Letters

Flammability as a biological concept

'No description of the variability and predictability of the environment makes sense without reference to the particular range of scales that are relevant to the organism or processes being examined.'
Levin (1992)

Recurrent fires enhance flammability

Studies examining plant flammability descriptors as fire-adaptive traits (e.g. Schwilk, 2003; Scarff & Westoby, 2006; Cowan & Ackerly, 2010; Saura-Mas *et al.*, 2010; Pausas *et al.*, 2012) are normally formulated within the framework of inclusive fitness theory. In such a framework, flammability-enhancing traits are considered to favour individuals if the elevated flammability confers fitness benefits. In post-fire seeder species (i.e. those with fire-stimulated germination from a persistent seed bank), higher flammability could increase the recruitment opportunities for the offspring of the individual with enhanced flammability by increasing the chance of opening spaces and by producing the necessary cues for triggering germination from the seedbank ('kill thy neighbour' hypothesis; Bond & Midgley, 1995). This might be particularly relevant in nonresprouting (obligate) seeders with strong spatial population structure (e.g. with short-distance dispersal). Because there is some evidence of heritability for both seed dormancy (e.g. Baskin *et al.*, 2000; Huang *et al.*, 2010) and flammability-enhancing traits (e.g. Sampedro *et al.*, 2010), we would expect a selection for higher flammability with repeated fires.

In a recent paper, we provided evidence that individuals of an obligate seeder species (*Ulex parviflorus,* Fabaceae; a shrub from the Mediterranean Basin) growing in populations recurrently burnt (HiFi populations) were more flammable than individuals of the same species in populations arising from old-field colonization that did not suffer any fire (NoFi populations, i.e. with fire-independent recruitment; Pausas *et al.*, 2012). Specifically, twigs of plants from HiFi populations ignited quickly, burnt slowly and released more heat than twigs of NoFi plants. In addition, HiFi plants had higher bulk density than NoFi plants. Previous studies have showed that bulk density in *U. parviflorus* (Fig. 1), as well as in other shrub species (e.g. Bradstock & Auld, 1995; Tachajapong *et al.*, 2008), is associated with higher temperatures and longer residence time of high temperatures in the soil during a fire. Thus, the results at the twig and the whole-plant scale were in agreement and suggested that HiFi plants should ignite easily and reach higher temperatures and

produce higher heat doses in the soil than NoFi plants (Fig. 1). This higher probability of ignition and higher heat in the soil would increase the chance of recruitment of *U. parviflorus* from the soil seed bank by opening spaces and by enhancing seedling emergence (the heat shock from fire breaks seed dormancy and stimulates germination in this species; Baeza & Vallejo, 2006; Moreira *et al.*, 2010). Thus, these results are in agreement with the kill thy neighbour hypothesis.

By including our data on *U. parviflorus* bulk density in a fire behaviour model, Fernandes & Cruz (2012; this issue pp. 606–609) predict lower fire spread rates in HiFi populations, which implies higher fire residence time and thus higher heat dose in the soil and in the seed bank (Bradstock & Auld, 1995; Gagnon *et al.*, 2010). Their simple modelling approach inadvertently provides further support for our results, although a modelling framework accounting for variability and uncertainty would have been much more appropriate. That is, the conclusions by Pausas *et al.* (2012) remain firm: in *U. parviflorus* shrublands there is a divergence on flammability traits between populations living in different selective environments, and the mechanism by which plant fitness would be enhanced is driven by the increase in both the probability of ignition and the heat released to the soil.

Diversity of paradigms, metrics and scales

Fernandes & Cruz (2012) criticize flammability experiments performed in laboratory conditions because they are not 'adequate surrogates for real-world, full-scale fire behaviour and dynamics', neglecting that predicting real-world broad-scale fire behaviour is not necessarily the objective of all flammability studies. Fire has effects at a diverse array of scales and the appropriate metric at which flammability should be measured depends on the scale and on the objective of the study (Levin, 1992). For instance, the durations of soil heating as well as maximum temperatures (Fig. 1) are closely tied to biological processes such as post-fire resprouting and seed regeneration (Beadle, 1940; Auld & O'Connell, 1991; Schwilk, 2003; Vesk *et al.*, 2004; Paula & Pausas, 2008). However, even though fireline intensity might be a useful metric for modelling fire behaviour, it is often not predictive of soil heating because heat is mainly transferred upwards (Hartford & Frandsen, 1992; Bradstock & Auld, 1995). This is why the use of fireline intensity has been discouraged for describing fire effects (Keeley, 2009). On the contrary, the rate of fire spread is related to soil heating, and the relationship is negative because faster fires tend to burn both with shorter residence times and higher above the ground than slower-moving fires (Bradstock & Auld, 1995). In fact, enhancing fire spread rates has been suggested as a mechanism for fire protection in plants (Gagnon *et al.*, 2010).
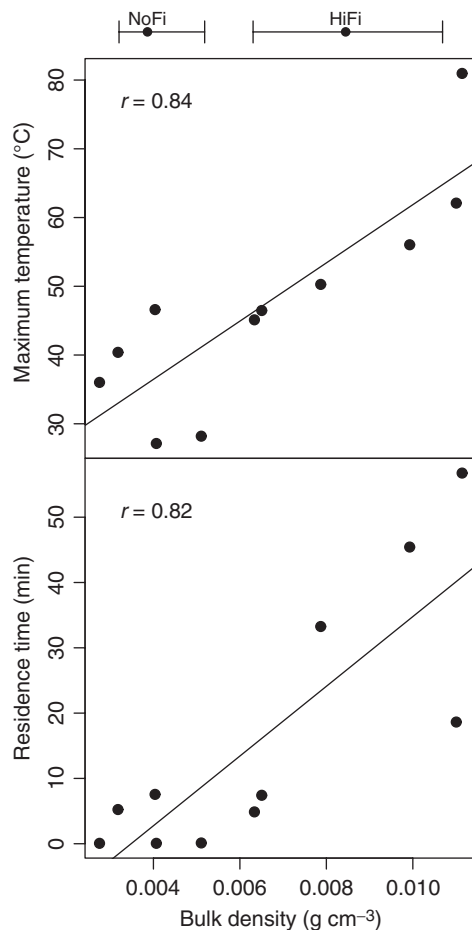
Fig. 1 Relation between bulk density (in g cm^{-3}) of different individuals of *Ulex parviflorus* and maximum temperature (°C) and residence time above 40°C (in min) in the soil profile (1 cm depth) during experimental fires in the Valencia region, eastern Spain (Santana *et al.*, 2011). Regressions are significant at *P* < 0.002. The segments on the top represent the median and the 25th and 75th percentiles of the bulk density values observed for NoFi (old-field colonization that did not suffer any fire) and HiFi (recurrently burnt) populations in Pausas *et al.* (2012).

Modelling fire behaviour requires detailed information of the spatial structure of the fuel bed in the landscape at a given time. Unfortunately, the simulation by Fernandes & Cruz (2012) does not consider parameters related to the structure of the ecosystem (e.g. flammability of the coexisting species, the size, cover density and spatial distribution of dead and live individuals, etc.) and thus their fire spread estimates may be unrealistic at the community and landscape scales. In contrast to fire behaviour modelling, ecological and evolutionary studies of flammability are mainly performed at the individual level and considering long-term processes (fire regimes), because natural selection (and the genetic control) acts on individual trait variation. Indeed, most of these studies perform standardized flammability measurements in leaves or small branches in controlled laboratory conditions (e.g. size or mass and moisture of the sample are standardized). Although burning full individuals in field conditions could conceptually be a better approach than working at a small scale in the laboratory, the dimensions and

logistics of such experiments and the difficulties of making standardized measurements limit the use of this approach. In addition, variability between whole individuals in the field might have various causes that are not genetically controlled, rendering them less informative for an evolutionary analysis. An extreme case may be illustrative: the number and cover of dead individuals in a community are important for modelling fire behaviour; however, these values might be of limited relevance for understanding evolutionary processes because they are not genetically controlled (mortality may be distributed among different species and depends on many other factors such as droughts, pests, age, competition, etc.).

Some species enhance their flammability by retaining dead biomass (Keeley & Zedler, 1998; Schwilk, 2003). For instance, the retention of dead biomass is an omnipresent trait in *U. parviflorus* (Pausas *et al.*, 2012). While the presence of this trait is probably genetically controlled (e.g. see references on architectural traits in many horticultural plants), the amount of dead biomass retained is unlikely to have a genetic basis, as many other local factors (e.g. water availability, microtopography, light incidence) are involved. Consistently, when analysing this trait in *U. parviflorus* populations with contrasted fire regime, we found high individual variability in standing dead biomass and no differences between fire regimes (Pausas *et al.*, 2012).

Flammability is a complex trait that can be defined in different ways (e.g. probability of ignition, heat released, temperature reached, velocity of combustion, fuel structure, chemical composition, etc.) and measured at different scales (from leaves to landscapes). Because all these indicators are not necessarily correlated, the simple use of the term flammability can generate some confusion. However, the results become clear when the flammability indicators are viewed in detail and at the scale that is relevant to the organism or process being examined (Levin, 1992).

Research directions

Fire science is multidisciplinary and researchers need to recognize the diversity of approaches and the importance of evolutionary biology. We definitively need experimentation in laboratories, even if they are (necessarily) reductionist, as is most experimental biology. Understanding the evolution of flammability is extraordinarily complicated and laboratory experiments can be considered a first step in sorting out this biological phenomenon. As our methods and technology advance, we will perhaps be able to account for the whole phenotypic variability, but currently we are forced to work at smaller scales, and risk being criticized for being reductionist. Experimentation cannot be replaced by computer models in which assumptions are embedded in the code; it is a basic tool in science and useful for the understanding of many biological processes. Laboratory experiments are also useful for calibrating models that are later used for fire modelling to test alternative management scenarios. Models can be a useful tool for scaling up laboratory experiments, because these experiments are performed at the scale of selection (individual level), but fire also spreads through communities and landscapes. Fire research

and landscape management have historically been based only on the physical paradigm of fire (i.e. fuel management and fire behaviour modelling). This physical framework has yielded remarkable results, yet it has failed to provide an integrative view of how fire shapes nature and how fire-prone ecosystems should be managed for a sustainable world. Only by considering the complementarity of the different disciplines (physics, forestry, ecology, evolution, genetics, etc.) can fire science make a significant advance in land management (Pyne, 2007).

Current trait-based flammability studies might have limitations for predicting broad-scale fire behaviour (but see Schwilk & Caprio, 2011). However, they contribute to understanding the role of fire in generating trait divergence, fire adaptations and, ultimately, species persistence in fire-prone ecosystems (Keeley *et al.*, 2011; Pausas & Schwilk, 2012). Fire modelling studies also have limitations, but contribute to understanding fire behaviour and might be valuable for fire management. Although the flammability concept is useful to foresters and engineers for predicting fire risk and modelling fire behaviour, it is a biological trait and its origin and variability are determined by biological processes. In fact, flammability is now becoming a key factor for understanding plant evolution (Keeley & Rundel, 2005; Bond & Scott, 2010; He *et al.*, 2011, 2012). With the recent advent of new generation sequencing and genotyping methods, we are closer to the possibility of genotyping whole populations with highly polymorphic makers to infer relatedness among individuals in the field, and thus to fully test the 'kill thy neighbour' hypothesis. In addition, the emerging trait-based discipline of community genetics and the concept of the extended phenotype (Whitham *et al.*, 2003) may provide an appropriate evolutionary framework for linking leaf traits and community flammability. Indeed, community genetics can potentially make a significant contribution to fire ecology (Wymore *et al.*, 2011). Current studies linking traits and flammability at different scales (Schwilk & Caprio, 2011; Pausas *et al.*, 2012) are contributing to build this promising approach. This is a very exciting time for fire ecology; we hope that fire modelling and landscape management will also benefit from these new emerging ideas.

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