REVIEW

Bark thickness and fire regime

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Summary

1. Bark is a vital and very visible part of woody plants, yet only recently has bark characteristics started to be considered as key traits structuring communities and biomes. Bark thickness is very variable among woody plants, and I hypothesize that fire is a key factor selecting for a thick bark, and thus, at the global scale, a significant proportion of the variability in bark thickness is explained by the variability in fire regimes. Previous research has focused on the importance of bark thickness mainly in surface-fire regimes; here I generalize this idea and present a conceptual framework to explain how the different drivers that affect fire intensity have shaped bark thickness, in conjunction with other plant traits.

2. I first review methods used to study bark thickness and then provide examples of bark thickness patterns from a wide range of ecosystems subject to different fire regimes (understorey fires, grass-fuelled surface fires, grass-fuelled crown fires and infrequent fires).

3. There are some fire regimes that select for thick barks, while some only in the base of the trunk (e.g. understorey fires), others select for a thick bark on the whole plant (e.g. grass-fuelled crown fires). There are also fire regimes in which allocating resources to a thick bark is not adaptive (e.g. woody-fulled crown fires).

4. Fire regime can explain a large proportion of the variability of bark thickness at the global scale, and thus, this trait varies across ecosystems in a predictable manner; however, the current paucity of data limits a fully accurate analysis.

Key-words: 'soft' plant traits, bark ecology, evolutionary, fire ecology, fire regimes, fire traits, woody plants

Introduction

Bark is the outermost covering of stems in woody plants. Behind the apparent simplicity of this concept, there is a complex of tissues located outside the vascular cambium that includes live and dead cells. Despite its importance and visibility, bark has been little studied from an ecological perspective in comparison with other plant parts such as leaves. Most previous work on bark ecology emphasizes the protective role of bark (e.g. Vines 1968; Harmon 1984; Peterson & Ryan 1986), and only very recently have bark traits been considered as key functional traits in structuring communities and biomes, and this has been greatly fostered by studies in species-rich tropical ecosystems (see references in Table 1).

Bark has two major components with different origins, structure and function: the inner bark (mainly the secondary phloem), which is produced by the vascular cambium and lies between this and the cork cambium, and the outer bark that is outside of, and originated by, the cork cambium (for anatomical details see Evert & Eichhorn 2006; Romero 2014). The primary function of the inner bark is the transport and storage of photosynthates and secondary compounds, and thus, it is of the paramount importance in plants; in some cases, the inner bark contains chlorophyll and contributes to plant photosynthesis (Pfanz & Aschan 2001). Major functions of the outer bark, which consists of dead cells, include reduction of water loss, barring against pathogen entry, mechanical stability, protection against mechanical injury, insulation of the stem against adverse climatic conditions (e.g. extreme cold) and protection against wildfires (e.g. Vines 1968; Niklas 1999; Paine *et al.* 2010; Ferrenberg & Mitton 2014; Romero 2014). Many of these functions were probably in place from the very origin of bark and contributed to the ability of early woody species to colonize and diversify in a range of environments. The diversity of bark functions is also reflected in its diverse anatomy and chemistry, as well as in the diversity of colours, textures, smells, densities and thicknesses.

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Table 1. Examples of studies that compare bark thickness values between different ecosystems. In each row, ecosystem are arranged starting from the one with the highest fire activity (A) as described in the corresponding reference. Symbols < and > refer to significant differences, while the symbol = refers to non-significant differences

Contrasts, ecosystem, region	Variable*	Results	Reference
Park-like forests and savannas (A) vs. forests (B); *Pinus* species, North America	Allometric coefficient	A < 1 < B	Jackson, Adams & Jackson (1999)
Park-like forests and savannas (A) vs. forests (B); *Quercus* species, North America	Allometric coefficient	A < 1 < B	Jackson, Adams & Jackson (1999)
Acacia woodlands (A) vs. Afromontane forest	BT	A > B	Eriksson, Teketay & Granström (2003)
Savanna (A) vs. Forest (B), congenerics, Brazil	BT	A > B	Hoffmann, Orthen & Do Nascimento (2003)
Savanna (A) vs. Forest (B), congenerics, Brazil	Allometric coefficient	A < 1 < B	Hoffmann, Orthen & Do Nascimento (2003)
Eucalypts (A) vs. non-eucalypts (B) saplings, tropical Australia	BT	A > B	Lawes *et al.* (2011)
Open savannas (A) vs. closed forests (B), cerrado mosaic, Brazil	BT/D	A > B	Dantas *et al.* (2013a)
Neotropical (A) vs. Afrotropical (B) savannas	BT ~ D	A > B	Dantas & Pausas (2013)
Savannas (A) vs. forests (B), South America	BT ~ D	A > B	Dantas & Pausas (2013)
Cerrado (A), Eucalypt savanna (B), Gallery forest (C), Monsoon forest (D), Amazon forest (E)	Slope of BT ~ D (linear, through origin)	A > B = C > D > E	Lawes, Midgley & Clarke (2013)
Savanna (A) vs. Forest (B) Tropical Australia	Cross-sectional bark area ~ D	A > B	Lawes, Midgley & Clarke (2013)
Savanna (A), temperate woodlands (B), xerophytic shrublands (C), dry forests (D), rain forests (E). Australia and Mexico	BTb BTb/Db	A > B = C = D = E	Rosell *et al.* (2014)
Drier habitats, shorter FRI and lower FI (A) vs. wetter habitats, longer FRI and higher FI (B); surface fires; *Quecus* species*	Allometric coefficient	A < B < 1	Schwilk, Gaetani & Poulos (2013)
Dry (A) vs. Moist (B) tropical forests, Bolivia	Allometric coefficient	A = B < 1	Poorter *et al.* (2014)
Dry (A) vs. Moist (B) tropical forests, Bolivia	Size-corrected BT	A = B	Poorter *et al.* (2014)
Acacia spp in wetter (A) vs. in drier (B) savannas (FRI = 2·9 vs. 3·8)	Slope of BT ~ D (linear section)	A > B	Hempson *et al.* (2014)

Abbreviations: BT: bark thickness (absolute value) measured at the main stem; D: stem diameter; BTb, Db: bark thickness and diameter measured in a branch (at fixed distance from the tip); BT ~ D: comparison made considering the full data set of BT and D (covariance-type analysis); FRI: mean fire return interval; FI: fire intensity.

Here I will focus on the variation of bark thickness in a global context with emphasis on fire-prone ecosystems. Bark thickness is very variable among woody dicotyledon plants, from less than a millimetre to a few decimetres, and because it determines the distance of external factors to vital tissues (e.g. the cambium), variability in this distance is likely to have protective function. Thus, developing a thick bark could be considered a protection mechanism against infections, herbivores, frost and extreme cold, or fire. My hypothesis is that fire is a very important factor selecting for a thick bark, and thus, at the global scale, a significant proportion of the variability in bark thickness is explained by the variability in fire regimes. Because fire regimes varies world-wide (Krawchuk *et al.* 2009; Pausas & Keeley 2009; Pausas & Ribeiro 2013), bark thickness should also vary across ecosystems in a predictable manner. That is, we predict that some fire regimes would favour disproportionately thick bark; while in others, having a thick bark provides little benefit. This does not mean that fire is the only selective factor for the variability in bark thickness; as we will see in this review,

in some fire regimes, and especially in ecosystems with infrequent fires, other factors can also be relevant (e.g. droughts); however, there is increasing evidence that contrasted fire regimes can generate different bark thickness (Table 1, Table S1, Supporting Information). By fire regimes, I refer to the characteristics of wildfires prevailing in a given ecosystems, including frequency, intensity, seasonality and spread pattern of fires (Keeley *et al.* 2012; Pausas & Keeley 2014a). Examples of ecosystems with different natural fire regimes are savannas that burn very frequently in low-intensity fires, Mediterranean shrublands that burn less frequently and more intensely or rain forest that burn very infrequently (or never).

Fire is expected to have a fundamental role in shaping bark thickness because it is predictable and a very efficient cause of tree mortality, and because the bark is a very good heat insulator, (thermal diffusivity is about 20% of wood of the same density and about two orders of magnitude lower than air; Martin 1963). The degree of heat insulation by bark is proportional to their thickness (specifically, it increases with the square of bark thickness;

Fig. 1, Table S2 and S3 (Supporting Information); Vines 1968; Harmon 1984; Peterson & Ryan 1986; Pinard & Huffman 1997). Bark not only protects meristemic tissues (cambium, buds) and phloem, but also the xylem, as stem mortality could also be caused by hydraulic failure (Ducrey *et al.* 1996; Midgley, Kruger & Skelton 2011; Michaletz, Johnson & Tyree 2012). That is, although the bark fulfils many functions and its origin may be unrelated to fire, there is increasing evidence that having a thick bark increases fitness in many fire-prone ecosystems, and thus, a significant proportion of the variability in bark thickness among ecosystems should be driven by their variability in fire regimes. Small differences in bark thickness may provide a great selective advantage for trees living under low-intensity fire regimes because it greatly increases stem protection and the likelihood of stem survival (Fig. 1). Stem mortality reduces plant fitness as it implies mortality (in non-resprouting plants) or a delay and reduction of reproduction and growth (in plants that resprout from basal buds). Developing a thick bark is costly, not only in terms of resource allocation, but also in opportunity costs caused by limiting the diffusion of water, oxygen, CO_2 and light through the stem (Pfanz & Aschan 2001; Cavaleri, Oberbauer & Ryan 2006; Teskey *et al.* 2008). Because of the costs, thick barks could only have appeared in ecosystems where a small difference in thickness would increase fitness (e.g. survival or reproduction) and ecosystems where fires are frequent and of low intensity are a clear example (Fig. 2). In ecosystems where fires are intense, small variations in bark thickness would provide no fitness benefits because stems would have no chance of survival (Fig. 2a); in such conditions, investing in a bark that will not protect the stem is not adaptive, and other traits such as basal resprouting, the presence of lignotubers and post-fire seeding are selected (Pausas *et al.* 2004; Keeley *et al.* 2011, 2012; Pausas & Keeley 2014b). In ecosystems where fires are rare, some variability in bark thickness is still observed, probably driven by other factors (Paine *et al.* 2010; Rosell & Olson 2014). That is, the differential selective pressure imposed by different fire regimes is likely to result in varying bark thickness, and in turn, bark thickness could provide some clues on the fire regimes where the species occurs. In fact, bark thickness is an evolutionary labile trait, and there is evidence in extant species of
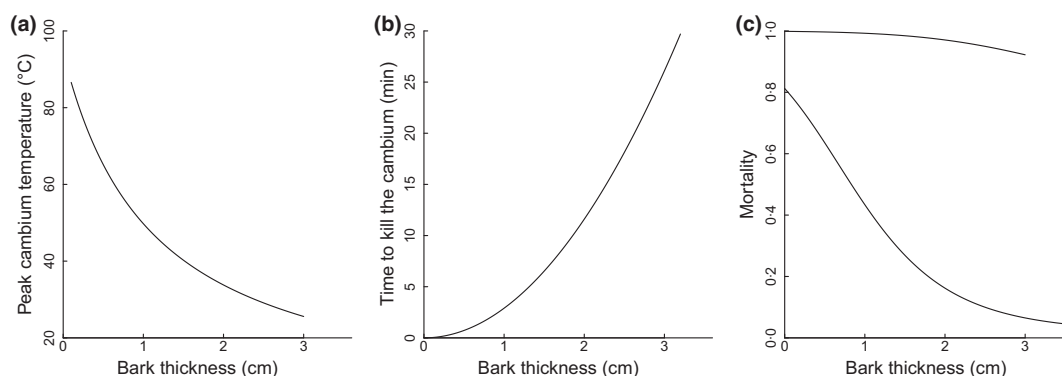
Fig. 1. Models showing the role of bark thickness (in cm) in protecting the cambium from fire heat: (a) peak temperature (°C) of the cambium in relation to bark thickness during experimental fires (Uhl & Kauffman 1990; see more details and other experiments in Table S2, Supporting Information). (b) Time to kill the cambium (i.e. to reach 60 °C), given an instantaneous fire temperature of 500 °C, based on Peterson & Ryan (1986); alternative models based on experiments are provided in Table S3 (Supporting Information). (c) Probability of mortality as a function of bark thickness after a crown-fire (upper line) and after a surface-fire (lower line) based on field observations in coniferous species from western USA (Ryan & Reinhardt 1988).
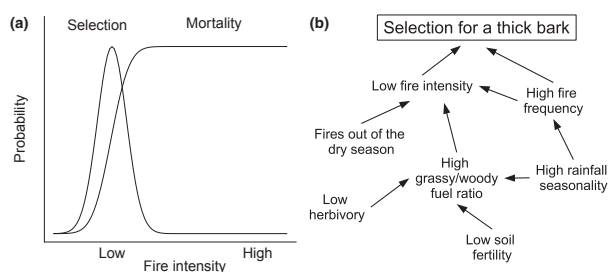
Fig. 2. Possible model for the selection of a thick bark in fire-prone ecosystems. For a thin-barked tree, selection for a thick bark occurs under recurrent low-intensity fires, as high-intensity fires kill all tree (a). The curves (a) move rightwards as the bark thickens over generations. There are several drivers that can generate low-intensity fires (b). For instance, low soil fertility decreases woody growth while high rainfall seasonality increases the grass component, thus increasing the grass-to-woody fuel ratio and so generating low-intensity fires. These low-intensity fires, when frequent, select for thick bark. Low herbivory may contribute to increased grassy fuels, while very high herbivory may increase unpalatable woody plants. Fires outside of the driest season tend to be of low intensity.

different bark thickness among populations as well as among congeneric species living under different fire regimes (Table S1, Supporting Information; Jackson, Adams & Jackson 1999; Hoffmann, Orthen & Do Nascimento 2003; Cavender-Bares *et al.* 2004; Simon & Pennington 2012). Also the presence of a thick and strongly suberized corky bark in distantly related species from fire-prone ecosystems in different continents can be considered an example of convergent evolution (Pausas, Pereria & Aronson 2009; Appendix Fig. S1, Supporting Information). Previous research has focused on the importance of having a thick bark in surface-fire regimes (e.g. Keeley & Zedler 1998; Jackson, Adams & Jackson 1999; Paine *et al.* 2010); here I will generalize this idea and present a conceptual framework for understanding how the different drivers affecting fire regimes, and especially intensity, have shaped bark thickness, in conjunction with other plant traits (Figs 2 and 3). I will focus on woody dicots, as arborescent monocots do not have either a secondary vascular cambium or a proper bark (Tomlinson 2006).

Understanding the ecology of bark thickness requires accurate measures of this trait. Although measuring bark thickness is relatively easy (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013), differentiating between inner and outer bark is more tedious (Appendix S1). Defining the most appropriate parameter for describing the functional role of bark thickness depends on the specific objective and the ecosystems involved. In addition, because bark thickness varies with tree size (Fig. 4), caution is needed when comparing bark thickness values among species or ecosystems, and there are different ways to standardize the measurements (Fig. 5, Appendix S1, Supporting Information).

Bark thickness in fire-prone ecosystems

Fire-prone ecosystems (also termed flammable or pyrophilic ecosystems) cover a large proportion of the world (Bond, Woodward & Midgley 2005; Krawchuk *et al.* 2009). They can be defined as those that have a history of fires that are frequent enough to exert an evolutionary pressure on the dominant species; that is, fire intervals are typically shorter than the longevity of plants, and thus, species need some adaptive traits for persistence. Having a thick bark is one of the key traits that can provide persistence to some fire regimes. An alternation of wet and dry conditions (with sufficient long wet period to permit biomass accumulation) is needed for recurrent fires (Figs 2 and 3), and this can be produced by seasonality or by frequent dry years. The two most distinctive fire regimes are
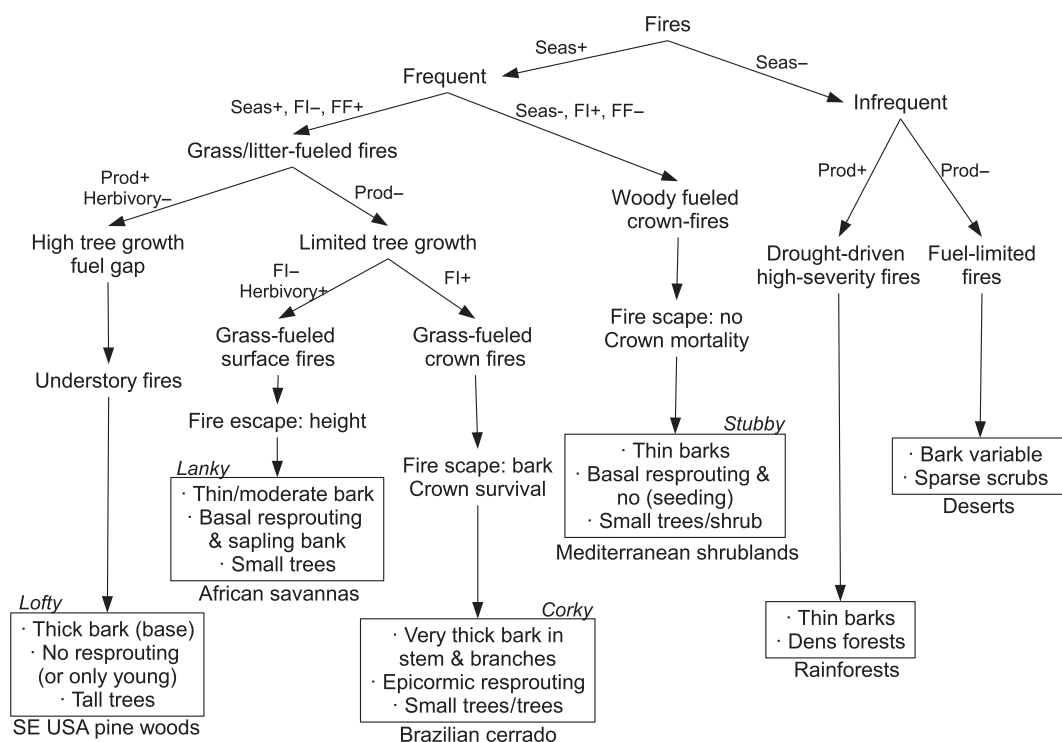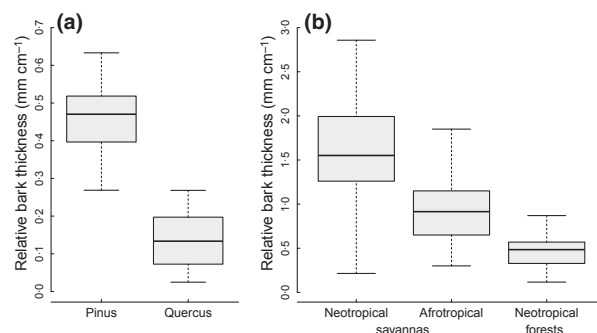

Fig. 3. Schematic diagram of the drivers that generate different fire regimes and different fire-related functional traits. The alternation of wet and dry periods (Seas) is a key parameter for determining fire-prone (with frequent fires) and non-fire-prone (with infrequent fires) ecosystems. The various components of the fire regime such as fire frequency (FF), fire intensity (FI) and type (crown or surface fire) together with productivity (Prod) determine bark thickness, resprouting ability and growth form (boxes) in dominant woody species (± refers to higher/lower and is relative for each bifurcation). Examples of ecosystems where the corresponding strategy is observed are given below the boxes. A nickname for the syndrome of plants living in frequent fire ecosystems is also included in *italics* on the top of the boxes. It is important to note that this in a schematic classification and there are intermediate cases and transitions between the examples provided.
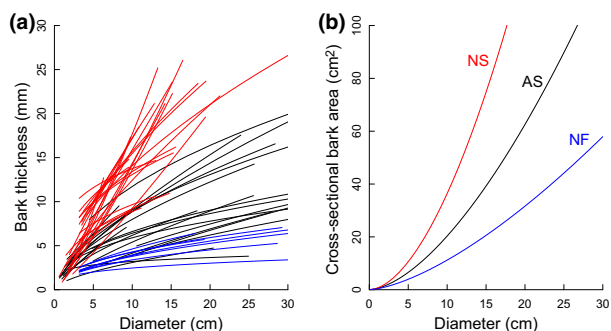
Fig. 4. (a) Relationship between bark thickness (mm) and diameter (cm) for 53 tropical woody plants (from Dantas & Pausas 2013). (b) Cross-sectional bark area (which is an estimation of the bark investment; Lawes, Midgley & Clarke 2013) for the same data set but grouping the species in three environments: Neotropical savannas (NS, Brazilian cerrado, red lines); Afrotropical savannas (AS, black lines); and Neotropical forests (NF, patches of forests in a cerrado landscape; blue lines). See also Fig 5b.

Fig. 5. Boxplots of the relative bark thickness (RBT, i.e. bark thickness/diameter; mm/cm) for different species and environments. (a) Outer bark thickness for adult individuals of 32 *Pinus* species and 16 *Quercus* species living in fire-prone ecosystems of North America (from Jackson, Adams & Jackson 1999); differences are statistically significantly ($F_{1,45} = 113$, $P < 0.0001$). (b) Bark thickness for Neotropical (e.g. cerrado) and Afrotropical savannas and Neotropical forests (62, 69 and 44 species, respectively, from Dantas & Pausas 2013; differences are statistically significantly: $F_{2,172} = 96$, $P < 0.001$); Fig. 4a shows the BT–D relationship for a subset of these species. RBT values are not directly comparable between the two studies due to different methodologies used in estimations; in brief, Jackson, Adams & Jackson (1999) used the full range of tree sizes (including small saplings) to predict the RBT of a standard adult size and considered the outer bark only; while the data from Dantas & Pausas (2013) represent the species mean RBT for the available data (small saplings are often excluded) and refer to total bark thickness.

surface fires and crown fires (Keeley *et al.* 2012; Pausas & Keeley 2014b). Surface fires typically spread through the herbaceous or litter layer and occur in a range of environments from open ecosystems (grasslands and savannas) to closed forests (understorey fires); when trees are present, they do not burn, and trees and grasses follow different dynamics. Crown fires only occur in woody-dominant ecosystems, and plants are fully burnt during the fire (including the crowns). That is, while surface fire is often fuelled by fine non-wooded fuels (grasses, litter), crown fires are typically fuelled by woody fuels. In highly seasonal climates, fires are very frequent and mainly driven by grasses, and thus, they are of relatively low intensity and often spread quickly across the surface (grass-driven surface fires, Fig. 3). In less seasonal climates, or in climates where fires are driven by drought, fires are less frequent, and so there is an accumulation of fine woody biomass that produces high-intensity fires (woody-fuelled crown fires, Fig. 3; e.g. Mediterranean ecosystems). However, within these broad fire regime types, there is considerable variability in the different parameters (e.g. intensity, frequency and season) depending on the different drivers that modify vegetation and fuel (e.g. climate, productivity, herbivory; Fig. 3). This wide variety of fire regimes has selected for different sets of adaptive traits. Below I present some examples to illustrate how different drivers may generate different optimal bark thicknesses (Fig. 2). Although there may be a continuum in many of the drivers and fire regimes, for simplicity, I propose to aggregate fire regimes as follows (from left to right in Fig. 3): understorey fires (forests and woodlands), grass-fuelled surface fires (open ecosystems), grass-fuelled crown fires (open ecosystems) and high-intensity woody-fuelled crown fires (forests and shrublands); in addition, regimes with infrequent fires can be driven by droughts or limited by fuel (rightmost in Fig. 3). Note that there are transitions and intermediate cases between these fire regimes, but still this simple group-

ing may help to describe the variability of bark thickness, and other fire-related plant traits, in different ecosystems world-wide.

UNDERSTOREY FIRES IN FORESTS AND WOODLANDS

In highly productive ecosystems with marked seasonal rainfall, the herbaceous layer develops profusely in biomass and height during each wet season, and thus, fires during the dry season can be relatively intense. In such conditions, trees quickly outgrow the flame height generated by the understorey vegetation. Thus, these ecosystems are typically dominated by tall trees with surface fires (understorey fires), and having a thick bark at the lower bole is then adaptive (Fig. S1, Supporting Information).

Examples of this strategy include many pines such as *P. ponderosa* and *P. palustris* in western and eastern North America (respectively). In fact, pines are an interesting group of species because they show a wide range of traits associated with different fire regimes (Keeley & Zedler 1998; He *et al.* 2012; Keeley 2012). The pine species with basal thick bark (i.e. in the lower part of the bole) mostly live in surface-fire ecosystems (Jackson, Adams & Jackson 1999; Fig. 5). They mostly live in highly productive environments, tend to be quite tall and have thin and long needles (i.e. high flammable litter); they self-prune dead branches (which helps maintain a significant fuel gap between the surface and the canopy) and lack serotiny. Consequently, these characteristics are evolutionary

correlated traits (Schwilk & Ackerly 2001; He *et al.* 2012) and conform the *fire tolerater pine syndrome* (Keeley 2012). Some of these fire tolerant pines have delayed height growth and trunk development as seedlings, whereby internode elongation is suppressed for a few years, with the resulting juveniles persisting in a bunch-grass growth form (the 'grass stage'; Keeley & Zedler 1998; Keeley 2012; He *et al.* 2012). During this stage, needles are decumbent, accumulate as a mantle over the apex, insulate the apical bud against fire heat – and thereby confer post-fire stem survival. Resources also accumulate in their roots. After 5–10 years, they produce a stem, quickly grow in height and, in a very short period, they are above the flame height zone of understorey fires and are protected by a thick bark. In some low productivity pine woodlands (e.g. Mediterranean mountain forests and the boreal forests of Eurasia), although trees grow more slowly, understorey vegetation is quite limited (e.g. by the cold) and there is still a fuel gap that maintains understorey fires. Fires in such conditions are of very low intensity, and probably, it does not select for the thickest barks (Fig. 2), but for a thick enough bark to protect the trunk.

Similarly to pines, there are other conifers that live in surface-fire ecosystems and have a very thick bark, grow very tall and tend to self-prune the lower branches. Prominent examples are *Araucaria araucana* and *Fitzroya cupressoides* in the Andes, and the giant sequoia (*Sequoiadendron giganteum*) and *Calocedrus decurrens* in western North America (Lara *et al.* 1999; Stephenson 1999; Beaty & Taylor 2007; González, Veblen & Sibold 2010). Some of these conifers form forests resembling what we believe Cretaceous forests looked like when surface fires enhanced the evolution of angiosperms (Bond & Scott 2010).

For trees living in ecosystems with understorey fires, the advantage lies in having a thick bark on the lower part of the trunk. For ontogenetic reasons, bark may also be thick in the upper part of the bole or in the branches. However, there is evidence that bark can be disproportionately thicker at the lower bole (Wiant & Koch 1974; Fernandes, Fernandes & Loureiro 2012; Odhiambo, Meincken & Seifert 2014; Graves, Rifai & Putz in press). It is possible that the lack of differences in bark thickness between ecosystems with different fire regimes reported by Rosell *et al.* (2014) could be because bark thickness was measured on branches (1 m from the tip) and not on the main stem.

GRASS-FUELLED SURFACE FIRES IN OPEN ECOSYSTEMS

In seasonal climates with low productivity or with high grazing pressure (e.g. African savannas), fuels are relatively low, and thus, fire intensities are also very low. In such conditions, the bark thickness determined by the tree size might be enough for survival, and seedlings do not necessarily allocate resource to develop an especially thick bark. In these ecosystems, there is a selection for seedlings

to grow fast in height during the interfire period to place the crown above the flame height (the escape hypothesis; Trollope 1984; Bond 2008; Dantas & Pausas 2013). By growing in height, the bark also reaches the minimal thickness for supporting low-intensity surface fires (the 'fire-safe' size). Resources are mostly allocated to fast growth and not to developing a especially thick bark (Afrotropical savannas in Fig. 5); in some species, saplings accumulate resources in underground structures (e.g. lignotubers) for later fuelling a fast growth. Browsers may act in a similar direction, that is selecting for fast height growth to escape the browsing height, without selecting for thick bark (Bond 2008; Moncrieff *et al.* 2011; Dantas & Pausas 2013). Saplings can be trapped in the flame/browsing zone for decades, where they are topkilled and resprout after each disturbance event to form a persistent sapling bank. Under these conditions, most individuals do not make it to adult sizes; and the effective recruitment is given by the few individuals that have a fast growth rate or thanks to rare long fire interval events (Wakeling, Staver & Bond 2011). Saplings surpassing the flame/browse height can be seen as seeds escaping predators; many seeds do not escape, but the few that do are the effective recruiters; that is, as in dispersal ecology, the tail of the distribution is extremely important. This strategy implies that the adult plants have a pole-like or lanky architecture (Gignoux, Clobert & Menaut 1997; Archibald & Bond 2003; Dantas & Pausas 2013; see an example in fig. 9b in Archibald & Bond 2003) and even may lose their resprouting ability with age and that populations may have a missing height class (e.g. Levick, Baldeck & Asner 2014) that act as a fuel gap. The specific threshold height at which plants scape topkilling might depend on the productivity, but it is typically between 2·5 and 3·5 metres in African *Acacia* ecosystems (Archibald & Bond 2003; Wakeling, Staver & Bond 2011). Another prominent example employing the height escape strategy is eucalypts in Australian savannas; in these systems, the dominance of eucalypts in high fire frequency areas is due to their much higher escape rate compared to coexisting non-eucalypts which are, in contrast, favoured by long fire intervals (Bond, Cook & Williams 2012). There are other types of savannas (e.g. some Neotropical savannas) with short trees and tall grasses and without a clear fuel discontinuity between grasses and trees, in which fast growth for escaping fire is difficult; because in these savannas fires select for different bark characteristics, they are discussed in the next section.

The existence of a resprouting sapling bank that persists in frequent disturbances until there is an opportunity to grow and become a successful recruiter is also common in temperate and Mediterranean broadleaved species (e.g. Peterson & Reich 2001; Pons & Pausas 2006); in fact, most temperate broadleaved species resprout, at least at the juvenile stage (Del Tredici 2001), which is adaptive for living in surface-fire regimes. A prominent example is oaks (*Quercus* species) living in surface-fire regimes (i.e. oak savannas) as their bark thickness is correlated with the regime

of surface fires (Cavender-Bares *et al.* 2004). Their bark can be generally thick, but not as thick as pines in surface-fire regimes, especially when considered relative to their size (Fig. 5a). In such ecosystems, the role of bark can be easily depicted when there is a change in fire regime. For instance, fire exclusion allows the entry of thin-barked trees (e.g. *Acer*, *Prunus*, *Amelanchier*, *Liquidambar*) in landscapes originally dominated by thick-barked oaks (Peterson & Reich 2001; Nowacki & Abrams 2008). Oak species are an interesting group of plants for understanding the variability of bark thickness in relation to fire regime as they inhabit very different fire regimes (surface and crown fires of a variety of intensities) and show a wide range of bark thickness from very thin to very thick. As it occurs in pines, oak species living in savannas and park-like woodlands with surface fires tend to allocate more on bark at early stages of development than congeneric species living in closed forests (Jackson, Adams & Jackson 1999), emphasizing the important role of bark thickness for sapling survival.

GRASS-FUELLED CROWN FIRES

In some tropical savannas, the woody vegetation is relatively short due to nutrient-poor soils, and grasses grow tall thanks to a high annual rainfall. Examples are some of the Brazilian *cerrados* (Dantas *et al.* 2013a,b), a type of tropical savanna found in South America (Neotropical savanna) that inhabit poor soils with rainfall often higher than 1200 mm (Dantas & Pausas 2013). This combination of short trees and tall grasses often precludes the formation of a fuel gap between the grasses and the canopy and thus favours the development of frequent grass-fuelled (low-intensity) fires that affect the crowns of many woody plants; I tentatively term this fire regime 'grass-fuelled crown fires'. Under these conditions of limited resources, escaping the fire by fast growth is not possible, and the fire protection is provided by a very thick bark from the early life stages, not only in the main stem but in the whole plant (the '*corky*' strategy in Dantas & Pausas 2013; Appendix Fig. S2, Supporting Information). That is, small differences in bark thickness at the early stages provide fitness benefits, and thus, a thick bark can be evolutionary selected (Fig. 2). This thick bark protects the stem buds from the heat of the fire (i.e. avoids topkill) and the plants resprout from epicormic buds found along the stems, including relatively thin branches. In some cerrado species, bark at the tip of the branches can be disproportionately thick (greater than the radius of the woody section; Fig. S2, Supporting Information). In these ecosystems, woody plants are relatively short, being mainly small trees and large shrubs (Fig. 3), because the limited resources are better allocated to stem protection and carbohydrate reserves for epicormic resprouting than to height growth. This strategy increases fitness as it enables survival and reproduction within the flame height; that is, they can complete their whole life cycle within the flame height. Some trees

may keep growing and finally overpass the flame height, but this is not necessary for survival and reproduction. As in savannas with typical grass-fuelled surface fires, there is a recruitment bottleneck in which seedlings are recurrently affected by fire and survive thanks to their resprouting capacity (sapling bank). Only when seedlings reach a bark thickness threshold (which depends on the fire intensity) can they resist fire, produce epicormic resprouts and reproduce. Fires continuously affect the top of the saplings and branches that have not attained the bark thickness threshold, and because they resprout epicornically from stem buds, saplings and young trees often show tortuous-looking stems that contrast with the vertical and lanky structure of trees in many of the typical grass-fuelled surface fires (e.g. African savannas). In short, while plants in African savannas escape fire by growing tall, plants in many cerrados escape fire by producing a thick bark, which makes a clear example of within biome divergence (Dantas & Pausas 2013). Even though the *corky* strategy is frequent in some Brazilian cerrados, it is not exclusive to this ecosystem as it occurs in other ecosystems world-wide.

Cork oak (*Quercus suber*) populations from poor acidic soils in the western Mediterranean basin are another prominent example of the *corky* strategy, that is, with very thick bark and epicormic resprouting (Pausas 1997; Pausas, Pereira & Aronson 2009; Catry *et al.* 2012; Appendix Fig. S1A, Supporting Information). The bark of this iconic tree is probably the most commercially important bark. Cork is harvested every 9 to 12 years when about three centimetre thick and used in a range of industrial products such as insulation and bottle tops (Aronson, Pereira & Pausas 2009; Bugalho *et al.* 2011); if not harvested, it can become much thicker (e.g. 27 cm in a 140-year-old oak, Natividade 1950). As explained before, this very thick and insulating bark should have evolved under low-intensity fires that affected the whole plant (i.e. under slow growth), and once the species had acquired a thick bark, they may withstand more intense crown fires, as is the case of the cork oak.

Another outstanding example of a tree with the *corky* strategy is *Pinus canariensis* (in the Canary Islands, north-western Africa), which has serotinous cones in addition to thick bark (Climent *et al.* 2004). The evolution of the thick bark in this species may be related to the volcanic origin of the Canary Islands, as volcanic activity would have generated fires (Fuentes & Espinosa 1986) regardless of the weather and thus probably of relatively low intensity, which could select for thick bark and epicormic resprouting (Fig. 2). Serotiny in this low-intensity crown fires would also be adaptive. There are other trees with relatively thick bark and some epicormic resprouting capacity that would also fit this strategy, although their epicormic resprouting might not be as strong as in previous examples (both *Q. suber* and *P. canariensis* can survive high-intensity crown fires). Examples may include some American oaks (e.g. *Quercus agrifolia*, *Q. kelloggi*, *Q. grisea*), *Protea nitida* (South African fynbos; Le Maitre *et al.*

1992), *Pinus rigida* and *P. serotina* (North America), and *Pseudotsuga macrocarpa* (Californian chaparral, Keeley *et al.* 2012). Some eucalypts and other Australian Myrtaceae also live in crown-fire systems (e.g. warm temperate forests) and resprout epicormically after fires as in the examples above; however, their bark in the branches is not disproportionately thick and corky. This is because eucalypts have an anatomical modification in which stem buds are more deeply embedded in the trunk than in most other trees (Burrows 2002), and thus, stem buds have a higher chance of survival. That is, eucalypts are the exception that proves the importance of protecting crown buds for epicormic resprouting; having a thick corky bark in the branches is the dominant mechanism, but it is not the only one.

HIGH-INTENSITY, WOODY-FUELLED CROWN FIRES IN FORESTS AND SHRUBLANDS

In less seasonal climates, and in environments where fires are driven by dry years, fires are less frequent. A relatively low frequency of fires enables the accumulation of fine woody biomass during the interfire period, and when fires arrive, it burns intensely and affects the whole community: crown fires driven by woody fuels. In most of these ecosystems, fire intensity is high and small differences in bark thickness become irrelevant for fire protection, and thus, a thick bark is not selected. Examples include the Mediterranean shrublands (chaparral-type ecosystems). In this environment, many plants tend to be short, stubby, multistemmed and with strong basal resprouting (Pausas *et al.* 2004; Keeley *et al.* 2011, 2012; see Fig. S3, Supporting Information). Such ecosystems are also the cradle for the lineages that abandoned the resprouting habitat and acquired the post-fire seeding strategy in which plants die after a fire, but the population recruits profusely from a seedbank (Pausas & Keeley 2014b). Both resprouting and especially seeding species have very thin barks (e.g. Hempson *et al.* 2014), although little data are available for species in these ecosystems. The Florida scrub is also an example of a crown-fire ecosystem dominated by resprouting shrubs, where bark has a very minor role in fire protection (Menges & Kohfeldt 1995).

High-intensity crown fires not only occur in warm (water-limited) environments, but also in cold environments. For instance, some of the boreal forests of North America in which return intervals of crown fires are shorter than tree longevity also fit within this category. In these cases, serotiny is the dominant post-fire seeding strategy (Gauthier, Bergeron & Simon 1996; Johnstone *et al.* 2009) and bark is thin (e.g. *Picea mariana*) or moderately thick (e.g. *Pinus banksiana*).

BARK THICKNESS, RESOURCE AVAILABILITY AND FIRE REGIME CHANGES

In landscapes where most trees have thick barks (as reviewed above), there may be patches of thin-barked trees. This is because there are parts of the landscape where fires are less frequent or the resource availability enables higher growth rates (e.g. gullies, soil fertility islands, etc.), and so thin-barked shade-tolerant forest trees can conform an alternative stable vegetation states (Pausas 2014). These forest species tend to have large leaf areas and quickly form low flammability patches as they prevent flammable light-demanding grasses from establishing. This process generates, for instance, savanna–forest mosaics with contrasting functional and diversity attributes, including a variety of bark thickness patterns (Hoffmann *et al.* 2012; Dantas *et al.* 2013b; Fig. 5b). In this framework, the transition from savanna to forests is expected to be less frequent in low productivity than in more productive environments where trees grow more quickly (Murphy & Bowman 2012).

In forest ecosystems that rely on a fuel gap between the understorey and the canopy for maintaining understorey fires, changes that reduce this fuel gap may be catastrophic. This is the case in some coniferous forests in which an exclusion of fire or grazing or changes in climatic conditions may close the gap between surface and crown fuels. This results in an increasing risk of high-intensity crown fires in dry years, which is a novel fire regime for the ecosystem. In these situations, a basal thick bark may become irrelevant for fire protection, leaving trees with no capacity to withstand these high-intensity fires (i.e. relative thin bark in the crown). These changes from surface to crown fires are among the most abrupt fire regime changes that our ecosystems are currently facing (Pausas & Keeley 2014a).

Ecosystems with grass-fuelled fires can also be sensitive to fire exclusion as an overly long fire interval may allow the growth of thin-barked forest trees that quickly accumulate sufficient canopy to reduce the highly flammable grass cover and thus transform open savanna into closed forests or thickets. In some cases, fire exclusion may also generate shrub encroachment on savannas (Archer 1995; Roques, O'connor & Watkinson 2001). Increased atmospheric CO_2 may have a similar effect of favouring tree invasion and disfavouring C4 grasses and thus thickening grass-dominated ecosystems (Bond & Midgley 2000; Pausas & Keeley 2014a). In pine and oak savannas, the entrance of thin-barked broadleaved forest trees due to fire exclusion (Gilliam & Platt 1999; Peterson & Reich 2001) has been termed 'mesophication' (Nowacki & Abrams 2008).

Bark thickness in fire-free ecosystems

Although a large part of our planet is susceptible to fire (Krawchuk *et al.* 2009; Pausas & Ribeiro 2013), there are woody ecosystems that in natural conditions rarely burn (Fig. 3 right). These ecosystems with infrequent fires are often call fire-free, non-flammable or pyrophobic ecosystems and include ecosystems where moisture levels are high throughout the year and only burnt under extreme droughts (infrequent drought-driven fires, Fig. 3; e.g. rain

forests) and ecosystems where fuels are too sparse for fire to spread (infrequent fuel-limited fire regimes, Fig. 3; e.g. arid or very cold ecosystems). Despite the name of these ecosystems (fire-free or non-flammable), fires do occur but are not sufficiently frequent and predictable to exert an evolutionary pressure (e.g. fire return intervals are longer than the life span of the plants). These ecosystems may be currently subject to increased fire activity due to anthropogenic factors such as increased droughts (Cochrane 2003) and plant invasion (Brooks *et al.* 2004; Pausas & Keeley 2014a).

INFREQUENT DROUGHT-DRIVEN FIRE IN FORESTS

Moist ecosystems with little rainfall seasonality only burnt under extreme weather conditions, and thus, fire is not an evolutionary pressure. In such conditions, barks tend to be very thin. This is the case of the Amazonian rain forests (mean bark thickness values for trees with DBH >20 cm are 7·1 and 6·4 mm; Uhl & Kauffman (1990) and Paine *et al.* (2010), respectively; for comparison, see Fig. 4). The thin bark of rain forest trees has been associated with the abundance of cauliflory (stem-flowering) in these ecosystems (Schimper & Fisher 1903), although a formal analysis remains to be done. Despite the low values, bark thickness still harbours variability. Paine *et al.* (2010) studied bark thickness for many species from the French Guiana (Amazonia) and found a large variability between taxa but were unable to find a functional explanation for this variability: bark appeared too thin and flexible to provide stem rigidity; there was no evidence of the role of defence against fire nor against herbivory; and there was no evidence that thickness limited trunk respiration. Lawes *et al.* (2014) showed that bark is thin in rain forest trees of Australia and New Zealand (BT/D ~ 0·4 mm/cm in trees D < 20 cm, for a reference, see Fig. 5) and also failed to understand its variability. Brando *et al.* (2012) found that bark thickness together with other stem traits (wood density and bark moisture) explains post-fire tree mortality in a transitional forests (from Amazonian forest to dry forests). Overall, these results suggest that, because bark fulfils many functions, in wet ecosystems where fires are absent, there may be no single function accounting for bark thickness variability.

Rain forest fires are understorey fires of very low intensity because of the high moisture and the lack of grass, and thus, many large trees may have sufficient bark to withstand these very cool, rare fires. However, these very low-intensity fires may be of high severity for some very thin-barked species and for young trees, and thus, the fires may kill some trees, opening up gaps that are filled with grasses. If there is another fire before the canopy closes to suppress the grasses, it spreads through the grass, and thus, this second fire is more intense and kills more trees. This process might be repeated, killing trees with the thinnest bark (Barlow, Lagan & Peres 2003), and thus generating a negative feedback loop driving the forest ecosystem

to an open, savanna-like, degraded system (Veldman & Putz 2011; Silvério *et al.* 2013). In natural conditions, this process rarely occurred as fires were infrequent and the grasses limited. However, the increased anthropogenic ignitions and frequency of droughts, as well as the high propagule pressure from alien grasses, have made this process more common and a threat to rain forests (Brando *et al.* 2014).

INFREQUENT FUEL-LIMITED FIRES IN ARID ECOSYSTEMS

In dry ecosystems with fuel discontinuities, fires are rare, very small, patchy or absent. In these ecosystems, variability of bark thickness is unlikely driven by fire. However, these ecosystems are strongly stressed by water limitations, and plants have acquired a plethora of traits to survive such adverse conditions. Very little data are available on bark thickness in these ecosystems; yet for some species, it is clear that a thick bark contributes to ameliorate the water deficit (Scholz *et al.* 2007; Poorter *et al.* 2014). In addition, some species can accumulate large amounts of water in the stem, and in some cases, in the inner bark, and this explains some of the variability in bark thickness in species inhabiting arid fire-free ecosystems (Rosell & Olson 2014). In cacti, the photosynthetic tissues are protected by a translucid epidermis that are replaced by a thick bark when aged (Gibson & Nobel 1990); this bark probably contribute to protection and stability. However, some arid ecosystems can burn, although infrequently (e.g. Abella 2009; Bradstock, Williams & Gill 2012), and given that many trees are very long lived, they can suffer multiple fires. Even though the role of fire in contributing to shape bark thickness cannot be fully excluded, it is unlikely to have a prominent role as other environmental pressures (drought) are stronger. Further research on the role of bark thickness in arid ecosystems is needed, and differentiating between inner (where most bark moisture accumulates) and outer bark may help us to better understand the functional role of bark in these environments.

Alternative hypotheses

We have shown that bark is a good heat insulator, and thus, a thick bark can increase the fitness of trees living in some fire regimes. Consequently, an important part of the variability in bark thickness across ecosystems may be due to the variability in fire regime (fire hypothesis). However, there are other alternative hypotheses for developing a thick bark that need to be considered, such as to protect from harmful organisms, from extreme climates or to provide mechanical support (biotic, climatic and biomechanical hypotheses).

The biotic hypothesis suggests that trees acquired a thick bark as a defence mechanism against pests, infections and herbivores. The bark certainly deters such organisms and

slows down infections, but the fact that such protection increases with bark thickness is not evident. For instance, different bark beetle species can be associated with different tree species that might differ in their bark properties (including thickness), but overall, bark beetles infest trees over a wide range of bark thicknesses, and different thickness might harbour different beetle communities (Bertheau *et al.* 2009a,b). In contrast, there is a bulk of evidence that the defence mechanism of tree against pests is more associated with the chemical (constitutive or inducible defences) than the physical properties of bark (Wood 1982; Hudgins, Krekling & Franceschi 2003; Franceschi *et al.* 2005; Ott *et al.* 2011). For instance, resins are a key mechanism in conifers to protect from insect and fungus attacks (Berryman 1972; Phillips & Croteau 1999; Franceschi *et al.* 2005), and latex, gums and the plethora of chemical compounds in the bark have a similar function in other plant groups (Agrawal & Konno 2009; Romero 2014). In addition, there are also physiological mechanisms of response to bark and stem damage as the ability to compartmentalize around wounds and repair them (Franceschi *et al.* 2005; Romero 2014). Some mammals also damage trees by stripping the bark; some ungulates do prefer to strip younger (i.e. with thinner bark) trees for a given tree species (Gill 1992; Månsson & Jarnemo 2013) although there is no clear evidence that bark thickness explains the different susceptibility among tree species (Gill 1992). Other bark properties, such as the amount of water, nutrients, lignins and deterring compounds, seem to be more important than bark thickness for large mammals (McNaughton 1988; Swanepoel 1993; Akashi & Nakashizuka 1999; Romero 2014). That is, bark may reduce the damage of the tree by pests and herbivores, but in most cases, small variations in thickness provides little change in survival from damage by large mammals, and there is no clear evidence that at large scale, the distribution of thick-barked trees reflects the distribution of a particular biotic interaction.

The climate hypothesis for bark thickness suggests that thick barks are a protection from extreme climatic conditions (frost, extreme cold, extreme warm, droughts). The fact that most tree species with thick bark are from warm environments (Table 1) and that the pine species with the thinnest bark are found in cold alpine environments (Keeley 2012) suggests that protection from cold is not a key driver of bark thickness; in general, boreal and tree line forest do not have tree with barks particularly thick. However, as we discussed earlier, thick barks may protect against water losses in arid non-fire-prone ecosystems, and thus, the climatic hypotheses cannot be fully excluded. In addition, some trees store water in the inner bark and thus have a relatively thick bark (Scholz *et al.* 2007; Poorter *et al.* 2014; Rosell & Olson 2014). That is, fire-independent factors, such as climate and fauna, might drive some variability in bark properties, although the evidence for shaping bark thickness at a global scale is limited and perhaps restricted to arid environments where fire is of little relevance.

The biomechanical hypothesis suggests that thick barks evolved as a mechanism to increase mechanical stability. The contribution of bark to the mechanical support of the main stem of an adult tree is probably negligible, but it could have an important role in small branches (Niklas 1999; Rosell & Olson 2014) or in thin/young trees. However, although bark may confer some mechanical stability in woody plants, there is no evidence that the variability in bark thickness is the response to a selective force affecting stem stability. In contrast, the ecosystem were many species have thick bark in branches is the Brazilian cerrado, an ecosystem that suffers repetitive fires and most trees grow within the flame height.

Final remarks

Bark thickness determines the degree of heat insulation and protection of vital tissues in the stem. Consequently, there is a link between fire regime and bark thickness across ecosystems (Fig. 3). There are some fire regimes that select for thick bark (some in the base of the trunk, others select for thick bark in the whole plant). There are other fire regimes in which allocating resources to a thick bark is not adaptive. Where fire is not an evolutionary pressure, we find ecosystems where bark tends to be thin (rain forest) and other ecosystems with very high bark thickness variability (arid ecosystems) where bark thickness is likely related to protection from factors other than fire (e.g. water stress or pests). However, the limited data on bark thickness in many world ecosystems preclude a more exhaustive analysis. Unfortunately, very little information on bark thickness is currently available in open trait data bases (Paula *et al.* 2009; Kattge *et al.* 2011), and when available, it often refers to some absolute values unrelated to diameter. For such data bases, it would be advisable to include individual values of bark thickness associated with the plant diameter at a given height, as depending on the question addressed, absolute values (thresholds), relative values (comparisons) or allometric coefficients (allocation) may be desired. In addition, differentiating inner and outer bark, and between basal bark and bark at the branches, would also be highly useful (Van Mantgem & Schwartz 2003; Graves, Rifai & Putz in press). An international effort is needed to measure and make available bark thickness data from a range of ecosystems and biomes in order to obtain a better picture of bark thickness patterns on a global scale. Such compilations would allow to test the model proposed here (Fig. 3).

Bark thickness is a defensive trait, relatively easy to measure (a '*soft*' trait; Appendix S1). It is correlated with other stem traits, but such correlations are still poorly understood and available for only a few ecosystems (e.g. Baraloto *et al.* 2010; Poorter *et al.* 2014). Data bases across biome would be desirable for a range of stem traits in order to properly validate the possibility of considering bark thickness as a proxy for the defence syndrome in woody plants. Given that bark thickness and stem traits

are strongly related to fitness and are clearly traits that contribute to the assembly of populations, communities and biomes (Tables 1 and S1, Supporting Information; Fig. 3), there is a possibility that bark thickness could better explain global patterns of vegetation than leaf traits such as SLA (Wright *et al.* 2004). I would suggest that bark thickness can explain a high proportion of the variability in world vegetation but that the current paucity of data limits a global analysis.

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Data accessibility

All data are included in the main article and supporting information.

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Supporting Information

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

Figure S1. Example of a grass-fuelled surface fire ecosystems.
Figure S2. Examples of trees with strongly suberized corky bark from different lineages.
Figure S3. Examples of plants living under a woody-fuelled crown-fire ecosystem.
Table S1. Examples of different bark thickness values among population living in different fire regimes.
Table S2. Effect of bark thickness on the maximum temperature reached by the cambium.
Table S3. Effect of bark thickness on the time to reach the temperature that kills the cambium.
Appendix S1. Methods for studying bark thickness.