

Species–habitat associations and demographic rates of forest trees

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Niche-driven effects on demographic processes generated in response to habitat heterogeneity partly shape local distributions of species. Thus, tree distributions are commonly studied in relation to habitat conditions to understand how niche differentiation contributes to species coexistence in forest communities. Many such studies implicitly assume that local abundance reflects habitat suitability, and that abundance is relatively stable over time. We compared models based on abundance with those based on demographic performance for making inferences about habitat association for 287 tree species from three large dynamic plots located in tropical, subtropical and temperate forests. The correlation between the predictions of the abundance-based models and the demography-based models varied widely, with correlation coefficients ranging nearly from -1 to 1 . This suggests that the two types of models capture different information about species–habitat associations. Demography-based models evaluate habitat quality by focusing on population processes and thus should be preferred for understanding responses of tree species to habitat conditions, especially when habitat conditions are changing and species–habitat interactions cannot be considered to be at equilibrium.

Ecologists have long studied species distributions in relation to habitat conditions to understand how population processes affect biodiversity through niche differentiation (Hubbell and Foster 1986, Harms et al. 2001, Legendre et al. 2005, Comita et al. 2007, Wang et al. 2009). In such studies, abundance observed at one point in time is generally assumed to be the equilibrium outcome of interactions of species and habitat conditions (Hubbell and Foster 1986, Harms et al. 2001, Legendre et al. 2005, Comita et al. 2007, Wang et al. 2009). However, all natural forests deviate from equilibrium to some degree due to extreme climate or weather events (Condit et al. 2004, Man et al. 2011) and other disturbances, such as insect outbreaks (Johnson et al. 2010, Nelson et al. 2013), wind damage (Zeng et al. 2009, Uriarte et al. 2012) and forest fires (Senici et al. 2010, Alencar et al. 2011, Morton et al. 2013). Because the equilibrium assumption is unlikely to reflect the dynamics of many forest communities, it is useful to consider the extent to which simple data about abundance adequately represents the overall performance of tree species populations and thus adequately indicates species niche.

Numerous factors, both abiotic and biotic, can influence abundance. One widely noted factor is the vagary of dispersal. On one hand a species may be rare or absent from a highly suitable habitat simply because its propagules fail to arrive, while on the other hand, a species can be abundant even in an unsuitable habitat if there is persistent influx of

propagules (Pulliam 2000, Zuidema et al. 2010). In addition, a species may not sustain a viable population even in optimal habitat because of intrinsic demographic properties, such as Allee effects or over compensatory dynamics (Lamont et al. 1993, Groom 1998). Biotic interactions can also influence local abundance through density-dependent effects driven by resource competition (Tilman 2004, Zurell et al. 2014) or species-specific pests and pathogens (Janzen 1970, Connell 1971). Recent studies conducted in large-scale forest dynamic plots indicate that biotic neighborhood interactions are widespread in forests (Lin et al. 2012, Wang et al. 2012). The fact that abundance is subject to the effects of so many factors suggests that abundance will be unreliable as a metric to describe associations between species and habitats, and furthermore, that reliance on simple abundance data could lead to inaccurate estimates of species niches (Schurr et al. 2012).

The recent availability of multiple repeated censuses of permanent forest plots (Condit et al. 1999, Wang et al. 2012, Shen et al. 2013) presents an opportunity to test the usefulness and reliability of abundance-based species–habitat models against more mechanistic, demography-based models (Schurr et al. 2012). We hypothesize that these latter models, which are based on a measure of overall demographic performance, will more reliably reveal effects of habitat conditions on species performance than those based on abundance (Clark et al. 2003, Lasky et al.

2013). There are two lines of support for this argument: 1) demography-based models are an integrated outcome of three vital rates (survival, growth and recruitment), not a single measure such as abundance that can be affected by factors other than on-site performance, and 2) demographic rates are calculated from observations of at least two times of a period, rather than from single-time observations as in surveys of abundance. Therefore, correlating demographic performance with habitat variables should be more suitable for understanding niche differentiation among coexisting species than relying on correlations with abundance (Schurr et al. 2012, Lasky et al. 2013).

In our study, we embrace the original definition of niche given by Hutchinson (1957), i.e. the collective biotic and abiotic conditions that allow populations of a species to persist. Although we have focused mainly on abiotic conditions, as have many niche studies of forest trees (Harms et al. 2001, Legendre et al. 2005, Wang et al. 2009), our demography-based models incorporate effects of both conspecific and heterospecific neighbors, thus taking biotic interaction into account. We compare inferences about species–habitat associations based on outputs from traditional abundance-based models with those from demography-based models based on repeated census.

Material and methods

Study sites

We studied species–habitat associations for forest trees in three large forest dynamics plots (Table 1). They were a 50 ha tropical forest plot on Barro Colorado Island (BCI) in Panama, a 20 ha subtropical forest plot located in Dinghushan Nature Reserve (DHS) in southern China, and a 25 ha temperate forest plot in Changbaishan Nature Reserve (CBS) in northeastern China. We used detailed data about topographic and edaphic variables collected at each plot to characterize habitats (Table 1). Topographic variables were calculated from the elevations measured at the nodes of 20 × 20 m grid system following the approach of Harms et al. (2001). Edaphic variables were measured from soil samples that were taken in 2003 in BCI (John et al. 2007) and in 2007 in both DHS (Lin et al. 2013) and CBS (Yuan et al. 2011).

In each plot, each stem with diameter at breast height (DBH) ≥ 1 cm was measured, tagged and identified to species, and its location was mapped.

Each plot is re-censused every 5 yr after establishment. At the time of re-census, death and recruitment are recorded and all stems are re-measured for DBH. A total of seven censuses have been conducted on the BCI plot (1981–1983, 1985, 1990, 1995, 2000, 2005, and 2010). The DHS and CBS plots were established, respectively, in 2005 and 2004, and subsequently re-censused in 2010 and 2009.

Selection of censuses and species for study

We used data from two complete censuses separated by five-year intervals at each plot. For the DHS and CBS plots we used the data from the only two censuses available while for the BCI plot we used the 2005 and 2010 censuses to avoid including the extreme disturbance effects of strong El Niño events in 1983 and 1997 (Condit et al. 2004).

Our analysis was restricted to species present in at least 30 quadrats at the initial census, so as to ensure sufficient sample sizes for reliable demographic analysis. As is typical in species–habitat association studies (Harms et al. 2001, Losos and Leigh 2004, Wang et al. 2009), all data were aggregated into 20 × 20 m quadrats. All analyses were done using R 3.0.3 (R Core Team).

Calculating demographic rates and abundance

We calculated quadrat-specific recruitment, basal area growth and survival as defined below in Eq. (1) through (4), using data about abundance (i.e. the number of individuals of species recorded within each 20 × 20 m quadrat), diameter and status (alive or dead) from the two successive censuses.

Recruitment rate (r) of a species in a quadrat was calculated following Condit et al. (1999) as

$$r = \frac{\ln N_t - \ln S_t}{\Delta t} \quad (1)$$

where N_t is the number of living stems at the second census; S_t is the number of stems present in the first census that are still alive at the second census, not including new

Table 1. Site descriptions for the Barro Colorado Island (BCI), Dinghushan (DHS) and Changbaishan (CBS) plots.

Plot	BCI	DHS	CBS
Location	9.15°N, 79.85°W	23.17°N, 112.52°E	42.38°N, 128.08°E
Altitude (m)	120–160	230–470	792–810
Vegetation type	Semideciduous lowland moist forest	Monsoon evergreen broad-leaved forest	Temperate broadleaved-Korean pine mixed forest
Annual mean precipitation (mm)	2551	1985	700
Annual mean temperature (°C)	23.2	20.9	3.6
Topography for 20 × 20 m quadrats	Aspect, convexity, elevation, slope	Aspect, convexity, elevation, slope	Aspect, convexity, elevation, slope
Adaphic for 20 × 20 m quadrats	Extractable soil cations including Al, B, Ca, Cu, Fe, K, Mg, Mn, Zn, available N and extractable P, nitrogen mineralization rate and pH	Relative soil water, volume weight, pH, total organic matter, available N, extractable P, extractable K and total N, P, K	Soil water content, pH, organic matter, available N, extractable P, extractable K, and total N, P, K

recruits. Δt is the time difference between the successive 5-yr measurements.

Because growth rate changes with tree size (Brown et al. 2004, Stephenson et al. 2014), we did not use the average basal area growth within a quadrat as a measure of ontogenetic growth. Instead, we fit a multi-level growth model that accommodated both variation in stem size and variation in quadrat-specific habitat conditions. The model was expressed as

$$G_{ij} = g_j B_{ij}^\beta + e_{ij} \quad (2)$$

where G_{ij} is basal area growth rate of the i th individual of the j th quadrat defined below in Eq. (3); B_{ij} is the original basal area, calculated as $\pi(DBH_{ij}/2)^2$; e_{ij} is the error term. We estimated β using all stems of the species in the plot with nonlinear least squares (the 'nls' function in R) first and then estimated g_j individually for each quadrat using ordinary least squares, i.e. by minimizing $\sum_{i=1}^n (G_i - g_j B_i^\beta)^2$, where

n is the number of stems in the j th quadrat. g_j describes the effect of habitat condition in the j th quadrat on growth. In Eq. (3), G_{ij} is the growth rate of basal area of the i th individual in the j th quadrat, calculated as

$$G_{ij} = \frac{\pi(DBH_{ijt}/2)^2 - \pi(DBH_{ij0}/2)^2}{\Delta t} \quad (3)$$

where DBH_{ijt} and DBH_{ij0} are the DBH of the i th individual of the j th quadrat at time t (re-census) and time 0 (first census), respectively. In BCI and CBS, the exact date of DBH measurement for each stem is available and hence Δt for trees in these two plots is accurate to days (but was converted to unit of years) that passed between the first and the second measurements of DBH. In the DHS plot, no stem-specific dates were available so Δt was set at five for all trees.

Because tree survival probability is also influenced by tree size (Bin et al. 2012, Wang et al. 2012), we fit a multi-level model that calibrated both the effects of size and quadrat-specific habitat condition on survival probability. Given that u-shaped mortality curves for tree species are common (Lorimer et al. 2001, Bin et al. 2012), we fit survival as a function of basal area with its first and quadratic form so that the model could capture an n-shaped curve (u-shaped mortality means an n-shaped survival function). The model was expressed as

$$\ln\left(\frac{p_{ij}}{1-p_{ij}}\right) = s_j + d_1 B_{ij} + d_2 B_{ij}^2 \quad (4)$$

where p_{ij} is the survival probability of the i th individual in the j th quadrat and B_{ij} is its basal area at the first census. The parameters d_1 and d_2 describe the size effect, and s_j describes the effect of quadrat-specific habitat condition on survival probability. This model was fit using maximum likelihood.

Survival, recruitment and growth contribute to different aspects of demographic performance, and thus different

combinations of the three could indicate equally suitable habitat conditions. Therefore, a useful measure should account for all three components. In this study, we calculated overall performance as a composite measure, including r in Eq. (1), g in Eq. (2), and s in Eq. (4). These three components were transformed to [0, 1] range as:

$$x_t = \frac{x - x_{\min}}{x_{\max} - x_{\min}} \quad (5)$$

where x_t is the transformed value, x is the original value, and x_{\min} and x_{\max} are the minimum and maximum values across quadrats for the same species (Legendre and Legendre 1998).

The overall performance of a species was calculated as

$$P = r_t + g_t + s_t \quad (6)$$

where r_t is the recruitment rate after transformation, and g_t and s_t are, respectively, quadrat specific parameters in Eq. (2) and (4) after transformation.

Simultaneous autocorrelation (SAR) models of species–habitat associations

Because of the large number of habitat variables (Table 1) and possible collinearity among them, principal component analysis was used to reduce the number of dimensions after transforming the habitat variables using Box–Cox transformation and then standardizing to 0 mean and unit standard deviation. The first three principal components (E1, E2, E3) together explained, 67.7, 71.0 and 64.6% of the original variation for the data, respectively for BCI, DHS and CBS (Fig. 1, Supplementary material Appendix 1). These principal components were used to represent habitat condition in subsequent analyses.

We analyzed demography-based species–habitat association while accounting for spatial autocorrelation by fitting simultaneous autoregressive models (SAR) using the R package `spdep` 0.5–71 (Bivand 2014) (referred to as model DH here after). We fit overall performance (Eq. 6) in terms of E1, E2, E3, their quadratic and cubic terms. Explanatory variables also included the original abundances of conspecifics and heterospecifics in the same quadrats so as to account for density-dependent effects. Variables were selected using a stepwise procedure based on the AIC. We first calculated partial correlations between response variables and each explanatory variable, controlling all the other variables. Explanatory variables were then added into the model in descending order of their partial correlations with the response variable. If adding a variable resulted in lower AIC, we kept that variable and checked whether the model could be further improved by removing any one of the other variables already in the model. If AIC was smaller after removing a variable, we removed that variable from our model. The remaining variables were tested one by one as described above. The procedure was terminated when no variable could be added to the model and no variable could be removed. Because of the advantage of greater generality, we sought the most

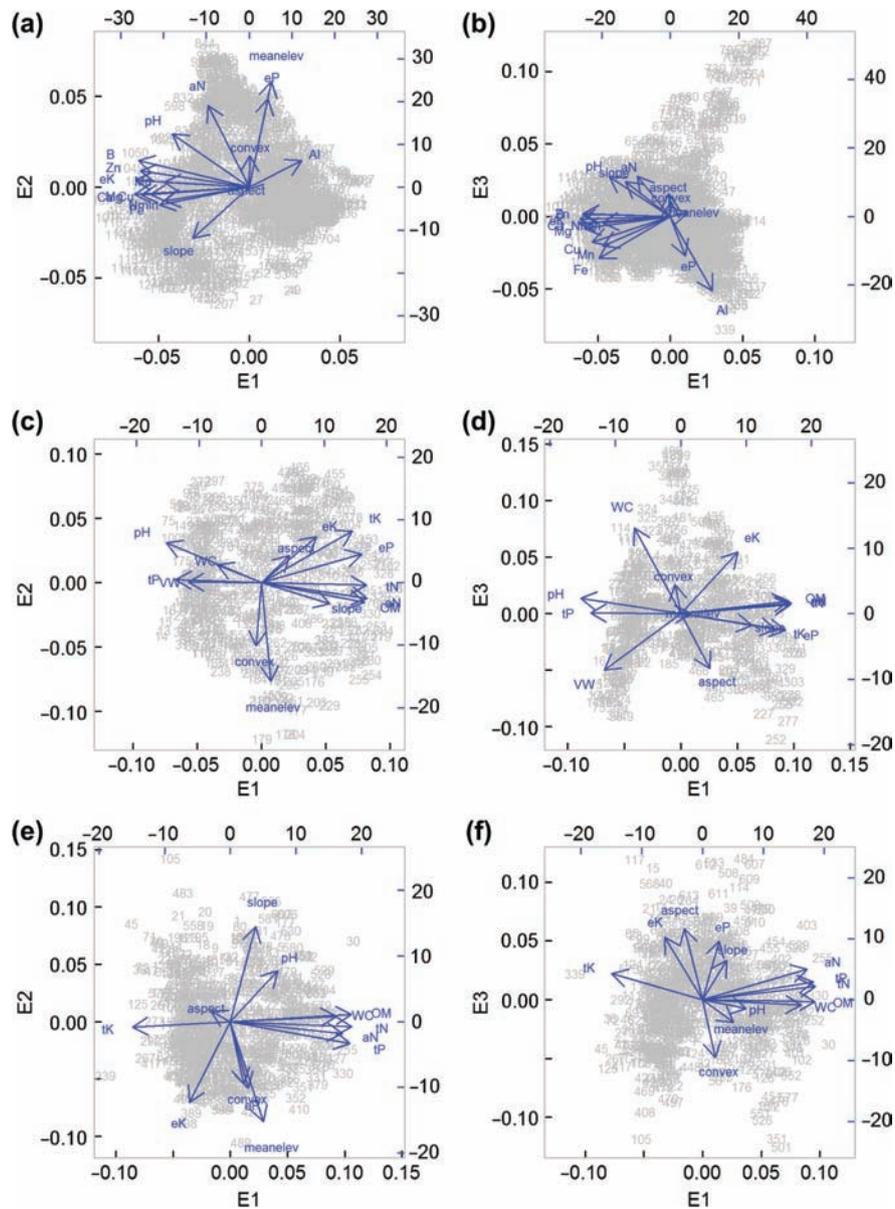


Figure 1. Biplots of the principle component analysis on topographic and edaphic variables for BCI, DHS and CBS plots. Panels (a), (c), (e) were the biplots between the first (E1) and the second (E2) principle components for the BCI (a), DHS (c) and the CBS (e) plots. Panels (b), (d) and (f) were the biplots between the first (E1) and the third (E3) principle components for the BCI (b), DHS (d), and the CBS (f) plots. meanelev: elevation; convex: convexity; aN: available nitrogen; eP: extractable phosphorus; eK: extractable potassium; Nmin: nitrogen mineralization rate; tN: total nitrogen; tP: total phosphorus; tK: total potassium; OM: organic matter; WC: water content; VW: volumn weight.

parsimonious model as shown in many studies when a lot of variables were involved (Legendre et al. 2005, Flinn et al. 2010). Though compared with the full model, this procedure could potentially bias parameter estimation when a variable was not kept due to non significant effect (Whittingham et al. 2006), evidence showed that the stepwise procedure had the highest accuracy on test data in a study of model performance (Parolo et al. 2008).

We also fit a SAR model with habitat variables to the log-transformed abundance data (called model AH hereafter) for each site, and then asked whether predictions of this model were consistent with those from the demography-based models for each species. With the demography-based model,

we first predicted overall performance of a species in each quadrat given the observed habitat variables and with zero conspecific or heterospecific individuals, i.e. overall performance was not influenced by the variation of neighborhood conditions. This required a slight extrapolation because when we fit model DH there were no demographic data about a quadrat with zero conspecifics. We next used the abundance-based model to predict abundance of the same species in each quadrat given the same observed habitat variables. We then calculated Pearson's r between these two predictions over all species included at each site. If the two model approaches were consistent in predicting habitat associations, we expected high positive correlation between them.

Results

Overall performance (as calculated from Eq. 6) of 72 (38.5%) species in BCI, 43 (59.7%) species in DHS and 22 (78.6%) species in CBS were influenced by at least one neighborhood variable (Supplementary material Appendix 2). According to DH models, at BCI, the number of species significantly affected by conspecifics (44) was similar to that of those affected by heterospecific neighbors (40) (Supplementary material Appendix 2). However, more species were affected by conspecific relative to heterospecifics in terms of overall performance at DHS (36 vs 15) and CBS (22 vs 8) (Supplementary material Appendix 2).

In the output of both the AH and DH models, >70% species in each of the three plots were found to be significantly associated with at least one of the three PCA habitat composite variables (Table 2). Among these species, only a small fraction (7.5 to 25.0%) was associated with all composite habitat variables at the three plots (Table 2). Both the AH and DH models showed that over 70% of the significant associations were curvilinear and included the second or the third order variables (Table 2).

We found little evidence for positive correlations between the predictions of the abundance- and demography-based models at any of the three sites. Only 7 species in BCI, 5 species in DHS showed modest positive correlations ($r > 0.5$). The correlations varied from almost -1 to 1 across species in the more diverse BCI and DHS plots, with means of -0.04 and -0.14, respectively (Fig. 2a, b). For species from CBS, the correlations were more negative (-0.20) and clearly showed a narrower distribution (Fig. 2c). The inconsistency of predictions between the abundance and the demography-based models suggests that these two models describe different aspects of species-habitat interaction.

Discussion

Species-habitat associations have been traditionally established by correlating measures of local abundance with habitat variables, usually based on field data collected at one point in time (Hubbell and Foster 1986, Harms et al. 2001, Gunatilleke et al. 2006, Yamada et al. 2006, Comita et al. 2007, Wang et al. 2009). However, in most natural forests abundance changes over time due to many unpredictable changes in driving factors (Condit et al. 1992). Consequently, inferences about habitat suitability based on patterns of abundance in one or a few locations are

probably unreliable for representing the suitable habitat of included species.

Compared with abundance, demographic rates capture better the spatial change in environmental conditions and the underlying physiological processes (Lasky et al. 2013). For example, the growth-mortality trade-off changed with respect to soil condition in a Bornean rain forest (Russo et al. 2008). The trade-off was steepest on the poorest soil, suggesting that fast-growing pioneer species might be eliminated from this habitat due to their higher mortality rates for a given growth rate (Russo et al. 2008). This was not manifested in the distribution of some of the pioneer species as 14 pioneer species aggregated in the poorest habitat (Russo et al. 2005). In another study, by correlating growth and survival with species traits and environmental conditions, Lasky et al. (2013) found strong filtering effects on demography were associated with low spatial variation in filters, suggesting that long-term processes in favour of habitat generalist may be affecting the species pool. This was a novel finding compared with the habitat analysis based on abundance previously done on this plot (Su et al. 2010).

We found that species-habitat associations revealed by demographic data differ from those revealed by patterns of abundance. Indeed, the average correlation across species between the predictions of our two different models was negative for all three plots. The study of soil-related tree growth and mortality also suggested that species might not necessarily perform best where they were abundant (Russo et al. 2005). In another study of subtropical rain forest tree communities, habitat-filtering functions for growth and survival were only partly in consistent with species' static distributions (Lasky et al. 2013). Because demographic rates are better indicators of habitat suitability, as argued above, demography-based models should be preferred to describe species-habitat association when communities cannot be assumed to be in static equilibrium.

We suggest several reasons why predictions from our demography-based model do not correlate well with those from the more traditional abundance-based model. Differences between demographic data and patterns of abundance, for example, can be driven by source-sink population dynamics. Continuous immigration from nearby 'source' habitats can maintain high abundance in 'sink' habitats even when demographic performance is poor and mortality is high (Pulliam 1988, Schurr et al. 2012). While abundance is generally determined from observations at one point in time, demographic rates are calculated using data from at least two censuses. These censuses were separated by five years in

Table 2. The number and proportion of species at each plot that was significantly associated with none, one, two, three and at least one composite habitat variables based on the abundance (model AH) and the overall performance (model DH) fitted using simultaneous regressive model.

Plot	Model	No significant variable	One significant variable	Two significant variables	Three significant variables	At least one significant variable
BCI	AH	55 (29.4%)	60 (32.1%)	54 (28.9%)	18 (9.6%)	132 (70.6%)
	DH	50 (26.7%)	73 (39.0%)	50 (26.7%)	14 (7.5%)	137 (73.3%)
DHS	AH	8 (11.1%)	19 (26.4%)	27 (37.5%)	18 (25.0%)	64 (88.9%)
	DH	16 (22.2%)	21 (29.2%)	25 (34.7%)	10 (13.9%)	56 (77.8%)
CBS	AH	5 (17.9%)	9 (32.1%)	10 (35.7%)	4 (14.3%)	23 (82.1%)
	DH	5 (17.9%)	7 (25.0%)	11 (39.3%)	5 (17.9%)	23 (82.1%)

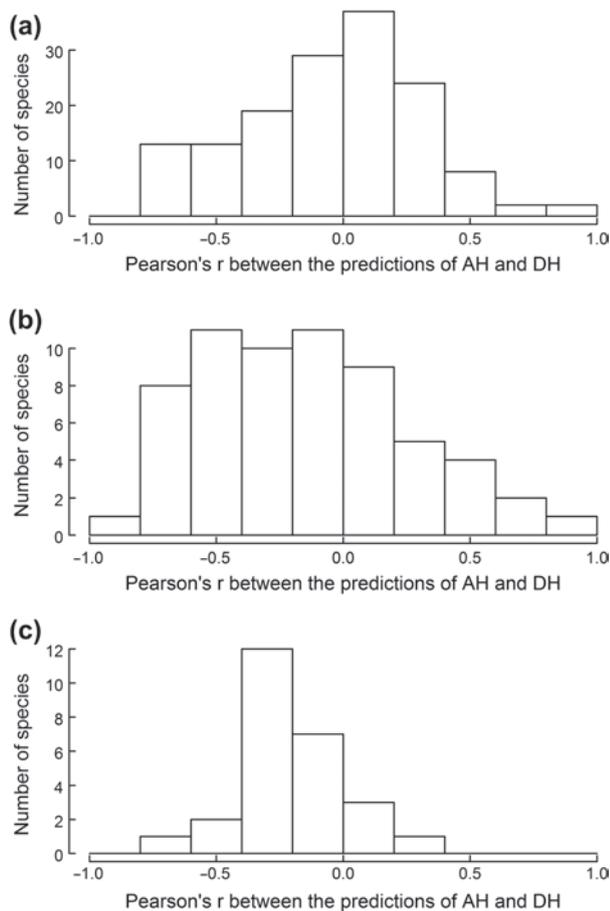


Figure 2. The distribution of Pearson's correlation coefficients between the predictions of the demography-based and the predictions of abundance-based models for individual species. The predictions were made using the observed habitat values for each species. An observed r -value in this figure denotes a single species. Panels (a), (b), and (c) showed the distribution of r for species in BCI (a), DHS (b), and CBS (c), respectively.

our study. Such differences in observation time could contribute to the inconsistency between predictions from demographic and abundance data, especially in rapidly changing forests such as the BCI plot (Condit et al. 2012). The modest extrapolation required to predict overall performance in the absence of neighborhood effects might contribute to the mismatch that we observed in predictions, but this should have minor impact on the results.

When a community is not at equilibrium, demography-based measures should provide more insightful understanding of niche differentiation of tree species in space (Eckhart et al. 2011, McLaughlin and Zavaleta 2012, Schurr et al. 2012). Demography-based models are especially useful for understanding responses of tree species to rapidly changing environment and identifying habitats in which demographic rates are most unstable. This can be useful for predicting local responses to change. Rapp et al. (2012), for example, used changes in tree diameter growth rate across an altitudinal gradient to predict ecosystem responses to global warming. Demography-based models are well suited to understand the impacts of global change on forest ecosystems, a matter of substantial current interest (Lawrence et al. 2013, Sardans and Peñuelas 2013).

Abundance-based species–habitat associations are generally modeled at the quadrat level (Harms et al. 2001, Comita et al. 2007, Wang et al. 2009). To facilitate comparison, we also constructed our demography-based models at this scale. It is worth noting, however, that demography can also be modeled at the individual level. This could be important for understanding diversity maintenance because variation among individuals contributes substantially to species coexistence (Clark et al. 2010). The individual-based approach is appealing for at least two reasons. First, neighborhood analysis using an individual-based approach can quantify the effects of the real neighbors for every individual. When modeled with a quadrat-based approach, part of the information about neighbor density for individuals near the edge of a quadrat is lost and replaced by information about the neighborhood relatively far away from the focus tree (Peters 2003). Second, sample sizes for individual-based models are larger than those obtained from quadrat-based models, leading to better estimates of habitat effects. Where comparison with abundance-based analysis is not of interest, the individual-based demographic models can be more powerful than quadrat-based models for studying species–habitat associations. Modeling details aside, our study demonstrates that the demographic approach in general yields more biologically realistic and accurate results than do correlations between abundance and environment.

Acknowledgements – This research was supported by National Natural Science Foundation of China (31300455), China Postdoctoral Science Foundation Grant (2012M521643), the Univ. of Alberta International (the China MOST-UofA Joint Research Lab program), and NSERC (Canada) to JP and FH. The work on the DHS and CBS plots was supported by the National Natural Science Foundation of China (41301057) and the BCI plot was funded by NSF DE Band OISE, the STRI Soils Initiative and CTFS. Many thanks to Honglin Cao, Dingliang Xing, Jim Dalling, Kyle Harms, Joe Yavitt, and many others for their contributions to the forest census, soil sample collection and analyses.

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Supplementary material (Appendix ECOG-00787 at <www.ecography.org/appendix/ecog-00787>). Appendix 1–2.