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Dissecting NDVI–species richness relationships in Hawaiian dry forests

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ABSTRACT

Aim A growing body of research has used the normalized difference vegetation index (NDVI) as a proxy for productivity to predict species richness. Yet the mechanisms that produce the relationship between NDVI and species richness remain unclear because of correlated biotic and abiotic factors that influence NDVI. In this study we investigated different biotic and abiotic effects that potentially drive plant species richness–productivity relationships.

Location Hawaiian Islands, USA.

Methods We quantified woody plant species richness, structure (density, basal area and canopy height), and species composition along a precipitation gradient of 14 Hawaiian dry forest plots. We then used structural equation models combined with 10 years of satellite data to disentangle the effects of precipitation, structure and NDVI-estimated productivity on species richness.

Results Underlying the simple correlation between NDVI and species richness was the indirect effect of precipitation and direct effect of forest structure. The best-fit model showed there was no direct effect of NDVI on species richness.

Main conclusions Our results demonstrate that complex relationships drive simple correlations between species richness and productivity. Considering the mechanisms and underlying factors driving NDVI–species richness relationships could improve predictions of species diversity as satellite measures of productivity have an increasingly important role in habitat mapping, species distribution modelling and predictions for global change.

Keywords

Diversity, ecosystem function, forest structure, habitat complexity, Hawaii, precipitation, tropical dry forest, woody plants.

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INTRODUCTION

Understanding factors that control species diversity is an increasingly important question in many habitats, particularly in diverse tropical forests that are especially at risk of species extinctions and rapid land-use change. The relationship between species richness and productive energy at regional to global scales is well established and can be used to predict species richness at broad spatial scales (e.g. Currie & Paquin, 1987; O'Brien, 1998). Recently, a large growing body of research has used satellite data observations of habitat productivity to explore patterns of species richness (Gould,

2000; Bawa *et al.*, 2002; Oindo & Skidmore, 2002; Waring *et al.*, 2002; Bailey *et al.*, 2004; Fairbanks & McGwire, 2004; Lee *et al.*, 2004; Gillespie, 2005; Ding *et al.*, 2006; Levin *et al.*, 2007; Nightingale *et al.*, 2008; Phillips *et al.*, 2010), or in species distribution models (Bradley & Fleishman, 2008; Buermann *et al.*, 2008; Maselli *et al.*, 2009).

One of the most commonly used satellite spectral indices is the normalized difference vegetation index (NDVI). NDVI provides an estimate of habitat productivity and has been shown both theoretically and experimentally to be associated with aboveground net primary productivity (Goward *et al.*, 1985; Tucker & Sellers, 1986; Box *et al.*, 1989; Prince, 1991;

Turner *et al.*, 2003) and photosynthetic activity (Asrar *et al.*, 1984; Sellers, 1985, 1987; Gamon *et al.*, 1995; Myneni *et al.*, 1995). Because chlorophyll *a* and *b* absorb light in the red portion of the electromagnetic spectrum whereas healthy leaf tissue reflects strongly in the near-infrared region, NDVI is calculated as a difference ratio between reflectance in the red and near-infrared wavelengths (Jensen, 2006). The advantages of using satellite measures of NDVI as an estimate of productivity include: (1) the temporal frequency of observations, which provides seasonal and interannual values; (2) the data are continuous observations and not modelled or interpolated; and (3) that it is globally available from numerous sources, often at no cost.

Yet, the mechanisms producing the relationship between NDVI and species richness are not well established. Whereas the species richness of birds and mammals has been shown to exhibit strong relationships with habitat structure and productive energy because they are dependent on the diverse resources provided by three-dimensional habitat complexity (e.g. Hurlbert, 2004; Rompre *et al.*, 2007; Jonsson *et al.*, 2011), in plant communities the underlying drivers of the relationship are less clear (Parmentier *et al.*, 2011). Available energy or productivity – often modelled as a function of climate (e.g. Currie & Paquin, 1987; O'Brien, 1998; Hawkins *et al.*, 2003) – has been proposed as a driver of plant species richness based on the species–energy hypothesis. The species–energy hypothesis proposes that species partition available energy so that energy is a limiting resource to the number of species in an area (Currie & Paquin, 1987; O'Brien, 1998). An increasing number of studies cite the species–energy hypothesis when using NDVI to predict plant species richness (see citations above); however, the relationship between plant species richness and NDVI as an estimate of productivity can be confounded by the influence of correlated biotic and abiotic factors known to influence NDVI.

In tropical forests, NDVI has been shown to increase with species richness, explaining between 30% and 60% of the variance in tree species richness (Bawa *et al.*, 2002; Feeley *et al.*, 2005; Gillespie, 2005; Cayuela *et al.*, 2006; Foody & Cutler, 2006; Gillespie *et al.*, 2009). However, NDVI also increases with precipitation (Asner *et al.*, 2005), and precipitation is a strong limiting factor in the structural development of tropical dry forests (Bullock *et al.*, 1995). Thus the relationship between NDVI and species richness may be an indirect result of precipitation and forest structure. Large differences in forest cover, canopy height, plant biomass and productivity are associated with structural development (Bullock *et al.*, 1995) and in turn, forest structure has also been shown to affect NDVI (Castro *et al.*, 2003; Arroyo-Mora *et al.*, 2005; Feeley *et al.*, 2005; Freitas *et al.*, 2005). NDVI has also been linked to changes in tree species composition associated with successional stages of tropical forests (Castro *et al.*, 2003; Arroyo-Mora *et al.*, 2005; Quesada *et al.*, 2009). Because these biotic and abiotic factors interact, disentangling their effects on NDVI is necessary for identifying the mechanisms that allow the use of NDVI to predict species

richness. Identifying causal mechanisms is important for both an empirical and theoretical understanding of distributional patterns of diversity, and for management decisions that rely on accurate predictions of species richness and wildlife habitat.

In this study we investigated different biotic and abiotic effects that potentially drive plant species richness–productivity relationships. We quantified woody plant species richness, structure (density, basal area and canopy height), and species composition along a precipitation gradient of Hawaiian dry forests. We then used structural equation models to partition the direct and indirect effects of precipitation, structure and NDVI-estimated productivity on species richness.

MATERIALS AND METHODS

Study sites and field measurements

Fourteen closed-canopy dry forest study sites were selected and surveyed in 2004–2006 (Table 1). Mean annual precipitation ranged from 642 to 1823 mm and mean annual temperature ranged from 19 to 22 °C (Giambelluca *et al.*, 1986). Field measurements of woody plant species at all sites followed Gentry (1988). 'Gentry transects' consist of belt transects totalling 1000 m^2 (0.1 ha), which thus control for area. Each sample consisted of 10 belt transects (2 m × 50 m) 10 m apart in which all woody plants ≥ 2.5 cm diameter at breast height (d.b.h.) rooted in the sample area were identified (Gentry, 1988). We quantified species richness, density (number of stems ≥ 2.5 cm d.b.h.), basal area (m^2 ha^{-1}), and canopy height (mean tree height in 2 m cohorts) for each site (Table 1).

Satellite data

We used NASA's Terra Moderate Resolution Imaging Spectro-radiometer (MODIS) Vegetation Indices (VI) Product (MOD13Q1), 16-day composite data with 250-m resolution. One pixel centred over each study site for a 10-year period (February 2000–December 2009) was used to calculate the mean and coefficient of variation (CV) of NDVI. Only pixels that had 'good quality' or 'check other QA' in the VI Quality dataset provided by the MODLAND Science Team were used for analyses (http://tbrs.arizona.edu/project/MODIS/MOD13.C5-UsersGuide-HTML-v1.00/index.html; downloaded 27 August 2010). Checking 'other QA' included filtering out pixels with clouds (adjacent cloud, mixed clouds and possible shadow), aerosols (high and climatology aerosols), and possible shadow. Whereas mean NDVI represents a temporally averaged measure of greenness and habitat productivity at each site, CV NDVI represents the seasonal and interannual variation in habitat productivity (see Appendix S1 in Supporting Information). We also examined the mean and CV of the enhanced vegetation index (EVI) from the same MODIS VI Product, which is thought to be less sensitive to saturation in high biomass regions (Huete *et al.*, 2002).

Table 1 Woody plant species richness and structure of all stems d.b.h. ≥ 2.5 cm in 0.1-ha plots from 14 dry forest sites in the Hawaiian Islands. Mean annual precipitation (MAP) and mean annual temperature (MAT) data are from Giambelluca *et al.* (1986).

Study site	Latitude	Longitude	Species richness	Density d.b.h. ≥ 2.5 cm	Density d.b.h. ≥ 10 cm	Basal area (m^2 ha^{-1})	Canopy height (m)	MAP (mm)	MAT (°C)	mean NDVI	CV NDVI
Kauai											
Awaawapuhi Trail	22.149	−159.666	21	245	74	45.0	7.11	1823	21	0.81	7.23
Nualolo Trail	22.139	−159.678	13	279	68	63.0	8.37	1520	22	0.82	3.93
Milolii Ridge	22.127	−159.684	9	313	68	25.0	8.88	1314	20	0.79	8.05
Waimea Canyon	22.061	−159.647	10	166	85	38.0	9.82	1452	19	0.79	10.92
Oahu											
Honouliuli	21.418	−158.094	12	161	62	36.0	9.44	1020	21	0.80	9.62
Kaluakauila Gulch	21.547	−158.224	13	326	70	21.0	5.98	1047	22	0.66	17.75
Molokai											
Kamiloloa Gulch	21.113	−156.959	7	41	35	9.2	4.89	970	20	0.62	19.02
Lanai											
Kanepuu 1	20.877	−156.977	4	173	61	26.0	4.37	664	21	0.48	27.18
Kanepuu 2	20.874	−156.967	10	133	60	19.0	4.08	678	21	0.46	27.82
Kanepuu 3	20.878	−156.989	5	135	60	23.0	4.00	642	21	0.67	19.76
Maui											
Kanaio	20.620	−156.339	7	33	42	12.2	6.81	750	19	0.56	31.78
Big Island											
Manuka 1	19.123	−155.806	10	258	77	38.8	8.38	1186	19	0.74	6.71
Manuka 2	19.128	−155.808	14	165	68	36.5	12.16	1195	19	0.76	5.13
Kaupulehu	19.768	−155.937	7	87	69	19.2	6.35	1007	21	0.31	18.28
Mean			9.6	180.0	63	29.4	7.2	1090.6	20.5	0.66	15.23
SD			4.4	93.5	13.0	14.4	2.5	353.9	1.0	0.16	9.17

CV, coefficient of variation; NDVI, normalized difference vegetation index; SD, standard deviation.

Structural equation modelling and partitioning direct and indirect effects

We then used structural equation models (SEMs) to partition the relative effects of precipitation, structure (density, basal area and canopy height), and NDVI on species richness. SEMs test the fit of the covariance matrix of observed data to hypothesized relationships regarding the functioning of the system. The relationships described indicate the magnitude of direct and indirect effects on the response variable, which here was species richness. The utility of SEMs to elucidate complex ecological relationships depends on their careful use (Petraitis *et al.*, 1996; Kline, 2010), especially when, as in this case (14 forests), sample size is low (Shipley, 2002). We carefully looked for instability associated with using SEMs with a small sample by checking that path estimates were stable between models and multiple fit metrics produced consistent model rankings (Grace, 2006). We used a common model fit index, Bayesian information criterion (BIC) (lower values indicate closer fit), to compare different model structures relative to each other but also examined *P*-values based on a chi-square test (χ^2) to ensure adequate fit of the observed data to the modelled data (thus *P*-values > 0.05 indicate that the modeled data are not significantly different to the observed data). We furthermore employed d-sep tests of our path models, which can be used with small sample sizes because they do not rely on an asymptotic probability distribution, assumptions of normality,

or iterative convergence in maximum likelihood estimations (Shipley, 2000, 2009). D-sep tests provide a *P*-value indicating if the model structure (but not coefficients) is unlikely to have occurred based on the observational data (again, *P*-values > 0.05 indicate that the modeled data are not significantly different to the observed data). D-sep tests the dependence or independence of each set of variables (e.g. is species richness dependent upon NDVI, which is in turn dependent upon precipitation?) in a path diagram without path coefficients, latent variables, or feedback loops. To avoid over-identifying the model, density, basal area and canopy height were reduced to one variable, from here on referred to as structure, using the first component (which explained 65% of the variance) from a principal components analysis (PCA). Larger values in the structure variable indicate greater structural complexity (more stems, greater basal area and taller canopy). As with any statistical modelling approach, analyses must protect against inflating Type I (α) error by fitting too many models, thus we developed four a priori models for mean and CV NDVI and EVI (16 total models; results referring to 'NDVI' or 'EVI' pertain to both mean and CV). These four a priori models were chosen because they maintained the link between NDVI/EVI and species richness while examining the direct and indirect effects of precipitation and structure. The full model examined all hypothesized direct and indirect (via structure and NDVI/EVI) effects of precipitation on species richness, while a second model removed the direct effect of precipitation.

A third model included the direct effect of structure on NDVI/EVI, while the fourth model again removed the direct effect of precipitation. We screened for collinearity of predictor variables by checking that all variance inflation factors (VIF) were < 5 (Petraitis *et al.*, 1996). A Moran's *I* coefficient based on a binary distance matrix ($d \leq 0.50$ considered connected) was examined for all variables. CV NDVI, precipitation and structure exhibited significant spatial autocorrelation (Moran's I = 0.64, 0.83, 0.60; $P < 0.05$, respectively). To assess relationships between these variables, generalized least squares (GLS) regressions with autocorrelated errors were performed. All statistical analyses were performed in R including the 'sem' and 'nlme' packages (Fox & Byrnes, 2011; R Development Core Team, 2011; Pinheiro *et al.*, 2012).

RESULTS

Floristic composition of Hawaiian dry forests

Hawaiian dry forests were represented by 64 species from 32 families (see Appendix S2, which shows species that occurred in two or more sites). Forty-nine species from 24 families were native, and Rubiaceae was the most species-rich family. The most common native dry forest species was *Diospyros sandwicensis* (569 individuals), followed by *Nestegis sandwicensis* (326 individuals), *Metrosideros polymorpha* (202 individuals), *Acacia koa* (193 individuals), and *Psydrax odorata* (113 individuals). Precipitation had a strong effect on species composition (the abundance of each species at a site) based on a permutational multivariate analysis of variance (MANOVA) using a distance matrix for dissimilarities in species composition ($F_{1,7}$ = 4.33,

$P < 0.001$) and these different communities displayed significantly unequal variance in seasonal and interannual NDVI (see Appendix S1). Species richness, density, basal area, canopy height and mean NDVI were all positively correlated with precipitation ($r = 0.78$, $P < 0.001$; $r = 0.54$, $P < 0.05$; $r = 0.72$, $P < 0.001$; $r = 0.60$, $P < 0.05$; $r = 0.67$, $P < 0.01$, respectively; Fig. 1), while CV NDVI was negatively correlated with precipitation ($r = -0.81$, $P < 0.001$). None of these variables were significantly correlated with temperature. Precipitation was positively and strongly related to mean NDVI and CV NDVI ($r = 0.67$, $P < 0.01$; $r = -0.81$, $P < 0.001$, respectively). Neither mean EVI nor CV EVI was significantly correlated with precipitation. CV NDVI, precipitation and structure exhibited significant spatial autocorrelation; however, relationships between these variables were still significant after accounting for autocorrelation in the residuals. Simple linear regressions suggest mean NDVI and CV NDVI can predict 30–40% of the variation in species richness ($R^2 = 0.33$, $P < 0.05$; $R^2 = 0.39$, $P < 0.05$, respectively). There was no significant relationship between mean EVI or CV EVI and species richness.

Partitioning direct and indirect effects on species richness

When the relationship between NDVI and species richness was simultaneously considered with other confounding biotic and abiotic effects, there was no direct relationship between NDVI and species richness. Instead, structural equation models consistently showed the importance of precipitation. Model fit always decreased when the direct path from precipitation to species richness was removed (Fig. 2, Table 2). BIC ranked
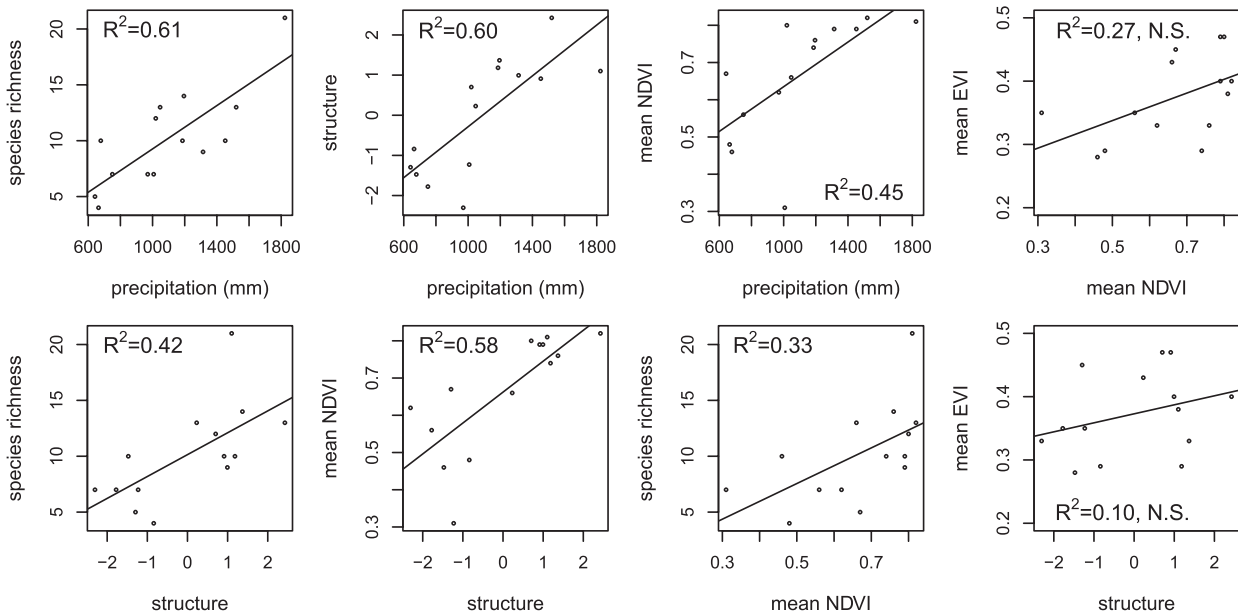
Figure 1 Scatterplots showing the relationship between woody plant species richness, precipitation, structure [a composite variable using the first component from a principal components analysis (PCA) of density, basal area and canopy height], normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) in 14 dry forest plots on the Hawaiian Islands. Relationships with EVI were not significant (n.s., $P > 0.05$).

Model A

Model B
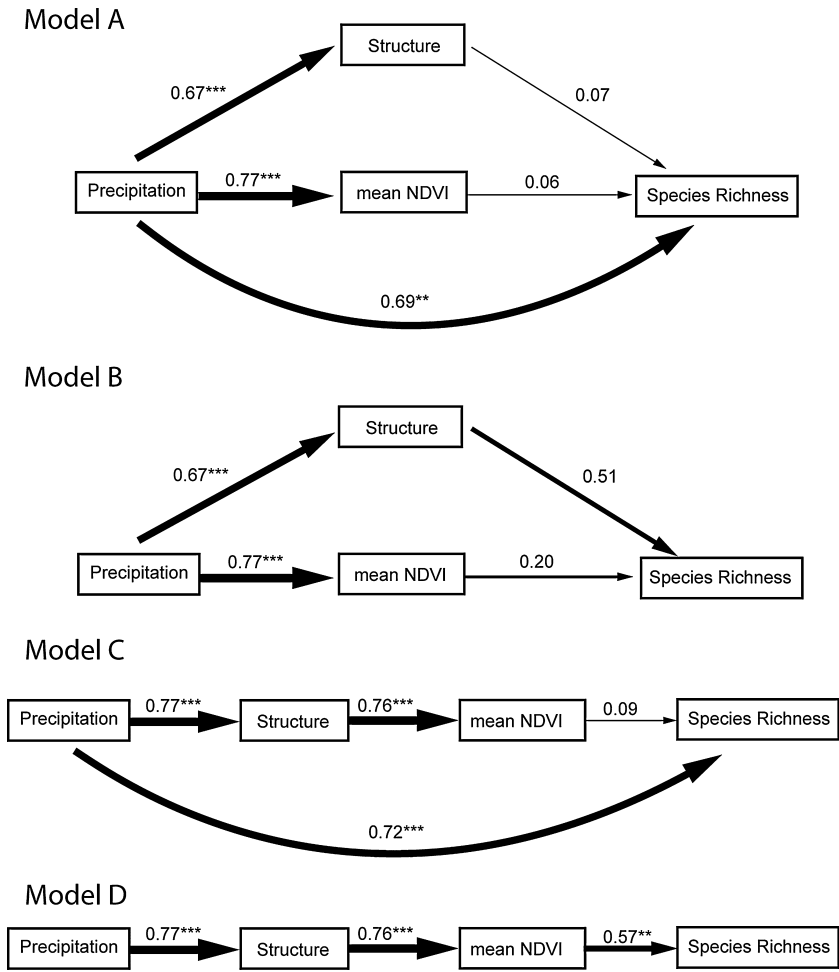
Model C

Model D

Figure 2 Structural equation models of the full model (Model A), excluding the direct path from precipitation to woody plant species richness (Model B), the best-fit model with structure driving the normalized difference vegetation index (NDVI) (Model C), and again excluding the direct path from precipitation to species richness (Model D). Path coefficients are shown with line weights representing the magnitude of the relationships. See Table 2 for all model descriptions and fit statistics. ***$P < 0.001$.

Model C the best-fit model and d-sep tests showed that Model C had the highest probability of occurrence. Model C demonstrated that precipitation had a strong direct effect on species richness and structure, and structure had a strong direct effect on NDVI, but the only significant direct effect on

species richness was through precipitation. BIC, as well as the d-sep test, ranked Model B (Fig. 2) the worst model. Model B did not consider the direct path from structure to NDVI and precipitation to species richness, and consequently the path from structure to species richness became stronger than NDVI

Table 2 Four structural equation models examining the direct and indirect effects of precipitation, structure and NDVI on woody plant species richness in 14 dry forest plots on the Hawaiian Islands (see Fig. 1 for all models with path coefficients). The full model examined the direct and indirect effects of precipitation and direct effects of structure and NDVI on species richness (Model A). Excluding the direct effect of precipitation from the full model worsened model fit (Model B). The best-fit model includes the direct effect of structure on NDVI (Model C). Again model fit worsened when the direct effect of precipitation was excluded (Model D). A C-value provided by d-sep tests is used for small sample sizes to provide further support for path models without coefficients (Shipley, 2000, 2009). P-values correspond to the preceding (left) column statistic.

Model	Description	Mean NDVI χ^2	P	BIC	C	P	CV NDVI χ^2	P	BIC	C	P
A	Full model	4.04	0.13	−1.24	5.30	0.07	7.63	0.02	2.36	8.71	0.01
B	Model A without direct effect of precipitation on species richness	9.16	0.03	1.24	11.19	0.03	13.12	0.00	5.20	14.91	0.01
C	Direct effect of structure on NDVI	0.59	0.90	−7.33	1.69	0.79	3.29	0.35	−4.63	5.23	0.27
D	Model C without direct effect of precipitation on species richness	7.89	0.10	−2.67	10.08	0.12	9.37	0.05	−1.18	12.50	0.05

BIC, Bayesian information criterion; NDVI, normalized difference vegetation index.

to species richness. The second best model was Model D, which showed that those of NDVI, had a direct effect on species richness only when structure was driving the relationship and the direct effect of precipitation on species richness was removed. Models including CV NDVI instead of mean NDVI showed that the direction of the relationship (the beta coefficient) with precipitation, structure and species richness became negative. The magnitude and significance of path coefficients were stable across different models structures. Results using EVI were generally similar to those using NDVI, with the best-fit model (Model C) showing the strong direct effect of precipitation on species richness and no direct effect of EVI on species richness (see Appendix S3). However, the relationship between structure and EVI was not significant, whereas structure exhibited a strong relationship with NDVI.

DISCUSSION

Mechanisms driving NDVI–species richness correlations in Hawaiian dry forests

Similar to previous papers, we found that NDVI can predict more than 30% of the variation in plant species richness (Bawa et al., 2002; Feeley et al., 2005; Gillespie, 2005; Cayuela et al., 2006; Foody & Cutler, 2006; Gillespie et al., 2009). However, our results reveal the biotic and abiotic factors that may influence the relationship between NDVI and species richness in our system. Recognizing these mechanisms is important for accurate predictions of species richness. Using NDVI has many advantages because the data have high spatial and temporal resolution, are not interpolated, and are globally available. However, considering the appropriate mechanisms and other underlying factors, such as precipitation or structure, would improve predictions.

Our models found that underlying the simple correlation between NDVI and species richness were the strong effects of precipitation and structural complexity (Fig. 2, Table 2). NDVI only showed a significant relationship with species richness if structure was driving the relationship and the direct effect of precipitation is not considered. Mature forests with greater structural complexity have multiple strata composed of different species, such as understorey, midstorey and emergent canopy species that 'fill space' (West et al., 2009). The relationship between structure and species richness in our statistical analyses was ultimately driven by precipitation. Precipitation had the only consistent direct effect on species richness and also had strong direct and indirect effects on structure and NDVI. NDVI has been shown to track changes in precipitation and its effect on canopy structure across space (e.g. Asner et al., 2005; Freitas et al., 2005), as well as across time (e.g. Asner et al., 2000; Jolly & Running, 2004).

Our results suggest that mapping and monitoring the species richness of regions using NDVI will only be accurate when a strong and consistent chain of relationships with precipitation and structure has been established. In areas where neither precipitation nor structure varies with species richness, NDVI may not be an accurate predictor of species richness. Indeed, research has shown that the importance of particular climatic factors for explaining species richness varies with latitude and taxonomic groups (Hawkins et al., 2003). For example, in contrast to plant communities, the species richness of birds and mammals may be directly dependent on the diverse resources provided by structural complexity independent from climate (Griffiths & Lee, 2000; Bailey et al., 2004; Hurlbert, 2004; Seto et al., 2004). In this case the direct relationship between NDVI and species richness may be stronger. In addition, habitat change and the invasion of non-native species may fundamentally alter ecosystem functions that maintain a connection between structure, NDVI and species richness; invasive plants have been shown to exhibit higher rates of productivity while reducing the structural complexity of more species-rich native communities (Baruch & Goldstein, 1999; Asner et al., 2008).

Comparison of NDVI and EVI for predicting species richness

Because our results suggest that structure may be important in determining NDVI–species richness relationships, we examined another related spectral index previously demonstrated to be more sensitive to vegetation structure compared to NDVI. EVI has been shown to be more responsive in high biomass regions because it responds primarily to the near infrared band, which does not saturate (Gamon et al., 1995; Huete et al., 2002). In our results, however, NDVI was more strongly associated with forest structure compared to EVI, which showed no significant relationship to structure or precipitation in our sites. This is likely to be due to the 500-m spatial resolution of the blue band that makes EVI distinct from NDVI. Aside from differences in spatial resolution, studies have shown that the relationship between NDVI and leaf area index (LAI), a common measure of green biomass related to forest structure, is maintained throughout the year, whereas the relationship between EVI and LAI breaks down during the leaf senescence stage (Wang et al., 2005). Additionally, previous work has shown that the relationship between EVI and productivity is weak for forests with little seasonal variation (Sims et al., 2006), a characteristic of our wettest sites (see Appendix S1).

CONCLUSIONS

Advances in satellite technology have generated valuable new approaches to mapping and quantifying plant community richness across large geographic gradients (Turner et al., 2003). Our results have important implications for understanding relationships between species richness and habitat productivity estimated using NDVI. Using extensive field data combined with remote sensing techniques we demonstrate how complex relationships drive simple correlations between species richness and productivity. This understanding is critical for accurate predictions of how species will respond to future change as satellite measures of productivity have an increasingly impor-

tant role in habitat mapping, species distribution modelling and predictions for global change.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 MODIS NDVI 250-m, monthly values from February 2000 to February 2009.
Appendix S2 Woody plant species that occurred in two or more sites within 0.1-ha plots.
Appendix S3 Four structural equation models examining the direct and indirect effects of precipitation, structure and EVI on species richness.

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