ESSAY REVIEW

Flammability as an ecological and evolutionary driver

Juli G. Pausas[1]*, Jon E. Keeley[2,3] and Dylan W. Schwilk[4]

[1]CIDE-CSIC, Ctra. Naquera Km 4.5 (IVIA), Montcada, Valencia 46113, Spain; [2]Western Ecological Research Center, Sequoia Field Station, US Geological Survey, Three Rivers, CA 93271, USA; [3]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA; and [4]Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA

Summary

1. We live on a flammable planet yet there is little consensus on the origin and evolution of flammability in our flora.

2. We argue that part of the problem lies in the concept of flammability, which should not be viewed as a single quantitative trait or metric. Rather, we propose that flammability has three major dimensions that are not necessarily correlated: ignitability, heat release and fire spread rate. These major axes of variation are controlled by different plant traits and have differing ecological impacts during fire.

3. At the individual plant scale, these traits define three flammability strategies observed in fire-prone ecosystems: the non-flammable, the fast-flammable and the hot-flammable strategy (with low ignitability, high flame spread rate and high heat release, respectively). These strategies increase the survival or reproduction under recurrent fires, and thus, plants in fire-prone ecosystems benefit from acquiring one of them; they represent different (alternative) ways to live under recurrent fires.

4. *Synthesis*. This novel framework based on different flammability strategies helps us to understand variability in flammability across scales, and provides a basis for further research.

Key-words: fire-prone ecosystems, flammability dimensions, plant flammability strategies, scale

Introduction

We live on a flammable planet where most terrestrial plants can burn under the right climatic conditions and many regions burn recurrently (Pausas & Keeley 2009; Krawchuk & Moritz 2011; Pausas & Ribeiro 2013). The flammability of our landscapes is sensitive to global change drivers (such as temperature and precipitation changes, fragmentation, biological invasion and CO_2 concentration) and there is evidence of important changes in flammability throughout geological time that affected the assembly of communities (Keeley & Rundel 2005; Bond & Scott 2010; Pausas & Keeley 2014a). However, there is little consensus on the role of this biological characteristic on the ecology and evolution of our biota (Keeley *et al.* 2011; Bowman, French & Prior 2014). One of the problems lies in the concept of flammability. In general, flammability can be defined as the capacity for plant biomass to burn, that is, to start and sustain a flame (Box 1). However, ecosystem fires are dependent on more than just particular plants igniting and sustaining a flame and rely on multiple factors that contribute to fire spread. Further complicating matters, there is not a single definition that captures variability in plant flammability and various authors have used this concept in different ways.

The evolution of flammability was first proposed at the community scale, suggesting that 'fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favoured development of characteristics that make them more flammable' (Mutch 1970). This hypothesis was strongly criticised, mainly for being group selectionist and for lacking a link between enhanced flammability and fitness (Snyder 1984; Christensen 1985; Troumbis & Trabaud 1989). More recent analyses have demonstrated that the evolution of plant flammability can be explained within the context of increased fitness (Bond & Midgley 1995; Kerr *et al.* 1999; Schwilk & Kerr 2002; Gagnon *et al.* 2010). However, we believe that further progress in this area requires greater clarity on what flammability is and how it is measured. In the present paper, we argue that 'flammability' should not be viewed as a single quantitative trait or metric, but rather it is a group of plant characteristic that influence fire probability and behaviour, and that can be measured with different metrics and at different scales (e.g. Pausas *et al.* 2012; Simpson *et al.* 2016) and for different fuels (e.g. canopy vs. litter fuels). Understanding this is critically important because neither the different flammability metrics nor the flammability at different scales are necessarily correlated. Previous research has proposed that flammability has different components such as

*Correspondence author. E-mail: juli.g.pausas@uv.es

ignitibility, combustibility, sustainability and consumability (e.g. Anderson 1970; Behm *et al.* 2004; Gill & Zylstra 2005; for definitions, see Box 1); however, they fail to frame these components in a unified ecological and evolutionary context, and empirical evidence does not support viewing these as independent axes. We propose that flammability has three major dimensions (Fig. 1), one associated with ignitability, another with flame spread rate (or rate of heat release) and another with heat released (standardised to fuel load); these dimensions explain the chance of burning given an ignition, and the different ways in which plant biomass can burn (e.g. slow vs. fast and high intensity vs. low intensity). These major axes of variation are controlled by different plant traits and have differing ecological impacts during fire. For example, the first axis determines the probability of ignition, the second is associated with the area burned, and the third is often associated with smouldering combustion and influences plant tissue damage and soil heating. For a given scale, these parameters can be independent of one another or even negatively related (e.g. Engber & Varner 2012; Magalhães & Schwilk 2012; Pausas & Moreira 2012; Cornwell *et al.* 2015). We propose that at the plant scale, these axes define three flammability syndromes, and because they have consequences for survival and reproduction under recurrent fires, they are likely to be adaptive strategies for persisting in fire-prone ecosystems (Fig. 1, Table 1). These strategies provide a novel framework for understanding variability in plant flammability.

Flammability strategies

Flammability is, of course, strongly dependent on moisture; however, for a given moisture level, there are plant traits that can enhance or reduce flammability. These flammability modifiers are scale dependent (Table 2). At the smallest scale, flammability depends on the size, thickness and shape of the organ (leaves and twigs) and on the tissue composition – such as the presence of organs that accumulate volatile organic compounds (VOCs), the lignin concentration and the dry matter contents (Ormeño *et al.* 2009; Pérez-Harguindeguy *et al.* 2013; Pausas *et al.* 2016). At this scale, flammability can be assessed directly by laboratory flammability tests (i.e. investigating how easily the organ under study burns when subject to an experimental heat source), or by investigating the specific relevant components (VOCs contents, lignin concentration, calorific value, DMC, etc.; e.g. Engber & Varner 2012; Pausas *et al.* 2016). However, this small-scale flammability does not necessarily predict how well a plant burns under field conditions because other plant characteristics may be relevant. For instance, at the individual level, the amount of standing dead biomass and plant structural traits (e.g. canopy bulk density, the continuity of the fuels across the plant and the branching pattern; Table 2) can influence plant flammability, especially the flame spread rate and heat release.

We propose that there are several plant flammability strategies that are selected under different evolutionary contexts; these strategies confer fitness benefits to plants living under

---

Box 1
Basic flammability concepts

Bulk density: Mass of the fuel per unit of volume (g cm^{-3}), e.g. dry weight of plant per volume occupied. See also *packing ratio* below.

Combustibility (rate of combustion): How well a material burns; it can be measured as the weight loss during combustion (mass loss rate; g s^{-1}). It is correlated with flame spread rate.

Consumability: The proportion of fuel consumed, which is correlated with the heat release (see below).

Fine fuel: The most available fuel for fire, typically includes leaves and twigs of less than 6 mm of diameter. The other fuels are often called *coarse fuels*.

Flammability: A general term for the ability to burn, that is, to start and sustain a flame. It refers to a set of plant characteristic that influence fire probability and behaviour. Flammability has three main axes of variation: ignitability, heat release and flame spread rate (Fig. 1). These terms define the different ways plant biomass burns.

Fuel loading: Plant biomass per unit of area (g m^{-2}); usually refers to fine fuel.

Heat release: Energy released as heat (kJ g^{-1}) which can be measured with a calorimeter. It is often estimated as the area below the time–temperature curve during the burning divided by the sample biomass (^{o}C per time per g).

Ignitability: Ability to start a fire. It can be measured as the time needed to start ignition once the material is exposed to a heat source (time-to-ignition or ignition delay time, in seconds), or as the probability of ignition given an ignition source (e.g. spark).

Packing ratio: The proportion of the space occupied by the plant (or litter) (cm^3 cm^{-3}). The opposite is *porosity*.

Rate of spread (flame spread rate): Speed of fire (distance/time), i.e. the time interval between flaming front passage at two points.

Residence time: Time the heating is above a temperature threshold at a given point.

Sustainability (burning time): Amount of time that the combustion is sustained; it can be restricted to the flame duration, or it can also include the smouldering phase.

---

recurrent fires. They correspond to variations in flammability at both the organ and individual levels because they are the scales that can be modified by natural selection. Specifically, we propose three general flammability strategies in species living in fire-prone ecosystems (Fig. 1, Table 1): the non-flammable, the fast-flammable and the hot-flammable strategy. As we will see below, the first and the second increase plant
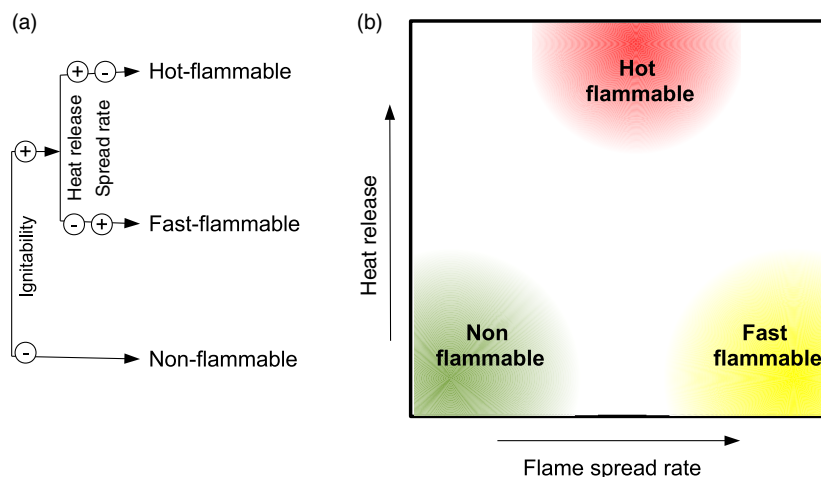
Fig. 1. Conceptual model describing the three plant flammability strategies in fire-prone ecosystems (a and b). The non-flammable strategy refers to plants that do not burn (or rarely) in natural conditions despite living in fire-prone ecosystems: this is because they have biomass with very low ignitability (low flammability at the organ scale, Tables 1 and 2) or because their plant structure does not allow the ignition of the biomass (low flammability at the individual scale). The hot- and the fast-flammable strategies refer to flammable plants with contrasted heat release (kJ g^{-1}; Box 1) and spread rate (m min^{-1}). While many plants fall at intermediate levels of these axes (i.e. the null model for flammability), plants in fire-prone ecosystems benefit from being at the extremes, forming the three flammability strategies considered in this review (Table 1). Note that some species may show different strategies at the different scales which can also be adaptive (e.g. fire-tolerator pines fit in the non-flammable strategy despite having fast-flammable needles; see main text). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Main fuel and plant characteristics for the three flammability strategies of plants living in fire-prone ecosystems

	Flammability strategy		
	Non-flammable	Fast-flammable	Hot-flammable
Fuel characteristics			
Standing dead biomass	Low	High	High
Bulk density	Low	Low	Moderate-High
Fine:coarse fuel ratio	Low	High	Moderate
Fuel continuity	Low	High	High
Leaves or branch tips	Thick	Thin	Thin
Branching	Low	–	High
Fire effects	Unaffected	Burnt, survival	Burnt, often high mortality
Fitness benefits	Survival	Survival, clonal spread, enhanced flowering	Fire-stimulated germination or dispersal
Regeneration	Fire-independent	Resprouting, enhanced growth and flowering	High post-fire recruitment
Examples	Woody species in grass-fuelled fire ecosystems (Fig. 1a)	Grasstrees (e.g. *Xanthorrhea*, *Kingia*; Fig. 1c), fire-promoting grasses	Post-fire seeders (Fig. 1b), including serotionus plants

survival, while the latter enhance post-fire recruitment (Table 1).

THE NON-FLAMMABLE STRATEGY

Some plants, despite living in fire-prone ecosystems, rarely burn. This is because they have characteristics that result in low tissue flammability (low ignitability) and/or low spread rate and heat release at the individual scale (e.g. a non-flammable plant architecture); this low flammability enables the plant to thrive in a highly flammable community. For instance, grasslands and savannas are fuel beds of very flammable plants where low intensity fire moves quickly (grass-fuelled surface fires). In these conditions, reducing flammability of woody species may confer fitness benefits as it allows woody plants to enter flammable communities (Fig. 2a). An

example of this strategy at the individual scale are pines that self-prune their lower branches (i.e. increasing the fuel gap between the forest floor and the canopy) to avoid understorey fires reaching their crowns (Pausas 2015a); in this case, the low tree flammability is coupled with thick basal bark to resist understorey fires (Keeley & Zedler 1998; Schwilk & Ackerly 2001; Pausas 2015a,b). Other species reduce flammability at a smaller scale (organs). This is the case of several woody species living in highly flammable savannas that have few non-flammable thick corky branches, and large leaves with very high leaf mass per area (Fig. 2a; Dantas, Batalha & Pausas 2013). Extreme examples of non-flammable plants may include several succulent plants from fire-prone ecosystems (Givnish, McDiarmid & Buck 1986; Thomas 1991); in some cases, succulent leaves or leaf bases protect meristems in a similar manner to thick corky bark in trees (Bond 1983;

Thomas 1991; Cousins, Witkowski & Pfab 2016). The persistence of slow-growing non-resprouting conifers (*Callitris*, *Juniperus*) in highly flammable landscapes (eucalypt forests, grasslands) has also been explained by the low flammability of their canopy (Trauernicht *et al.* 2012) or litter (Twidwell *et al.* 2013a,b).

Table 2. Example of factors determining plant flammability at different scales. These factors are cumulative from the smallest scale (organs) to the largest (regional) scale. For some quantitative factors, signs in square brackets refer to the main directional effect on a flammability axis (I = ignitability axis, H = heat axis, S = spread rate axis)

Scale	Factors
Organ	VOCs [I+], lignin [H+], C:N ratio [H+], mineral contents [H+], SLA [S+], DMC [H+], thickness [IS−], size [canopy: S−, litter: S+], shape
Individual	Plant architecture (branching pattern, biomass distribution), canopy bulk density [H+], litter bulk density [S−], branch diameter distribution, dead branch retention [IH+]
Population	Age, dead individuals [IHS+], litter, spatial pattern
Community	Composition, time since fire
Landscape	Topography, nutrients
Ecoregion	Climate, productivity

VOCs, volatile organic compounds; SLA, specific leaf area; DMC, dry matter contents.

In all these cases, the low flammability of the plant confers survival in fire-prone ecosystems, and these species can enter into flammable communities only because they are little affected by the frequent fires in their ecosystem. The reduced flammability allows them to survive and reproduce throughout multiple fire cycles (polypyric species sensu Pausas & Keeley 2014b) without being significantly affected by fire. However, research on the selection of non-flammable traits in fire-prone ecosystems is still needed.

THE FAST-FLAMMABLE STRATEGY

Some plants living in fire-prone ecosystems have traits that make them ignite easily and burn quickly, and thus they generate fires with high spread rate (i.e. high rate of heat release) but with a relatively low overall heat release. There is evidence that having traits conferring fast-flammability increases fitness because it decreases fire-residence time and the heat shock to the meristems and roots of the plant (Gagnon *et al.* 2010). This strategy is typical of plants that burn during fire (as opposed to non-flammable plants) but survive; the buds are preserved undamaged. This strategy is typical of some grasstrees (*Xanthorrhea,* some *Dasylirion*) as they have thin highly ignitable leaves and often retain dead leaves; it is also found in some pines at the young stage (pines with the 'grass-stage', Keeley & Zedler 1998; Pausas 2015a). This strategy is sometimes linked to post-fire-stimulated flowering as in some *Xanthorrhea* species from Australia (Fig. 2c; Lamont, Wittkuhn & Korczynskyj 2004); that is, the light fire
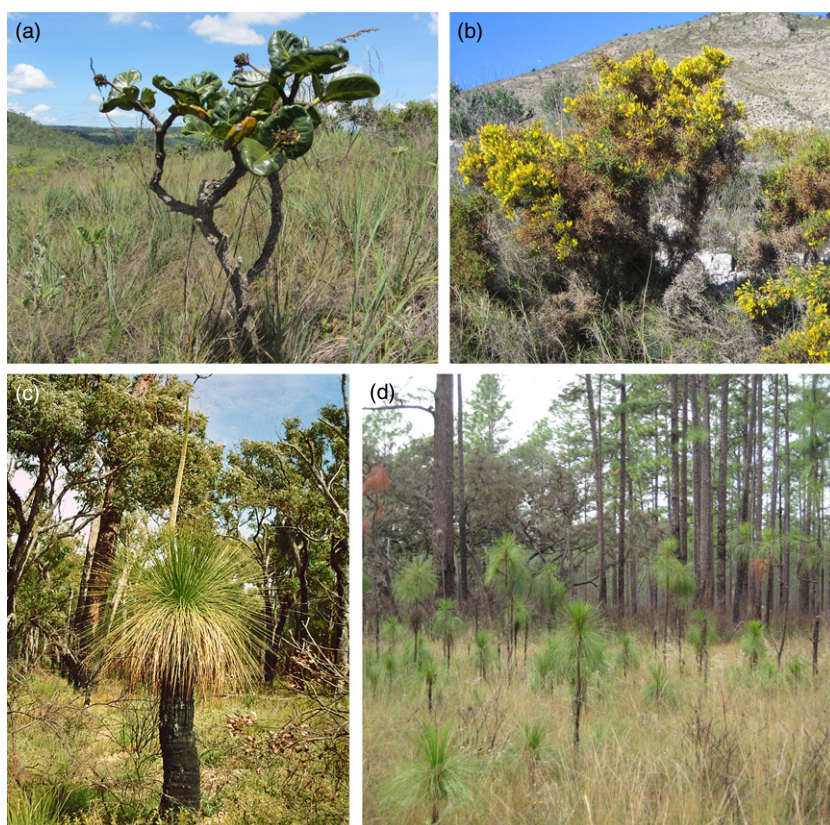
Fig. 2. Examples of species with different flammability strategies. (a) A non-flammable plant (*Palicourea rigida*, Rubiaceae) living in an ecosystem dominated by fast-flammable grasses in a Brazilian savanna (cerrado); note the large and thick leaves and a trunk and branches covered by a thick non-flammable corky bark. (b) A hot-flammable plant (*Ulex parviflorus,* Fabaceae) in a Mediterranean shrubland of eastern Spain; note its fine biomass, the high bulk density and the high amount of standing dead biomass. (c) A recently burnt fast-flammable plant (*Xanthorroea preissi*, Xanthorrhoeaceae) in Australia; note the fine leaves and the post-fire flowering; this species accumulates dead leaves that facilitate burning (not shown in the picture because they were consumed by the recent fire). (d) A forest gap of a frequently burned pine woodland in Florida that shows a fast-flammable (grassy) understorey together with pines (*Pinus palustris*) that have fast-flammable needles but the trees grow quick, and they self-prune the lower branches and thus become non-flammable (photos a, b, d by J.G. Pausas, c by B.B. Lamont). [Colour figure can be viewed at wileyonlinelibrary.com]

not only does not kill buds but it also breaks the dormancy of floral buds.

Fire-promoting grasses also fit in this category as they burn very easily and quickly, that is, with higher ignitability and fire spread rates than woody plants (Simpson *et al.* 2016), and with lower heat release. Many of these grasses grow very quickly during the wet season and produce a large amount of very fine biomass. Fast-flammable fuel beds are the cradle for the evolution of non-flammable woody species, and thus they often coexist (Fig. 2a). However, grasses are always relatively fast-flammable (non-woody), and currently there is only weak evidence of increasing fast-flammability associated with fitness benefits. One line of evidence is the linkage between flammability and post-fire success in savanna grasslands (Ripley *et al.* 2015). Given that grasses have their meristems at the leaf base, they benefit from a fast fire because it stimulates new growth (and often increase flowering, e.g. Caturla *et al.* 2000); fast fires also enable clonal spread by opening resource space (critical because tillers are often shade-intolerant; Everson, Everson & Tainton 1988) without affecting growth tissues. Invasion ecology research provides many lines of evidence that suggest that disturbance favours flammable grasses (D'Antonio & Vitousek 1992; Grigulis *et al.* 2005; Pausas & Keeley 2014a). There is some research on the interspecific variability of flammability in grasses (Simpson *et al.* 2016); however, research on the selection of flammability traits (intraspecific) and their fitness benefits is still lacking.

THE HOT-FLAMMABLE STRATEGY

Some flammable plants produce fires that generate high temperatures with high residence time (high heat release). These species do not rely on survival as the fires they generate are lethal to themselves, but their offspring make use of the newly available space and favourable post-fire conditions (i.e. a niche construction mechanism, Box 2); examples include many mediterranean-climate post-fire seeders (e.g. Keeley *et al.* 2012).

The kill-thy-neighbour hypothesis (Bond & Midgley 1995) is a possible mechanism underlying the evolution of the hot-flammable strategy. Under this hypothesis, traits conferring hot-flammability could be favoured in individuals if the elevated flammability creates hot fires that increase the mortality of neighbours, and thus open space for recruitment opportunities of the flammable individual's offspring. For this flammability strategy to evolve, it needs to be linked to efficient post-fire recruitment (Bond & Midgley 1995; Kerr *et al.* 1999; Pausas & Moreira 2012), and thus is especially relevant in species that form a fire-resistant seed bank in the soil or canopy (serotiny) because fire enhances their recruitment. In these cases, massive post-fire recruitment generates a high-density cohort that may benefit from the killing of conspecific neighbours. Invasion ecology also shows examples of increasing species dominance under certain recurrent disturbances (D'Antonio & Vitousek 1992; Grigulis *et al.* 2005) that may enable the kill-thy-neighbour process to act. Even if there is

---

Box 2
Flammability as a niche construction mechanism

Many organisms modify their environment and, when these modifications have evolutionary consequences, we call this process 'niche construction' (Laland, Odling-Smee & Feldman 1999). Flammability is a clear example of a niche construction mechanism, as it determines the fire regime, which in turn selects for a set of persistence and regeneration traits (Keeley *et al.* 2011). In fact, flammability and other plant traits have evolved in a correlated manner. For instance, hot-flammable crowns evolved concomitantly with serotiny (e.g. in pines; Schwilk & Ackerly 2001; He *et al.* 2012), or with seed traits for heat resistance (e.g. in mediterranean post-fire seeders; Pausas & Moreira 2012). However, niche construction not only refers to the modifications of their own niche, as in the cases just mentioned, but also to the modification of the niche of other coexisting species (ecological spillovers). For instance, the expansion of high flammable grasses in tropical biomes drove the evolution of a range of traits in coexisting woody species, including thick barks (Pausas 2015b), different bud protection mechanisms (Bond 1983; Maurin *et al.* 2014; Charles-Dominique *et al.* 2015), and traits conferring low flammability such as self-pruning in pines (Keeley & Zedler 1998; He *et al.* 2012) or corky twigs and large thick leaves in cerrado trees (Fig. 2a, Dantas, Batalha & Pausas 2013). Given that fires spread to most plants of the community, all species in flammable communities need to adapt to the fire regime, by evolving traits either to resist fire (e.g. thick bark, resprouting), to escape from the fire (e.g. non-flammable strategy) or to quickly recruit after fire (e.g. post-fire seeders).

---

no direct fitness benefit (fire-enhanced recruitment), simulation models also suggest that flammability can evolve based on gap dynamics (e.g. in non-resprouters with limited gene flow; Schwilk & Kerr 2002). Certainly, there may be plants, often in non-fire-prone ecosystems, with apparent high flammability that do not have high post-fire recruitment, and the populations are too widely spaced for the kill-thy-neighbour hypothesis to operate. In such cases, flammability might require an alternative (fire-independent) explanation.

Consistent with the existence of the hot-flammability strategy is the macro-evolutionary correlation between pines that retain their lower branches (generating a vertical continuity of fuels that produce hot fires) and serotiny (accumulation of a canopy seed bank that is released after fire) (Keeley & Zedler 1998; Schwilk & Ackerly 2001; He *et al.* 2012). In fact, changes in individual flammability in pines is a key parameter that drive fires to the understorey (species that self-prune lower branches; non-flammability strategy) or to the crowns (species with branch retention; hot-flammability strategy), and these two contrasted strategies have appeared very early in the evolution of pines (He *et al.* 2012; Pausas 2015a). Recent micro-evolutionary studies also show field and genetic

evidence suggesting that recurrent fires can increase heat release and maximum temperatures in an obligate seeder shrub in which hot fires stimulate recruitment (Pausas & Moreira 2012; Pausas *et al.* 2012; Moreira, Castellanos & Pausas 2014).

Flammability across scales

As described above, the main flammability strategies of plants can be driven by changes in flammability at the small (organ) scale and/or at individual scale. Some species may have similar flammability at different scales (e.g. Pausas *et al.* 2012), while in others, flammability may differ with scale. For instance, some *Banksia* species in Australia concentrate their hot-flammable organs next to the serotinous cones (retention of dead florets), which ensures cone opening during fire (Lamont & Cowling 1984; He, Lamont & Downes 2011). The most clear-cut example of different flammabilities across scales is the case of pines with the fire-tolerator syndrome (Pausas 2015a) because they have a non-flammable strategy (at the plant level) despite their flammable leaves (Fig. 2d). These pines generate fast-flammable litter with low packing ratio (e.g. thin and large leaves) that enhance understorey (litter-driven) fires (Varner *et al.* 2015). The low flammability at the individual level prevents understorey fires from reaching the crowns (e.g. self-pruning pines; Pausas 2015a). This strategy often occurs in high productivity environments, where litter production and accumulation is high and could limit seed germination of the tree. Thus, the benefit for the tree is that quick fires remove the litter and so generate an ideal bed for the success of their offspring, without generating high intensity fires that could damage their own stem. Some pine species have the additional benefit of having a fast-flammable early stage (the 'grass-stage'; Keeley & Zedler 1998; Pausas 2015a) that allow them to survive fires at the sapling stage, i.e. before growing taller than the flame height (Fig. 2d). Congeneric comparisons of litter flammability among pines and oaks (Fonda 2001; Kane, Varner & Hiers 2008) and comparisons among coexisting species (Scarff & Westoby 2006; Magalhães & Schwilk 2012) support the existence of species with different litter flammabilities, and those with a faster flammable litter are mostly living in understorey-fire ecosystems. Overall, these examples suggest that acquiring different flammability attributes at different scales can also be adaptive.

The evolution of the different flammability strategies is based on how individual plants burn; however, fires spread across populations, communities and landscapes, and thus it is also important to consider the flammability concept above the individual scale in order to accurately describe ecological processes related to flammability and fire behaviour (Table 2). Fire spread is influenced by the composition, structure and fuel load of the community and thus highly flammable species juxtaposed with non-flammable species may not gain a flammability advantage if fire never reaches them. The number of dead individuals, plant density, the proportion of grass and woody fuels, the amount of litter, the individual fuel load, or the flammability of the coexisting species, are all components of flammability at the community scale. Many of these characteristics are influenced by age or time since the most recent fire. The three flammability types mentioned above (Fig. 1) may also be translated at this scale: there are non-flammable communities (e.g. closed forests), fast-flammable communities where fires spread quickly (e.g. tropical grasslands) and hot-flammable communities with high heat release (ecosystems with woody-fuelled fires such as mediterranean shrublands dominated by post-fire seeder species). These different communities may appear in different environmental conditions, but they may also appear in the same environment and maintained by different feedback processes (Box 3).

Topography and soil nutrients are also important drivers of flammability at the landscape scale, because topographic depressions may be enough to locally increase moisture and so directly reduce flammability and thereby enable the growth of less flammable plants (e.g. broad-leaved species that shade out flammable grasses). Patches of high nutrient soils may trigger a similar shift in vegetation composition and flammability (Hoffmann *et al.* 2012). Examples of communities with contrasted flammability living in a given climate are observed in many biomes (Box 3). Climate also plays a role in determining flammability at a regional scale (Pausas & Ribeiro 2013), and is strongly linked to long-term fire regimes, that is, the regimes to which the species are adapted.

Fire spread is also influenced by traits that promote spot fires, and this can be due to characteristics that affect the ember production that spread fires kilometres ahead of the fire front (Koo *et al.* 2010; Hall *et al.* 2015), as well as traits that favour the ignition of embers where they fall. Some traits such as shaggy bark on some eucalypts have been postulated to have a potentially adaptive advantage by increasing ember production (Jackson 1968). In forests, it is generally understood that spot fires ignite when embers land on dead surface fuels. However, embers can ignite in shrub canopies with sufficient fine dead fuels. One trait that might be thought of as an 'ember-catcher' is the dead floral displays of the chaparral shrub *Adenostoma fasciculatum* (Fig. 3). Floral clusters often dominate the upper canopy of these shrubs, and in late summer, they dry down to masses of very fine dead fuels that persist into the autumn fire season. Much more research and thought needs to be given to this aspect of flammability.

Given the multiscale nature of flammability (Table 2), it is interesting to ask, 'To what extent can we predict flammability at one scale with information from another scale?' For example, how much variability in flammability at the regional or landscape scale is explained by the flammability at the tissue or individual scale? In many ecosystems, there is a consistency across scales. For example, many shrublands of the Mediterranean Basin are flammable from the smallest scale (e.g. many species are rich in VOCs, have small leaves, retain dead biomass, etc.) to individuals, communities and landscapes (Pausas *et al.* 2012, 2016). In a very different fire regime, leaf length explains a significant proportion of the variability in surface fire severity in Californian mixed conifer forests (Schwilk & Caprio 2011), suggesting that upscaling is

possible. However, there are other ecosystems in which it is important to explicitly consider the different scales to understand flammability. The fast-flammable needles of some pines of the fire-tolerator syndrome do not confer high flammability at the individual level in these species as they self-prune the lower branches to prevent fire spread to the crowns (a non-flammable strategy). The low flammability of some savannas trees may be consistent at organ (thick corky branches) and individual level (open branching structure; Fig. 2a), but they live in highly flammable ecosystems. Downscaling is also difficult; for instance, for a given climate appropriate for fire spread (e.g. with seasonal droughts), alternative vegetation states with contrasted flammability are possible (Box 3). Estimating the explained variance in flammability across scales is a challenge.

Evolution of flammability: remarks and challenges

Despite the increasing evidence of flammability as a key factor in the ecology and evolution of plants at different spatial and temporal scales, there is still debate as to what extent evolution can modify plant flammability (Midgley 2013; Bowman, French & Prior 2014). One limitation to flammability research has been the tendency to consider a single axis of flammability. By understanding that there are different flammability axes and strategies, we can now explain many of the problems raised by flammability-skeptics. For instance, Midgley (2013) found inconsistencies when applying the Bond & Midgley (1995) and the Gagnon *et al.* (2010) models to a set of species. We propose that these two models refer to very different strategies, the hot-flammable and the fast-flammable, and they are related to a different set of species with different regeneration mechanisms, that is, different solutions to similar problems (Table 1). In addition, not all species living in fire-prone ecosystems have necessarily evolved changes in flammability, just as not all species living in grazing systems have evolved thorns. For instance, fast-flammability may be a protection mechanism, but other mechanisms for bud protection exist (Charles-Dominique *et al.* 2015; Pausas 2015b). Our framework explains the coexistence of species with contrasted flammability traits in fire-prone ecosystems, in the same way that species with different life histories do coexist (Loehle 2000; Vilagrosa *et al.* 2014). For instance, both fast-flammable and non-flammable strategies can be adaptive in a given fire-prone ecosystem (Fig. 1a), despite presenting strongly contrasted flammability traits. High canopy bulk density (that generates high heat release, Table 2) may be beneficial for hot-flammable species (Pausas & Moreira 2012) but not for fast-flammable ones (Table 1). That is, accounting for the different flammability strategies, we are better able to understand flammability variations in fire-prone ecosystems.

Certainly, it is difficult to unambiguously demonstrate evolutionary changes in flammability (as in any other trait), but the evidence is accumulating at both the macro- (He, Lamont & Downes 2011; He *et al.* 2012) and micro-evolutionary scales (Pausas *et al.* 2012; Moreira, Castellanos & Pausas 2014). In addition, there is evidence that even small amounts of niche construction can significantly alter ecological and evolutionary patterns (Laland, Odling-Smee & Feldman 1999; Box 2). However, more research is needed to unambiguously

Fig. 3. Ember-catching plants. California chaparral in late summer dominated by the widespread shrub *Adenostoma fasciculatum* that retains dead flower clusters may act to increase probability of ember ignition during fires (photo by J. Keeley). [Colour figure can be viewed at wileyonlinelibrary.com]

demonstrate increased fitness with changes in flammability. The recent boost in genetic resources for kinship analysis could help to test some of the proposed models such as the kill-thy-neighbour hypothesis. Global changes provide another opportunity: increased fire frequency in some ecosystems, together with the invasion by flammable plants, may provide an opportunity for improving our understanding of rapid flammability changes (especially if studied together with the genetic changes). The use of dated phylogenies can be used to trace back the origin of the different flammability strategies; for example the origin of the savanna biome in South America (Simon *et al.* 2009) is likely to have driven the evolution of non-flammable savanna trees. Many flammability-related traits are chemical and structural characteristics with adaptive value for other selective pressures (e.g. herbivory and drought); understanding the proportion of variability in these traits that is driven by recurrent fires is another challenge. We hope that the non-fast-hot-flammable scheme may provide a framework for better addressing these challenges and thus improving our understanding of variability in flammability.

Authors' contributions

J.G.P. conceived the idea and wrote the first version of the manuscript. All authors contributed to the final version of the manuscript and gave final approval for publication.

Acknowledgements

Data accessibility

This paper does not use data.

References

Anderson, H.E. (1970) Forest fuel ignitibility. *Fire Technology*, **6**, 312–319.
Behm, A.L., Duryea, M.L., Long, A.J. & Zipperer, W.C. (2004) Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface. *International Journal of Wildland Fire*, **13**, 355–365.
Bond, W.J. (1983) Dead leaves and fire survival in Southern African tree aloes. *Oecologia*, **58**, 110–114.
Bond, W.J. & Midgley, J.J. (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos*, **73**, 79–85.
Bond, W.J. & Scott, A.C. (2010) Fire and the spread of flowering plants in the Cretaceous. *New Phytologist*, **188**, 1137–1150.
Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
Bowman, D.M.J.S., French, B.J. & Prior, L.D. (2014) Have plants evolved to self-immolate? *Frontiers in Plant Science*, **5**, 590.
Caturla, R.N., Raventós, J., Guàrdia, R. & Vallejo, V.R. (2000) Early post-fire regeneration dynamics of *Brachypodium retusum* Pers. (Beauv.) in old fields of the Valencia region (eastern Spain). *Acta Oecologica*, **21**, 1–12.
Charles-Dominique, T., Beckett, H., Midgley, G.F. & Bond, W.J. (2015) Bud protection: a key trait for species sorting in a forest–savanna mosaic. *New Phytologist*, **207**, 1052–1060.
Christensen, N.L. (1985) Shrubland fire regimes and evolutionary consequences. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 85–100. Academic Press Inc., Orlando, FL, USA.
Cornwell, W.K., Elvira, A., van Kempen, L., van Logtestijn, R.S.P., Aptroot, A. & Cornelissen, J.H.C. (2015) Flammability across the gymnosperm phylogeny: the importance of litter particle size. *New Phytologist*, **206**, 672–681.
Cousins, S.R., Witkowski, E.T.F. & Pfab, M.F. (2016) Beating the blaze: fire survival in the fan aloe (*Kumara plicatilis*), a succulent monocotyledonous tree endemic to the Cape fynbos, South Africa. *Austral Ecology*, **41**, 466–479.
Dantas, V.L., Batalha, M.A. & Pausas, J.G. (2013) Fire drives functional thresholds on the savanna–forest transition. *Ecology*, **94**, 2454–2463.
Dantas, V.L., Hirota, M., Oliveira, R.S. & Pausas, J.G. (2016) Disturbance maintains alternative biome states. *Ecology Letters*, **19**, 12–19.
D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
Engber, E.A. & Varner, J.M. (2012) Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research*, **42**, 1965–1975.
Everson, C.S., Everson, T.M. & Tainton, N.M. (1988) Effects of intensity and height of shading on the tiller initiation of six grass species from the Highland sourveld of Natal. *South African Journal of Botany*, **54**, 315–318.
Fonda, R.W. (2001) Burning characteristics of needles from eight pine species. *Forest Science*, **47**, 390–396.
Gagnon, P.R., Passmore, H.A., Platt, W.J., Myers, J.A., Paine, C.E.T. & Harms, K.E. (2010) Does pyrogenicity protect burning plants? *Ecology*, **91**, 3481–3486.

Gill, A.M. & Zylstra, P. (2005) Flammability of Australian forests. *Australian Forestry*, **68**, 87–93.

Givnish, T.J., McDiarmid, R.W. & Buck, W.R. (1986) Fire adaptation in *Neblinaria celiae* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. *Oecologia*, **70**, 481–485.

Grigulis, K., Lavorel, S., Davies, I.D., Dossantos, A., Lloret, F. & Vilà, M. (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, Ampelodesmos mauritanica in Catalan shrublands. *Global Change Biology*, **11**, 1042–1053.

Hall, J., Ellis, P.F., Cary, G.J., Bishop, G. & Sullivan, A.L. (2015) Long-distance spotting potential of bark strips of a ribbon gum (*Eucalyptus viminalis*). *International Journal of Wildland Fire*, **24**, 1109–1117.

He, T., Lamont, B.B. & Downes, K.S. (2011) *Banksia* born to burn. *New Phytologist*, **191**, 184–196.

He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W. & Lamont, B.B. (2012) Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist*, **194**, 751–759.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, **15**, 759–768.

Jackson, W. (1968) Fire, air, water and earth—an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, **3**, 9–16.

Kane, J.M., Varner, J.M. & Hiers, J.K. (2008) The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. *Forest Ecology and Management*, **256**, 2039–2045.

Keeley, J.E. & Rundel, P.W. (2005) Fire and the Miocene expansion of C4 grasslands. *Ecology Letters*, **8**, 683–690.

Keeley, J.E. & Zedler, P.H. (1998) Evolution of life histories in *Pinus*. *Ecology and Biogeography of Pinus* (ed. D.M. Richardson), pp. 219–250. Cambridge University Press, Cambridge, UK.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406–411.

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G. & Rundel, P.W. (2012) *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge University Press, Cambridge, UK.

Kerr, B., Schwilk, D.W., Bergman, A. & Feldman, M.W. (1999) Rekindling an old flame: a haploid model for the evolution and impact of flammability in resprouting plants. *Evolutionary Ecology Research*, **1**, 807–833.

Koo, E., Pagni, P.J., Weise, D.R. & Woycheese, J.P. (2010) Firebrands and spotting ignition in large-scale fires. *International Journal of Wildland Fire*, **19**, 818–843.

Krawchuk, M. & Moritz, M. (2011) Constraints on global fire activity vary across a resource gradient. *Ecology*, **92**, 121–132.

Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. (1999) Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 10242–10247.

Lamont, B.B. & Cowling, R.M. (1984) Flammable infrutescences in *Banksia*: a fruit-opening mechanism. *Australian Journal of Ecology*, **9**, 295–296.

Lamont, B.B., Wittkuhn, R. & Korczynskyj, D. (2004) Ecology and ecophysiology of grasstrees. *Australian Journal of Botany*, **52**, 561–582.

Loehle, C. (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *American Naturalist*, **156**, 14–33.

Magalhães, R.M.Q. & Schwilk, D.W. (2012) Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology*, **100**, 1153–1163.

Maurin, O., Davies, T.J., Burrows, J.E., Daru, B.H., Yessoufou, K., Muasya, A.M., van der Bank, M. & Bond, W.J. (2014) Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist*, **204**, 201–214.

Midgley, J.J. (2013) Flammability is not selected for, it emerges. *Australian Journal of Botany*, **61**, 102–106.

Moreira, B., Castellanos, M.C. & Pausas, J.G. (2014) Genetic component of flammability variation in a Mediterranean shrub. *Molecular Ecology*, **23**, 1213–1223.

Murphy, B.P. & Bowman, D.M.J.S. (2012) What controls the distribution of tropical forest and savanna? *Ecology Letters*, **15**, 748–758.

Mutch, R.W. (1970) Wildland fires and ecosystems–a hypothesis. *Ecology*, **51**, 1046–1051.

Nowacki, G.J. & Abrams, M.D. (2008) The demise of fire and "mesophication" of forests in the eastern United States. *BioScience*, **58**, 123–138.

Ormeño, E., Céspedes, B., Sánchez, I.A., Velasco-García, A., Moreno, J.M., Fernandez, C. & Baldy, V. (2009) The relationship between terpenes and flammability of leaf litter. *Forest Ecology and Management*, **257**, 471–482.

Pausas, J.G. (2015a) Alternative fire-driven vegetation states. *Journal of Vegetation Science*, **26**, 4–6.

Pausas, J.G. (2015b) Bark thickness and fire regime. *Functional Ecology*, **29**, 315–327.

Pausas, J.G. (2015c) Evolutionary fire ecology: lessons learned from pines. *Trends in Plant Science*, **20**, 318–324.

Pausas, J.G. & Keeley, J.E. (2009) A burning story: the role of fire in the history of life. *BioScience*, **59**, 593–601.

Pausas, J.G. & Keeley, J.E. (2014a) Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, **204**, 55–65.

Pausas, J.G. & Keeley, J.E. (2014b) Abrupt climate-independent fire regime changes. *Ecosystems*, **17**, 1109–1120.

Pausas, J.G. & Moreira, B. (2012) Flammability as a biological concept. *New Phytologist*, **194**, 610–613.

Pausas, J.G. & Ribeiro, E. (2013) The global fire–productivity relationship. *Global Ecology and Biogeography*, **22**, 728–736.

Pausas, J.G., Alessio, G.A., Moreira, B. & Corcobado, G. (2012) Fires enhance flammability in *Ulex parviflorus*. *New Phytologist*, **193**, 18–23.

Pausas, J.G., Alessio, G.A., Moreira, B. & Segarra-Moragues, J.G. (2016) Secondary compounds enhance flammability in a Mediterranean plant. *Oecologia*, **180**, 103–110.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E. *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.

Peterson, D.W. & Reich, P.B. (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*, **11**, 914–927.

Ripley, B., Visser, V., Christin, P.-A., Archibald, S., Martin, T. & Osborne, C. (2015) Fire ecology of C3 and C4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, **96**, 2679–2691.

Scarff, F.R. & Westoby, M. (2006) Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology*, **20**, 745–752.

Schwilk, D.W. & Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos*, **94**, 326–336.

Schwilk, D.W. & Caprio, A.C. (2011) Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology*, **99**, 970–980.

Schwilk, D.W. & Kerr, B. (2002) Genetic niche-hiking: an alternative explanation for the evolution of flammability. *Oikos*, **99**, 431–442.

Simon, M., Grether, R., De Queiroz, L., Skema, C., Pennington, R. & Hughes, C. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 20359.

Simpson, K.J., Ripley, B.S., Christin, P.-A., Belcher, C.M., Lehmann, C.E.R., Thomas, G.H. & Osborne, C.P. (2016) Determinants of flammability in savanna grass species. *Journal of Ecology*, **104**, 138–148.

Snyder, J.R. (1984) The role of fire: much ado about nothing? *Oikos*, **43**, 404–405.

Thomas, P.A. (1991) Response of succulents to fire: a review. *International Journal of Wildland Fire*, **1**, 11–22.

Trauernicht, C., Murphy, B.P., Portner, T.E. & Bowman, D.M.J.S. (2012) Tree cover–fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna. *Journal of Ecology*, **100**, 958–968.

Troumbis, A.Y. & Trabaud, L. (1989) Some questions about flammability in fire ecology. *Acta Oecologica*, **10**, 167–175.

Twidwell, D., Fuhlendorf, S.D., Taylor, C.A. & Rogers, W.E. (2013a) Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology*, **50**, 603–613.

Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R., Kreuter, U.P. & Taylor, C.A. (2013b) The rising Great Plains fire campaign: citizens' response to woody plant encroachment. *Frontiers in Ecology and the Environment*, **11**, e64–e71.

Varner, J.M., Kane, J., Kreye, J. & Engber, E. (2015) The flammability of forest and woodland litter: a synthesis. *Current Forestry Reports*, **1**, 91–99.

Vilagrosa, A., Hernández, E.I., Luis, V.C., Cochard, H. & Pausas, J.G. (2014) Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. *New Phytologist*, **201**, 1277–1288.