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The relevance of phylogeny to studies of global change

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Phylogenetic thinking has infiltrated many areas of biological research, but has had little impact on studies of global ecology or climate change. Here, we illustrate how phylogenetic information can be relevant to understanding vegetation–atmosphere dynamics at ecosystem or global scales by re-analyzing a data set of carbonic anhydrase (CA) activity in leaves that was used to estimate terrestrial gross primary productivity. The original calculations relied on what appeared to be low CA activity exclusively in C4 grasses, but our analyses indicate that such activity might instead characterize the PACCAD grass lineage, which includes many widespread C3 species. We outline how phylogenetics can guide better taxon sampling of key physiological traits, and discuss how the emerging field of phyloinformatics presents a promising new framework for scaling from organism physiology to global processes.

Introduction

The integration of phylogenetics with other areas of biology has grown more prevalent in recent years. The first and most obvious connections were made in evolutionary biology (e.g. character evolution and adaptation, molecular evolution, developmental biology and historical biogeography), but important links have also been made in fields as far-reaching as community ecology [1] and medicine [2]. By contrast, phylogenetic thinking and analytical methods appear to have had little impact in ecosystem ecology or global change research. Is this because there are no meaningful connections between these areas, or is it that this particular intersection has yet to be explored?

We argue here that a productive area of overlap between these fields does exist. Understanding biogeochemical cycles (for example) depends upon understanding how compounds are processed by the biosphere, which ultimately is influenced by the physiology of individual organisms. We know that physiological traits vary among different groups of organisms, and that these differences originated as evolutionary innovations along the branches of the tree of life. It stands to reason, therefore, that knowing how organisms are related to one another will help us to better understand how key physiological traits are distributed across species and, in turn, across biomes.

The existence of significant physiological differences among organisms has been recognized by those modeling global processes. This is most evident in the widespread recognition of functional types (most commonly plant functional types, or PFTs) [3,4], particularly among dynamic global vegetation models [5–7]. Different authors use different categories of PFTs, but in general, these are meant to capture observed differences in functional traits that influence ecosystem-level processes. Two particularly well-used PFTs are C3 versus C4 plants: C4 plants utilize an evolutionarily derived photosynthetic pathway that concentrates CO₂ at the site of carbon assimilation inside the leaf. This results in C4 plants having typically higher maximum photosynthetic rates and higher water and nitrogen use efficiencies compared with C3 plants, key traits that can affect global carbon, water and nutrient cycles.

The use of PFTs is an improvement over assuming that all plants are functionally equivalent. However, the species assigned to any particular PFT will usually represent multiple evolutionary origins of that PFT: standard growth form categories (trees, shrubs, herbs and succulents) and even photosynthetic pathways (C4 and crassulacean acid metabolism) have evolved independently many times, and in distantly related plant lineages. Each separate origin of a particular PFT occurred within a different organismal context, and will be associated with distinct anatomical and biochemical traits that could result in different functional performance (e.g. grass species representing separate origins of C4 photosynthesis respond differently to elevated CO₂ [8]). In addition, species that have been assigned to different PFTs (e.g. trees versus herbs) might perform similarly if they both happen to be members of a lineage that evolved a key physiological trait. That is, relevant physiology can be conserved through evolutionary transitions in growth form. For these reasons, a phylogenetically based classification scheme might be a good alternative to traditional PFTs for organizing physiological diversity into functional units for modeling purposes.

We illustrate this point by re-analyzing data from a study that used the differential isotopic discrimination of atmospheric CO₂ by PFTs during photosynthesis to estimate terrestrial gross primary productivity (GPP). We conclude that phylogenetics is highly relevant to global-scale problems. However, establishing practical collaborations between phylogeneticists and global ecologists depends upon the further development of ‘phyloinformatics’, especially the

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ability to mine data on the geographical distributions of species within a phylogenetic framework.

Photosynthetic discrimination of C¹⁶O¹⁸O and the global carbon cycle

Current estimates suggest that approximately half of the increased atmospheric CO₂ resulting from fossil fuel combustion and deforestation is re-absorbed into terrestrial and oceanic systems [9–13]. It is still unclear, however, how this carbon sink is distributed among and within marine and terrestrial ecosystems, despite this knowledge being crucial for projecting future atmospheric CO₂ levels [14]. Understanding the mechanisms underlying terrestrial carbon fluxes and their temporal variation is thus a major goal of carbon cycle science.

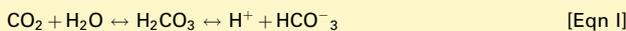
Stable isotope chemistry has proven useful in helping to resolve processes within the global carbon cycle [11]. For instance, it is now clear that the terrestrial biosphere is primarily responsible for setting the ¹⁸O:¹⁶O ratio of atmospheric CO₂ (referred to as δ¹⁸O_a) [15–17]. Furthermore, photosynthesis and respiration, the two main biological processes involved in land–atmosphere carbon exchange, each produce a unique isotopic imprint on δ¹⁸O_a. This

results mainly from an effective discrimination against the heavier C¹⁶O¹⁸O molecule by terrestrial photosynthesis (Box 1). Because of this, analysis of δ¹⁸O_a potentially enables estimation of terrestrial ecosystem GPP and, thus, changes in GPP in response to climate variation. There is additional potential for δ¹⁸O_a to resolve differences in GPP among different types of terrestrial ecosystem (e.g. grasslands versus forests [18]), which could become an important tool in monitoring ecosystem responses to climate change.

Photosynthetic discrimination against C¹⁶O¹⁸O (Δ¹⁸) is caused by several processes. First, water in plant leaves is typically enriched in the heavier molecule H₂¹⁸O because the lighter H₂¹⁶O evaporates more easily into the atmosphere. Second, there is an exchange of oxygen atoms between leaf water and dissolved CO₂ in the leaf mesophyll, such that many of the heavy ¹⁸O atoms are transferred to CO₂ molecules. The degree of oxygen isotopic equilibration between leaf CO₂ and H₂O, termed θ_{eq}, depends upon the activity of the enzyme carbonic anhydrase (CA). Lastly, much of the atmospheric CO₂ that diffuses into the leaf and becomes dissolved then diffuses back into the atmosphere before it can be incorporated into the next step of photosynthesis. Owing to the isotopic

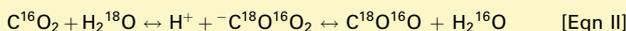
Box 1. How does C¹⁶O¹⁸O discrimination by photosynthesis work?

When the stomata of a plant are open, atmospheric CO₂ passively diffuses into the leaf along a concentration gradient, where it is then dissolved in mesophyll cell water. CA is found in the leaves of all plants and catalyzes the hydration reaction (Equation I):



This results in the formation of bicarbonate ions (HCO₃⁻), which react with PEP carboxylase in the first step of the C₄ photosynthetic pathway [31]. The importance of CO₂ hydration in C₃ plants is less clear, but it is presumed to aid in CO₂ diffusion into the chloroplast and in the maintenance of a steady supply of CO₂ for the Calvin cycle [32,33], the metabolic pathway that fixes carbon in all photosynthetic organisms.

The hydration of CO₂ in the mesophyll results in an isotopic fingerprint of photosynthesis on atmospheric CO₂ because of two factors. First, leaf water is generally enriched in H₂¹⁸O relative to source (soil) water, owing to the differential evaporation of the lighter H₂¹⁶O molecules through the stomata. During the CO₂ hydration reaction, oxygen atoms from CO₂ and H₂O are often switched, resulting in ¹⁸O-labeled CO₂ molecules (Equation II):



Second, it is estimated that up to 60% of the gross CO₂ flux into leaves each year returns to the atmosphere without being fixed by photosynthesis [15,34]. Because many of these molecules have been labeled with ¹⁸O owing to CA activity, this retroflux causes an ¹⁸O enrichment of the CO₂ outside of the leaf.

But how much of the ¹⁸O from leaf water is transferred to CO₂? Previous work on estimating global values of C¹⁶O¹⁸O discrimination by photosynthesis has assumed that the oxygen isotopic equilibrium between CO₂ and H₂O (θ_{eq}) results from a temperature-dependent fractionation factor [35] and is not limited by CA activity [15–17]. Gillon and Yakir [19] investigated this assumption by calculating the sensitivity of θ_{eq} to potential variation in CA activity of an individual plant (Equation III):

$$\theta_{\text{eq}} = 1 - e^{-k\tau/3} \quad [\text{Eqn III}]$$

where the $k\tau$ is the product of a CA rate constant (k) and CO₂ in-leaf residence time (τ) [36]. The authors translated this term into two measurable components: *in vivo* CA activity (which is an estimated variable based on CA leaf assays, gas exchange measurements and

leaf temperature) and gross flux of CO₂ from the atmosphere to the leaf. Their survey of 52 plant species demonstrated extreme variation in θ_{eq}, from 0.03 in *Digitaria sanguinalis* (a C₄ grass) to 1.00 in a variety of species representing woody and herbaceous eudicots, monocots and conifers (Figure 1) [19]. They argue that low equilibrium values result in a significantly reduced isotopic imprint of photosynthesis on atmospheric CO₂, and that this has major implications for estimating global GPP (see main text).

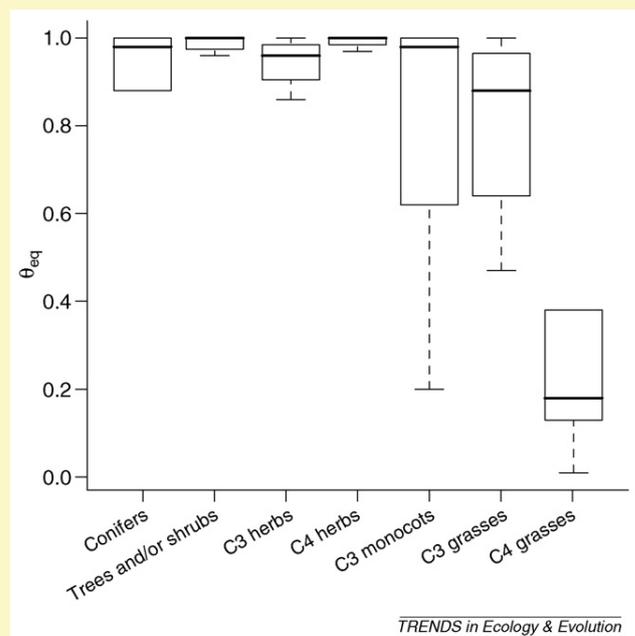


Figure 1. Mean values of θ_{eq} (using supplemental data from [19]) sorted into the PFT categories used by Gillon and Yakir [19]. In this case, the 'C₃ Monocot' PFT refers to all C₃ monocots other than grasses; the 'C₄ Grass' PFT also includes a C₄ sedge, *Cyperus*; and the 'Herb' PFT refers to herbaceous eudicots. Bold lines inside the box are median values; 95% confidence intervals are represented by the dashed lines.

exchange with leaf water, many of these molecules are now labeled with ^{18}O .

Estimates of global Δ^{18} have been made with the assumption that CA activity is universally high in all plants and so isotopic equilibration between CO_2 and H_2O (Θ_{eq}) is complete ($\Theta_{\text{eq}} = 1$) [11,15,16] (Box 1). However, work by Gillon and Yakir [19–21] challenges this assumption. In particular, the authors demonstrate an extreme variation in effective CA activity and Θ_{eq} among 52 plant species that would lead to large differences in Δ^{18} [19]. They argue that, as a group, C4 grasses show the greatest reductions in Δ^{18} (Box 1, Figure I), and that previous estimates of C4 Δ^{18} have led to a significant underestimation of C4 GPP. This has major implications for global GPP, as C4 plants are currently estimated to account for 18–25% of global photosynthesis [22,23], and their prevalence is increasing in tropical areas, where they often replace lowland forests following deforestation. Gillon and Yakir [19] suggest that the miscalculation of global Δ^{18} is currently underestimating global GPP by as much as $\approx 20\%$.

It is clear that the C4 grasses sampled by Gillon and Yakir [19], when averaged as a unit, have a significantly different mean value in CA activity and in resulting Θ_{eq}

compared with the other PFT categories (Box 1, Figure I). However, when the data are viewed in a phylogenetic context, the situation is not so straightforward. Fortunately, the complexities that emerge open up several new and productive avenues of research.

Insights from phylogeny

To explore the data set of Gillon and Yakir [19] in a phylogenetic context, we constructed a composite phylogeny of their 52 sampled species from previously published studies (Figure 1, Box 2). Using this tree in a simple trait-mapping exercise can provide important clues about the relationships between Θ_{eq} , PFTs and major plant lineages. Focusing first on Figure 1a, it appears that there have been several reductions in Θ_{eq} , but the lowest values correspond with a major lineage of grasses known as the PACCAD clade (consisting of the panicoid, arundinoid, chloridoid, centothecoid, aristidoid and danthonioid grass lineages [24]). From this perspective, *Echinochloa*, in view of its nested position within the PACCAD clade, has an unexpectedly high value of 0.88.

Onto the tree in Figure 1b, we have mapped the functional types referred to by Gillon and Yakir [19].

Box 2. Assessing trait correlations using phylogenetic methods

Figure 1 (main text) depicts the phylogenetic relationships of the 52 species used in the Gillon and Yakir [19] study, with the exception of an unidentified C4 grass, which we excluded from our analyses. Relationships among the major plant lineages were assigned using the classification of the Angiosperm Phylogeny Group [37] and resolution within major clades was determined according to individual studies [24,26,38,39] and the Angiosperm Phylogeny Website (<http://www.mobot.org/MOBOT/research/APweb/>). All branch lengths were arbitrarily assigned to 1.0. This approach to tree building does not provide meaningful branch length information; for example, in our composite tree *Cyperus* sp. 1 and *Cyperus* sp. 2 are sister species, as are *Dais continifolia* and *Hibiscus* sp., and as such these species are separated by similar branch lengths. However, it is likely that *Dais* and *Hibiscus* diverged from one another much earlier than did the two *Cyperus* species. In an attempt to account for this, we constructed a second tree with identical topology but with branch lengths scaled to time using independently calculated node age estimates of major clades [40]. This second tree is also imperfect, but better represents the relative phylogenetic distance between taxa.

To test for significant phylogenetic signal of physiological traits, we used the AOT software module in Phylocom v. 3.22 [41]. For a given trait, we generated a null distribution of mean divergence values of sister lineages by randomly redistributing tip values of traits across the tree (1000 replications). We then compared divergence values of the real data with our distribution: a trait was considered significantly labile if real data trait divergences were greater than the greatest 50 of 1000 replicates ($p < 0.05$), and significantly conserved if real data trait divergences were smaller than the smallest 50 of 1000 replicates ($p < 0.05$). We ran these analyses using both sets of branch lengths and with normal and ln-transformed trait data.

Taxon sampling did not enable us to test directly for the correlated evolution of C4 grass and low Θ_{eq} , as there are only two transitions between C3 and C4 photosynthesis captured in the grasses (although the C4 grasses included probably do represent multiple origins of C4 photosynthesis). However, there are four potential transitions from C3 to C4 photosynthesis across the entire tree and, in some parts of their discussion, Gillon and Yakir [19] associated low CA activity with C4 photosynthesis in general rather than with C4 grasses in particular. We therefore tested directly for correlations between photosynthetic pathway and shifts in Θ_{eq} as well as the other physiological traits

measured. Significance of independent contrasts were assessed by calculating 95% confidence intervals around the mean contrast value using a one sample t-distribution [42]; traits were considered either positively or negatively correlated with the evolution of C4 photosynthesis if the value zero fell outside the 95% confidence interval ($p < 0.05$) (Figure I).

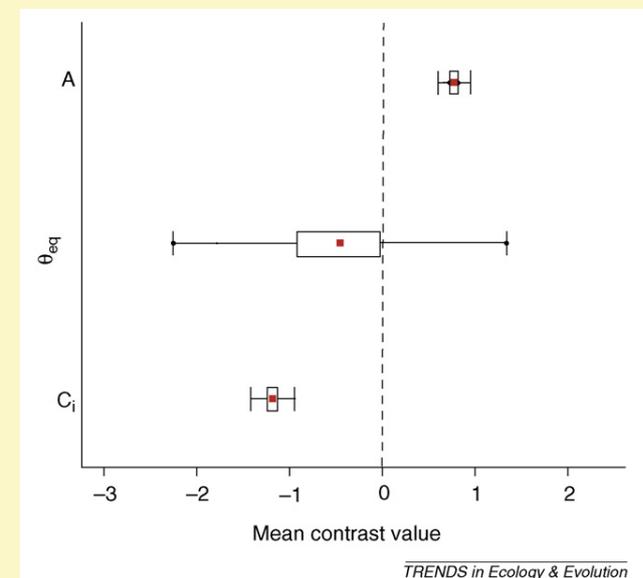


Figure I. Means and confidence intervals for independent contrast analyses of three physiological traits and C4 photosynthesis (using supplemental data from [19]). Means are represented by the red square, 50% confidence intervals are represented by the box, and 95% confidence intervals are represented by the tails. A mean contrast value of zero indicates that the two traits are not significantly correlated. As zero falls within the 95% confidence interval for Θ_{eq} , we cannot reject the null hypothesis of zero correlation between Θ_{eq} and C4 photosynthesis. Two other traits, photosynthetic rate (A) and internal leaf CO_2 concentration (C_i), show significant correlation with C4 photosynthesis, as would be expected based on what we know about C4 plant physiology. Physiological data were ln-transformed before analysis.

How well do these PFTs correlate with the Θ_{eq} values in Figure 1a? On the surface, there does not appear to be a strong correlation between the evolution of C4 photosynthesis and low Θ_{eq} values. Thus, we do not see reduced values in C4 eudicot herbs (i.e. *Amaranthus*) or in C4 monocots outside of the grasses (i.e. *Cyperus* sp. 2). The best correlation is within the grasses, where the C4 grasses generally show low values, with the exception of *Echinochloa* already noted. However, in this context, the C3 grass *Phragmites*, with its low Θ_{eq} value, appears out of place.

We return to these apparent exceptions later, but it is first important to test more rigorously these initial perceptions derived by inspection of Figure 1. Using the methods described in Box 2, we can ask whether any of the physiological traits measured by Gillon and Yakir [19] exhibit significant phylogenetic signal, suggesting that they are evolutionarily conserved traits; and whether low Θ_{eq} or any of the other physiological traits are correlated with C4 photosynthesis in general or with the C4 grass PFT in particular.

All the physiological traits measured by Gillon and Yakir [19] demonstrate a significant phylogenetic signal ($p < 0.01$) when tested using either set of branch lengths and analyzing normal or ln-transformed data (Box 2). This is due mainly to values in the PACCAD grass clade being distinctly different from all other taxa. In our tests for correlated evolution between C4 photosynthesis and the measured physiological traits, we could not reject the hypothesis of a mean shift of zero in Θ_{eq} , indicating that the evolution of C4 photosynthesis is not significantly correlated with a change in Θ_{eq} . It should be stressed, however, that the small number of transitions between photosynthetic pathways in the dataset ($n = 4$) afforded limited statistical power. Despite this, there was a significant correlation between C4 photosynthesis and two other traits commonly associated with the C4 pathway: photosynthetic rate (A) was positively correlated with C4 photosynthesis, and internal leaf CO_2 concentration (C_i) was negatively correlated (Box 2, Figure I). Unfortunately, it was not possible to evaluate the statistical significance of a possible correlation between low Θ_{eq} and C4 grasses in particular, because the sampling of species in the original data set only captured (at most) two transitions between photosynthetic pathway within the grasses.

Echinochloa, *Phragmites* and Θ_{eq}

We have highlighted what we feel is the most important pattern to emerge from these analyses: the lowest values of Θ_{eq} are found primarily in the PACCAD clade of grasses. Because all the sampled C4 grasses are also from the PACCAD clade, it might still seem reasonable to associate low Θ_{eq} values with the C4 grass PFT. Focusing in on this clade, however, the two exceptions mentioned earlier lead us to think otherwise. First, although *Phragmites australis* is a C3 species, it exhibits similarly low values to other PACCAD clade members. Without the knowledge that *Phragmites* is a member of the PACCAD clade (as opposed to another major grass lineage, the 'BEP' clade [24], which consists of exclusively C3 species and to which all other sampled C3 grasses belong), one might dismiss the low *Phragmites* value as 'anomalous,' just as Gillon and Yakir

[19] ignored the higher Θ_{eq} values in *Amaranthus*. When regarded within a phylogenetic context, however, the *Phragmites* Θ_{eq} is consistent with its nearest relatives (the PACCAD grasses), as are the *Amaranthus* species with their relatives (other eudicots). The value that instead stands out as anomalous is that of *Echinochloa crus-galli*, a C4 PACCAD member with a high Θ_{eq} of 0.88. Why might *Echinochloa* have such a different value from the other sampled PACCAD species?

Although it is not evident from Figure 1, *Echinochloa* probably represents an independent origin of C4 photosynthesis from the other C4 grasses included in the study. It is the only C4 member of a C3 lineage of forest understory grasses, referred to as the 'forest-shade' clade [25,26]. Although we do not currently have data on the Θ_{eq} values of other members of this clade, the high Θ_{eq} value of the sampled *Echinochloa* makes it clear that the transition to C4 photosynthesis was not associated with a dramatic reduction in Θ_{eq} , providing a second argument that low Θ_{eq} and the C4 grass PFT are not necessarily linked.

To investigate the matter further, one could use phylogenetic information to guide a more strategic sampling of grasses to survey for CA activity and resulting Θ_{eq} values. It is estimated that there have been 11 independent origins of C4 photosynthesis in the grasses [27], at least seven of which occurred in the Panicoideae alone [25,27]. To test whether being a grass and performing C4 photosynthesis is correlated with low Θ_{eq} , one could measure Θ_{eq} in representative taxa from each of the 11 C4 lineages and their respective C3 relatives. If one found a significant correlation between the evolution of C4 photosynthesis and a reduction in Θ_{eq} , then that would provide strong support for modeling the C4 grass PFT with low Θ_{eq} values.

If one instead found that shifts in photosynthetic pathway are not associated with shifts in Θ_{eq} , and that low Θ_{eq} is highly conserved and largely representative of the PACCAD grasses, how would that understanding inform global biogeochemical modeling efforts? One might argue that it makes no difference, as all C4 grasses are found in the PACCAD clade and would, thus, all have low Θ_{eq} values anyway. As discussed earlier, however, there are also many C3 grasses in this clade that would also have low Θ_{eq} values and these include some of the most ecologically dominant grasses (e.g. *Phragmites*, the common reed; *Arundo*, the European reed grass; and *Cortaderia*, the pampas grass of South America). *Phragmites australis*, for example, is now common in many temperate areas of the world and, in North America, it is rapidly expanding its range and forming dense, monospecific stands over large areas [28,29] (Figure 2). Taken together, we believe that the C3 PACCAD ecological dominants could significantly influence global Δ^{18} , which suggests that assigning them an erroneously high value of Θ_{eq} would lead to large miscalculations in carbon cycling on a global scale.

Global change research and phyloinformatics

So how do we incorporate phylogenetic information into studies of global ecology and climate change? This knowledge could be immediately utilized by those modeling $C^{16}O^{18}O$ ecosystem-atmosphere exchanges at a particular

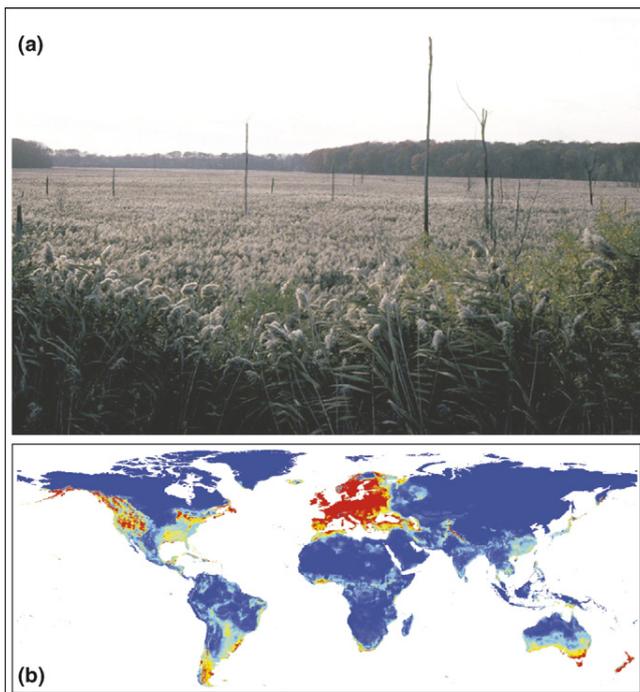


Figure 2. Ecological dominance and global distribution of *Phragmites australis*, a C3 grass of the PACCAD clade. *Phragmites australis* is a good example of some of the dominant C3 grasses that our phylogenetic analyses indicate might share low Θ_{eq} values with their C4 relatives. Such C3 grasses represent highly productive and ubiquitous species, and assigning them erroneous Θ_{eq} values could significantly affect estimations of global GPP. (a) In many regions, *P. australis* is an aggressive invader and will form dense monocultures that cover vast areas, as depicted here in Mentor Marsh, Ohio, USA. Reproduced with permission from John M. Randall. (b) Global geographical distribution of *P. australis* predicted from 8319 georeferenced herbarium collections (<http://www.GBIF.org>), 19 climate variables derived from a global temperature/precipitation dataset (WorldClim, <http://www.worldclim.org>), and ecological niche modeling (MAX-ENT [43]). Areas in red represent the highest probability of *P. australis* occurrence, whereas those in dark blue represent zero probability. With further development of phyloinformatics, we envision being able to model geographical distributions of entire clades as easily as a single species.

site that is known to have PACCAD clade C3 grasses. It is currently more difficult to translate this knowledge to regional-scale and global-scale analyses. Our argument is that the area that is assigned a lower Θ_{eq} value for purposes of global calculations should be increased to include the distributions of *Phragmites* and other ecologically dominant C3 PACCAD grasses. There are many global vegetation models that currently estimate the location and extent of C4 grass-dominated ecosystems [23,30], but not PACCAD-clade dominated ecosystems. One possibility would be to estimate the distribution of individual species through analyses of satellite imagery or other remote-sensing techniques. This might be possible in certain cases (e.g. *Phragmites*), where large monospecific stands could be detected, but we doubt that the geographical ranges of many species could be determined in this way.

A different, and we believe quite promising, approach will be enabled by the further development of 'phyloinformatics'. Digitization efforts now being undertaken by natural history institutions worldwide are yielding open online access to the geographical data associated with museum specimens (e.g. the Global Biodiversity Information Facility; <http://www.gbif.org>). At the same time, the development of georeferencing tools and GIS-based

modeling methods make it possible to generate predictive range maps for species from data on specimen labels (Figure 2). If these capabilities could be linked with rapidly expanding knowledge on phylogenetic relationships (e.g. TreeBASE; <http://www.treebase.org>) it would be possible to automate the assembly of geographical range information for entire clades. Thus, for example, we could infer the geographical range of the PACCAD grasses by connecting information on clade membership to specimen databases, and submitting these data to a linked cascade of georeferencing, niche-modeling and mapping web-services. These results could then be used in more nuanced models designed to estimate global ecosystem parameters, such as GPP. Accuracy could be improved still further with the inclusion of relative abundance information gathered from online databases of vegetation plot surveys (e.g. <http://www.salvias.net>; <http://www.vegbank.org>), which might also be available in some cases.

Conclusion

In summary, we see both the need and the real possibility to develop a productive link between phylogenetics and global biology. Phylogenetic knowledge is expanding rapidly and it can now be used to orient and to improve studies, including those of global change, that concern the evolved functional traits of organisms. As we have shown, variation in the relevant physiological attributes does not always correspond neatly with the traditional plant functional categories used in ecosystem-level studies. We are confident that the accuracy of modeling efforts can be improved by taking the phylogenetic distribution of these key traits into account, and we look forward to the design of the phyloinformatics tools that are necessary for practical applications on a global scale.

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