciduous broad-leaved species (DBT): open circles, and evergreen conifers: grey circles. EBT includes: *Castanopsis eyrei* (Castey), *C. sclerophylla* (Castsc), *Cyclobalanopsis glauca* (Cyclgl), *C. myrsinifolia* (Cyclmy), *Lithocarpus glaber* (Lithgl), *Machilus thunbergii* (Machth), *Syzygium buxifolium* (Syzybu). DBT includes: *Dalbergia hupeana* (Dalbhu), *Grewia biloba* (Grewbi), *Ligustrum quihoui* (Liguqu), *Liquidambar formosana* (Liqufo), *Pteroceltis tatarinowii* (Pterta), *Quercus variabilis* (Querva), *Tilia miqueliana* (Tilimi). Evergreen conifers include: *Pinus massoniana* (Pinuma), *Cunninghamia lanceolata* (Cunnla).

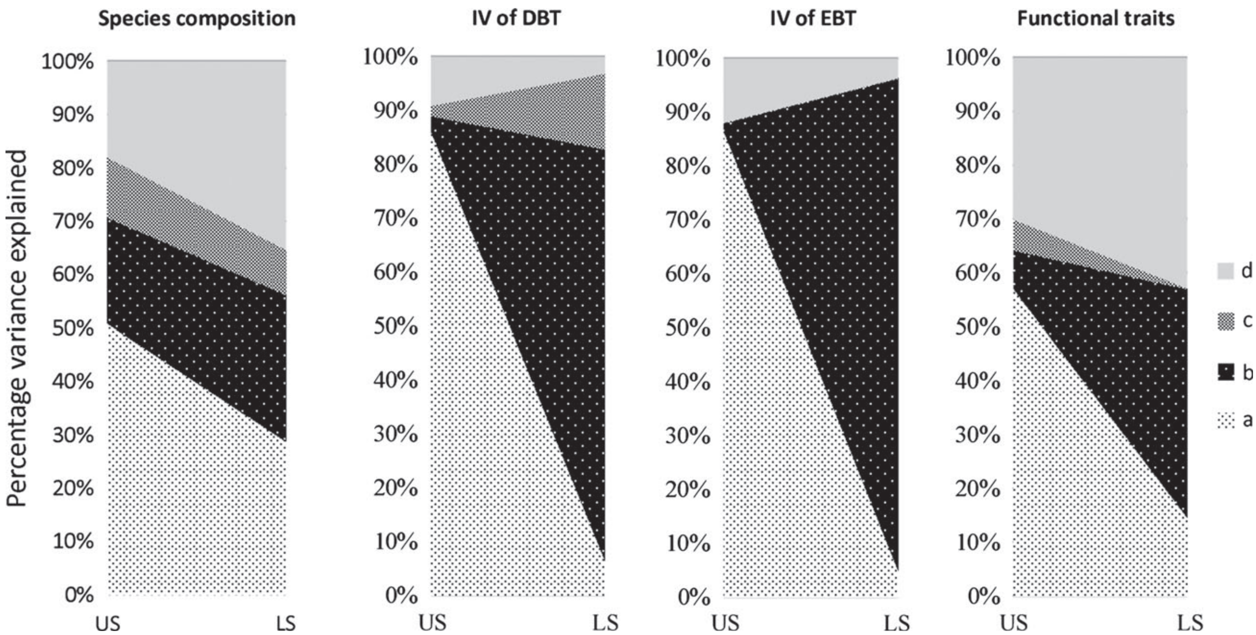


Fig. 4. Results of variance partitioning of species composition, relative importance value (IV) of evergreen (EBT) and deciduous (DBT) broad-leaved species, and plot-based functional traits. Fractions of partitioning analysis show the percentage of variation explained by measures of (a) thermal conditions; (b) water availability; (c) combination of thermal conditions and water availability; and (d) residual unexplained variance.

show the transition of EBT and DBT dominance across the EDF ecotone and variables that explain the transition patterns differed between upper and lower slope plots, with a more abrupt change primarily explained by thermal conditions on the upper slope and a gradual change conditioned by water availability on the lower slope.

Previous studies concluded that cold temperatures or climatic water variables primarily determined the northern extent of evergreen broad-leaved forest (Ohsawa 1990; Song 1999; Fang et al. 2002). In contrast, we concluded that both thermal conditions and water availability greatly impact forest transitions across the EDF ecotone, but their relative roles differed between the upper and lower slopes. Thermal condition was the best predictor of variations in species- and functional trait-based community structure on the upper slope, and water availability was the key variable on the lower slope. This was also confirmed by the different evergreen–deciduous replacements on the two slope types from the point of view of dominant species. The drought-tolerant dominant evergreen *Castanopsis* was replaced by deciduous species on the dry upper slopes, while the cold-tolerant *Cyclobalanopsis* was replaced by deciduous species on the wet lower slope. Deng et al. (1985) found that the lowest CI tolerated by *Cyclobalanopsis glauca* and *Castanopsis sclerophylla* in eastern China was near −15 °C·mo, and > −8 °C·mo, respectively. The northern distribution of *Castanopsis* trees was defined by a coldest monthly mean temperature of 2 °C (cited in Ohsawa et al. 1985), compared to −1 °C for *Cyclobalanopsis*-dominated evergreen broad-leaved forest in East Asia (Ohsawa 1990). These limitations indicate that *Castanopsis* species are sensitive to variations in thermal conditions across the EDF ecotone, where they exist near the limit of their cold tolerance. With respect to the more cold-tolerant *Cyclobalanopsis*, however, the climate of even the northernmost sites studied here (Huangcangyu Mountain) was within the cold tolerance limits of this species. *Cyclobalanopsis* species were usually dominant in wet valleys or near rivers and lakes in the EDF ecotone (Deng et al. 1985), which suggests that they prefer wet habitats and are sensitive to variations in water availability.

We therefore conclude that species–habitat associations cause the variation in transition patterns among topographies across the EDF ecotone, which is a widespread occurrence in nature. In the prairie–forest boundary of Minnesota, climatic water availability explained most variance in occurrence of prairie vs woody vegetation (Danz et al. 2011). Although *Populus tremuloides* is a relatively drought-intolerant tree, it can grow in regions of lower climatic water availability in northwestern Minnesota due to its preference for wet depressions (Danz et al. 2012). Conversely, *Quercus macrocarpa*, a relatively drought-tolerant tree, is restricted to southeast Minnesota where climatic water availability is high, due to its preference for well-drained, south-facing slopes (Danz et al. 2012). In the tree line ecotone of subarctic Finland, mountain birch forests (*Betula pubescens* subsp. *czerepanovii*) become increasingly scattered at 240–300 m a.s.l on dry, wind-swept landscapes, but within wet valleys and on wind-sheltered slopes tree groves (mainly *Empetrum* sp., *Betula nana*, *Vaccinium uliginosum* and *V. myrtillus*) occur at up to ca. 370 m a.s.l. (Broll et al. 2007). In the tropical montane forest ecotone, cloud forests composed of broad-leaved trees are limited to the lower warm zone and attain maximum elevation in humid gullies, while mono-dominant pine forest prevails from the higher cold zone to the lowest elevation on dry ridges (Martin et al. 2007). The primary mechanisms underlying diverse transition patterns across climatic ecotones appear to be variability in soil water content or humidity among topographies, together with soil fertility and fire regime.

According to variance partitioning analysis, although the climate explains more than 90% of the variation in dominance of EBT and DBT in our study, it was less important in explaining species composition and plot-based functional traits, especially on the lower hill slopes where climate explained no more than 60% of the variation (Fig. 3). Even the combination of climate and edaphic factors only increased the explained variance in plot-based functional traits by 9% and 5% for the upper and lower slopes, respectively, compared to the variance explained by climate alone (Appendix S3). We hypothesize that the unexplained residuals were associated with soil water balance. On the upper slope, soil moisture was dependent on actual precipitation due to high or excessive drainage and serious erosion (Broll et al. 2007). In contrast, high water content of the lower slope soil is likely maintained by continuous subsurface run-off in forested regions (Enoki et al. 1996; Hara et al. 1996). Therefore, compared with predictions for the upper slope, climatic proxies were poor predictors for the lower slope, with abundant water-dependent species, which are likely better predicted from available water and soil water balance measurements (Piedallu et al. 2012). Furthermore, temperature and disturbance regimes vary among topographies (Nagamatsu & Miura 1997; Lenoir et al. 2013) and thus also likely contributed to the unexplained residuals.

Undoubtedly, the geographic limits of the EDF ecotone are coupled with variations in climate. Over the past 5000 yr, EDF ecotone boundaries have varied with climate, with the southern boundary at 35° N during the warmest periods and approaching 29° N during the coldest periods (Liu 1992). Current trends of increasing temperature in eastern China (Ge et al. 2011) favour evergreen broad-leaved trees, but heterogeneous habitats, supported

Doi: 10.1111/jvs.12156

by topographic differences, increase local spatial buffering of climate warming effects on species distributions (Scherrer & Körner 2011; Lenoir et al. 2013). On the other hand, climate change-induced drought stress has reduced the ecological resilience of subtropical evergreen broad-leaved forests (Zhou et al. 2013) and reduced their vegetative activity (Wu et al. 2009). Therefore, for the EDF ecotone, it seems that the transition pattern on the upper hill slope, which was highly influenced by thermal conditions, will continue to shift northward. Conversely, the transition pattern on the lower hill slope, which is dependent on water availability, will be more sensitive to drought and, therefore, likely shift southward with increasing temperature in eastern China. We predict these differing effects of warming on the upper and lower slopes will result in a narrowing of the EDF ecotone, producing a sharper boundary between the evergreen and deciduous broad-leaved forests in eastern China under a warmer and drier climate.

Acknowledgements

The authors are grateful for comments from Han Ye-Liang, plant identification of Wang Wen-Ge and field assistance of Yu Qian, Sun Wen, Shang Kan-Kan and Wang Jie. We also thank the editor Otto Wildi and two anonymous referees for constructive comments. We acknowledge the help of Wang Zhi-Heng (University of Copenhagen) for calculating climate indices. We would also like to thank Cindy Q. Tang (Yunnan University) and Christine Verhille (University of California, Davis) for assistance with English language and grammatical editing of the manuscript. This study was funded by the '211 Project' of the key academic discipline program of ECNU and the National Natural Science Foundation of China (40971041).

References

Blanchet, F.G., Legendre, P. & Borcard, D. 2008. Forward selection of explanatory variables. *Ecology* 89: 2623–2632.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

Broll, G., Holtmeier, F., Anschlag, K., Brauckmann, H.O.R., Wald, S. & Drees, B. 2007. Landscape mosaic in the treeline ecotone on Mt Rodjanoaivi, Subarctic Finland. *Fennia* 185: 89–105.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., (…) & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Curtis, J.T. & McIntosh, R.P. 1951. An upland forest continuum in the prairie–forest border region of Wisconsin. *Ecology* 32: 476–496.

Danz, N.P., Reich, P.B., Frelich, L.E. & Niemi, G.J. 2011. Vegetation controls vary across space and spatial scale in a historic grassland–forest biome boundary. *Ecography* 34: 402–414.

Danz, N.P., Frelich, L.E., Reich, P.B. & Niemi, G.J. 2012. Do vegetation boundaries display smooth or abrupt spatial transitions along environmental gradients? Evidence from the prairie–forest biome boundary of historic Minnesota, USA. *Journal of Vegetation Science* 24: 1129–1140.

Deng, M., Wei, H. & Yao, G. 1985. Evergreen plants and evergreen broad-leaved forests in Huoshan and Jinzhai counties of the Dabie mountain region. *Acta Phytoecologica et Geobotanica Sinica* 9: 142–149.

Editorial Committee for Vegetation of Anhui. 1981. *Vegetation of Anhui*. Anhui Science and Technology Press, Hefei, CN.

Editorial Committee for Vegetation of China. 1980. *Vegetation of China*. Science Press, Beijing, CN.

Enoki, T., Kawaguchi, H. & Iwatsubo, G. 1996. Topographic variations of soil properties and stand structure in a *Pinus thunbergii* plantation. *Ecological Research* 11: 299–309.

Fang, J.Y. & Yoda, K. 1991. Climate and vegetation in China (5). Effect of climatic factors on the upper limit of distribution of evergreen broadleaf forest. *Ecological Research* 6: 113–125.

Fang, J.Y., Song, Y.C., Liu, H.Y. & Piao, S.L. 2002. Vegetation–climate relationship and its application in the division of vegetation zone in China. *Acta Botanica Sinica* 44: 1105–1122.

Ge, Q.S., Dai, J.H., Zheng, J.Y., Bai, J., Zhong, S.Y., Wang, H.J. & Wang, W.C. 2011. Advances in first bloom dates and increased occurrences of yearly second blooms in eastern China since the 1960s: further phenological evidence of climate warming. *Ecological Research* 26: 713–723.

Goldblum, D. & Rigg, L.S. 2010. The Deciduous Forest-Boreal Forest Ecotone. *Geography Compass* 4: 701–717.

Han, Y.L. 1990. *Scientific survey of the Guniujiang natural reserve*. China Expectation Press, Beijing, CN.

Han, W., Fang, J., Guo, D. & Zhang, Y. 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist* 168: 377–385.

Hara, M., Hirata, K., Fujihara, M. & Oono, K. 1996. Vegetation structure in relation to micro-landform in an evergreen broad-leaved forest on Amami Ohshima Island, south-west Japan. *Ecological Research* 11: 325–337.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hou, H.Y. 1983. Vegetation of China with reference to its geographical-distribution. *Annals of the Missouri Botanical Garden* 70: 509–548.

Kikuchi, T. & Miura, O. 1993. Vegetation patterns in relation to microscale landforms in hilly land regions. *Vegetatio* 106: 147–154.

Kikuzawa, K. & Lechowicz, M. 2011. *Ecology of leaf longevity*. Springer, New York, NY, US.

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. 2012. Assessing species and

community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23: 805–821.
Legendre, P. & Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.
Legendre, P. & Legendre, L. 1998. *Numerical ecology*, 2nd edn. Elsevier, Amsterdam, NL.
Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G., Bergendorff, C., Birks, H.J.B., Bråthen, K.A., (…) & Svenning, J. 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology* 19: 1470–1481.
Liu, B. 1992. *A study on evergreen and deciduous broadleaved mixed forest of China*. PhD Thesis, East China Normal University, Shanghai, CN.
Liu, P. 1993. A study on the flora of the Dabeishan and the interrelationship between the southern and the northern slope. *Guihaia* 13: 225–233.
Markesteijn, L., Poorter, L., Paz, H., Sack, L. & Bongers, F. 2011. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment* 34: 137–148.
Martin, P.H., Sherman, R.E. & Fahey, T.J. 2007. Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *Journal of Biogeography* 34: 1792–1806.
Nagamatsu, D. & Miura, O. 1997. Soil disturbance regime in relation to micro-scale landforms and its effects on vegetation structure in a hilly area in Japan. *Plant Ecology* 133: 191–200.
Ohsawa, M. 1990. An Interpretation of Latitudinal Patterns of Forest Limits in South and East Asian Mountains. *Journal of Ecology* 78: 326–339.
Ohsawa, M., Nainggolan, P.H.J., Tanaka, N. & Anwar, C. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of East Asia. *Journal of Tropical Ecology* 1: 193–216.
Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.
Piedallu, C., Gégout, J., Perez, V., Lebourgeois, F. & Field, R. 2012. Soil water balance performs better than climatic water variables in tree species distribution modelling. *Global Ecology and Biogeography* 22: 470–482.
Sakai, A. & Ohsawa, M. 1994. Topographical pattern of the forest vegetation on a river basin in a warm-temperate hilly region, central Japan. *Ecological Research* 9: 269–280.
Scherrer, D. & Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38: 406–416.
Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.
Shen, Z.H., Hu, Z.W., Zhao, J. & Wang, H. 2007. Altitudinal patterns of plant diversity on Mt Guniujiang, Anhui, China – with a discussion on the ecological impacts of hilltop condition. *Journal of Mountain Science* 25: 160–168.
Song, Y.C. 1999. Perspective of the vegetation zonation of forest region in Eastern China. *Acta Botanica Sinica* 41: 92–103.
Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water-balance. *The American Naturalist* 135: 649–670.
Wang, Z.H., Fang, J.Y., Tang, Z.Y. & Lin, X. 2011. Patterns, determinants and models of woody plant diversity in China. *Proceedings of the Royal Society B-Biological Sciences* 278: 2122–2132.
Wu, X.C., Liu, H.Y., Ren, J., He, S.Y. & Zhang, Y.K. 2009. Water-dominated vegetation activity across biomes in mid-latitudinal eastern China. *Geophysical Research Letters* 36: L04402.
Xie, Z.W., Cai, Y.L., Zhou, L.L. & Zhang, F.L. 1995. The flora and forest vegetation of Huangcangyu nature reserve, Anhui province. *Journal of Wuhan Botanical Research* 13: 310–316.
Yang, Y.C., Da, L.J. & You, W.H. 2005. Vegetation structure in relation to micro-landform in Tiantong National Forest Park, Zhejiang, China. *Acta Ecologica Sinica* 25: 38–48.
Zhang, M., Xie, Z., Xiong, G. & Zhang, J. 2006. Variation of soil nutrition in a *Fagus engleriana* Seem.- *Cyclobalanopsis oxyodon* Oerst. Community over a small scale in the Shennongjia area, China. *Journal of Integrative Plant Biology* 48: 767–777.
Zhang, L., Luo, T., Zhu, H., Daly, C. & Deng, K. 2010. Leaf life span as a simple predictor of evergreen forest zonation in China. *Journal of Biogeography* 37: 27–36.
Zhang, S., Slik, J.W.F., Zhang, J. & Cao, K. 2011. Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Global Ecology and Biogeography* 20: 241–250.
Zhang, S., Zhang, J., Slik, J.W.F. & Cao, K. 2012. Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment. *Global Ecology and Biogeography* 21: 809–818.
Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., Liu, J., Yan, J., Zhang, D. & Chu, G. 2013. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. *Global Change Biology* 19: 1197–1210.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Map showing the study region.

Appendix S2. Correlation between measured data and mean value of other data sources for functional traits.

Appendix S3. Results of variance partitioning using thermal conditions, water availability and edaphic variables for explanation.

Appendix S4. Results of permutation test of variance partitioning analysis using thermal conditions and water availability as explanatory variables.