

## Alternative biome states challenge the modelling of species' niche shifts under climate change

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Type: Mini-review

Number of words: 3614 (excluding abstract, references, figures, boxes, and tables)

Number of figures: 1

Number of tables: 1

Number of boxes: 1

### Abstract

1. It is common to characterise the species niche using climate and global species distribution maps. This is then used to predict changes in distribution under a warming climate. This approach assumes that climate is a major driver of species distribution and that each species responds individually (*sensu* Gleason) to climate.

2. However, in many world landscapes, for a given climate, strikingly different vegetation types co-occur: forests and non-forests. These two alternative biome states are maintained by different feedback processes and have radically different species with contrasting shade and disturbance tolerance traits.

3. We propose that to improve predictions of species distribution changes under a novel climate we need to consider the presence or absence of forest shade, as species are likely to respond individually only within their forest or non-forest biome, and not across biomes.

4. *Synthesis*. By considering shade as a biotic filter in niche modelling, we are not only improving our predictive capacity, but we are also reconciling the two views of communities: both the individualistic (within biome) and the organismal (across biomes) views of the community concept become relevant and complementary.

*Key words*: alternative stable states, biomes, community, light environment, open ecosystems, shade, species niche, species response.

## 1. Gleason's individualistic assumption reconsidered

The question of whether species are organised as collectives of integrated interacting assemblages (Clements, 1936) or behave individualistically (Gleason, 1926) is a century-old debate in ecology that is still to be resolved (Loreau, 2020). The debate has re-emerged in recent decades with an initial widespread acceptance of the Gleasonian assumption when using species distribution models (SDMs) for exploring climate change impacts on biodiversity (Thuiller et al. 2005; Conradi et al., 2020). Climate change can be predicted from general circulation models while species responses to those changes can be explored using statistical models of their niche dimensions along environmental axes. The latter assumes that climate factors are major causes of species distributional changes over a template of varying geologies, and that each species responds individually along climatic axes (Fig. 1a). Here we challenge both assumptions.

Conceptually, the abundance and distribution of a plant species can be represented as a function of light, temperature, soil nutrients, water, CO<sub>2</sub>, disturbance, and biota (Austin & Van Niel, 2011). In practice, climate variables are the most widely used in SDMs, probably because they are more available at broad scales. There have been attempts to include biological interactions in predictive models (Boulangeat et al. 2013, Wisz et al., 2013); however, the underlying assumption remains that the main drivers are climate and soil variables; interactions are often inferred from co-occurrence along those main gradient (Wilkinson et al. 2021). A few studies consider differing light regimes in SDMs, recognising that different aspects and topographies generate distinct light environments that favour different sets of species (Austin & Van Niel, 2011; Higgins et al., 2012, Nieto-Lugilde et al. 2014, ).

Here we argue that the light regime created by canopy trees, i.e., forest shade and its presence or absence, profoundly influences the distribution of many species across the world as it filters the assembly of species by their shade tolerance. And, as we will see below, this filter generates different environmental conditions associated with different disturbance regimes, and thus requiring divergent physiological adaptations (Valladares & Niinemets 2008, Zellweger et al., 2020) and disturbance response traits (Bond, 2019; Pausas & Bond, 2020a). The presence or absence of forest shade is therefore a major factor in determining species distribution and global biodiversity. Given that many open (light-demanding) ecosystems are threatened, it is important to be able to predict their fate under global change. We propose that considering forest shade in SDMs, or using mechanistic models that explicitly consider vegetation feedbacks, may help in this regard while improving our understanding of community assembly.

## 2. Alternative biome states: exceptions to deterministic climate control

In climates suitable for forests, ecosystems with low levels of tree cover, and therefore open to sun-loving species, are anomalies for the hypothesis that climate determines vegetation (Bond 2019). Yet over the last decade, mosaics of closed forest and open (non-forest) ecosystems dominated by shade-intolerant grasses or shrubs have been recognised as alternative stable states in a diversity of environments (Bond, 2019; Dantas et al., 2016; Hirota et al., 2011; Overbeck et al., 2015; Ratajczak et al., 2014; Ratnam et al., 2016; Staver et al., 2011; Cramer et al. 2019). These states can be considered 'biomes' (Box 1) since they differ in the dominant growth forms (Alternative Biome States, ABS; Pausas & Bond, 2020a). The open and closed biomes are stable as they can persist over generations at a site. They are 'alternative' because they can occupy the same substrate and occur in the same climate; and they can switch states rapidly relative to periods of stability (Bond, 2019; Hirota et al., 2011; Pausas & Bond, 2020a; Staver et al. 2011).

Open ecosystems in landscapes also supporting forests have long been considered as early successional. The supposed anthropogenic origins of open biomes have stifled research for most of the 20th century and this continues to lead to misconceptions today (Noss et al. 2015; Pausas & Bond, 2019). However, both fossil and phylogenetic studies have shown that sun-loving lineages are ancient and millions of years older than human deforestation (Edwards et al. 2010; Carpenter et al. 2015; Maurin et al., 2014; Simon et al., 2009; Feurdean et al. 2015; Bond, 2019). Fire, often considered the most destructive human tool, has been burning vegetation for over 400 million years (Pausas & Keeley, 2009; Scott, 2000). Livestock ‘degradation’ of vegetation was preceded by millions of years of consuming and trampling plants by mammalian megafauna, and before them, by dinosaurs and other tetrapods for at least 300 million years. Open biomes and their biota are now known to be ancient and diverse, and so must be included in global change assessments of biodiversity responses (Veldman et al., 2015).

### **3. Feedback processes maintain contrasted environments**

Open (non-forests) and closed (forest) biomes are maintained by different stabilising feedback processes that are generated by contrasted disturbance regimes (Bowman et al. 2015; Dantas et al 2016; Pausas & Bond, 2020a). Frequent fires and/or large herbivores maintain open biomes and enable a dominance of shade-intolerant graminoids or shrubs; and these plants further enhance frequent fires and/or grazing that maintain the open light-saturated state. In contrast, in closed biomes, shade limits the growth of understory plants, and thus limits fuel for fires and forage for large herbivores (Charles-Dominique et al. 2018). Forests create microenvironmental conditions (e.g., higher humidity, lower temperatures, and lower wind speed) that inhibit fire spread while enhancing the growth of forest trees (Hoffmann et al., 2012; Newberry et al., 2020). These two feedback processes are essential for maintaining different biomes in a given environment, and they generate divergent microenvironmental conditions.

The forest feedback creates environmental conditions different from the macroclimate (Zellweger et al., 2020, De Frenne et al. 2021), including higher humidity, lower temperatures, and lower wind speed. Environmental conditions in open biomes are a mirror image, with lower humidity, higher temperatures, higher windspeeds, and sufficient light to grow a dense vegetation of highly flammable, or palatable, grasses, and shrubs (Hoffmann et al., 2012; Little et al. 2012, Newberry et al. 2020). Forests may also diverge from open grasslands and shrublands in accumulating nutrients such as nitrogen, potassium, and calcium in the topsoil whereas these are depleted in open biomes, especially when frequently burnt (Table 1; Cramer et al., 2019; Pausas & Bond, 2020b). Root systems of both juvenile and adult forest woody plants diverge from those of open biomes (Hoffmann et al. 2004; Ma et al. 2018), so that a suite of physiologically divergent traits develops around the presence or absence of a forest canopy.

### **4. Taxonomic and functional differences in the biota**

The consequences of different conditions between open and closed biomes are profound and not only related to different physiognomy and growth patterns; they imply different species composition with contrasting traits in each biome (Dantas et al., 2013; Charles-Dominique et al. 2017, 2018; Aleman et al., 2020), even under the same climate (Table 1). Open biomes are dominated by shade-intolerant species that cannot colonise forests, while forests maintain shade-tolerant trees that are burnt or browsed to death in open environments. Forest trees can colonise the open biomes only if disturbance is excluded, probably coping with high light levels thanks to their high plasticity (Power et al., 2019). In such conditions, savanna trees

may require some time to die but will fail to recruit (e.g., transitional forests with coexisting forest and savanna trees). Dynamics and elimination by shade are much faster for the ground layer of open biomes (Newberry et al., 2020), which include a large proportion of their biodiversity (Baker et al. 2020). When tropical forests have patches or glades of grasses, they are often  $C_3$  species, in contrast to adjacent savannas and grasslands that are dominated by  $C_4$  grasses (Charles-Dominique et al., 2018, Solofondranohatra et al. 2018, Edwards et al., 2010, Pilon et al., 2021).

Given the different disturbance regimes in each biome, plants in open and closed biomes have dramatically different traits related to fire and herbivore resistance. These include higher insulation of buds limiting fire injury in open biomes (Burrows, 2002; Charles-Dominique et al. 2015), thinner bark in forests (Charles-Dominique et al. 2017; Lawes et al. 2013; Pausas, 2015), higher prevalence of resprouting structures in open biomes (Pausas et al., 2018), and different structural defences such as spinescence (common in open biomes where mammal browsing is high; Charles-Dominique et al., 2016; Dantas & Pausas, 2020). The net effect is a pronounced floristic and functional divergence between forest and open biomes (Table 1).

The importance of shade (or its mirror opposite, openness) is also conspicuous for fauna, as it provides contrasting habitat for a myriad of animals. And this distinction is not exclusive for large vertebrates that dominate open habitats (Bond, 2019). For instance, the most important factor determining the assembly of ant species in Australia is whether they live in an open or closed biome (Andersen, 2019); and South African forests and shrublands also differ in the assembly of Collembola, with contrasted functional traits in each biome (Liu et al. 2020). Open/closed environments have also generated species divergences in animals, including elephants (Rohland et al., 2010), birds (Slabbekoorn & Smith, 2002), and even hominids (Roberts et al. 2016).

## 5. Implications for global change impacts on biodiversity

If open biomes were determined primarily by climate and soils, then predicting the future of species from these physical variables would be reasonable (e.g., Conradi et al., 2020; Gardner et al. 2020). However, the existence of open biomes where forests can grow forces consideration of the existence of feedback processes that maintain open states. Mosaics of open and closed biomes are globally widespread and occur under many climates (Staver et al. 2011; Pausas & Bond, 2020a). Forest/grassy biome mosaics are common in the tropics and sub-tropics of Africa and South America (Staver et al. 2011), and occur in Australia (Wood & Bowman 2012, Barker et al. 2020), south-east Asia (Ratnam et al 2016), and North America (Noss 2012). Forest-steppe mosaics are common in a vast area of Eurasia (Feurdean et al 2015; Erdős et al. 2017). Based on ecoregion maps, open biomes cover about one-third of the world's vegetated land surface (Bond, 2019). By ignoring the biotic response to shade in species distribution models we are likely to fail to predict the different biodiversity futures in open versus closed biomes.

For instance, despite the many examples of ABS from Africa, a recent vegetation modelling exercise for this continent (Conradi et al. 2020) only used climate and soils, and thus was not able to model alternative biome states (as admitted by the authors). A striking example is Madagascar, a biodiversity hotspot where grasslands are widespread, diverse, and include numerous species endemic to open habitats on the island (Solofondranohatra et al. 2018, 2020). In the Madagascar highlands (and in other parts of Africa), Conradi et al (2020) predicted a mix of trees, climbers, and grasses rather than the observed mosaic of forest patches in grassland. Grassland fires are lethal to forest trees while forest trees are lethal for shade-intolerant grasses (which hardly coexist in Madagascar). Considering shade as an environmental filter would have prevented the prediction of an unrealistic coexistence. The

distinction between forested and open habitat is also crucial for Madagascar rich fauna, and the forest-dwelling mouse lemur is an emblematic example (Quéméré et al 2012). The failure to recognise feedback processes and the associated forest/non-forest environmental filter is just as important in other regions with grassy biomes (Bond 2016, 2019; Veldman et al. 2015; Murphy et al. 2016; Buisson et al. 2019; Pausas and Bond 2020). If a significant part of the world vegetation and diversity is strongly controlled by fire and herbivory, then it is not possible to predict the distribution of species by just climate and soil alone.

While there has been considerable public and scientific concern over loss of forests and their ‘savannisation’ due to extreme fires, there has been far less concern over loss of biodiversity in open biomes due to expanding forests (e.g., Baker et al. 2020). Yet disruption of consumers, especially through fire suppression, or changing the type and density of herbivores, can cause cascading effects to these systems. Fire suppression caused the loss of large tracts of the species-rich southern grasslands in the USA (Noss, 2012) and forest expansion is swallowing up what is left (Nowacki & Abrams, 2015). Fire suppression in nature reserves in the Brazilian cerrado caused the loss of the rich sun-loving cerrado plant species, especially the herbaceous layer, and their replacement by shade-tolerant trees and shrubs (Durigan and Ratter 2016; Abreu et al., 2017). And conifer plantations in old growth grasslands have led to the loss of the rich forb flora which has failed to re-colonise areas many decades after the forests were felled (Veldman et al., 2015). These cascading losses had nothing to do with climate change and everything to do with human interventions in managing the consumers that maintain open biomes. Restoring ecological processes that maintain open biomes (e.g., rewilding; prescribed grazing; wildfire management; prescribed burns) are slowly being promoted for biodiversity conservation (Driscoll et al., 2010; Perino et al., 2019).

Changes in the growing conditions for woody plants should also affect the tree layer and the mix of forest and non-forest. An important global change impact is the effect of increasing CO<sub>2</sub> on trees. Fires maintain open biomes by limiting the growth of tree saplings to adults (fire-trap). Faster sapling growth under CO<sub>2</sub> fertilisation should enable more trees to reach the size threshold to escape the flames, thus speeding forest expansion into open biomes (Bond & Midgley, 2012). In fact, when incorporating CO<sub>2</sub> into vegetation modelling, woody plants largely increase (Higgins & Scheiter, 2012). Because of the open/closed dichotomy of species and their traits, major loss of open habitat biodiversity can be expected as they close over with trees (Midgley & Bond, 2015, Baker et al. 2020) and this may go unnoticed if our models are unable to predict it.

An additional concern is an intentional massive increase in tree cover as a form of geoengineering intended to decarbonise the Earth. There are several high-profile tree-planting programmes endorsed by the UN, the IUCN, governments, and industry. These are being targeted at areas of low tree cover – open biomes – without consideration of their unique and diverse biota (Bond et al. 2019; Veldman et al. 2015). There is clearly a need to explicitly consider the future of alternative closed and open biomes in global change modelling.

## **6. Modelling beyond Gleasonian assumptions**

The Gleasonian view of communities suggests that communities are assembled by species that respond individually along environmental gradients and thus cannot form bounded units (Gleason 1926). This view lacks any consideration of stabilising feedback processes generating divergent biotically-determined environments and mosaics in a given climate. The overlapping response curve along a climate gradient (Fig. 1a) may indicate plant coexistence (and potentially competitive interactions) only if they occur in the same biome (Fig. 1b). That is, the individualistic continuum of species along climatic gradients is expected within the



same biome but not across biomes. Thus, responses to climate and geology do not necessarily reflect the species niche; the physical environmental axes are relevant only if nested within the appropriate physiognomically-defined biome. Fitting species distribution models or using climate limits in biome modelling for projecting future distributions are inappropriate for extensive regions with alternative biome states.

Is it possible to incorporate the biological effect of shade as a major environmental filter in SDMs? The availability of large databases of species, localities, and habitat preferences have made it possible to consider responses to climate change for thousands of species (Conradi et al., 2020). A few studies have demonstrated that shade (i.e., tree cover) can also be added as a significant habitat requirement for plants (Nieto-Lugilde et al. 2014). However, defining biologically determined light environments may not be straightforward, as the resolution of global tree cover maps may not be the most appropriate for depicting ABS. Among the difficulties are divergent views on the meaning of ‘forest’. For instance, FAO describes ‘forests’ as ecosystems with tree cover as low as 10% thereby muddling ecologically and functionally distinct closed and open biomes (Sasaki & Putz, 2009). The increasing availability of quantitative field-based vegetation data at the global scale (Bruehlheide et al., 2019) may facilitate the estimation of the shade factor. The use of new remote sensing technologies including new satellites, drones, and airborne LiDAR (Valbuena et al., 2020, Ferraz et al. 2020, Emilien et al. 2021) can also provide quantitative data to discriminate between closed and open ecosystems at large scales. Field information is also available to calibrate remote sensing data. For instance, both in Brazil and in southern Africa, field studies suggest thresholds of leaf area index (LAI) above which grasses (and fire) are absent (Charles-Dominique et al., 2018; Hoffmann, et al., 2012; Pilon et al., 2020). Field measurements of microclimate (e.g., Zellweger et al. 2020) can also be used for calibration; when the appropriate data is available, it can be incorporated into SDM (Nieto-Lugilde et al. 2014, Lembrechts et al. 2019). There are also a range of statistical methods for fitting complex SDM including species interactions that could indirectly include the shade factor (for a recent revision see Norberg et al. 2019). The joint species distribution models may prove especially promising (Warton et al. 2015, Wilkinson et al. 2021; see caveats in Poggiate et al. 2021) as they can model entire species assemblages to environmental conditions assuming common responses to some factors (e.g., shade tolerance). Thus, these tools may help moving from Gleasonian assumptions to a more Clementsian view of communities.

Another approach for accounting for ABS is including the processes that maintain open biomes (fire, grazing) into correlative SDMs. For instance, fire-related variables explained additional variation not captured by climatic variables, resulting in increased model performance when modelling species distribution in the Cape Floristic Region of South Africa (Tucker et al. 2012). More difficult may be including variables related to grazing especially at broad (global) scales. In fact, there is limited tradition to simultaneously consider the three ecological dimensions, i.e., environmental parameters, species interactions, and disturbance, to understand biogeographic patterns (Pausas & Lamont 2018).

Process-based models, such as dynamic vegetation models (DVM) can also be used at the community level for inferring ABS (Moncrieff et al. 2014, Lasslop et al. 2016); their added advantage is their dynamic nature and the possibility of including other global change drivers (e.g., CO<sub>2</sub> effects, disturbance regime shifts; Higgins & Scheiter, 2012, Sato et al. 2021). Some of these models do not directly simulate the feedback process that generate ABS, but they are used for testing different initial conditions. For instance, results simulating African biomes in response to changing CO<sub>2</sub> (Moncrieff et al. 2016) suggest that DVM are highly sensitive to initial conditions; predictions showed extensive savannas and grasslands (similar to 20<sup>th</sup> century African vegetation) when using initial conditions resembling late glacial vegetation, but forests were much more widespread if the historical initial condition was

ignored. The simulations also showed widespread loss of conditions favouring alternative biome states and the expansion of forests primarily because of elevated CO<sub>2</sub> effects (Moncrieff et al 2016). Consequently, species associated with open ecosystems would be at high risk of extinction because of the spread of forest, regardless of their individualistic responses to changing climate. A few DVMs explicitly simulate feedbacks and ABS; for instance, a local scale simulation study in southern Brazil highlighted the importance of the initial spatial pattern (not just abundance) of the different alternative states (Blanco et al. 2014). More research is needed to be able to explicitly simulate feedback processes at broad scales, and thus to predict expansions and contractions of biomes in landscape mosaics and across biogeographic units.

Overall, a wide range of tools are available for exploring the global change responses of the biodiversity in alternative biome states; it is the conceptual framework that has been missing.

## 7. Concluding remarks

Ancient open biomes are common in climates that can support forests (alternative biome states). They encompass a significant proportion of world regions, including many biodiversity hotspots such as Brazilian cerrado, Cape fynbos, Mediterranean-type shrublands, and other major centres of species richness such as the Campos rupestres of Brazil, African grasslands and savannas, pine savannas of the southern USA, or Eurasian forest-steppes. We know a little about their response to global drivers, and models not considering alternative biome states are likely to fail in their biodiversity projections. There is an immediate and major threat to the future of many of these open habitats, not only because of increasing tree cover with declining herbivory and fire and the continuous increase in atmospheric CO<sub>2</sub>, but also because of the international support for planting trillions of trees or expanding forested areas to millions of km<sup>2</sup> worldwide. Failure to model the implications, or to acknowledge the importance of non-forested ecosystems and their sun-loving biota, could lead to a major loss of species over the next few decades as trees start shading out the forest floor. Lacking appropriate modelling tools may mean unpredictable and unnoticed biodiversity losses with little room for management actions for conservation.

There is a need to incorporate ABS in vegetation modelling. For process-based models, the most appropriate would be to include the necessary feedback processes. For correlative-based niche models, incorporating forest shade as a biotic filter may provide a way to incorporate ABS, and thus improve our biodiversity response predictions under global change. By doing so, we are also reconciling the two community concept views (Fig. 1): both the individualistic (within biome) and the organismal (across biomes) are relevant and complementary. That is, both Gleason's and Clements's perspective of community remain useful concepts in ecology.

## Acknowledgements

This research has been performed under the framework of the projects FIROTIC (PGC2018-096569-B-I00, Spanish government). Authors declare no conflict of interest.

## Authors contribution

J.G.P. and W.J.B. conceived the idea; J.G.P. wrote the first draft; J.G.P. and W.J.B. wrote the final version and gave final approval for publication.

## Data Accessibility

No original data was used in this study.

### Box 1. The biome concept

Humboldt & Bonpland (1807) noted that there were analogous vegetation formations in geographically disjunct but climatically similar regions. These vegetation formations (*sensu* Schimper, 1903) correspond to a current common use of the term ‘biome’, that is, vegetation dominated by the set of life-forms prevailing in a given climate (for a historical review, see Mucina, 2019). This definition, in which vegetation physiognomy and climate are linked, has been the basis of many global vegetation/ecosystem classifications (Walter, 1973; Whittaker, 1975) and it is based on the idea of strongly convergent evolution by climate. More recently, Woodward et al. (2004) recognised that this biome definition makes vegetation and climate indistinguishable, and thus it limits our understanding of the processes behind vegetation patterns; and they suggested defining biome in terms of only plant physiognomy (i.e., based on the dominant, or the mixture of dominant, growth forms). Defining biomes based on the vegetation physiognomy (see below) enables assessing the relative influence of various environmental factors (including climate, soil type, herbivory, or fire regimes).

Table in Box 1. Examples of structurally based (climate-independent) biomes at different resolution levels (the coarsest on the left).

Closed biomes	Forests	Needle-leaved forests
		Broad-leaved winter deciduous forests
		Broad-leaved summer deciduous forests
		Broad-leaved evergreen forests
		Sclerophyllous forests
Open biomes	Savannas	C4 savannas with broad-leaved trees
		Coniferous woodlands
		Eucalypt woodlands
	Shrublands	Sclerophyllous shrublands
		Heathlands
		Low shrublands
		Eucalypt woodlands
	Grasslands	C3-dominated grasslands/steppes
		C4-dominated grasslands



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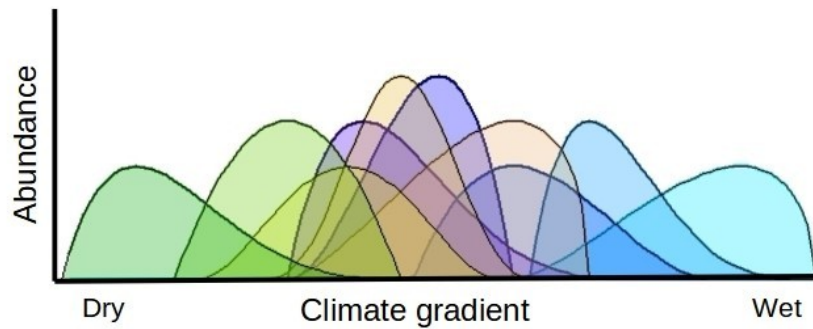
**Table 1.** Contrasted characteristics between open and close biomes are produced by the different feedbacks influencing tree density and shade with cascading effects at different scales. In open biomes, several traits are variable among different types (e.g., grasslands, shrublands) or disturbance type (fire, grazing). Examples of open and close biomes are given in Box 1.

Trait	Open biomes	Closed biomes	Examples*
<i>Woody plants</i>			
Tree bark thickness, bark growth	Variable	Low	1, 2, 3
Stem bud protection	Variable	Low	4
Resprouting ability	High, basal	Low	
Belowground bud bank	Common	Rare	5
Hydraulic fire resistance	High	Low	6
Root/Shoot	High	Low	7
Leaf area (m <sup>2</sup> /g)	Lower	Higher	8
Spines	Variable	Low	9
Shade tolerance	Intolerant	Tolerant	10, 11
Shape (height, width)	Shorter, wider	Taller, narrower	12, 2
Leaf area / branch mass	Lower	Higher	11
Light plasticity	Lower	Higher	13
<i>Herbaceous plants</i>			
Grass photosynthesis	C <sub>4</sub>	C <sub>3</sub>	11, 14, 15
<i>Community and ecosystem</i>			
Leaf Area Index	Lower	Higher	13
Grass cover	Variable	Low	11
Vertebrate herbivory	Higher	Lower	9
Fire frequency	Higher	Lower	16
Dominant biogeochemical feedback driver	Fire, herbivores	Microbes (litter decomposition)	17
Local effect on soils	Leaching	Enriching	17, 18
Topsoil fertility	Lower	Higher	18
Microclimate (in relation to macroclimate)	Similar	Colder, moister, less wind	19, 20, 21

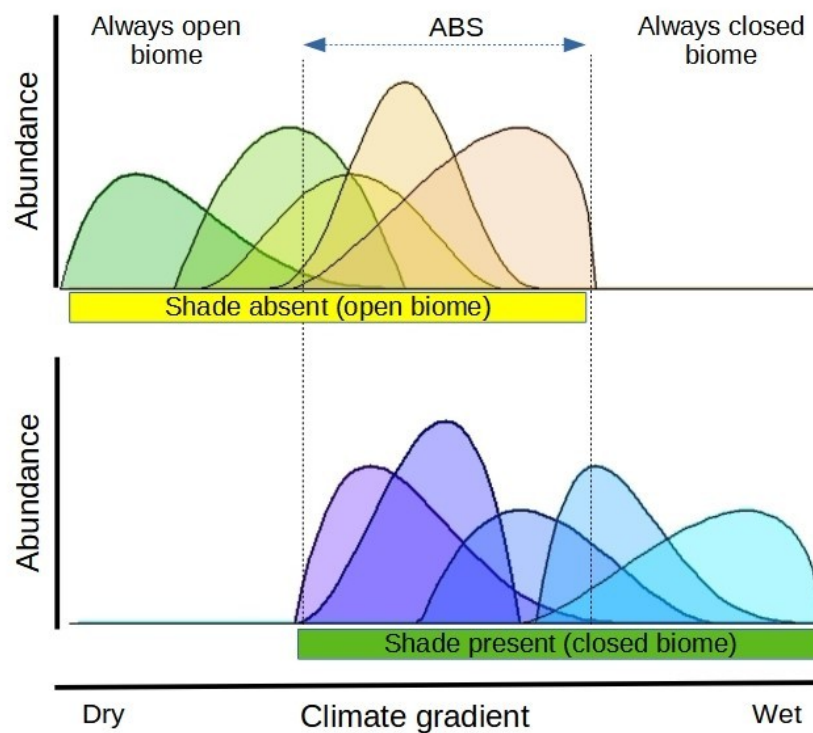
\* 1 Charles-Dominique et al., 2017; 2 Hoffmann, Orthen, & Do Nascimento, 2003; 3 Pausas 2015; 4 Charles-Dominique et al., 2018; 5 Pausas et al., 2018; 6 West et al., 2012; 7 Hoffmann et al., 2004; 8 Hoffmann & Franco, 2003; 9 Charles-Dominique et al., 2016; 10 Bazzaz, 1979; 11 Charles-Dominique et al., 2018; 12 Dantas & Pausas, 2020; 13 Power et al., 2019; 14 Edwards et al., 2010; 15 Pilon et al., 2020; 16 Dantas,

Batalha, & Pausas, 2013; 17 Pausas & Bond, 2020b; 18 Cramer et al., 2019; 19 Newberry et al., 2020; 20 Zellweger et al., 2020; 21: De Frenner et al. 2021.

### A. Classical



### B. Alternative



**Figure 1.** Classical pattern of species response curves along a climate gradient (A), and the alternative pattern along the same climatic gradient when considering the shading factor (B). Note that in the driest and the wettest section of the gradient, we find open (e.g., grassland) and closed (forest) biomes, respectively; but at intermediate levels of the gradient, both are possible depending mainly on the disturbance regimes and feedback processes (alternative biome states, ABS; Pausas & Bond, 2020a). Thus, under the intermediate levels of the gradient, species that may seem to coexist when considering climate only (A) are not really coexisting but occurring in drastically different biomes.