

Fire and plant evolution

MEDECOS Special session on 'Fire as an evolutionary pressure shaping plant traits', University of California, Los Angeles, CA, USA, September, 2011.

Throughout much of the history of ecological science, wildfires were viewed as disasters that destroyed ecosystems. Currently, however, most scientists and managers have overcome this short-sighted view and now consider fires as ecological processes that influence structure and function in many ecosystems worldwide. Despite this, there remain several outstanding controversies regarding fire's role. One area of research and controversy is the potential of plant traits to result in feedback effects on fire regime (e.g. Bond & Midgley 1995, Schwilk & Caprio 2011). There is increasing recognition that wildfires are old phenomena on the Earth as there is charcoal evidence during the whole history of terrestrial plants (Glasspool et al. 2004). In addition, past periods with high atmospheric oxygen concentration made vegetation highly flammable even in wet conditions (Glasspool & Scott 2010, Belcher et al. 2010). Consequently, vegetation-fire feedbacks may have had major effects on past vegetation and even on biome shifts. For instance, fire may have favoured the expansion of angiosperms during the Cretaceous (Bond & Scott 2011), a time with high concentrations of O₂ (possibly exceeding current values by 25%). Similarly, the expansion of C₄ grasses during the Miocene was favored by fire in extensive seasonally dry areas (Keeley & Rundel 2005). These studies point to the increasing recognition that fire has been an ancient process on the Earth (Pausas & Keeley 2009). However, the role of fire as an evolutionary force shaping plant adaptations has remained controversial (Keeley et al. 2011).

During the recent MEDECOS (Mediterranean Ecosystems) XII conference we organised a special session focused on compiling evidence of fire as an evolutionary process shaping plant traits (i.e., fire adaptations). The session benefited from an initial presentation by William Bond (University of Cape Town, South Africa) who provided an overview on the role of fire in biome distribution, with new evidence on the link between fire regime and the Cretaceous expansion of angiosperms (Bond & Scott 2010). Bond emphasized the feedback role of vegetation on fire regime and pointed out that in many fire-prone ecosystems alternative vegetation types with quite different flammabilities coexist on landscapes ('open' and flammable vs 'closed' non-flammable communities). These community types often represent groups of taxa with distinct life-histories and phylogenetic origins. Bond pointed out that the size and dynamics of these coexisting patches has been changing during the history in response to changes in fire regime and O₂ and CO₂ atmospheric concentration (with low CO₂ and high fire activity favoring open ecosystems and with high CO₂ and low fire favoring closed ecosystems). Consequently, vegetation has been shaped during the evolutionary history by complex atmospheric processes modifying resource allocation and flammability.

Micro-evolutionary approaches

The role of fire as an evolutionary pressure can be elucidated using both macro- and micro-evolutionary approaches (Fig. 1). Susana Gómez-González (Universidad Bío-Bío, Chile) provided a clear example of the micro-evolutionary approach to demonstrate natural selection driven by fire. She showed that populations of an annual species growing under different recent fire histories have different seed traits, and these traits are proven to be heritable and that increase fitness in frequently burnt ecosystems. Another micro-evolutionary study was presented Juli G. Pausas (CIDE-CSIC, Spain) suggesting that individuals of *Ulex parviflorus* (Fabaceae; a shrub of the Mediterranean Basin) growing in populations recurrently burnt were more flammable than individuals of the same species growing in populations arising from old-field colonisation (i.e., with fire-independent recruitment). Because *U. parviflorus* does not resprout but recruits from a soil seed bank after fire

(a post-fire seeder species), high flammability increases the chance of opening space for offspring recruitment after fire (Pausas et al. 2012). Thus, if this flammability is heritable, repeated fires would select for individuals with higher flammability, and thus driving trait divergence among different fire regimes. These results provide some field support for the ‘kill thy neighbour’ hypothesis (Bond & Midgley 1995), but they also highlighted the need for heritability studies to unambiguously demonstrate natural selection driven by fire.

Macro-evolutionary approaches

While the micro-evolutionary approach searches for trait divergences in different current selective environments, the macro-evolutionary approach uses dated phylogenies to trace the evolution of traits over long time scales (My) (Fig. 1). Previous uses of phylogenies for understanding trait evolution in fire-prone ecosystems were able to find evolutionary correlations among traits as well as patterns in the order of appearance of different fire-related traits (Schwilk & Ackerly 2001, Pausas & Verdú 2005); however, these studies were limited by the lack of molecular data for dating the phylogenies. The recent blooming of such data is allowing researchers to generate time calibrated phylogenies that can be used to date the origin and evolution of fire-related traits. Byron Lamont (Curtin University, Australia) presented an example of this macro-evolutionary approach for Australian and South African species. He presented recent results on the origin of several fire traits (e.g., lignotuber resprouting, epicormic resprouting, and serotiny) in the Proteaceae. For example, the origin of serotiny and dead floret retention around the cones (enhanced flammability around serotinous cones) was traced back to 61 Ma in *Banksia* (He et al. 2011), a similar age to the origin of epicormic resprouting in *Eucalyptus* (Crisp et al. 2011). The simultaneous and independent origin of fire traits in these two Australian families suggests that fire was an effective agent of selection as far back as the early Paleocene. The use of older clades could provide an opportunity to trace the origin of fire as a selective force even earlier (Midgley & Bond 2011), as there is evidence of fire persistence and regeneration traits in old lineages such as conifers and ferns.

Evolutionary role of some fire-related traits

In mediterranean-climate shrublands, alternative life-histories coexist, including species that resprout after fire but lack fire-cued seed germination (“obligate resprouters”), species that resprout and also have fire-cued seed germination (“facultative seeders”), and those that are killed by fire and are depended upon post fire seedling establishment (“obligate seeders”). Brandon R. Pratt (California State University, CA, USA) focused on physiological trade-offs between facultative and obligate resprouters from Californian chaparral growing in a common garden experiment. He presented evidence suggesting that facultative species have higher growth and lower root to shoot ratios than obligate resprouters (Pratt et al. 2009), a result in the same direction to those reported for the Mediterranean Basin (Paula & Pausas 2006, 2011). Jon Keeley (US Geological Survey, CA, USA) proposed a model of evolution from obligate resprouters (ancestral state) to facultative resprouters, and then to obligate seeders (Keeley et al. 2012). This model is consistent with phylogenetic studies (Pausas & Verdú 2005), and it is based on two evolutionary steps driven by different environmental conditions. Resprouting is hypothesized to contribute to persistence on a wide variety of fire-prone landscapes. With increases in aridity and the predictability of high intensity fires capable of creating gaps for seedling recruitment, selection has led to delayed reproduction and a single post-fire pulse of seedling establishment (evolutionary step 1). Further changes in fire regimes that placed a greater premium on seedling recruitment and limited the value of resprouting have led to some lineages abandoning the resprouting habit and evolution of the obligate seeding life history (evolutionary step 2) (Keeley et al. 2012).

Two researchers presented information on two less-studied fire related traits. Byron Lamont presented a review of fire-stimulation flowering. He compiled data on 550 species in Australia and

South Africa for which there is evidence of fire-stimulated flowering and pointed to the fitness benefits of this trait (Lamont & Downes, in press). Parker V. Thomas (San Francisco State University, CA, USA) provided evidence that the caching activities of rodents may be a fire adaptation by which *Arctostaphylos* species place their seeds in safe and protected sites for post-fire germination. However, it remains to understand why rodents would cache *Arctostaphylos* fruits given that apparently they do not retrieve and consume them (due to the little reward offered by *Arctostaphylos* fruits). One possible explanation is that caching activities are an anachronism from a time when similar plant species provided larger and palatable fruits, and thus current *Arctostaphylos* species benefit from what appears to be maladaptive animal behavior.

Conclusions

This session highlighted several key aspects on the role of fire in plant evolution. First, there is good evidence for vegetation-fire regime feedbacks at different spatial and temporal scales, in such a way that plant flammability is a major driver of plant evolution and vegetation distribution. Second, the evidence that fire acts as a selective force is apparent on both micro- and macro-evolutionary scales, suggesting that fire shapes plant traits and generates fire adaptations. And third, that fire is a complex selective pressure – plants adapt to (and, in turn, influence) particular fire regimes rather than fire in the abstract. This is an exciting time for fire ecologists, as fire is now recognized as fundamental for many ecological and evolutionary processes; the coming macro- and micro- evolutionary studies will certainly reinforce many of the ideas drawn during the meeting.

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References

- Belcher CM, Mander L, Rein G, Jervis FX, Haworth M, Hesselbo SP, Glasspool IJ, McElwain JC. 2010.** Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. *Nature Geoscience* **3**: 426-429.
- Bond WJ, Midgley JJ. 1995.** Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* **73**: 79-85.
- Bond WJ, Scott AC. 2010.** Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* **188**: 1137-1150.
- Crisp MD, Burrows GE, Cook LG, Thornhill AH, Bowman DMJS. 2011.** Flammable biomes dominated by eucalypts originated at the Cretaceous-Palaeogene boundary. *Nature Communications* **2**: 193.
- Glasspool IJ, Edwards D, Axe L. 2004.** Charcoal in the Silurian as evidence for the earliest wildfire. *Geology* **32**: 381-383.
- Glasspool IJ, Scott AC. 2010.** Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. *Nature Geoscience* **3**: 627-630.
- He T, Lamont BB, Downes KS. 2011.** Banksia born to burn. *New Phytologist* **191**: 184-196.
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011.** Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406-411.
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012.** *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. UK: Cambridge University Press.
- Keeley JE, Rundel PW. 2005.** Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* **8**: 1-8.
- Lamont BB, Downes KS. in press.** Fire-stimulated flowering among resprouters and geophytes in

Australia and South Africa. *Plant Ecology* **xx**: xx-xx.

- Midgley J, Bond W. 2011.** Pushing back in time: the role of fire in plant evolution. *New Phytologist* **191**: 5-7.
- Paula S, Pausas JG. 2006.** Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* **20**: 941-947.
- Paula S, Pausas JG. 2011.** Root traits explain different foraging strategies between resprouting abilities. *Oecologia* **165**: 321-331.
- Pausas JG, Keeley JE. 2009.** A burning story: The role of fire in the history of life. *BioScience* **59**: 593-601.
- Pausas JG, Verdú M. 2005.** Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. *Oikos* **109**: 196-202.
- Pausas JG, Alessio G, Moreira B, Corcobado G. 2012.** Fires enhance flammability in *Ulex parviflorus*. *New Phytologist*. **193**: xx-xx. (doi:10.1111/j.1469-8137.2011.03945.x)
- Pratt RB, North GB, Jacobsen AL, Ewers FW, Davis SD. 2009.** Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. *Functional Ecology* **24**: 70-81.
- Schwilk DW, Ackerly DD. 2001.** Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* **94**: 326-336.
- Schwilk DW, Caprio AC. 2011.** Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* **99**: 970-980.

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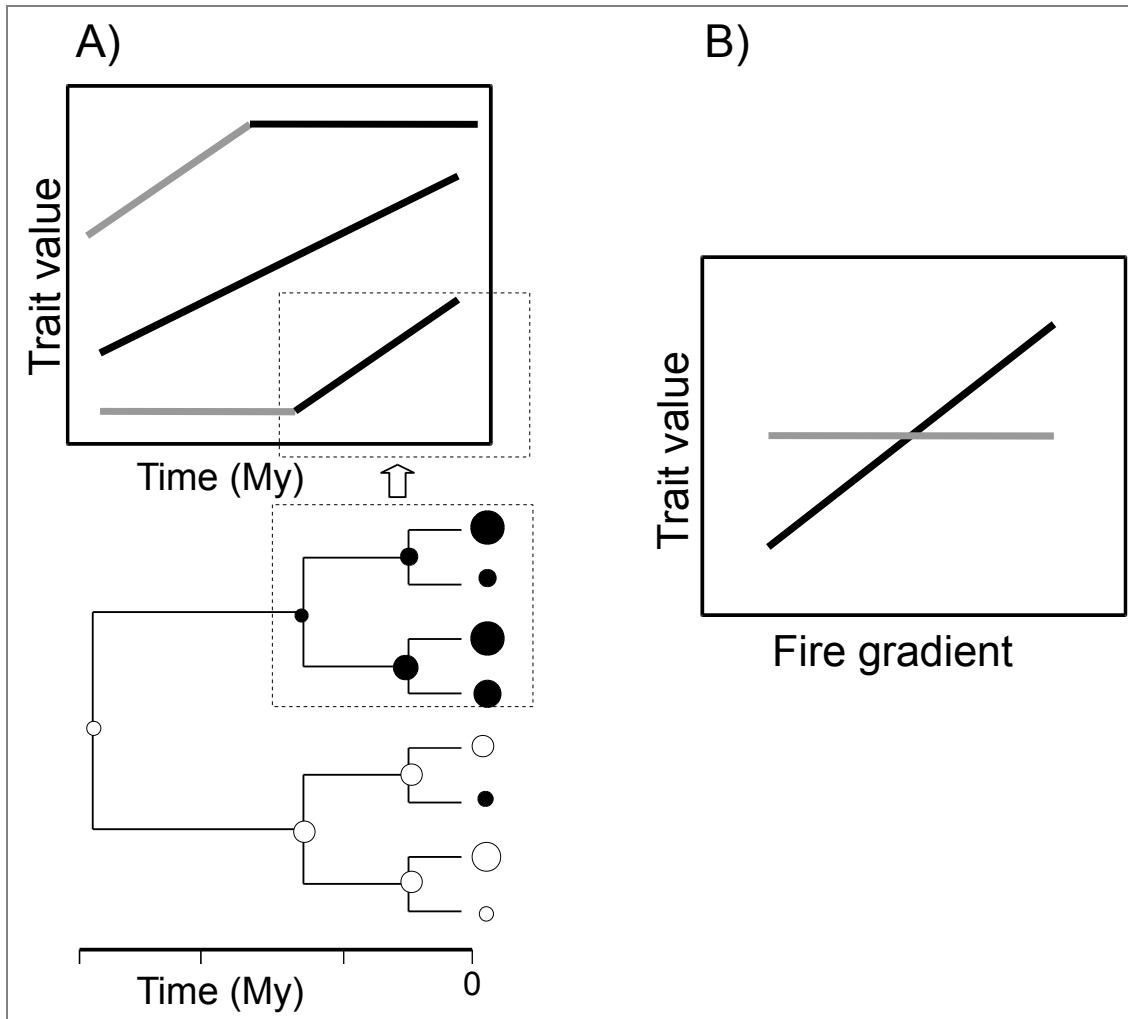


Fig. 1. Approaches to elucidate the role of fire as evolutionary pressure: The macro-evolutionary approach (A) is based on understanding changes in the trait in relation to the different evolutionary pressures (top figure: different lines are different possible scenarios; different line shades represent periods of different evolutionary pressures; see Keeley et al. 2011), based on the ancestral reconstruction of trait values in dated phylogenies (bottom figure; symbols of different size and color represent different trait values). The micro-evolutionary approach (B) is based on searching for trait divergences along a current fire activity gradient (dark line suggest local adaptation, while gray line represents a trait independent of the fire regime).