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Citation	Griffith, D. M., Anderson, T. M., Osborne, C. P., Strömberg, C. A. E., Forrestel, E. J., & Still, C. J. (2015). Biogeographically distinct controls on C_3 and C_4 grass distributions: merging community and physiological ecology. Global Ecology and Biogeography, 24(3), 304–313. doi:10.1111/geb.12265
DOI	10.1111/geb.12265
Publisher	John Wiley & Sons Ltd.
Version	Accepted Manuscript
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Article Title: Biogeographically distinct controls on C_3 and C_4 grass distributions: merging community and physiological ecology

Authors:

Daniel M. Griffith; Department of Biology, Wake Forest University, Winston-Salem, NC, 27109, USA; grifdm1@wfu.edu

T. Michael Anderson; Department of Biology, Wake Forest University, Winston-Salem, NC, 27109, USA; anderstm@wfu.edu

Colin P. Osborne; Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK; c.p.osborne@sheffield.ac.uk

Caroline A.E. Strömberg; Department of Biology & Burke Museum of Natural History and Culture, University of Washington, WA, 98195, USA; caestrom@u.washington.edu

Elisabeth J. Forrestel; Department of Ecology and Evolution, Yale University, New Haven, CT, 06520, USA; elisabeth.forrestel@yale.edu

Christopher J. Still; Forest Ecosystems and Society, Oregon State University, Corvallis, OR, 97331, USA; chris.still@oregonstate.edu

Short running title (45): **Climate disequilibrium in C_4 grass distributions**

Keywords: **Biogeography, C_3, C_4, crossover temperature, tree cover, invasive, fire**

Type: **Research Paper**

Number of words in the abstract including key words (10): **300** of 300

Main text, including Biosketch (32): **5632** of 5000

Number of references: **50** of 50

Number of figures: **4** of 6

Tables: **1**

Corresponding author:

Daniel M. Griffith

048 Winston Hall; 1834 Gulley Dr.

Department of Biology, Wake Forest University

Winston-Salem, NC, 27109, USA

Email: grifdm1@wfu.edu; Tel: (910) 545-0632; Fax: (336) 758-6008

ABSTRACT

Aim C_4 photosynthesis is an adaptation that maintains efficient carbon assimilation in warm and low-CO_2 conditions. Due to the importance of C_4 grasses for carbon and surface energy fluxes numerous models have been proposed to describe their spatial distribution and forecast responses to climate change. These models often rely on broad climate predictors (e.g., temperature and precipitation) but fail to integrate other ecologically relevant factors, such as disturbance and competition, which may modify realized C_3/C_4 grass distributions. We evaluate the contribution of ecological factors, in addition to climate predictors, to C_3/C_4 grass distributions across multiple biogeographic regions of North America in a multi-source database of >40,000 vegetation plots.

Location Conterminous United States of America (USA).

Methods We identified a comprehensive pool of physiological-climatic models in the literature and used information theoretic criteria to select a primary physiological predictor of C_3 and C_4 grasses. Subsequently, the climate model was combined with ecological predictors using a multiple regression framework and tested within eight regions within the USA.

Results Surprisingly, grass-dominated communities across the USA exist largely in a C_3 or C_4 dominated state. Transitions between C_3/C_4 dominance were best explained by models that integrated temperature and precipitation with ecological factors that varied according to region. For some regions, such as Eastern Temperate Forests, local, ecological factors were comparable in strength to broad climate predictors of C_3/C_4 abundance.

Main conclusion Local, ecological factors modify C_3/C_4 grass responses to broad-scale climatic drivers in ways that manifest at regional scales. In Eastern Temperate Forests, for example, C_4 grass abundances are maintained below climatic expectations where tree cover creates light

limitation, but above expectations where frequent fires reduce tree cover. Thus, local ecological factors contribute to major among-region differences in the climate responses of C_3/C_4 grasses.

Main Text:

INTRODUCTION

As humans continue to modify ecosystems and alter the Earth's climate, predicting future species' distributions and shifting range limits has become a paramount goal in ecology. Many contemporary methods for modeling species distributions (e.g., climate envelope, process-based) are largely based on the assumption that species' physiological tolerances to environmental variation (e.g. temperature, precipitation, etc.) determine species occupancy across the landscape (Merow *et al.*, 2013). However, an alternative perspective argues that local ecological processes (e.g. disturbance, predation, facilitation, storage effects) interact with species' ecophysiological and life history traits to determine species distributions (e.g., Callaway, 1995; Weiher & Keddy, 1995; Araújo & Pearson, 2005; Maestre *et al.*, 2009). Approaches that merge species distribution modeling based on physiological tolerances to variation in climate with community ecological theory (e.g., Guisan & Rahbek, 2011; Scheiter *et al.*, 2013) show tremendous promise in predicting species distributions, as well as assessing the contributions of relevant abiotic and biotic drivers (Araújo *et al.*, 2013). However, integrative methods are not commonly applied in contemporary modeling approaches, especially at large scales (Araújo & Rozenfeld, 2014).

The Poaceae (grasses) are a cosmopolitan family of flowering plants that dominate the herbaceous layer of several major biomes which together cover as much as half the Earth's land surface (grasslands, savannas and managed rangelands - Asner *et al.*, 2004). A central factor determining the primary production of grass-dominated ecosystems is the proportion of species that fix carbon using the C_4 photosynthetic pathway. This is because C_4 species have evolved an efficient mechanism for reducing the negative effects of photorespiration in warm climates compared to C_3 species (Ehleringer *et al.*, 1997), creating differences in carbon capture, water use, phenology, and quantum yield (Still *et al.*, 2003a,b; Randerson *et al.*, 2005; Taylor *et al.*, 2010, 2014). In contrast, C_3 grasses have a competitive advantage in cool environments where photorespiration is reduced (Sage, 2004). As such, C_3 and C_4 grasses are often observed to segregate along temperature gradients; historically, broad-scale climate predictors such as temperature and precipitation have been seen as the predominant determinants of C_3/C_4 grass distribution. While, local, and often stochastic, factors like fire, herbivory, and competition (in addition to temperature) are known to modify the C_3:C_4 grass ratio (e.g., Heckathorn *et al.*, 1999), these various drivers have not been incorporated into a single framework for predicting C_3/C_4 grass distributions. Thus, the history of climate-based research combined with community ecological research on C_3 and C_4 grasses provides an ideal system for testing models that merge physiological and ecological processes in order to predict the abundance and distribution of these functional types.

Several studies have investigated the distribution of C_3 and C_4 grasses along temperature gradients across a range of spatial scales. Teeri & Stowe (1976) first showed that the percentage of C_4 grass species in regional floras was closely tied to the minimum July temperature and the length of the frost-free period, suggesting that cold growing season temperatures limit C_4 grasses (while warm temperatures favor them). Numerous other studies have confirmed a role for temperature in C_4 grass distributions (reviewed in Ehleringer *et al.*, 1997; Sage *et al.*, 1999). However, additional factors such as soil texture (Epstein *et al.*, 1997) and growing season precipitation (Paruelo & Lauenroth, 1996; Winslow *et al.*, 2003; Murphy & Bowman, 2007; von

Fischer *et al.*, 2008) often add considerably to explained variance and to predicting the spatial distribution of C_3 or C_4 grasses.

The prevailing physiological hypothesis for explaining temperature-driven patterns of grass functional-type distributions is that C_3 and C_4 species differ in the temperature sensitivity of their quantum yield (the amount of carbon fixed per unit of light absorbed; Ehleringer *et al.*, 1997). At higher temperatures C_3 quantum yield is reduced by photorespiration while at lower temperatures the additional energetic requirements of the C_4 carbon concentrating mechanism generally result in lower quantum yield for C_4 grasses (Ehleringer, 1978). This model implies the existence of a ‘crossover temperature’ at which the photosynthetic gains of C_3 and C_4 grasses are equal; above this temperature, C_4 grasses have higher photosynthetic and growth rates, whereas the opposite holds below this crossover temperature. For global-scale distribution and carbon models, crossover temperatures have been combined with assumptions about the minimum quantity of precipitation necessary for grass growth to predict the climates in which C_4 or C_3 grasses should dominate. The resulting prediction is that in months with mean air temperature $\geq$ 22 °C and rainfall >25 mm C_4 should out-compete C_3 grasses (Collatz *et al.*, 1998; Still *et al.*, 2003a). However, studies which take a phylogenetic approach have found that air temperature does not always explain the distributions of closely related C_4 and C_3 species, implying that thermal adaptations in grasses may be indirectly associated with photosynthetic functional type (Edwards & Still, 2008; Pau *et al.*, 2013; Still *et al.*, 2013).

Where C_4 and C_3 grasses coexist, C_3 grasses may gain a competitive advantage if they can acquire resources (e.g. space, nutrients) early in the growing season before C_4 plants become most active (Ode *et al.*, 1980; Barnes *et al.*, 1983; Tieszen *et al.*, 1997). Conversely, locations with cool spring/fall seasons that should favor C_3 grasses may be completely dominated by C_4 grasses which preempted resources during the warm summer season (Tieszen *et al.*, 1997). These seasonal competitive effects have the potential to promote dominance of grasses that are not climatically favored at a given location and time. Similarly, in forested areas, shading from trees also has potential to favor C_3 grasses over C_4 because they generally have a carbon gain advantage under low light conditions (Sage *et al.*, 1999; Peterson *et al.*, 2007).

Several other traits related to photosynthetic pathway alter the competitive interactions between C_3 and C_4 grasses, such as how species respond to disturbances such as herbivory and fire (Monson *et al.*, 1983; Heckathorn *et al.*, 1999). Compared to C_3 grasses, C_4 species are often better equipped for rapid regrowth in the high-light conditions following defoliation (Heckathorn *et al.*, 1999). Furthermore, C_4 grasses in savannas are believed to express traits that promote understory fires, such as leaf flammability, which then maintain high light environments by reducing tree cover in savannas (Ratnam *et al.*, 2011; Veldman *et al.*, 2013). From the perspective of community ecologists, the mechanisms promoting coexistence or dominance of C_3 and C_4 species at individual sites are best explained by temporal or spatial resource partitioning by species with different resource requirements (Monson *et al.*, 1983; Tilman & Pacala, 1993; Fargione & Tilman, 2005). Finally, species and lineages are likely to have distinct and independent responses to temperature, precipitation, and other environmental factors (regardless of functional type) that we expect to contribute to the variation in grass distributions (Edwards & Still, 2008).

While the broad-scale distribution of C_3 and C_4 grasses has been studied extensively in North America, previous studies have been limited because they (i) relied upon indirect proxies of relative abundance (e.g., floral survey lists, soil organic carbon stable isotopes and land cover classifications), (ii) have been limited in spatial extent, and (iii) focused largely on climatic and physiological explanations (Teeri & Stowe, 1976; Paruelo & Lauenroth, 1996; Epstein *et al.*, 1997; Tieszen *et al.*, 1997; Sage *et al.*, 1999). Using plot level abundance data, we set out to explore the degree to which direct measurements of vegetation abundance support hypothesized models of C_3/C_4 distributions, including those used to estimate global carbon budgets. Specifically, we intend to identify if ecological mechanisms not directly related to the efficiency of photosynthesis produce disequilibrium with climate that is discernible in species distribution models at broad scales. Finally, we ask whether integrating a selection of ecological predictors can increase the explanatory power of the climate model and provide support for specific local mechanisms.

METHODS

Vegetation plot data

Vegetation plots with cover abundance measurements were sourced from databases, literature sources, and unpublished sources (Appendix S1 in Supporting Information). Plot data met the following criteria: (1) sample areas were between 100 and 1000 m^2, (2) accurate spatial data were provided, (3) plant abundance in the herbaceous layer was collected by species, and (4) plots contained species from the Poaceae (mean grass abundance was 65 %). Criterion (4) was included because our primary goal was to understand the controls over the ratio of C_3:C_4 grasses, not those factors that determine the abundance of grass relative to other plant taxa (herbaceous forbs, shrubs, etc.). Consequently, our response variable, proportion of C_4 grass, was calculated for each plot as the sum of C_4 grass abundance divided by the total grass abundance. Abundance was measured as aerial estimates of percent cover, but where cover classification systems (e.g. Carolina Vegetation Survey cover classes) were used, we converted cover ranges to the midpoint percent cover. Photosynthetic functional types were assigned to species using (Osborne *et al.*, 2014).

Explanatory variables

We reconstructed several previously published statistical models of C_3/C_4 grass distributions using climate 30 year (1971-2000) climate normals for the USA, sourced from the PRISM Climate Group (http://www.prism.oregonstate.edu/; details in Appendix S1). These are: (1) Teeri & Stowe's (1976) July minimum temperature and consecutive frost-free months predictors, (2) Paruelo & Lauenroth's (1996) growing season precipitation model, the (3) Epstein *et al.* (1997) soil texture and climate model, the (4) July temperature and rainfall model of von Fischer *et al.* (2008), and (5) the Collatz *et al.* (1998) crossover temperature model. The construction of the crossover model is describe below as it is the predominant model in the literature and requires some additional explanation.

The model representing the C_3/C_4 crossover temperature was created by applying a set of climatic criteria (temperature and rainfall thresholds) to all grid cells in the monthly climate dataset, following the work of Collatz et al. (1998) and Still et al. (2003a). Because multiple crossover temperature values have been reported in the literature, we created separate models spanning the entire range of empirical temperature thresholds (5-31 °C) separately for minimum, mean, and maximum monthly temperatures (Ehleringer *et al.*, 1997). Within each grid cell, each month with sufficient simultaneous rainfall (≥25 mm) and temperatures above the crossover threshold were classified as favoring the growth of C_4 grasses over C_3 grasses (Still *et al.*, 2003a; Pau *et al.*, 2013; summarized in Fig. S2). We then summed the number of months in each grid cell that favored C_4 growth to produce a metric, hereafter referred to as the number of "months favoring C_4 grasses" or the "crossover temperature model", to be used as a predictor of the expected C_4 grass proportion. This model, often called the Collatz model in the literature, always refers to both the temperature and rainfall criteria together. The best minimum, mean, and maximum monthly temperatures for use in the crossover temperature model was selected by comparing their variance explanations when each was regressed against the proportion C_4 grasses in the plot as a response variable.

In addition to minimum and maximum temperatures, mean annual temperature (MAT), mean annual precipitation (MAP), the crossover temperature model, frost-free months, and seasonal rainfall, we also extracted non-climatic predictors such as tree cover, soils (cation exchange capacity, organic carbon, pH, and texture), fire frequency, and proportion invasive grasses (Appendix S1). We included invasive grasses as a predictor because of the observation that exotic species may possess different relationships with disturbance regimes or otherwise interact with native species in a way that increases their representation in the community (D'Antonio & Vitousek, 1992; Smith & Knapp, 1999).

Data analysis

Data analyses were aimed at (1) determining the best possible model that predicts C_3/C_4 grass abundance based of physiological limits to temperate and precipitation (i.e. climate variables) and (2) to what extent the predictions of the climate model were modified by local ecological factors (e.g., fire, competition, see introduction) at regional scales. In the first step, an appropriate analytical model of grass physiology was chosen using formal model selection procedures based on the Akaike Information Criterion (AIC; Appendix S1) to compare the support among previously published C_3/C_4 distribution models (e.g., Teeri & Stowe, 1976; Paruelo & Lauenroth, 1996; Epstein *et al.*, 1997; Still *et al.*, 2003a; von Fischer *et al.*, 2008) across the entire dataset. Then, we inspected the fit of the physiological-climatic C_3/C_4 distribution model to the observed vegetation data from across the USA. To control for phylogenetic, biogeographic, and historical differences (e.g., history of competition, disturbance) between regions of North America, we partitioned our data into geographical subsets based on the regions described by Omernik (see Appendix S2).

In the second step, we developed a series of "verbal" models to represent various potential interactions between climate and ecological drivers (Fig. 1) as a framework for exploring the ways that local ecological factors might cause C_3/C_4 grass distributions to be in disequilibrium with climate. Our intention is not to provide an exhaustive set of models or directly infer specific ecological processes from these patterns; rather the goal of this exploratory analysis is to provide a rational for statistically testing for the effects of various ecological predictors in the next step of analysis. Fig. 1A shows our expectation if C_3/C_4 grasses are in climate equilibrium—C_4 species exist when and where they are favored and are absent when conditions are never physiologically suitable (Araújo & Pearson, 2005). The remaining "verbal" models (Fig. 1B-F) illustrate patterns that can be expected when other mechanisms (interspecific competition, disturbance feedbacks, and species interactions) play important roles in addition to the purely physiological model. For example, if C_3 grasses are able to persist in a grassland, perhaps because they can capture and store resources during the cool season, then C_4 species may never attain the level of dominance predicted by the local climate until C_3 grasses are incapable of growing (Fig. 1B). On the other hand, disturbance favoring C_4 grass species (e.g., fire) might maintain dominance of C_4 grasses at sites where the climate favors C_3 grasses (Fig. 1C). Competition and disturbance are just two straight-forward examples that would produce disequilibrium with climate. Furthermore, multiple factors might operate in conjunction—for instance, cool season competition from C_3 grasses could prevent establishment of C_4 species in low temperatures environments, but in warmer conditions C_4 grasses might be promoted by fire (Fig. 1D). Another possibility is that C_4 species do not grow in areas where temperatures favor them for only short periods (e.g., one month) because there is not sufficient time to establish a population (Fig 1E). Finally, in warm environments where C_4 grasses are expected to dominate exclusively, C_3 species may continue to persist if they store resources gained during temporarily beneficial environmental conditions, such as following a frost event that kills competing C_4 grasses (Fig. 1F; "storage effect"; Chesson, 2000).

Treating each ecoregion separately, we compared the physiological model expectations (e.g., Fig. 1A) to the observed plot-based C_4 grass proportions with the goal of identifying patterns of deviation indicative disequilibrium processes (e.g., Fig 1B-F, described above). For each ecoregion containing vegetation data, we statistically tested whether the observed versus expected relationship reflected climatic equilibrium (i.e., a linear fit) or disequilibrium (i.e., nonlinear, requiring a second or third degree polynomial term in a regression model). Linearity is a good representation of climate equilibrium because it indicates that as climate changes there are corresponding changes in C_4 grass abundances. In addition to assessing linearity, we tested the hypothesis that plots existed largely in either low or high C_4 states by applying Hartigan's dip test to test for and quantify the degree of multimodality in each ecoregion (Maechler 2013).

Finally, in ecoregions in which grass distributions were likely to be in disequilibrium with climate, we assessed the degree of statistical support for a selection of other potential mechanisms that could produce the observed patterns. We did this by fitting models which test for partial effects of additional predictors on the proportion of C_4 grasses after the climate-related predictor variable was accounted for. These additional predictors were: (1) fire, (2) tree cover, (3) proportion of grasses that are invasive, and (4) soil characteristics (Appendix S1). While temperature and rainfall are already included in the Collatz crossover model, min and max temperature and rainfall were included in our regressions because we considered that additional temperature thresholds (tolerance to extremes) and interactions with rainfall might operate in addition to the crossover model and be important in particular regions (Still *et al.*, 2013). Due to the spatial autocorrelation and bounded nature of our proportional plot data we fit models using boosted beta regression (Appendix S1). This approach is appropriate for modeling spatial data with beta distributed responses (i.e. bounded zero to one) when accounting for partial effects and modeling how variance responds to predictors. For example, our regressions modeled variance through phi (ϕ), which is a parameter of beta distributions that describes the degree to which a variable (in this case, proportion of C_4 grass) is either hump-shaped (large ϕ) or U-shaped (small ϕ)—this shape can change in response to predictor variables. In this case a positive effect of a predictor on ϕ would indicate that variance decreases around the mean response; conversely, variance increases as ϕ decreases.

There are several aspects of our analytical approach that deserve a caveat. First, the sampling dates for our plot data were skewed towards summer months and to reduce bias we restricted our analysis to summer month to represent the height of the growing season; this means we may have missed patterns that might only be evident when all seasons are fully sampled. Second, in this study we have lumped species into functional type even though these species will have individualistic responses to the environment that could explain additional variation or be confounded with our other predictors. Lastly, our modeling approach mostly considers main effects of temperature and ecological predictors even though temperature likely interacts with biotic factors to produce ecological outcomes (Dillon *et al.*, 2009).

RESULTS

The number of months that favor C_4 grasses (i.e. the Collatz crossover model) based on a monthly maximum of 27 °C and a minimum 25 mm rainfall emerged as the best physiological predictor of the observed C_4 grass proportion (R^2 = 0.40; Fig. 2); the max 27 °C Collatz model had the lowest AIC (and highest R^2) of all single predictor models from the literature (Table S3) and had a strong positive effect in all ecoregions (Tables 1 and S3). The quality and spatial coverage of the plot data allowed us, for the first time, to empirically derive the best crossover temperature for the Collatz model (Fig. 2) and to compare it to other models with a modern statistical approach. The next best models were 9 °C and 18 °C for the minimum and mean temperature Collatz crossover models, respectively. Consequently, in downstream analyses the crossover temperature model was used to represent the best physiological-climate predictor of the proportion of C_4 grasses.

When the proportion of C_4 grasses in a plot was regressed upon the number of months favoring C_4 growth, all of the ecoregions, with the exception of the Mediterranean, showed a non-linear relationship best fit by either a second or third degree polynomial (Table S3). To better visualize the middle range and upper boundary of these responses we used quantile regression to model the median and upper 95^{th} quantile of C_4 proportion; because the relationships were non-linear we fit these models with additive components (Fig 3). The modeled upper limit of C_4 grasses was consistently above 50% C_4 in all regions except for the Mediterranean regions. In the Great Plains, Temperate Sierras, and Southern Semiarid Highlands, the median C_4 response is higher than expected when just one month favors C_4 grasses. The Eastern Temperate Forests and North American Deserts have sigmoidal relationships between predicted and actual C_4 proportion, and their median curves (and the Northern Forest and Northwestern Forested Mountain curves) remain below the physiology-climate predictions even when several months favor C_4 (Fig. 3). One particularly compelling results was that the distribution of C_4 grass proportions in all regions (except Mediterranean) could not be explained by a unimodal distribution (for all regions: D=0.01-0.13 and $p < 0.001$ from Hartigan's dip test) —i.e., they were at least bimodal with peaks near 0 and 1 (Fig. 3). The Mediterranean showed a linear pattern and was unimodal which might reflect C_3 competitive dominance or simply that C_4 is only favored for up to two months.

These results establish that seven of eight ecoregions showed nonlinear relationships between observed and expected C_4 proportion. Because we found significant deviations from our predictions, we used boosted beta regression in order to determine if fire, tree cover, invasiveness, soils, min and max temperature, or rainfall could explain additional variation in C_4

grass proportion after accounting for physiological-climate effects based on the crossover temperature model (with 27 °C temperature and 25 mm rainfall criteria). The explanatory power of all models was increased by the addition of these variables (Table 1; Appendix S1), compared to models with only the number of months favoring C_4 grasses as the predictor. R^2 values increased from 0.18 to 0.30 in Eastern Temperate Forests, 0.19 to 0.41 in Great Plains, 0.33 to 0.51 in North American Deserts, 0.23 to 0.42 in Temperate Sierras, and from 0.49 to 0.53 in Southern Semiarid Highlands.

In Eastern Temperate Forests, there was a strong negative effect of tree cover on C_4 grass proportions, whereas invasive grass proportion, soil organic carbon, and minimum temperature each had positive effects (Table 1). Fire did not have a main effect but decreased the variance associated with C_4 (ϕ coefficient = 0.06; see Methods) meaning that where fire is common it is rare to find C_3 grass species. In the Great Plains, the crossover temperature model was the only significant predictor of the mean response, but, tree cover (ϕ coefficient = -0.009) and increasing minimum temperatures (ϕ coefficient = -0.005) tended to increase variance there. In contrast, increasing maximum temperatures were positively associated with C_4 grasses in the Deserts, and both minimum and maximum temperatures were important in the Temperate Sierras. MAP was associated with decreasing C_4 grass presence in both Temperate Sierras and the Semiarid Highlands. Unexplained spatial patterns were present in the Great Plains, Temperate Sierras, and North American Deserts datasets as demonstrated by the significant fit of geographic coordinates to the data in our boosted beta regressions (Table 1; Appendix S1). Finally, in three regions where invasiveness was important, an associated decreased in variance of proportion of C_4 grass was observed.

DISCUSSION

To our knowledge this is the first time that the C_4 grass fraction from plot abundance measurements of specific taxa (rather than floral lists, aggregated presence/absence, or herbarium collections data) has been compared quantitatively at a broad scale to the state-of-the-art models of C_4 distribution (Teeri & Stowe, 1976; Sage *et al.*, 1999; Murphy & Bowman, 2007; Still *et al.*, 2013). In doing so, we revealed that there are major, biogeographically distinct deviations from climate equilibrium that exist in the broad scale spatial distributions of two highly studied grass functional types.

Based on previous work (Still *et al.*, 2003a), we expected to find that the physiological model using a mean 22 °C crossover temperature criteria (and 25 mm rainfall screen) for counting the number of months favoring C_4 grasses would best account for the variation in the data. Instead, we found that a maximum temperature of 27 °C was a better predictor of C_4 grass abundance than all other models (Fig. 1 and Table S3). One possible explanation for this result is that mean temperatures integrate daytime and nighttime temperatures, while maximum temperature better represents the daytime growing conditions (especially mid-morning when stomata are most open) of grasses and should reflect the C_4 advantage in reducing photorespiratory costs relative to C_3 grasses. Our result is consistent with empirical data suggesting that, when temperature is represented by daytime measurements, it results in high crossover temperatures (Ehleringer *et al.*, 1997; Sage *et al.*, 1999). Although it is not surprising that temperature was a good predictor of C_4 grass distribution, the more significant and novel finding is that the temperature model is not adequate to explain these distributions on its own. Whereas the number of months favoring C_4 grasses explained the highest percentage of the variance in C_4 grass abundance across the entire dataset (40 %), the residual variation not explained by temperature is considerable and the region-specific analyses show that ecological variables, such as fire and tree cover, play an important role in determining C_3/C_4 grass distributions.

Seven of our eight regions were characterized by non-linear relationships between the observed and predicted results from the temperature/precipitation model, indicating that there are factors other than climate that are determining grass functional type distributions at large scales (Fig. 3). Moreover, deviations from climate equilibrium were unique to different regions which suggests the presence of region-specific processes or mechanisms that modify grass climate responses in areas with different biogeographic histories. These non-linear patterns suggest different types of factors that might modify climate-determined grass distributions (introduced in Fig. 1), such as seasonal competition favoring either C_3 or C_4, disturbance factors like fire or herbivory favoring either C_3 or C_4, minimum growing season thresholds, or coexistence mechanisms such as storage effects (Brown & Maurer, 1989; Chesson, 2000; Araújo & Pearson, 2005; Araújo *et al.*, 2013). In two regions, Eastern Temperate Forests and North American Deserts, the median quantile regression results exhibit a sigmoidal-shaped curve implying processes that suppress C_4 grasses in shorter warm growth seasons but promote C_4 above expected beyond a five month warm growing season. Two generally forest-dominated ecoregions, Northern Forests and Northwestern Forested Mountains, have a restricted number of months favoring C_4 grasses because they occupy limited climatic space. Interestingly, these regions have their median responses suppressed below expectations, whereas regions with more open canopy or generally non-forest habitat tend to approach maximum C_4 proportions rapidly (Southern Semiarid Highlands, Temperate Sierras, and Great Plains but not North American Deserts). Altogether, these patterns point to the existence of biogeographically and ecologically distinct factors and processes influencing the observed distributions of C_4 and C_3 grasses.

In the boosted beta regressions, where we modeled the C_4 proportion of grasses as a function of several covariates, the strength of the relationship and the degree to which other predictors were needed to explain variance in C_4 grass proportion varied among regions. These results support the assertion that North America ecoregions differ in the degree to which temperature and physiology control C_4 distributions. It is also consistent with the hypothesis that the global rise to dominance of C_4 grasses cannot be explained solely by photosynthetic pathway; instead, other adaptations may be equally important to explaining dominance (Edwards *et al.*, 2010). For example, one proposition is that fire-adapted C_4 grasses facilitated the expansion of the grass-dominated savanna systems in the late Miocene (Scheiter *et al.*, 2012). For example, in our dataset the two most dominant species in the southeast were the fire-adapted C_4 species *Aristida stricta* and *A. beyrichiana*, whereas across the rest of the temperate eastern US the dominant grasses were C_3, and likely less fire-prone species *Brachyelytrum erectum* and *Danthonia spicata*. However, the dominant C_4 species still include fire-adapted species like *Andropogon gerardii* and *Schizachyrium scoparium* in addition to the invasive *Microstegium vimineum*.

The only effect of fire regime found in this study was a negative correlation between fire frequency and the variance associated with C_4 proportion in Eastern Temperate Forests. This supports the frequently reported association of C_4 with fire, including in North America, because at the scale of our analysis fire maintains a high proportion of C_4 grass (D'Antonio & Vitousek, 1992; Scheiter *et al.*, 2012; Veldman *et al.*, 2013). This result introduces the possibility that in the warmer areas of Eastern Temperate Forests (e.g., Florida) high relative abundances of C_4 are already explained by the physiological model, and the influence of fire is mediated through a negative impact on tree cover. A known indirect effect of fire that promotes C_4 grasses is the reduction of forest trees (as opposed to savanna trees) that would otherwise negatively influence the C_4 understory (Veldman *et al.*, 2013). Therefore, fire effects on C_4 might be masked by the negative impact of tree cover, found in three ecoregions. To explore the potential for indirect effects and the influence of scale on our results, we conducted a heuristic analysis comparing the effects of fire on C_4 grass proportion within and outside of the natural range of Longleaf pine (*Pinus palustris*), a species characteristic of the pyrogenic grasslands of the Southeastern United States (see Appendix S3). This analysis showed that C_4 proportion was still bimodal, whether within or out of the range of Longleaf pine. However, C_4 grasses were more common within this range, whereas C_3 grasses were more common in the rest of the Eastern Temperate Forests (Fig. 4; D = 0.06-0.11, $p < 0.001$). Furthermore, a simple path analysis revealed direct (fire increasing C_4 abundance) and indirect (mediated through reduced tree cover) effects of fire on C_4 grasses inside of the Longleaf pine range but not outside the range (Fig. 4; Appendix S3). This pattern is likely the indirect consequence of shading and the creation of a cool microclimate, relating to the fact C_4 grass species are thought to be at a competitive disadvantage in shade and less able to utilize sunflecks than C_3 grasses (Horton & Neufeld, 1998; Sage *et al.*, 1999). This effect seems to be modified by the presence of the invasive, apparently shade tolerant C_4 grass *M. vimineum* (Horton & Neufeld, 1998). Accordingly, invasive grass (*M. vimineum*) abundance had a positive influence on the proportion of C_4 grass in the Eastern Temperate Forests.

In contrast, grass invasiveness had negative effects on the abundance of C_4 grasses in both North American Deserts and Temperate Sierras, where the C_3 invasive *Bromus tectorum* is responsible for reducing the C_4 proportion to below expected values. The numerous other invasive grasses in the dataset (e.g., *Eragrostis curvula*—C_4 and *Dactylis glomerata*—C_3) are all in low abundance and appear to have less of an influence on C_4 cover. Invasives may shift the proportion of C_4 grasses through diversity reduction and competitively exclusion or through interaction with disturbance (D'Antonio & Vitousek, 1992; Smith & Knapp, 1999). In general, all mean effects of invasive grasses on C_4 proportion (positive and negative) in our analysis were accompanied by decreased variance around the mean, indicating that sites tend to be dominated by the functional type of the invading species.

Another surprising result was the prevalence of bimodal C4 abundance distributions across the entire dataset indicating that, at the plot scale, plant communities tend to be dominated largely by one functional type with few mixed C_3/C_4 intermediates. In fact, C_3- and C_4-dominated sites are largely separated in climate space, with overlap existing primarily where coexistence of functional types exists (Fig. S7). Whether or not these observations provide direct evidence for the existence of alternative stable states for different photosynthetic pathways is not known; however, the strongly suggestive nature of our data warrants future investigation of these patterns. For example, temporal demographic data from grasslands would be valuable for testing for alternative attractors. If grassland vegetation plots do exist in largely monocultures of either C_3 or C_4, one likely explanation is that ecological conditions create feedbacks favoring a particular photosynthetic pathway creating non-linearity in species distributions. For example, the direct and indirect promotion of C_4 grass by fire leads to nonlinearity in the climate responses the Eastern Temperate Forests and the highly bimodal abundance distribution observed (Fig. 4).

Soil type was a notably poor predictor of C_4 proportion, despite the frequent dominance of C_4 grasses on highly disturbed and low nutrient sites (Wilson & Tilman, 1993; Smith & Knapp, 1999); although, soil organic carbon was positively correlated with C_4 grasses in Eastern Temperate Forests. Climatic factors such as min/max temperature and precipitation, on the other hand, had stronger influence on grass distributions. In both Temperate Sierras and Southern Semiarid Highlands, higher MAP was associated with decreased C_4 proportions, in agreement with work on the Hawaiian Islands (Pau et al. 2013, Still et al. 2013), and potentially indicating that either increased rain favored C_3 grasses or that low rainfall favored C_4 (Paruelo & Lauenroth, 1996). Maximum temperatures positively affected C_4 grasses in Temperate Sierras and North American Deserts, which suggests that high temperatures have a particular negative effect on C_3 grasses in these areas (e.g., von Fischer *et al.* 2008). Similarly, higher minimum temperatures in Eastern Temperate Forests and Temperate Sierras were accompanied by higher C_4 proportions, indicating that cold may indeed limit C_4 production (Long, 1999).

Conclusion

We used vegetation abundance data to determine that counting the number of months favoring C_4 grasses, based on a max crossover temperature of 27 °C, was the best predictor of C_4 abundance. Furthermore, seven of eight biogeographical regions of North America examined had distinct and non-linear relationships with proportion of C_4 grasses predicted from the number of months favoring C_4 indicating that separate ecological processes might contribute differently to distributional patterns among regions. In particular, invasive species, tree cover, and fire had important and regionally distinct modifying effects on C_4 grass abundance. In our study of C_3 and C_4 grass distributions in North America we found that climate disequilibrium was commonplace and biogeographically distinct at large scales.

Acknowledgements The authors would like to thank Matthias Schmid, Florian Wickler, Simone Wahl for providing both R code and detailed discussion regarding the application of Boosted Beta Regression. Susan Carr kindly provided data for the southeastern United States. Additional thanks to Tom Morrison, Frances Morris, and Kathleen Quigley for discussions. DG was supported by National Science Foundation Graduate Research Fellowship under Grant No. 0907738 and National Evolutionary Synthesis Center (NESCent), NSF #EF-0905606.

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BIOSKETCH

Daniel M. Griffith’s conducts plant ecological research in savanna and grassland ecosystems with specific focus on the interactions of abiotic and biotic factors. His fieldwork is concentrated on African grazing ecosystems.

Tables:

Table 1. Results from boosted beta regression analyses. Effect sized for variables are only presented if they were selected in the final model. A significant influence of space, which doesn't have a single effect size, is indicated as an asterisk. The symbols ($+\sigma^2$) and ($-\sigma^2$) indicates a positive and negative influences on the variance of C_4 proportion, indicated by the model as the inverse of beta distribution precision parameter (see methods). Only regions with models with significant mean effects are reported; these are Eastern Temperate Forest (ETF), Great Plains (GP), North American Deserts (NAD), Temperate Sierras (TS), and Southern Semiarid Highlands (SSH).

	ETF	GP	NAD	TS	SSH
Crossover model with max 27 °C	0.16	0.13	0.29	0.18	0.31
MAP				-0.4	-0.18
TREE COVER	-0.22	($+\sigma^2$)		-0.07	-0.005
Invasive grass (%)	0.1 ($-\sigma^2$)		-0.12 ($-\sigma^2$)	-0.09	($-\sigma^2$)
Soil CEC					
Soil OC	0.06				
Soil pH	($+\sigma^2$)				
Soil Clay (%)					
Fire frequency	($-\sigma^2$)				
Minimum temperature	0.17	($+\sigma^2$)		0.06 ($+\sigma^2$)	
Maximum temperature			0.03	0.02	
Space		*	*	*	

Figure legends:

Figure 1. Predicted patterns for the relationship between modeled and actual C_4 grass proportions. The gray line is the one-to-one “pure-physiology” prediction and the dotted black lines are alternative patterns. Capital letters identify the panel and lowercase letters identify the processes expected to produce the patterns observed. (A) A one-to-one relationship between expected and observed C_4 grasses would suggest that (a) physiology drives their distribution. (B) C_4 grasses might be represented below expected values in nature suggesting (b) C_3 competitive priority effects or disturbance favoring C_3. (C) C_4 grasses may be over represented and might imply (c) C_4 priority effects or disturbance favoring C_4. Further alternatives include (D) a sigmoidal relationship (d) where there are alternative states, thresholds, or opposing processes. (E) A lagged pattern where (e) the minimum threshold conditions for C_4 are not met. (F) An asymptotic curve that could suggest (f) storage effects buffering populations of C_3 species.

Figure 2. The R^2 values from separate linear models for minimum, mean, and maximum temperature based crossover models across a range of potential values. The vertical line indicates the crossover temperature that maximizes the explanatory power of the model given the entire plot dataset.

Figure 3. Map of the study extent, the conterminous USA, showing the biogeographic (Omernik) ecoregions analyzed (Datum: WGS84). Each region is associated with a plot using quantile regression to visualize the non-linear relationships (Appendix S2) between predicted and observed C_4 grasses. These graphs follow the framework developed in Fig 1, but use the crossover temperature model as the x-axis. The gray line is the one-to-one, “climate equilibrium”

prediction. The data are represented with density curves within each bin on the x-axis (C4-favored months). To visualize the median and upper limit of C_4 distributions, median and 95^{th} quantile regressions were fit in the R package ‘quantreg’ (Koenker 2013).

Figure 4. The Eastern Temperate Forest ecoregion was divided according to the historical range of Longleaf pine. The figure shows the frequency distribution of C_4 grass proportion of the Northeastern Temperate Forests (outside of the Longleaf pine range) as compared to the range of Longleaf pine in the Southeastern USA. Each histogram has an inset depicting the results of a path analysis testing the direct and indirect (mediated by tree cover) effects of fire on proportion of C_4 grass. Significant regressions are labeled with standardized effect sizes.

Figures:

Figure 1.

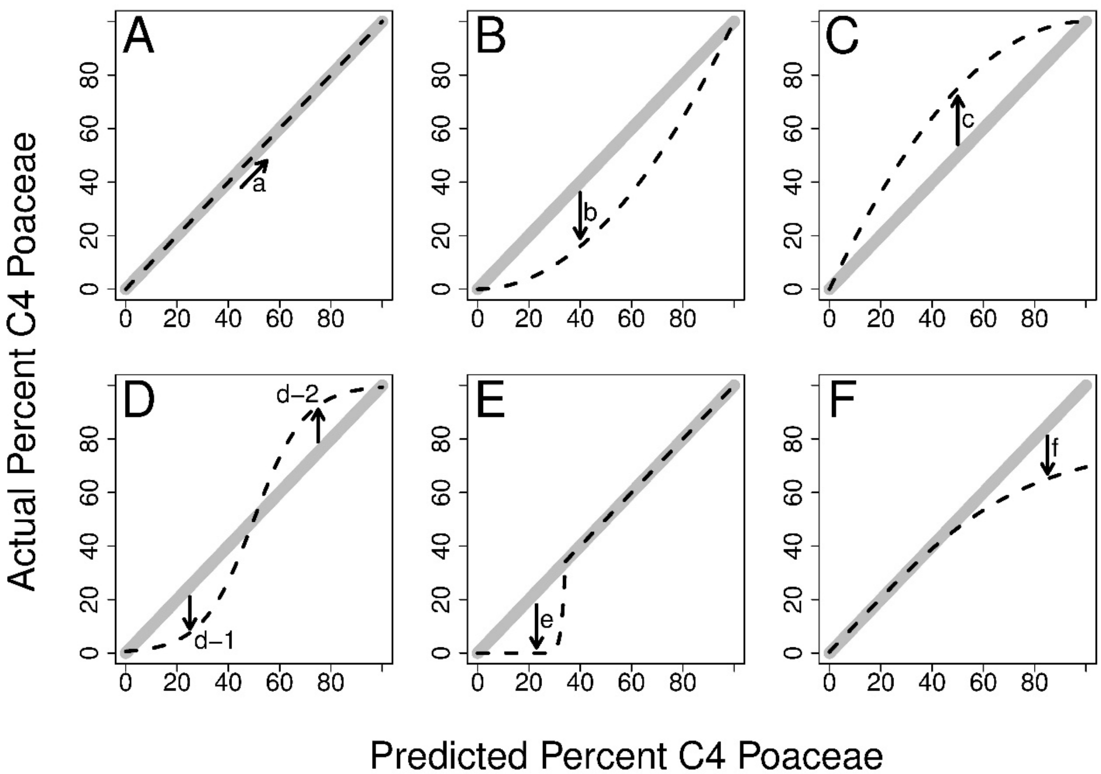


Figure 2.

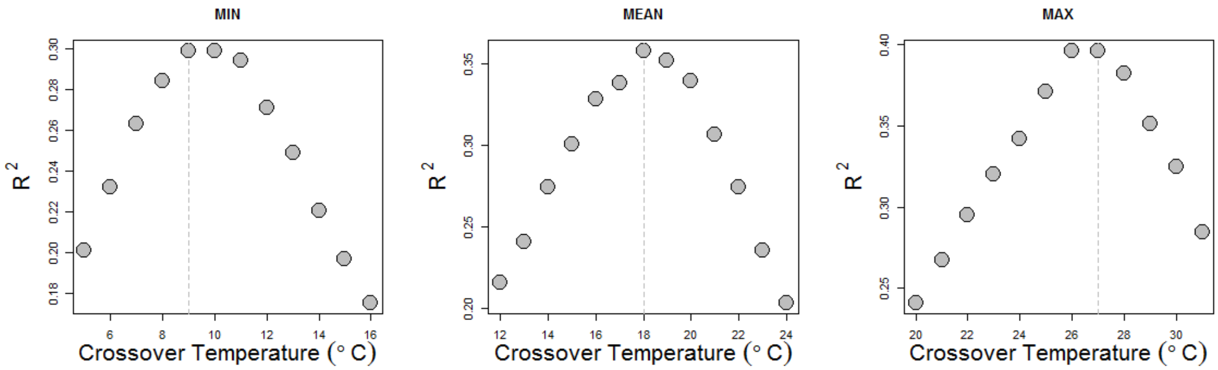


Figure 3.

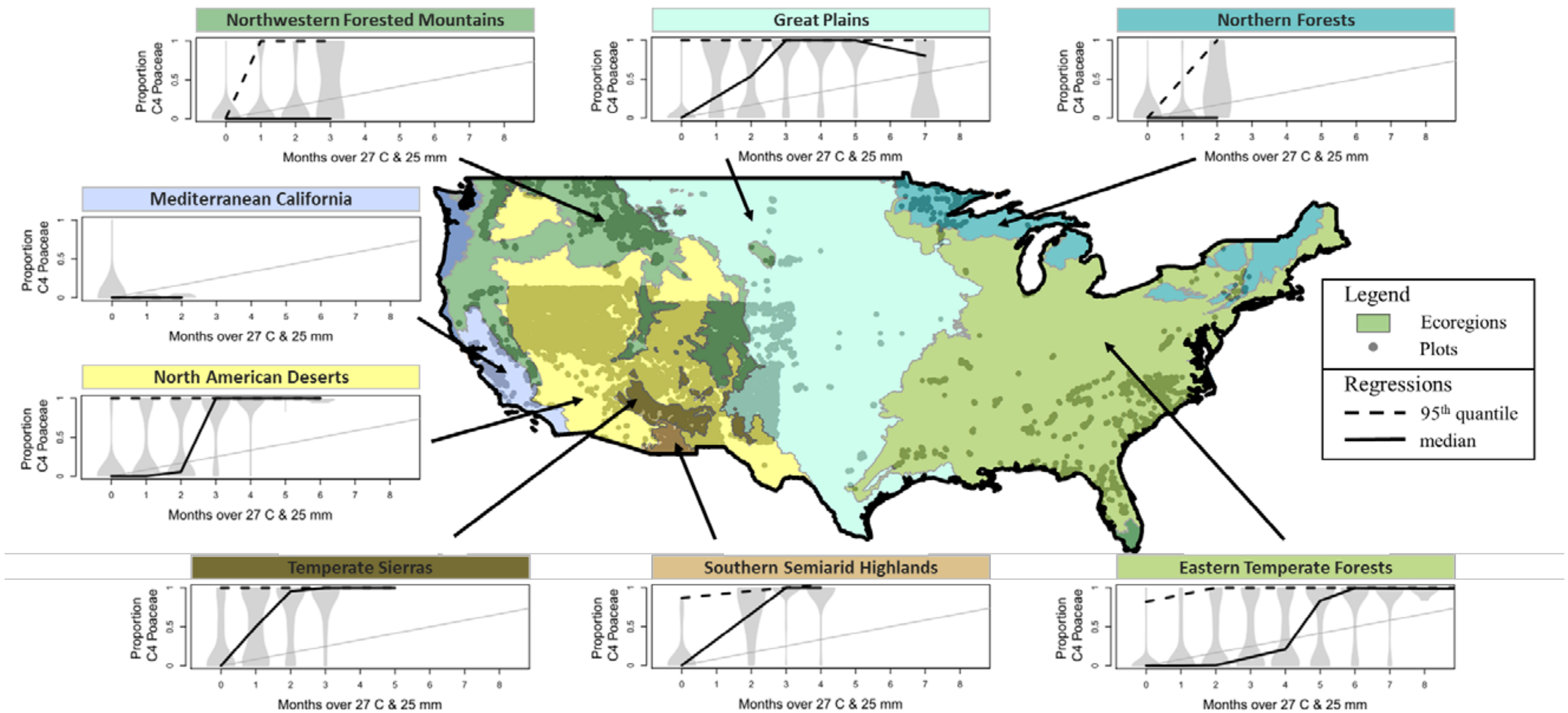
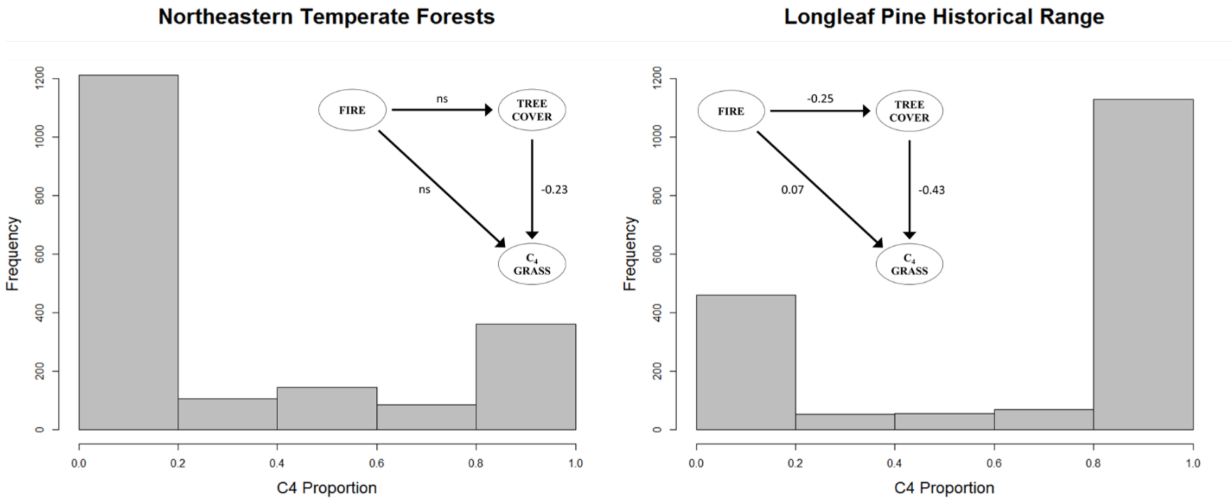

Northwestern Forested Mountains
Great Plains
Northern Forests
Mediterranean California
North American Deserts
Temperate Sierras
Southern Semiarid Highlands
Eastern Temperate Forests
Proportion C4 Poaceae
Months over 27 C & 25 mm
Legend
Ecoregions
Plots
Regressions
95th quantile
median

Figure 4.


Northeastern Temperate Forests
Longleaf Pine Historical Range
FIRE
TREE COVER
C4 GRASS
ns
ns
-0.23
-0.25
0.07
-0.43
Frequency
C4 Proportion
0
200
400
600
800
1000
1200
0.0
0.2
0.4
0.6
0.8
1.0

SUPPORTING INFORMATION

Appendix S1 Additional methods
Appendix S2 Additional results
Appendix S3 Details for path modeling