Journal of Ecology

Ecology's cruel dilemma, phylogenetic trait evolution and the assembly of Serengeti plant communities

T. Michael Anderson[1]*, Joey Shaw[2] and Han Olff[3]

[1]*Department of Biology, Wake Forest University, 206 Winston Hall, Winston-Salem, NC 27109, USA;* [2]*Department of Biological and Environmental Sciences, University of Tennessee, Chattanooga, TN 37403, USA; and* [3]*Community and Conservation Ecology Group, University of Groningen, Box 14 Haren, The Netherlands*

Summary

1. Ecologists debate the importance of neutral versus niche-based explanations for patterns of species coexistence and whether small-scale data can inform ecological understanding of communities, referred to by McNaughton [*Ecological Monographs*, 1983, **53**, 291] as 'ecology's cruel dilemma.' Research on phylogenetic relationships, traits and species co-occurrence has attempted to address this topic, with results considerably mixed.

2. We address the hypothesis that plant community assembly is influenced by trait similarity across ecological gradients and this affects mean phylogenetic distance (MPD) of species within sites. We analysed specific leaf area (SLA), maximum plant height and phylogenetic relationships among Serengeti grasses, a system ideally suited to study community assembly because of an ecological gradient in which the dominant plant stress shifts from drought to light competition.

3. Phylogenetic community assembly theory predicts that MPD would be lowest (under-dispersed) at dry sites and greatest (over-dispersed) at sites with higher rainfall. Similarly, theory predicts that low soil nutrient concentrations should filter intolerant species, so that MPD is expected to be under-dispersed at infertile, low-elevation sites and over-dispersed at fertile, higher-elevation sites. However, as gradients of rainfall and soil fertility run counter to one another across the Serengeti, it was unclear how this covariation would influence MPD.

4. Surprisingly, traits showed different evolutionary patterns: SLA displayed convergent evolution while maximum plant height displayed Brownian evolution across the phylogeny. As predicted, statistically under-dispersed assemblages occurred at lower rainfall, infertile sites while statistically over-dispersed assemblages occurred at higher rainfall, fertile sites. However, the pattern across all plots was weak, with most plots showing no statistical pattern of MPD.

5. Multivariate analyses using structural equation modelling, which statistically controlled for covariation among environmental effects, revealed complex direct and indirect effects of environmental variation on MPD, including offsetting direct effects of SLA and maximum plant height due to their different patterns of trait evolution.

6. *Synthesis.* Spatially counteracting gradients of moisture and soil fertility across the Serengeti, combined with contrasting patterns of trait evolution, obscured the relationship between MPD and any single environmental variable. Our study shows that integrating trait and phylogenetic relationships across ecological gradients yields considerable insight into the ecological mechanisms that determine community composition, but that multivariate techniques may be required to appropriately reveal such patterns.

Key-words: abiotic gradients, community assembly theory, environmental filters, grass phylogeny, K-statistic, plant population and community dynamics, plant species richness, species coexistence, structural equation modelling, trait dispersion

*Correspondence author. E-mail: anderstm@wfu.edu

Introduction

'Ecology is confronted by a cruel dilemma: either communities have an order expressed in their species compositions, population abundances and diversities, or community ecology has been on the wrong track since its inception.' – McNaughton (1983).

The concept captured in this quote, hereafter referred to as 'ecology's cruel dilemma', is even more salient today than when it was published because of the debate over neutral versus niche processes in determining the species composition of local communities (Alonso, Etienne & McKane 2006; Gewin 2006; Adler, HilleRisLambers & Levine 2007; Clark *et al.* 2007). This debate has emphasized two separate, but related, themes: the importance of species interactions, held by the niche perspective, versus the importance of stochastic processes such as dispersal and ecological drift, held by the neutral perspective (Chave 2004; Leigh 2007). The dramatic rise in the popularity of neutral mechanistic explanations for community compositions (e.g. Clark 2009), in combination with calls to disintegrate the idea of the local community entirely (Ricklefs 2008), imply that ecologists studying local species assemblages are working at inappropriate spatial and temporal scales. In other words, there is debate about whether many contemporary ecologists are, as portended by ecology's cruel dilemma, on the wrong track.

In response to the neutral theory and calls to abandon research on local community diversity, there has been a surge of studies arguing for the importance of niche-based mechanisms in maintaining stable and diverse assemblages of organisms at relatively small scales (Adler 2004; Harpole & Tilman 2006; Levine & HilleRisLambers 2009). Attempts to incorporate functional traits and long-term evolutionary mechanisms into theories of local coexistence have lead to the theory of 'phylogenetic community assembly' (Webb *et al.* 2002; Cavender-Bares *et al.* 2004; Kraft *et al.* 2007; Hardy 2008; Kembel 2009; Vamosi *et al.* 2009). The theory suggests that the assembly process can result in communities composed of species that are more closely related than expected by chance (called attraction or 'under-dispersed') or less closely related (called repulsion or 'over-dispersed') (Cavender-Bares *et al.* 2004). Moreover, the theory hypothesizes that the degree of phylogenetic relatedness in a community varies in a predictable way and depends on two conditions: first, whether interspecific competition or environmental filtering (i.e. exclusion of intolerant species) is the dominant ecological process and secondly, whether functional traits of species tend to be evolutionarily conserved (similar among related taxa) or convergent (similar among distantly related taxa) across the phylogeny (Bloomberg, Garland & Ives 2003; Kraft *et al.* 2007). The theory suggests that when traits are conserved, filtering should select for related species with common traits that can tolerate environmental conditions, while competition should select for distantly related taxa that can coexist due to decreased trait overlap. In contrast, when traits are convergent, theory suggests that environmental filters should assemble communities of distantly related species that share common traits, while

competition should drive the assembly of related communities with little trait overlap.

Among plants, evolutionary trait conservatism is a common and widespread mode of evolution (Lord, Westoby & Leishman 1995; Prinzing *et al.* 2001; Patterson & Givnish 2002; Chazdon *et al.* 2003; Ackerly 2004; Swenson *et al.* 2007). However, because spatial scale, the evolutionary time separating nearest common ancestors, and different evolutionary forces can lead to a broad range of trait evolution, the conservation of niches across taxa should not be considered as the default model of evolution (Ackerly & Reich 1999; Cavender-Bares *et al.* 2004; Losos 2008).

Despite the attention received by phylogenetic community assembly (e.g. Kraft *et al.* 2007; Hardy 2008; Cavender-Bares *et al.* 2009; Kembel 2009; Vamosi *et al.* 2009; Cadotte *et al.* 2010), key aspects of the theory remain untested. For example, even though both phylogenetic attraction and repulsion have been demonstrated to operate simultaneously within communities (Anderson, Lachance & Starmer 2004; Cavender-Bares *et al.* 2004; Kembel & Hubbell 2006; Lovette & Hochachka 2006; Helmus *et al.* 2007), the hypothesis that communities should essentially flip from phylogenetic over- to under-dispersion across a gradient of shifting ecological processes (i.e. from abiotic filtering to competition) has not been fully tested under natural conditions. In addition, the empirical results of phylogenetic community assembly are mixed: reports vary from no signal (e.g. Silvertown *et al.* 2006), to significant phylogenetic dispersion, both over- and under- (Anderson, Lachance & Starmer 2004; Cavender-Bares *et al.* 2004; Kembel & Hubbell 2006; Lovette & Hochachka 2006; Helmus *et al.* 2007; Verdu & Pausas 2007), and effects being derived from facilitation (Valiente-Banuet & Verdu 2007) as well as competition and filtering.

The disparate results from the literature may arise because of a high degree of among-community variation in processes that govern community assembly; i.e. from filters, competition, facilitation and dispersal (Kembel 2009). Another reason for the lack of consensus among results in the literature could be due to the simplification of inherently complex multivariate gradients that influence the way that traits respond to the environment and interact with each other. Understandably, gradients are often represented by the dominant abiotic variable and rarely incorporate environmental interactions (e.g. direct versus indirect effects). Yet another possible reason for inconsistent results is proposed by Mayfield & Levine (2010): when competition predominates, it can have quite different effects on communities, resulting in the exclusion of species with either similar or dissimilar traits. As an example, Mayfield & Levine (2010) describe a system in which plant species compete along two primary axes, a soil texture gradient and a light competition gradient. Across the soil texture gradient, competitive exclusion eliminates species that overlap too much in their preference for a particular soil texture due to niche differences, leading to high-trait variability among competitive dominates. In contrast, across the light competition gradient, taller species can eliminate shorter species because of superior competitive ability, resulting in low trait variability among competitively

dominant species. Thus, the effects of competition are difficult to discriminate from environmental filtering, especially when exclusion occurs due to differences in competitive ability.

Serengeti National Park (SNP) in Tanzania is characterized by a relatively long, uninterrupted ecological gradient that matches closely the hypothetical gradients described by Mayfield & Levine (2010). The annual cycle of wet season herbivory by migratory ungulates in the Serengeti planes, combined with a prominent dry season and a rain shadow from the Ngorongoro crater highlands, has produced a striking gradient in standing plant biomass that increases from south-east to north-west. Grasses in the Serengeti planes to the south-east are < 20 cm high throughout the year and experience little light competition, while grasses in the north-west can exceed 1 m in height and are commonly limited by light competition (McNaughton 1983, 1985). Counter to this water availability gradient is a gradient in elevation that slopes down from the crater highlands in the south-east towards Lake Victoria in the west. Due to the rich, fine-particulate, volcanic soils associated with the highlands in the south-east, elevation is positively correlated with soil nutrients and texture, meaning that elevation is a decent proxy for soil fertility (see Appendix S1 in Supporting Information). Thus, as rainfall increases from the planes to the north-west, the factors that limit plant growth gradually change from plant-available water and herbivory to competition for light with other plants (McNaughton 1983, 1992; Dyer *et al.* 1991; Hartvigsen & McNaughton 1995). As a result, plants experience a trade-off between environmental and competitive adversity across the Serengeti environmental gradient; according to phylogenetic community assembly, this should be associated with a change in genetic relatedness across the same gradient.

The goal of this study was to determine if phylogenetic community assembly could explain the co-occurrence of species among the rich graminoid communities spanning an ecological gradient in the Serengeti ecosystem. First, we explore patterns of trait evolution (i.e. conservatism, Brownian or convergence) for specific leaf area (SLA) and maximum plant height, two key traits known for their functional importance in plants (Westoby 1998) but which have special significance for herbaceous species along the Serengeti environmental gradient. Our hypothesis is that traits will show Brownian evolution, if not phylogenetic niche conservatism. Subsequently, we ask whether mean phylogenetic distance (MPD) varies across abiotic gradients in Serengeti as predicted by phylogenetic community assembly theory. We predict that in seasonally dry sites, harsh conditions (drought and herbivory) will limit the range of traits that are viable in these areas, leading to phylogenetic under-dispersion. This is consistent with studies showing a relatively small and stable pool of species that can colonize and persist under these conditions (Belsky 1985; Anderson 2008). At wet, productive sites, where competitive exclusion is expected, phylogenetic community assembly theory predicts phylogenetic over-dispersion (Webb *et al.* 2002). However, as species are likely to compete strongly for light at these sites, it is conceivable that tall, low-SLA species will exert competitive dominance over inferior species leading to phylogenetic clus-

tering (Mayfield & Levine 2010). We address these hypotheses within the framework of a multivariate model that incorporates relationships among environmental variation, trait dispersion, species richness and MPD.

Materials and methods

STUDY SYSTEM

Our study was conducted in Serengeti National Park, Tanzania, part of the *c.* 30 000 km^2 Serengeti ecosystem. The major ecological characteristics of the ecosystem, such as the savanna nature of the vegetation, are believed to have existed throughout much of the Pleistocene (Peters *et al.* 2008). We focus our analyses on grasses because they typically account for > 85% of the above-ground herbaceous biomass across plots in SNP (Anderson, Metzger & McNaughton 2007), they are species rich with several multispecies genera, and they are characterized by trait and life-history variation ideal for investigating community assembly while controlling for effects of taxonomic scale, which can have pronounced influence on DNA sequence similarity (Cavender-Bares *et al.* 2009).

GRASSLAND VEGETATION SAMPLING

Grassland plant community composition was studied at 133 sites across the Serengeti environmental gradient; these sites have been the focus of prior research on Serengeti plant communities (Anderson, Metzger & McNaughton 2007; Anderson 2008). Each site consisted of one 50 × 20 m Modified-Whittaker plot (MWP) constructed from a series of ten 1-m^2 plots within the 1000 m^2 whole plot. Here, we focus on the presence of plant species recorded within the 1-m^2 plots; additional information on sampling techniques and site locations can be found elsewhere (Anderson, Metzger & McNaughton 2007).

TRAIT SAMPLING AT CORE SITES

At eight study sites widely dispersed across the ecosystem (Anderson 2008), hereafter referred to as core sites, morphological measurements were collected from a total of 52 focal grass species; these focal species account for > 86% of the total basal area covered by all plant species encountered during the study (including grasses, forbs, trees, etc.). For each focal species encountered at each core site, five individuals were randomly located inside the plot and measured for SLA and maximum height. These traits were chosen because they represent different grass allocation strategies (Westoby 1998) and, in the case of SLA, are identified with the world-wide leaf economics spectrum (Shipley *et al.* 2006). We also emphasize these traits because they are a proxy for grass life-history variation in SNP. For example, in a separate laboratory experiment on 15 Serengeti grass species, SLA was correlated with defoliation tolerance and species growth rate (see Appendix S1), while maximum height correlates with the position of a species along an axis from strong light competitors that are grazing intolerant to poor light competitors that are tolerant of herbivory (Hartvigsen & McNaughton 1995). Specific leaf area was calculated by dividing leaf area by leaf dry weight (m^2 kg^{-1}). Leaf area was determined with the software SigmaScan (Systat Software Inc., San Jose, CA, USA) by analysing digital photographs of 3–5 fully expanded leaves from each individual. Leaves were photographed under plate glass on a white background adjacent to rectangles of known area to correct for focal length. Leaves were dried at 70 °C and weighed to the nearest 0.1 mg on a digital

balance. Maximum height was measured at each site as the maximum leaf height of five ungrazed adult plants. For both SLA and maximum plant height, field collected trait averages were highly correlated with average trait values of the same species raised under identical conditions in a controlled environment, demonstrating that despite phenotypic plasticity that may occur, our trait measurements were highly representative of differences among species (see Appendix S1).

PHYLOGENETIC RECONSTRUCTION

Fresh leaf tissue was collected from 52 grass species (see Appendix S2) across the eight core study sites. Samples were preserved in silica gel until DNA was extracted. For all 52 accessions, regions of the chloroplast genome were initially screened to identify a region that would provide enough characters to genetically separate all of the taxa (Shaw *et al.* 2005). In the end, the *psbA-trnH*^{GUG} intergenic spacer region and sequences from the *rpL16* intron region of the chloroplast sufficiently resolved evolutionary relationships among our taxa. Specific laboratory methods are reported in Appendix S3.

CONSTRUCTION AND TESTING OF THE INITIAL HYPOTHESES

Our first step was to evaluate evolutionary patterns of SLA and maximum height across the tips of the phylogeny. We then evaluated the abundance phylogenetic deviation index (APD), which tests for non-random patterns of abundance across a phylogeny (Hardy 2008). Non-random phylogenetic abundance patterns create bias in the randomizations used to identify phylogenetic under- and over-dispersion. Subsequently, we tested the hypothesis that community phylogenetic distance is influenced by trait dispersion, which itself is under environmental control. Our initial hypothesis was that traits would show Brownian trait evolution, if not phylogenetic conservatism, due to the prominence of trait conservatism in plant traits across wider taxa (Patterson & Givnish 2002; Chazdon *et al.* 2003; Ackerly 2004). Moreover, we hypothesized that species would be included or

excluded from sites because of abiotic filters and competitive interactions that act upon species' traits (Webb *et al.* 2002; Cavender-Bares *et al.* 2004). In addition, we hypothesized that abiotic filters and competitive interactions would change across gradients of rainfall, seasonality and soil fertility. For example, we hypothesized abiotic filtering at dry sites would select for species with similar traits and thus promote phylogenetic under-dispersion. In contrast, at wet, productive sites, phylogenetic community assembly predicts that the increasing strength of light competition should drive differences between species light capturing ability (e.g. height and SLA), thus promoting phylogenetic over-dispersion. On the other hand, differences in species' competitive ability at productive sites may select for a single, successful strategy: tall species with low SLA (Mayfield & Levine 2010).

Patterns of trait evolution across the phylogeny for SLA and height were tested with the K-statistic (Bloomberg, Garland & Ives 2003) using the R-package PICANTE (Kembel *et al.* 2008). Patterns of dispersion for MPD were tested for significance with the software PHYLOCOM (Webb, Ackerly & Kembel 2008). Mean trait distances were tested for significant under- and over-dispersion using separate randomization tests in R (version 2.10.1). To explore the relationships among phylogenetic patterns, traits and environmental variation, MPD and trait distances were regressed against average annual rainfall, proportion of dry season rainfall and elevation, all identified as key environmental gradients affecting patterns of plant diversity in the Serengeti (McNaughton 1983; Anderson, Metzger & McNaughton 2007). Elevation was included because it is a strong proxy for soil and landscape variation across the system, such as soil nutrient status (see Appendix S1).

We recognize that trait dispersion and phylogenetic distance are influenced by the number of species within a sample. For example, trait and phylogenetic distances tend to increase as more species are included in a sample. This is analogous to a 'sampling effect' in biodiversity research that can bias analyses aimed at understanding variation in trait and phylogenetic distance. Consequently, we explicitly control for sampling effects by including species richness in a multivariate analysis using structural equation modelling (Grace *et al.* 2010). We evaluated an *a priori* model (Fig. 1) that
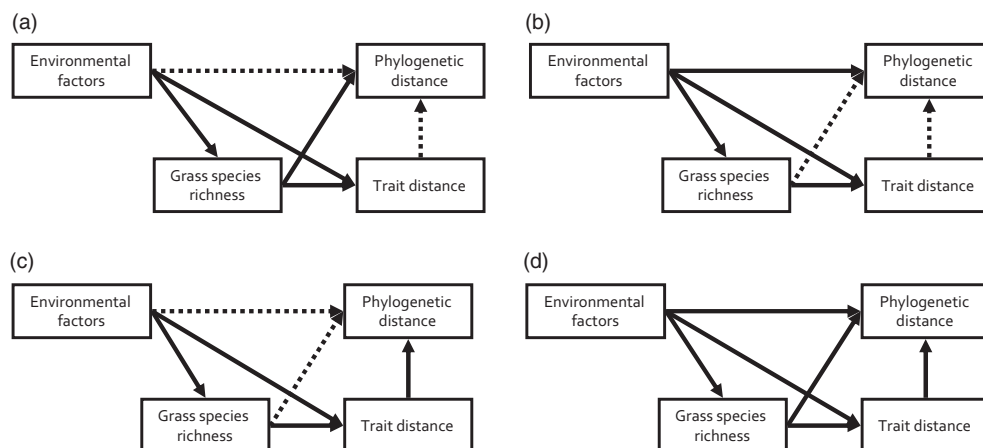

Fig. 1. *A priori* multivariate models relating environmental variation, species richness and trait distance to mean phylogenetic distance (MPD) of plant communities across an environmental gradient in Serengeti National Park (see Appendix S3). Model A occurs when spurious correlations among environmental variables, trait distances and MPD are explained by direct effects of species richness on MPD. Model B occurs when environmental variables, but not trait relationships, directly explain variation in MPD. Model C occurs when traits directly affect MPD, while environmental variation and species richness have only indirect effects on MPD. Model D occurs when some combination of traits, environmental variation and species richness directly explain variation in MPD across plots. Arrows represent either statistically significant (solid lines) or insignificant (dashed lines) effects of one variable on another.
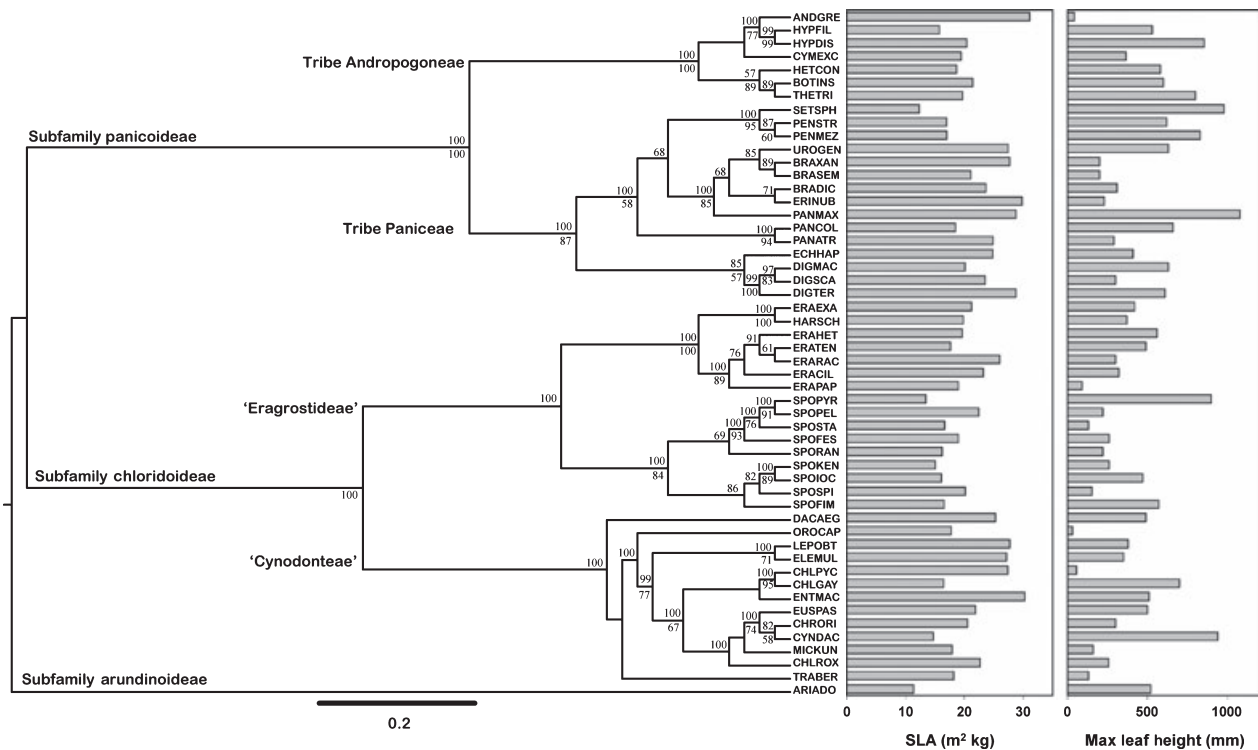
Fig. 2. Phylogenetic reconstruction of 52 Serengeti grasses based on two non-coding chloroplast DNA regions (see Appendix S3). Grey bars to the right represent average SLA (m^2 kg^{-1}) and maximum height (mm) values based on five replicate samples at eight widely dispersed sites across Serengeti (see methods).

distinguished between direct and indirect effects of environmental factors, trait relationships and species richness on MPD across plots (see Appendix S3).

Results

PHYLOGENETIC RECONSTRUCTION

The final structure of the phylogeny was extremely consistent with the current, accepted relationships among clades in the Poaceae and among taxa within the major clades (Fig. 2); a more detailed comparison between our phylogeny and previously published works appears in Appendix S3.

PATTERNS OF TRAIT EVOLUTION AND ABUNDANCE PHYLOGENETIC DEVIATION

As expected, the distribution of maximum plant height across the tips of the phylogeny was consistent with Brownian evolution (Fig. 2; $K = 0.341$; observed variance $= 4.03 \times 10^6$; randomized variance $= 3.95 \times 10^6$; $P = 0.64$). In contrast however, the distribution of SLA values across the tips of the phylogeny showed a significant pattern of phylogenetic convergence (Fig. 2; $K = 0.597$; observed variance $= 1057.7$; randomized variance $= 1420.9$; $P = 0.032$). This unexpected result demonstrates that SLA values for Serengeti grasses are more highly differentiated within clades than among different clades. Species abundances were randomly distributed across the phylogeny, as indexed by an abundance phylogenetic devi-

ation (APD) that was not significantly different from zero for either species frequency (APD $= -0.009$; 95% CI -0.043 to 0.023) or percentage cover (APD $= 0.017$; 95% CI -0.075 to 0.059). Thus, subsequent randomization tests used to identify statistically significant phylogenetic over- and under-dispersion were not biased by the abundances of taxa.

MEAN PHYLOGENETIC DISTANCE ACROSS SITES

Across all 1-m^2 plots, MPD showed essentially no univariate relationships with average annual rainfall, the average proportion of dry season rainfall or elevation (Fig. 3). However, when only significantly non-random plots are considered (filled circles in Fig. 3), over-dispersed plots tend to occur at higher average annual rainfall, proportion dry season rainfall and elevation compared with under-dispersed plots (regression lines in Fig. 3). Notably, these effects are strongest for elevation and weakest for average annual rainfall. However, contrary to our expectation that under- and over-dispersed sites would only occur at the extremes of the environmental gradient, many of the statistically under- and over-dispersed sites occurred at intermediate positions along the environmental gradients (Fig. 3), suggesting that covariation among environmental variation may contribute to the distribution of MPD across sites. The structural equation model (SEM) presented in the following section provides a multivariate framework for understanding the variation in MPD across sites, with standardized path coefficients presented to facilitate comparisons among effects.
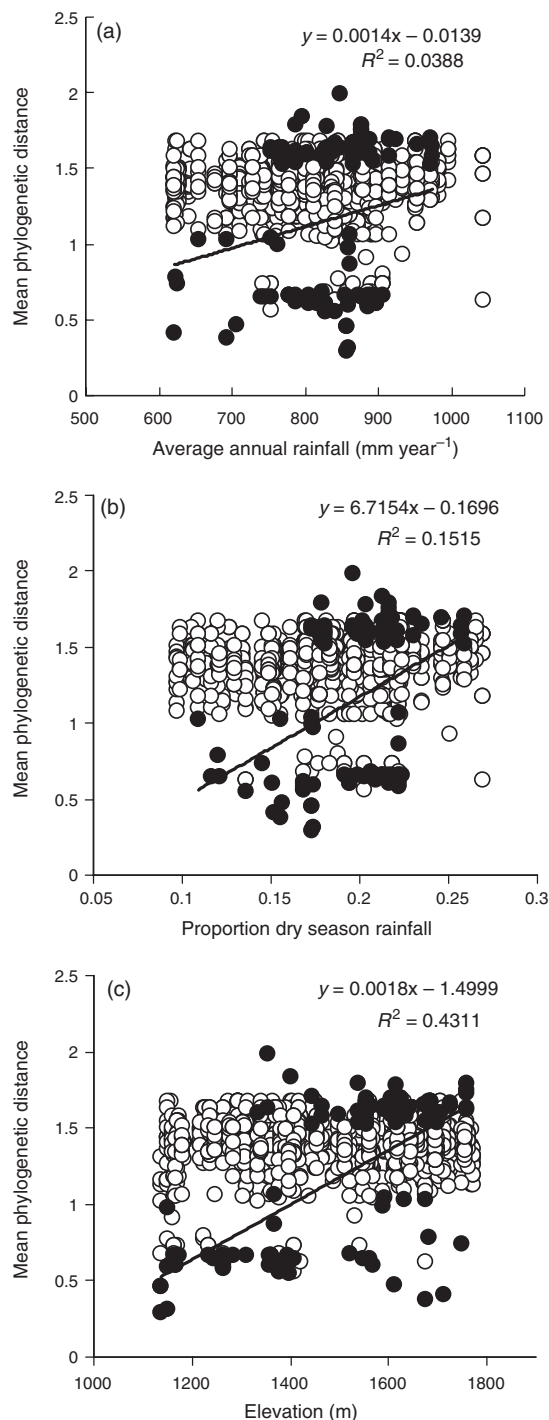
Fig. 3. Bivariate scatter plots showing mean phylogenetic distance (MPD) within 1 m² plots across Serengeti as a function of rainfall (a), average proportion of dry season rainfall (b) and elevation (c). Points represent plots that show random MPD (unfilled circles) or statistically significant over- or under-dispersion (filled circles). Equations and lines are from best-fit regressions for the over- and under-dispersed plots only.

STRUCTURAL EQUATION MODELLING PREDICTING MPD

After eliminating insignificant paths, the final SEM was not significantly different from the *a priori* model ($\chi^2 = 5.88$,

d.f. = 5, $P = 0.32$, AIC = 51.88; see Appendix S3). The final accepted model was most consistent with the *a priori* model C (Fig. 1), in which variation in MPD is largely controlled by trait distances with plots. Inclusion of a relatively weak correlation between elevation and MPD (curved arrow in Fig. 1) strongly improved the model fit and suggests additional, potentially indirect, influence of soil characteristics (fertility or texture). The variation explained in MPD across all plots ($R^2 = 0.17$, Fig. 4), while not substantial, was far superior to any of the univariate relationships considering all plots and only a single environmental axis (Fig. 3). Additionally, the results suggest that univariate relationships (Fig. 3) are actually mediated by relationships between traits and the environment. Across sites in the Serengeti, average rainfall and proportion dry season rainfall are correlated with elevation and strongly correlated themselves (curved arrows in Fig. 4). Grass species richness increased with average annual rainfall, but also with increasing elevation. As expected, plots with greater grass species richness were associated with larger trait distances in SLA and maximum plant height. Moreover, SLA and plant height, which were themselves both response variables and predictors of MPD, showed a positive correlation. After controlling for covariation among environmental variables and species traits in the SEM, environmental variables had largely indirect effects on MPD, which were mediated by their effects on either SLA or maximum plant height (Fig. 4).

Despite a large bivariate correlation between average annual rainfall and proportion dry season rainfall, these variables had different direct effects on trait distances in the model. Dry season rainfall had a strong direct negative effect on SLA trait distance among species, while a lesser direct negative effect on plant height trait distance. Across all plots, average plant height increased and average SLA decreased with greater proportion dry season rainfall (average plant height = $459.7 \times$ P-DRY + 457.1, $F_{1,132} = 9.81$, $P = 0.0021$, $R^2 = 0.07$; average SLA = $-13.4 \times$ PDRY + 22.0, $F_{1,132} = 28.6$, $P < 0.0001$, $R^2 = 0.18$), with comparable relationships between these traits and rainfall (average SLA $R^2 = 0.13$; average plant height $R^2 = 0.16$; equations not shown). Moreover, the SD of maximum plant height and SLA decline with greater proportion dry season rainfall (plant height SD = $-259.3 \times$ PDRY + 271.5, $F_{1,132} = 10.2$, $P = 0.0018$, $R^2 = 0.07$; SLA SD = $-10.9 \times$ PDRY + 5.5, $F_{1,132} = 23.5$, $P < 0.0001$, $R^2 = 0.15$). Thus, as moisture availability increases, species assemblages are limited to a smaller range of maximum plant heights (e.g. taller) and SLA (e.g. denser leaves), despite having more species.

The strongest direct effects on MPD within the context of the model were those from the average trait distance of SLA and plant height. However, SLA and maximum height had opposite direct effects on MPD, apparently due to different patterns of trait evolution. These results suggest that the trait relationships themselves are directly affecting MPD within plots and that environmental factors influence MPD indirectly through their effects on trait distances among species.
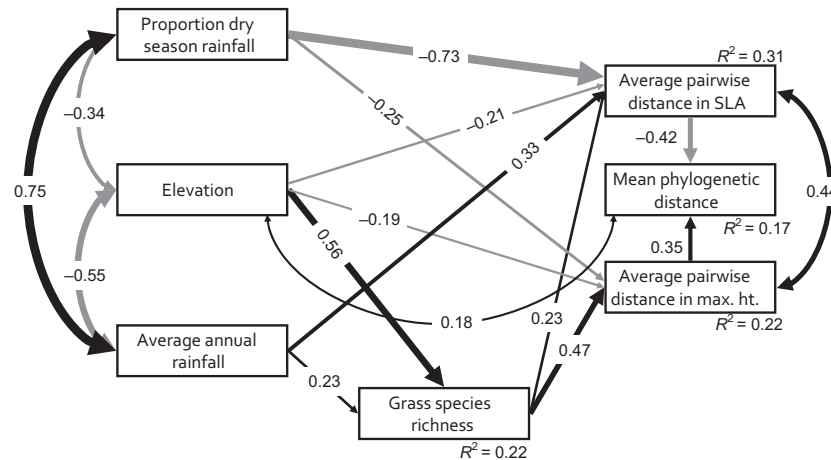
Fig. 4. Final structural equation model showing multivariate relationships among environmental variables, species richness, mean trait distances and mean phylogenetic distances. Curved arrows represent correlations, straight arrows represent direct effects while the values are either positive (black lines) or negative (grey lines) standardized path coefficients. The model was not significantly different from the *a priori* model after deleting all non-significant paths (χ^2 = 5.88, d.f. = 5, *P* = 0.32, AIC = 51.88). Note that data were averaged by site (*n* = 133) prior to analysis with SEM to avoid sample size inflation and pseudoreplicate (see Appendix S3).

Discussion

According to the theory of phylogenetic community assembly (e.g. Webb *et al.* 2002) when species' traits are evolutionarily conserved, MPD should vary from under- to over-dispersed across an environmental gradient such as the one in the Serengeti ecosystem. The pattern of MPD among dominant savanna grasses that we observed across plots in the Serengeti was weak (Fig. 3), but varied in a way that was consistent with theory: under-dispersed plots tend to occur in dry, seasonal sites while over-dispersed plots tend to occur in moist, less-seasonal sites. When tested with a multivariate model based on interactions among environmental factors, species richness and plant traits, the results were stronger, explaining 17% of the variation in MPD. While this is only a modest amount of variance explained, it is a considerable improvement over univariate models, which only minimally (if at all) account for variation in MPD. It is conceivable, if not highly likely, that the inclusion of seed size data, the third axis of Westoby's (1998) leaf-height-seed plant strategy model, would provide an improved fit and greater variance explained. Even without seed size, the model provides general support for the application of phylogenetic data to understand community assembly, but in ways that differ from standard phylogenetic community assembly theory.

While the analysis revealed non-random patterns of phylogenetic distance within communities, several unexpected results emerged. First, phylogenetically over- and under-dispersed sites were found throughout the range of variation in rainfall, seasonality and elevation. According to our *a priori* expectation, over- and under-dispersed sites should occupy the extremes of the environmental gradient because these sites should be those typified by habitat filtering on the one end (dry, seasonal, high-elevation sites) and competition on the other (wet, less-seasonal, low-elevation sites).

A second unexpected result was that SLA and maximum height displayed different evolutionary trait relationships

across the tips of the phylogeny: phylogenetic convergence by SLA and Brownian evolution by maximum plant height. The expectation that plant traits behave according to Brownian evolution or even phylogenetic niche conservatism is widespread throughout ecology, even if this *a priori* expectation is not particularly justified (Losos 2008).

A third unexpected result was that, despite a strong bivariate correlation (*r* = 0.75; Fig. 4), average annual rainfall and proportion dry season rainfall had different direct and indirect influences in the models that were often off-setting in terms of their influence on mean trait distances and MPD within plots (see Appendix S4). This observation reveals an important point about variation among environmental factors that are themselves positively correlated. Ecological gradients are often composed of multiple, correlated abiotic factors (Grace *et al.* 2010); our results suggest that variation among correlated factors has subtle but important consequences for trait differences among species, and thus for the outcome of species interactions along gradients. In this instance greater rainfall was associated with larger average trait distances in SLA, indicating increased trait differences with great resource inputs. In contrast, a greater proportion of rainfall falling in the dry season was associated with smaller average trait distances, which suggests that less-seasonal sites are dominated by competitively dominate plants which are taller and have lower SLA (Mayfield & Levine 2010).

A fourth unexpected result was that elevation had a correlative relationship with MPD that significantly improved the model fit (Fig. 4). One possible explanation for this relation is that it results from unmeasured traits, such as roots or seed size, that respond to the strong variation in soil texture and fertility created by the Ngorongoro volcanic highlands in the south-eastern Serengeti and which is significantly correlated with elevation (see Appendix S1). Another plausible explanation is that grazing, which can be substantial in the low-eleva-

tion planes near Lake Victoria (McNaughton 1985), exerts a strong filter for species that cannot tolerate intense and repeated herbivory. This is consistent with the observation that average trait distances of both plant height and SLA decrease with elevation (Fig. 4), because the strong evolutionary selection pressure of grazing has selected for species of low stature and higher SLA (see Appendix S1).

Clearly the unexpected results just discussed are related, and we argue that weak bivariate relationships between MPD and environmental variation (unexpected result 1) is a consequence of functional traits with different evolutionary relationships (unexpected result 2) and environmental drivers that are themselves correlated but produce effects that obscure the bivariate relationship between any one factor and MPD (unexpected results 3 and 4). The offsetting effects of the environmental drivers are measured by the sum of their direct and indirect influences on MPD, which in this case are mediated by their effects on plant traits (Fig. 4; see Appendix S4). This is one of the primary advantages to using SEM in this type of analysis: univariate predictors rarely provide sufficient explanatory power across complex, natural gradients. An additional advantage was that, after accounting for the environmental effects, SEM was able to reveal the opposing forces of SLA and maximum leaf height on MPD. In systems characterized by multiple counteracting environmental gradients, such as with moisture availability and soil fertility in the Serengeti (Fig. 4), SEM provides a way to tease apart environmental effects on traits and MPD that are obscured in univariate space.

In a study across lakes in WI, USA, Helmus *et al.* (2007) showed that 11 species of sunfish showed no pattern of phylogenetic dispersion in the community data. However, analyses revealed that this observation was driven by simultaneous phylogenetic over-dispersion (called repulsion) and under-dispersion (called attraction) which obscured each other in the raw community data. Closely related species tended to co-occur in lakes of similar water clarity and latitude, but within lakes phylogenetic repulsion was apparent, which they hypothesized could be potentially caused by interspecific competition. Similarly, the lack of a phylogenetic signal among tropical rainforest trees within plots appears to be driven by the simultaneous interactions of opposing over- and under-dispersed traits within closely related species (Swenson & Enquist 2009). As in these studies, Serengeti grasses show divergent evolutionary patterns in two key plant life-history traits, SLA and maximum height, which have opposing effects in the assembly process that appear to operate in a hierarchical manner.

Conclusions and future directions

We propose it may be common that multivariate, hierarchical explanations are required to mechanistically explain what appears like noise or lack of a pattern in phylogenetic distance across ecological gradients (Silvertown *et al.* 2006; Helmus *et al.* 2007; Schamp, Chau & Aarssen 2008). Therefore, the finding of a random or weak phylogenetic signal does not imply the absence of a significant mechanism maintaining coexistence (Swenson & Enquist 2009). If this is the case, the original theory of phylogenetic community assembly may have to be revised to allow for the simultaneous effects of phylogenetic repulsion and attraction and the possibility that competition can favour both clustering and over-dispersion (Mayfield & Levine 2010).

Disagreement over the degree to which communities act according to 'assembly rules' based on traits and species interactions represents one of the better-known controversies in ecology (reviewed in Fox 1999). The possibility that species abundances and distributions are not mechanistically linked to their interactions with other species or adaptive traits was presented as a cruel dilemma faced by a majority of ecologists (*sensu* McNaughton 1983). Today, support for purely neutral theories as explanations of species abundances and calls to disintegrate the study of local communities entirely (e.g. Ricklefs 2008) continue to fuel this dilemma. The theory of phylogenetic community assembly provides a framework for diffusing this dilemma by integrating trait distributions and genetic relatedness across ecological gradients. Our study, and others (e.g. Anderson, Lachance & Starmer 2004; Cavender-Bares *et al.* 2004; Helmus *et al.* 2007; Swenson & Enquist 2009), suggest that incorporating data on adaptive traits and phylogenetic relationships, even at relatively small scales, provides insight in to the mechanisms that govern community composition. However, these studies also suggest that a multivariate, hierarchical framework is appropriate and may unify studies with seemingly inconsistent results.

References

Ackerly, D.D. (2004) Evolution of leaf form in the California chaparral: adaptation and community assembly. *American Naturalist*, **163**, 654–671.

Ackerly, D.D. & Reich, P.B. (1999) Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany*, **86**, 1271–1281.

Adler, P.B. (2004) Neutral models fail to reproduce observed species area and species time relationships in Kansas grasslands. *Ecology*, **85**, 1265–1272.

Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007) A niche for neutrality. *Ecology Letters*, **10**, 95–104.

Alonso, D., Etienne, R.S. & McKane, A.J. (2006) The merits of neutral theory. *Trends in Ecology and Evolution*, **8**, 451–457.

Anderson, T.M. (2008) Plant compositional change over time increases with rainfall in Serengeti grasslands. *Oikos*, **117**, 675–682.

Anderson, T.M., Lachance, M.A. & Starmer, W.T. (2004) The relationship of phylogeny to community structure: the cactus yeast community. *American Naturalist*, **164**, 709–721.

Anderson, T.M., Metzger, K.L. & McNaughton, S.J. (2007) Multi-scale analysis of plant species richness in Serengeti grasslands. *Journal of Biogeography*, **34**, 313–323.

Belsky, A.J. (1985) Long-term vegetation monitoring in the Serengeti National Park, Tanzania. *Journal of Applied Ecology*, **22**, 449–460.

Bloomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Cadotte, M.W., Davies, T.J., Regetz, J., Kembel, S.W., Cleland, E. & Oakley, T.H. (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters*, **13**, 96–105.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. (2004) Phylogenetic overdispersion in Floridian oak communities. *American Naturalist*, **163**, 823–843.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Chave, J. (2004) Neutral theory and community ecology. *Ecology Letters*, **7**, 241–253.

Chazdon, R.L., Careaga, S., Webb, C. & Vargas, O. (2003) Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecological Monograph*, **73**, 331–348.

Clark, J.S. (2009) Beyond neutral science. *Trends in Ecology and Evolution*, **24**, 8–15.

Clark, J.S., Dietze, M., Chakraborty, S., Agarwal, P.K., Ibanez, I., LaDeau, S. & Wolosin, M. (2007) Resolving the biodiversity paradox. *Ecology Letters*, **10**, 647–659.

Dyer, M.I., Acra, M.A., Wang, G.M., Coleman, D.C., Freckman, D.W., McNaughton, S.J. & Strain, B.R. (1991) Source-sink carbon relations in two *Panicum Coloratum* ecotypes in response to herbivory. *Ecology*, **72**, 1472–1483.

Fox, B. (1999) The genesis and development of guild assembly rules. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & P. Keddy), pp. 23–57. Cambridge University Press, Cambridge.

Gewin, V. (2006) Beyond neutrality – ecology finds its niche. *PLoS Biology*, **4**, e278.

Grace, J.B., Anderson, T.M., Olff, H. & Scheiner, S.M. (2010) On the specification of structural equation models for ecological systems. *Ecological Monographs*, **80**, 67–87.

Hardy, O.J. (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology*, **96**, 914–926.

Harpole, W.S. & Tilman, D. (2006) Non-neutral patterns of species abundance in grassland communities. *Ecology Letters*, **9**, 15–23.

Hartvigsen, G. & McNaughton, S.J. (1995) Trade-off between height and relative growth rate in a dominant grass from the Serengeti ecosystem. *Oecologia*, **102**, 273–276.

Helmus, M.R., Savage, K., Diebel, M.W., Maxted, J.T. & Ives, A.R. (2007) Separating the determinants of phylogenetic community structure. *Ecology Letters*, **10**, 917–925.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, **12**, 949–960.

Kembel, S.W. & Hubbell, S.P. (2006) The phylogenetic structure of a neotropical forest tree community. *Ecology*, **87**, S86–S99.

Kembel, S., Ackerly, D.D., Blomberg, S., Cowan, P., Helmus, M. & Webb, C. (2008) Picante: Tools for Integrating Phylogenies and Ecology, Version 0.4-0.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist*, **170**, 271–283.

Leigh, E.G. (2007) Neutral theory: a historical perspective. *Journal of Theoretical Biology*, **20**, 2075–2091.

Levine, J.M. & HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature*, **461**, 254–256.

Lord, J.M., Westoby, M. & Leishman, M.R. (1995) Seed size and phylogeny in six temperate floras: constraints, niche conservatism and adaptation. *American Naturalist*, **146**, 349–364.

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology letters*, **11**, 995–1003.

Lovette, I.J. & Hochachka, W.M. (2006) Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology*, **87**, S14–S28.

Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.

McNaughton, S.J. (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs*, **53**, 291–320.

McNaughton, S.J. (1985) Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs*, **55**, 259–294.

McNaughton, S.J. (1992) Laboratory-simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. *Ecology*, **73**, 170–182.

Patterson, T.B. & Givnish, T.J. (2002) Phylogeny, concerted convergence, and phylogenetic niche conservatism in the core Liliales: insights from rbcL and ndhF sequence data. *Evolution*, **56**, 233–252.

Peters, C.R., Blumenshine, R.J., Hay, R.L., Marean, C.W., Livingstone, D.A., Armour- Chelu, M., Andrews, P., Bernor, R., Bonnefille, R., Harrison, T. & Werdelin, L. (2008) Paleoecology of the Serengeti-Mara ecosystem. *Serengeti III: Human Impacts on Ecosystem Dynamics* (eds A.R.E. Sinclair, C. Packer, S.A.R. Mduma & J. Fryxell), pp. 47–94. University of Chicago Press, Chicago.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London, Series B*, **1483**, 2383–2390.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *American Naturalist*, **172**, 741–750.

Schamp, B.S., Chau, J. & Aarssen, L.W. (2008) Dispersion of traits related to competitive ability in an old-field plant community. *Journal of Ecology*, **96**, 204–212.

Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R. (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany*, **92**, 144–166.

Shipley, B., Lechowicz, M.J., Wright, I. & Reich, P.B. (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, **87**, 535–541.

Silvertown, J., McConway, K.J., Gowing, D.J., Dodd, M.E., Fay, M.F., Joseph, J.A. & Dolphin, K. (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society of London, Series B*, **273**, 39–44.

Swenson, N.G. & Enquist, B.J. (2009) Opposing assembly mechanisms in a neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, 2161–2170.

Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.

Valiente-Banuet, A. & Verdu, M. (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, **10**, 1029–1036.

Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, **18**, 572–592.

Verdu, M. & Pausas, J.G. (2007) Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, **95**, 1316–1323.

Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098.

Webb, C.O., Ackerly, D.D., Mcpeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.

Supporting Information

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

Appendix S1. Supplemental figures pertaining to the assembly of plant communities along an environmental gradient in the Serengeti ecosystem.

Appendix S2. Table of grass species used in the phylogenetic analysis of community assembly across the Serengeti ecosystem.

Appendix S3. Supplemental methods, results and discussion pertaining to the assembly of plant communities along an environmental gradient in the Serengeti ecosystem.

Appendix S4. Tables of standardized direct, indirect and total effects from the structural equation model analysis.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.