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effects have the potential to be influential agents of natural selection (25). Imbalances of expectation and reward may therefore have broad effects on health and physiology in humans and may represent a powerful evolutionary force in nature.

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Savanna Vegetation-Fire-Climate Relationships Differ Among Continents

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Ecologists have long sought to understand the factors controlling the structure of savanna vegetation. Using data from 2154 sites in savannas across Africa, Australia, and South America, we found that increasing moisture availability drives increases in fire and tree basal area, whereas fire reduces tree basal area. However, among continents, the magnitude of these effects varied substantially, so that a single model cannot adequately represent savanna woody biomass across these regions. Historical and environmental differences drive the regional variation in the functional relationships between woody vegetation, fire, and climate. These same differences will determine the regional responses of vegetation to future climates, with implications for global carbon stocks.

Savannas cover 20% of the global land surface and account for 30% of terrestrial net primary production (NPP) and the vast majority of annual global burned area (1–3). Savanna ecosystem services sustain an estimated one-fifth of humans, and savannas are also home to most of the remaining megafauna (1). Tropical savanna is characterized by the codominance of C_3 trees and C_4 grasses that have distinct life forms and photosynthetic mechanisms that respond differently to environmental controls (4). Examples include the differing responses of these functional types to temperature and atmospheric CO_2 concentrations, predisposing savannas to altera-

tions in structure and extent in the coming century (4–6).

Tropical savannas are defined by a continuous C_4 herbaceous layer, with a discontinuous stratum of disturbance-tolerant woody species (7). Although savanna tree cover varies greatly in space and time (8, 9), the similarities in structure among the major savanna regions of Africa, Australia, and South America have led to an assumption that the processes regulating vegetation structure within the biome are equivalent (10, 11). Current vegetation models treat savannas as a homogenous entity (12, 13). Recent studies, however, have highlighted differences in savanna extent across continents (14, 15), and it remains unknown how environmental drivers interact to determine the vegetation dynamics and limits of the biome (10, 14, 15).

We sought universal relationships between savanna tree basal area (TBA, m^2 ha^{-1}), a key metric of woody biomass within an ecosystem, and the constraints imposed by resource availability (moisture and nutrients), growing conditions (temperature), and disturbances (fire). Ecologists have devoted considerable effort to the identification of universal relationships to describe the structure and function of biomes (16). However, it has not been clear whether such relationships exist. Any such relationships may be confounded by the unique evolutionary and environmental histories of each ecological setting (11).

Across Africa and Australia, TBA scales similarly with rainfall, but the intercepts and the 95th quantile differ substantially (Fig. 1, A to C). On average, at a given level of moisture availability, TBA is higher in Africa and lower in Australia. However, in South America there is almost no relationship between rainfall and TBA, which is probably in part attributable to the narrow range of rainfall that savanna occupies on this continent (Fig. 2). Further, across the observed range of rainfall, the upper limits of TBA increase linearly with effective rainfall for Australian savannas (Fig. 1B) but show a saturating response in African and South American savannas (Fig. 1, A and C). When TBA is used to estimate aboveground woody biomass (AWB) (17), the large differences in intercepts between Africa and Australia are reduced but substantial differences in the limits remain (fig. S1, A to C). By con-

verting TBA to AWB, we attempted to quantify how variation in biomass allometry, modal tree size, maximum tree size, and the mean number of stems per hectare affects our interpretation of the functional relationships between savanna woody vegetation, climate, and fire. These regional differences imply that savanna vegetation dynamics are region-specific and are influenced by both regional climates and the allometric traits specific to the woody species of each region (17). We interpret the fact that so few sites reach the maximum values as being partially a result of variation in soil properties and disturbance processes. Fire is a prevalent agent of vegetation change, as shown by experimental, landscape, and modeling studies (8, 15, 18).

To investigate the drivers underlying the observed continental differences in TBA, we constructed a conceptual model of the determinants of woody vegetation structure based on a priori hypotheses about the direct and indirect effects of climate, soils, and fire on TBA (Fig. 3A) (1, 8, 10, 14). The model estimates the effects of resource availability (moisture availability and soil properties), growing conditions (temperature), and disturbance (fire) on TBA. Globally, data availability on herbivore abundance is sparse and unreliable and, as a result, we could not include herbivore abundance as a predictor (17). We used our conceptual model to develop a series of structural equation models (SEMs) to quantify the response of TBA to functionally related composite

variables (17). Composite variables in our analysis were (i) moisture availability, composed of effective rainfall, rainfall seasonality, and Foley's drought index; (ii) soil properties, composed of percent of organic carbon and percent of sand; and (iii) temperature, composed of mean annual temperature and annual temperature range [described in detail in (17)]. Specifically, our model allowed us to test the extent to which TBA is directly determined by climate and edaphic factors, versus the extent to which TBA is indirectly effected by these factors through their effects on fire.

Our results highlight that interactions among moisture availability, fire, and TBA are a defining characteristic of savannas. Increasing moisture availability simultaneously promotes increases in both TBA and grass-fueled fire frequencies (Fig. 3, B to D). As moisture availability increases, mean TBA can approach a maximum value, which is different in each region (Fig. 1, A to C). Fire, by preventing the accumulation of TBA, generally maintains TBA below a maximum value.

Therefore, on a qualitative level there is universality in savanna vegetation dynamics, evidenced by our analysis of each region identifying the same network of factors influencing TBA. The exception was that soil properties influenced TBA in South America and did not influence fire frequency, in contrast to Africa and Australia.

Interactions between moisture, fire, and TBA are unequal across continents. Moisture availability explains approximately two to three times more of the variation in both TBA and fire frequency in Africa and Australia as compared to South America (Fig. 3). Similarly, the negative effect of fire explains 1.5 to 2.5 times more of the variation in TBA in Africa as compared with South America or Australia, with only a very weak effect of fire on TBA is in Australia (Fig. 3). Our findings are consistent with studies that have shown that the importance of the effect of fire on TBA is conditional on seedling and sapling growth rates, fire resilience traits, and fire intensity (10, 18, 19). Woody plant growth rates determine the post-fire rates of TBA accumulation,

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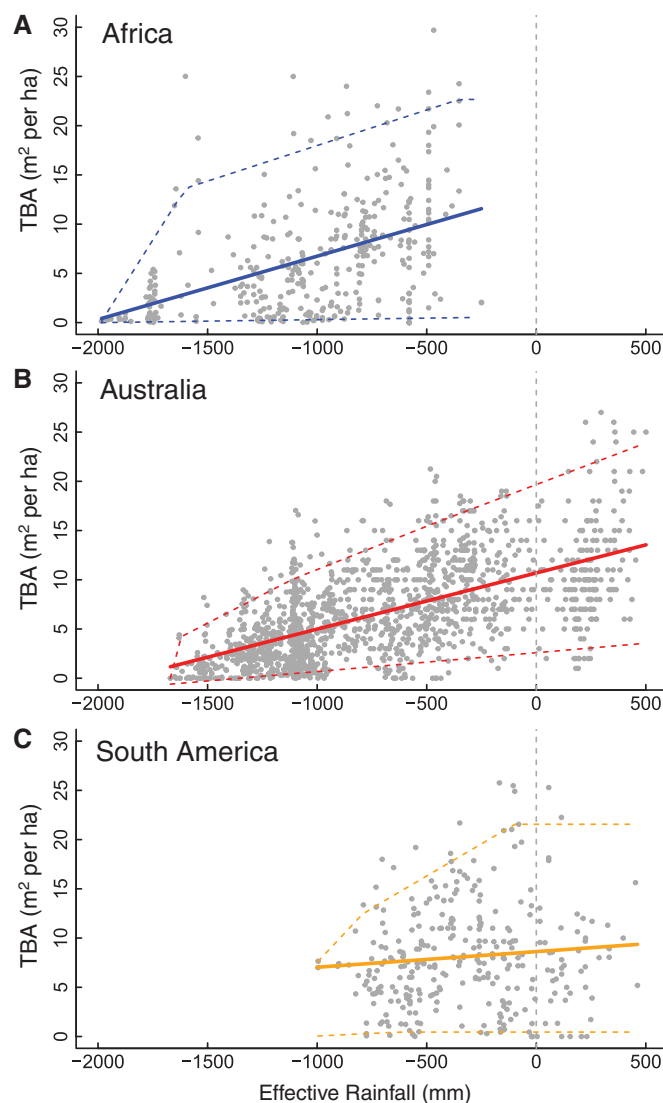
Fig. 1. Change in TBA of savannas relative to effective rainfall. The relationships between TBA and effective rainfall (in millimeters per year) across (**A**) Africa [coefficient of determination (r^2) = 0.203, $F(1, 363)$ = 92.4, P value = <0.001]; (**B**) Australia [r^2 = 0.385, $F(1, 1485)$ = 930.9, P value = < 0.001]; and (**C**) South America [r^2 = 0.008, $F(1, 300)$ = 2.6, P value = 0.111] are shown. Also depicted are the piecewise quantile fits of the 5th and 95th quantiles.

whereas fire frequency and intensity are a product of grassy fuels (*19*). Differences among continents in the effect of fire on TBA probably reflect differences in woody plant traits and the fuel loads and flammability of C_4 grasses.

In Africa, moisture availability has a strongly positive relationship with fire, implying that fire and the accumulation of C_4 grasses in African savanna are more tightly controlled by

yearly variation in the timing and amount of rainfall than in either Australia or South America. These cascading relationships appear weaker in Australia, and less so in South America, and can be partially explained by the differences in the climatic domain occupied by the savanna of each region (Fig. 2). Thus, continental differences in TBA and AWB relate to a combination of differences in the climatic drivers of fire fre-

quency and intensity, as well as to differences in the growth and fire resilience traits of woody plants.

In Africa and Australia, temperature has a strong effect on fire (Fig. 3, B to C, and tables S1 and S2), probably determined by a composite of two factors. First, at warmer sites, fuels are more likely to cure, facilitating more frequent fire (*3*). Second, the physiology of C_4 grasses means

Fig. 2. Climate domain of savannas in Africa, Australia, and South America. The savanna climate domain relative to (**A**) mean annual rainfall versus mean annual temperature and (**B**) effective rainfall versus annual temperature range. Black points represent all vegetated 0.5° grid cells within 30° of the equator across Africa, Australia, and South America. Gray points represent all 0.5° grid cells where savanna is present as in (*14*). Lines represent the 95th quantile of the density of these points for savanna on each continent.
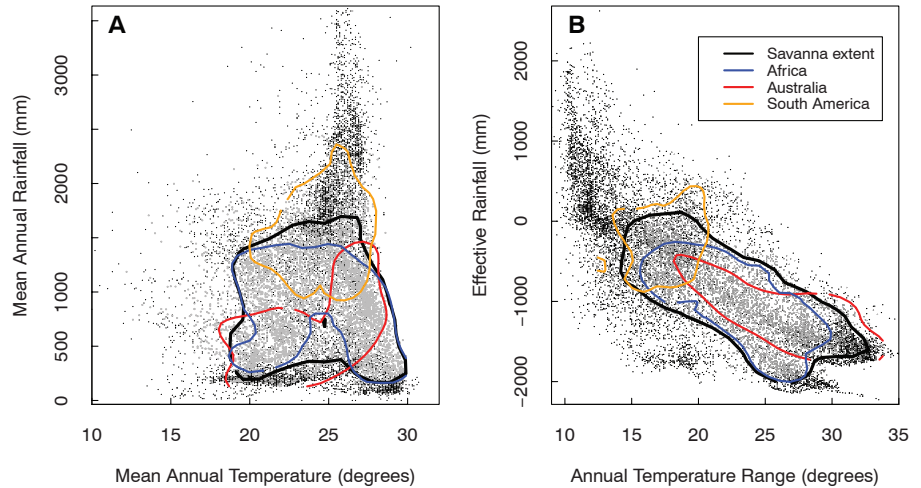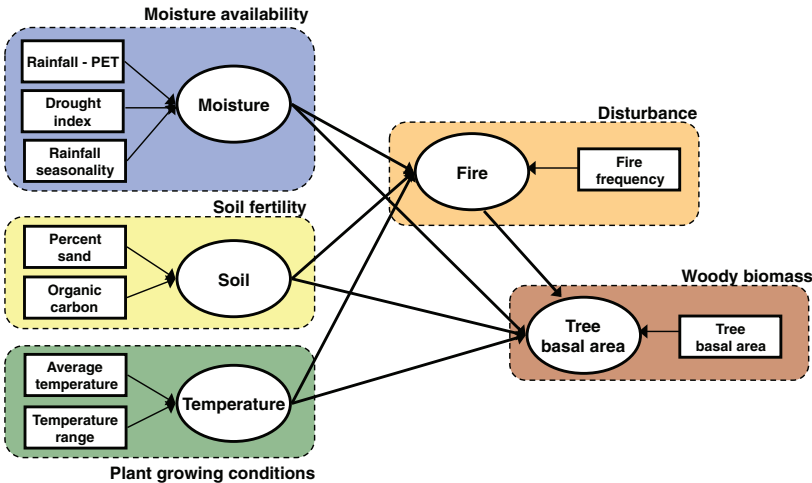

Fig. 3. Structural equation modeling of TBA for Africa, Australia, and South America. Structural equation modeling of TBA for Africa, Australia, and South America. (**A**) Conceptual model depicting theoretical relationships among moisture availability, soil fertility, plant growing conditions (temperature), and disturbance (fire frequency), and their effects on TBA either directly or indirectly as mediated by fire frequency. (**B** to **D**) The final model for each continent. Values associated with arrows are absolute path strengths, which combine positive and negative effects of indicators into a composite effect (*17*); the arrow thickness is proportional to the absolute path strength. The arrows from fire to TBA represent standardized path coefficients and are depicted in gray to express their negative impacts. Full models results are presented in (*17*).
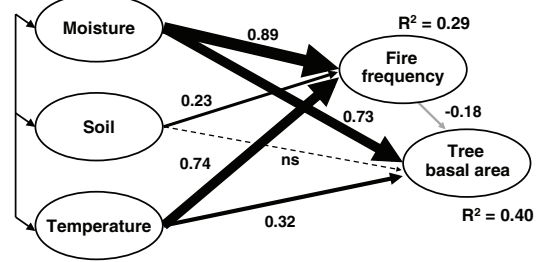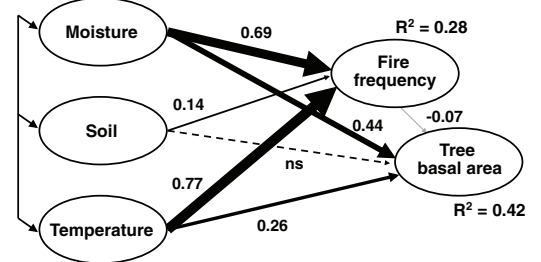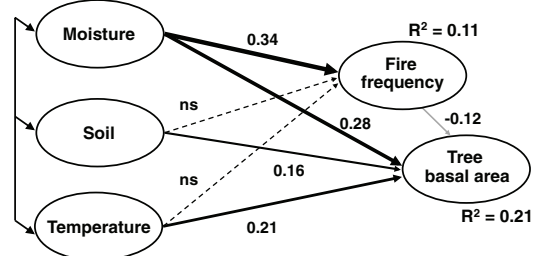
that they have a higher temperature optima for photosynthesis and growth (relative to C_3 plants), facilitating the potential for rapid biomass accumulation in hot seasonally dry environments (4, 20), conditions that are more extensively found in the savannas of Africa and Australia (Fig. 2).

In South America, we found a limited explanation of TBA (Fig. 3D). This is consistent with previous studies that have examined savanna extent and found that the limited explanatory power was not simply a product of South American savanna being wetter (14, 15). A previous study found that if the climatic range of South American savanna were projected to Africa or Australia, the global extent of savanna would diminish (14). One potential explanation is that acid and infertile soils may act as constraints on both the distribution and vegetation structure of South American savanna, as discussed in numerous studies (14, 15, 21), although the quality of global soils data limits any ability to detect the regional influence of soils.

Taken together, our findings illustrate how a common set of environmental drivers shape savannas across the globe in qualitatively similar ways. However, the quantitative details of how these factors interact (Fig. 3) and the climatic domains occupied (Fig. 2) differ substantially among continents, so that for practical purposes we must dismiss the use of a single global model relating savanna TBA and AWB to environmental drivers. Instead, we make a case for

regionally calibrated models to investigate the response of savanna vegetation to climate change. For example, we show that our global analysis, in which the role of continent is ignored, fails to capture regional differences in the predicted response to a hypothetical 4°C increase in mean annual temperature (Fig. 4). In particular, for Africa our global analysis predicts a net decrease in woody biomass, whereas the regional model predicts a net increase (Fig. 4) due to fire-temperature interactions within our model. Our regional analyses show that changing climates could set these three savanna regions on different paths of vegetation change.

Why are these structurally similar ecosystems in different geographic regions regulated in different ways by the same environmental drivers? The answer may lie in the evolutionary history of this biome. Tropical savanna is relatively new, originating with the global expansion of C_4 grasses 3 to 8 million years before the present (22). When savannas arose, the southern continents had been separated for >40 million years. C_4 grasses and the coincident increase in fire frequency (and also megaherbivory) exerted novel selective pressures on regional woody floras, while the phylogenetic and geographic distance between savanna regions led to the development of analogous but not identical solutions in woody plants to these new selective pressures. Today, savanna tree canopies are dominated by Myrtaceae in Australia and in Africa by Mimosaceae, Combretaceae, and

Caesalpiniaceae (23). In South America, there is a mix of dominance, with savanna taxa derived from forests in the past 10 million years (24). These distantly related woody taxa are disturbance-tolerant but differ in their phenology (23), growth rates (19), resilience to fire (19), canopy architecture, and biomass allometry (17).

The global ensemble of regions constituting modern savannas has, over millennia, converged on a similar open-canopy vegetation structure due to the evolution and invasion of C_4 grasses (22) and the resulting ubiquity of disturbance (3, 14). The environmental space occupied by modern savanna allows for the multiple interactions among moisture availability, temperature, fire, and vegetation. However, the functional and architectural traits of the woody species dominating each region determine the form and strength of the functional relationships to environmental drivers. Our data indicate that each savanna region may respond differently to changes in climate. Currently, remote sensing evidence suggests differing trajectories of change in Australian and southern African savannas (9, 25). The one climate–one vegetation paradigm is an underpinning of many global vegetation models (12, 13), and these models are a primary tool for anticipating the response of vegetation to future climates (5, 26), but are based on a notion that the same environmental controls will produce the same vegetation structure irrespective of environmental and evolutionary history. We show
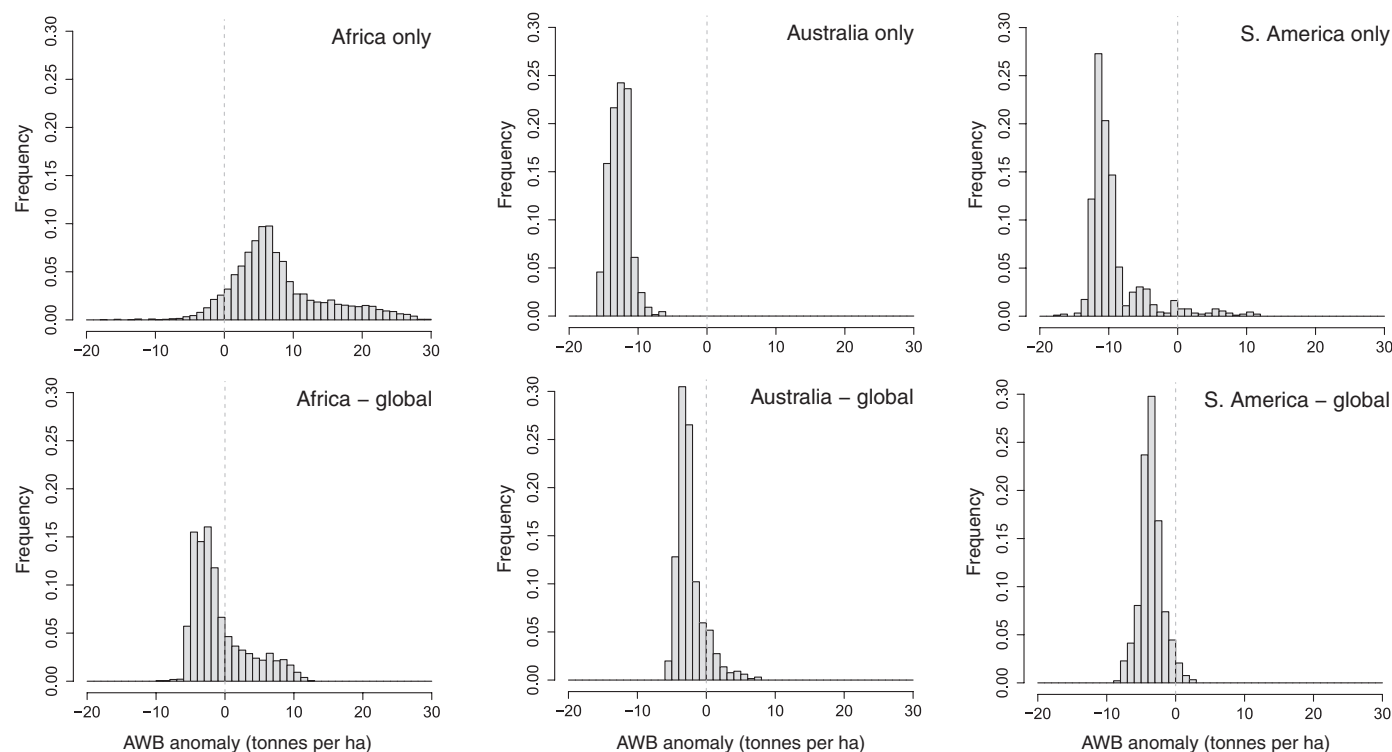
Fig. 4. Hypothetical shifts in AWB on three continents relative to a 4°C increase in mean annual temperature. Frequency distributions of the predicted anomalies in AWB (metric tons per hectare) with a 4°C increase in mean annual temperature, where a region-specific model and a global model are compared. Distributions are calculated at a 0.5° resolution. The global model shows the results of an analysis where "continent" is ignored (table S4).

that the convergence of structure in savanna conceals substantial differences in the relationships between savanna woody vegetation, climate, and fire. Just as the regional evolutionary and environmental histories underpin differences in these relationships, these same differences will determine the contemporary vegetation response of each region to future climates.

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Effector Specialization in a Lineage of the Irish Potato Famine Pathogen

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Accelerated gene evolution is a hallmark of pathogen adaptation following a host jump. Here, we describe the biochemical basis of adaptation and specialization of a plant pathogen effector after its colonization of a new host. Orthologous protease inhibitor effectors from the Irish potato famine pathogen, *Phytophthora infestans*, and its sister species, *Phytophthora mirabilis*, which is responsible for infection of *Mirabilis jalapa*, are adapted to protease targets unique to their respective host plants. Amino acid polymorphisms in both the inhibitors and their target proteases underpin this biochemical specialization. Our results link effector specialization to diversification and speciation of this plant pathogen.

The potato blight pathogen, *Phytophthora infestans*, is a recurring threat to world agriculture and food security. This funguslike oomycete traces its origins to Toluca Valley, Mexico, where it naturally infects wild *Solanum* plants (*1*). In central Mexico, *P. infestans* co-occurs with closely related species in a tight phylogenetic clade known as clade 1c. These species evolved through host jumps followed by adaptive specialization on plants belonging to different botanical families (*2*, *3*) (fig. S1). One species, *Phytophthora mirabilis*, is a pathogen of four-o'clock (*Mirabilis jalapa*). It split from *P. infestans* about 1300 years ago (*1*), and the two species have since specialized on their *Solanum* and *Mirabilis* hosts. Adaptive evolution after the host jump has left marks on the genomes of *P. infestans* and *P. mirabilis* (*3*). Comparative genomics analyses revealed signatures of accelerated evolution, structural polymorphisms, and positive selection in genes occurring in repeat-rich genome compartments (*3*). In total, 345 genes induced within plants show signatures of positive selection between the two sister species (*3*). These include 82 disease effector genes, rapidly evolving determinants of virulence that act on host target molecules. We lack a molecular framework to explain how plant pathogen effectors adapt and specialize on new hosts, even though this process affects pathogen evolution and diversification (*4–6*).

To gain insight into the molecular patterns of host adaptation after host jumps, we selected the cystatinlike protease inhibitor EPIC1, an effector protein of *P. infestans* that targets extracellular (apoplastic) defense proteases of the *Solanum* hosts (*7*, *8*). The *epiC1* gene and its paralogs *epiC2A* and *epiC2B* evolved relatively recently in the *P. infestans* lineage, most likely as a duplication of the conserved *Phytophthora* gene *epiC3* (*7*) (Fig. 1). To reconstruct the evolution of these effectors in the clade 1c species, we aligned the *epiC* gene cluster sequences, performed phylogenetic analyses, and calculated variation in selective pressure across the phylogeny (Fig. 1, fig. S2, and table S1) (*9*). We detected a signature of positive selection in the branch of *PmepiC1*, the *P. mirabilis* ortholog of *P. infestans epiC1* [nonsynonymous to synonymous ratio (ω) = 2.52] (Fig. 1B). This is consistent with our hypothesis that PmEPIC1 evolved to adapt to a *M. jalapa* protease after *P. mirabilis* diverged from *P. infestans*.

To test our hypothesis, we first determined the inhibition spectra of the EPIC effectors using DCG-04 protease profiling, a method based on the use of a biotinylated, irreversible protease inhibitor that reacts with the active site cysteine of papainlike proteases in an activity-dependent

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