Research review

Towards understanding resprouting at the global scale

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Summary

Understanding and predicting plant response to disturbance is of paramount importance in our changing world. Resprouting ability is often considered a simple qualitative trait and used in many ecological studies. Our aim is to show some of the complexities of resprouting while highlighting cautions that need be taken in using resprouting ability to predict vegetation responses across disturbance types and biomes. There are marked differences in resprouting depending on the disturbance type, and fire is often the most severe disturbance because it includes both defoliation and lethal temperatures. In the Mediterranean biome, there are differences in functional strategies to cope with water deficit between resprouters (dehydration avoiders) and nonresprouters (dehydration tolerators); however, there is little research to unambiguously extrapolate these results to other biomes. Furthermore, predictions of vegetation responses to changes in disturbance regimes require consideration not only of resprouting, but also other relevant traits (e.g. seeding, bark thickness) and the different correlations among traits observed in different biomes; models lacking these details would behave poorly at the global scale. Overall, the lessons learned from a given disturbance regime and biome (e.g. crown-fire Mediterranean ecosystems) can guide research in other ecosystems but should not be extrapolated at the global scale.

Introduction

Resprouting refers to the ability of some plants to form new shoots after destruction of living tissues from disturbance. It is common in many plants worldwide and thought to be common in ancient floras (Pausas & Keeley, 2014). Because resprouting enables the survival of individuals after disturbance, it is a key plant functional trait in many ecosystems and has been reviewed elsewhere (Bellingham & Sparrow, 2000; Clarke *et al.*, 2013; Pausas & Keeley, 2014). Given the important shifts in disturbance regimes in our changing world, understanding resprouting and predicting post-disturbance responses is of paramount importance.

Resprouting is often considered a species-specific binary trait (Pausas *et al.*, 2004), with some species able to resprout and others lacking this ability (but see Vesk & Westoby, 2004). However, this is an overly simplistic view; resprouting is a mode of regeneration and therefore it is better considered in the context of other modes such as seeding (Box 1). Classification of species as resprouters vs nonresprouters coupled with seeding response, has been successfully used in specific contexts (i.e. Mediterranean ecosystems with crown-fire regimes; Pausas *et al.*, 2004; Ackerly, 2004; Pausas & Keeley, 2014), but it is uncertain that this would provide significant explanatory power at the global scale. This is because resprouting is a trait that increases fitness under many different disturbance types, occurs in a wide range of environments, is widespread in many lineages and is morphologically very diverse (Keeley *et al.*, 2012). Below we review important considerations in understanding

Box 1 Basic concepts

Postfire traits and strategies

Postfire resprouting (R): the ability to generate new shoots from dormant buds after stems have been fully scorched by fire. This term is preferable to sprouting, which refers to initiation of new shoots throughout the life cycle of a plant. Species are typically classified as resprouters (R+) or nonresprouters (R−) depending on their resprouting ability.

Postfire seeding (S): the ability to generate a fire-resistant seedbank with seeds that germinate profusely after fires (fire-cued germination). Typically, such species restrict recruitment to a single pulse after a fire. Seeds may be stored in the soil or in the canopy. Species are typically classified as seeders (S+) or nonseeders (S−) depending on whether seeds display fire-cued germination and recruitment in postfire pulses. Note that the term 'seeders' refers strictly to postfire conditions, and cannot be attributed to plants that regenerate by seeds in other conditions.

Obligate resprouters (R+S−): plants that solely rely on resprouting to regenerate after fire (resprouters without postfire seeding ability). These plants do not germinate after fire because they lack a fire-resistant seedbank. Note that obligate resprouters might reproduce by seeds during the fire-free interval, but the terminology of seeders and resprouters refers to the postfire conditions.

Facultative seeders (R+S+): plants that have both mechanisms for regenerating after fire, that is, they are able to resprout and to germinate seeds after fire.

Obligate seeders (R−S+): plants that do not resprout and rely on seeding to regenerate their population after fire (nonresprouters with postfire seeding ability).

Postfire colonizers (R-S−): plants that lack a mechanism for local postfire persistence, but they can recruit after fire from seeds dispersed from unburned patches or from populations outside the fire perimeter (metapopulation dynamics).

Drought-related strategies

Water stress, drought stress, dehydration stress: the stress due to a water deficit.

Drought regime: different aspects of a drought that can have different effects on plants. Two key aspects are intensity and duration of water deficits (Box 2); two additional factors are temperature and vapour pressure deficits.

Drought resistance: the ability to survive a drought. This can be achieved by tolerating or avoiding tissue dehydration.

Dehydration (drought) avoidance: the strict meaning of 'drought', as a meteorological term, is a prolonged absence of precipitation, extending over geographical space, and thus cannot be 'avoided' by plants *per se*. However, plants can avoid tissue dehydration caused by drought through deep roots, stomatal closure, growth near a water source, tissue water storage and shedding of leaves (in the case of drought deciduous species).

Dehydration (drought) tolerance: a drought resistance mode whereby tissues experience significant dehydration but avoid injury. In some cases injurious strain may be sustained, but plants are able to either tolerate it or repair it.

Anisohydric: a form of stomatal regulation that leads to tissue water deficits, measured at midday, when the available water in the environment declines.

Isohydric: a form of stomatal regulation that leads to stable water status, typically measured at midday, in response to fluctuating water availability.

resprouting at the global scale and using this trait for accurate predictions in a changing world. Specifically we address the following questions: (1) Because global change includes regime changes in many disturbances (e.g. drought, fire, herbivory, wind), to what extent is a single qualitative trait, such as resprouting ability, useful for predicting global change responses? (2) One of the main global change drivers is the increased frequency and intensity of droughts; the higher resources allocated to the root system by resprouters allows them not only to accumulate reserves for resprouting, but also to access more stable water sources. Thus, we ask to what extent do the differences between resprouters and nonresprouters affect their resistance to drought? And (3) can we use resprouting to improve our prediction of vegetation responses to global change in global vegetation models? By answering these questions, we highlight some progresses and pitfalls in understanding plant resprouting at the global scale.

Does disturbance type matter?

Resprouting has been studied as a response to many disturbances, including wind, freezing, drought and large animals; however, much focus has been on fire. Consequently, there is considerable information on postfire resprouting ability in trait databases (e.g. FEIS-USDA Forest Service, Paula *et al.*, 2009). This information is mostly binary at the species level. If the ability to resprout was intrinsic to the species and independent of the type of disturbance (e.g. Zeppel *et al.*, 2015) then the cumulative information in the databases could be used for predicting vegetation responses to any disturbance. The basis of this hypothesis is that resprouting species have dormant buds (or bud-forming tissues) and accumulate reserves (nonstructural carbohydrates) that are mobilized in response to a biomass removal from any disturbance or stress factor. In this framework, it has been suggested that the ability to resprout after fire could be an indicator of the capacity to recover

after drought, and thus be a useful proxy for predicting vegetation dynamics in a warming world (Zeppel *et al.*, 2015).

However, there are major differences between fire and other disturbances that may influence resprouting and limit generalizations. Although disturbance typically leads to defoliation, fire causes additional impacts due to high temperatures and some species with an innate capacity for resprouting may not resprout after fire due to the lethal effects of the fire. Some plants have resprouting buds with very little protection that are killed by the heat of a fire but not by other disturbances. Even for fire survivors, the heat from fire may nucleate cavitation and deform xylem conduits leading to postfire water stress (Michaletz *et al.*, 2012). Consequently, most plants that resprout after fire are also likely to resprout after many other types of disturbances, but the opposite is not necessarily true. Supporting this, there is evidence for lower resprouting ability after fire than after clipping (see compilation by Vesk & Westoby, 2004; Vesk *et al.*, 2004). There are also cases in which plants resprout after fire but may fail to regenerate after drought. For instance, root systems are often protected from fires by the soil, but they are vulnerable to drought disturbance (cavitation; Pratt *et al.*, 2007a,b); thus, in the case of a very intense drought, extensive embolism formation in the shoot and root may preclude resprouting, even for a species that commonly resprouts after a fire (see next section, Resprouting and drought resistance).

Additionally, fire not only defoliates a plant and has lethal effects on meristemic tissues (buds, cambium), it also depletes the litter layer, changes nutrient dynamics and kills interacting species (antagonistic, mutualistic and pathogen species). There is also a flush of new resources after fire, but not after other disturbances. Consequently, many disturbances produce different community and ecosystem dynamics compared with fire (e.g. Nguyen-Xuan *et al.*, 2000; Te Beest *et al.*, 2015).

When determining whether or not a species is a postfire resprouter, it is important to consider that on a landscape scale fires are heterogeneous. There may be some plants that experience low fire intensity and are only partially defoliated; these plants may successfully recover by resprouting new leaves and shoots. However, this resprouting is not indicative of the postfire resprouting ability of the species. Postfire resprouters are defined as those species that generate new shoots following full scorching of the plant (Box 1; Gill, 1981; Pausas *et al.*, 2004; Pausas & Keeley, 2014). Many postfire nonresprouters can also produce new shoots and survive when they are only partially scorched (e.g. Hanson & North, 2006; Fernandes *et al.*, 2008).

Even in the case of fire, different fire regimes can generate different pressures that select for different traits (Pausas, 2015a,b). Fire affects plants very differently in ecosystems under crown fire regimes (e.g. shrublands) and those under understorey fire regimes (e.g. some conifer forest and open woodlands), and these two fire regimes can coexist at the landscape scale. The sharp boundary between them represents a tipping point in which the selective factors for life history characteristics change state abruptly (Keeley *et al.*, 2012). Despite radical differences in fire intensity and frequency, both ecosystems have resprouting and nonresprouting species, but for very different reasons that are tied to the different selective environments. For example, crown fires select for

nonresprouters that recruit seedlings after fire from *in situ* seed-banks, whereas forest ecosystems with understorey fire regimes often comprise trees that are nonresprouters but persist due to their tall stature, clear boles due to self-pruning of dead branches, and thick bark (Pausas, 2015b).

Overall, it seems that not all disturbances act with the same mechanism and produce the same plant and ecosystem responses, and equating the recovery from postfire resprouting with recovery from any other disturbance is an oversimplification. To what extent this simplification may be useful would depend on the specific question addressed, but the differences need to be kept in mind. Specifically, in the context of global change, predicting the response of plants to the disturbance by frequent droughts is of paramount importance. A clear example of the dissimilarity between resprouting and post-drought recovery includes species that survive drought periods by initially dropping their leaves and recover them after the drought; among these species there are a number of nonresprouters (e.g. *Cistus* species; Werner *et al.*, 1999). Given that postfire resprouting is not equivalent to drought response, we now ask, what is the relationship between these two processes?

Resprouting and drought resistance

Resprouters vs nonresprouters

Resprouting carries a cost of storing resources belowground to maintain and protect a bud bank and support rapid post-disturbance regrowth (Pate *et al.*, 1990; Schwilk & Ackerly, 2005; Moreira *et al.*, 2012). By contrast, nonresprouters allocate the corresponding resources to other functions such as rapid growth and reproduction. In addition, resprouters survive and accumulate additional belowground biomass through multiple disturbances, and thus their roots are frequently older and larger (i.e. they can explore a larger soil volume) than those of nonresprouters, even though shoots may be equal in height. All this implies that resprouters tend to have a higher root-to-shoot ratio which could provide greater access to water resources than nonresprouters. However, nonresprouters often coexist with resprouters in the same environment, and even tend to dominate in dry environments. Thus, we hypothesize that nonresprouters have developed physiological mechanisms for higher dehydration tolerance than resprouters (Keeley *et al.*, 2012; Vilagrosa *et al.*, 2014). Our global analysis suggests that the xylem of nonresprouting species is more resistant to dehydration-induced cavitation (P_{50}) than that of resprouters (Fig. 1a; Supporting Information Notes S1, S2). This result contrasts with the conclusions of Zeppel *et al.* (2015) and is likely attributable to their smaller dataset with some errors in assignment of resprouting (see Notes S1 for details).

Our observation that nonresprouters are more resistant to cavitation (Fig. 1, left) is driven mainly by species in the Mediterranean biome (Fig. 1, centre; Notes S2). Comparisons between resprouting and nonresprouting species have been most extensively examined in this biome, and thus it is instructive to focus on it as a model. Numerous studies of cavitation resistance in California chaparral (Jacobsen *et al.*, 2007; Pratt *et al.*, 2007a,b),
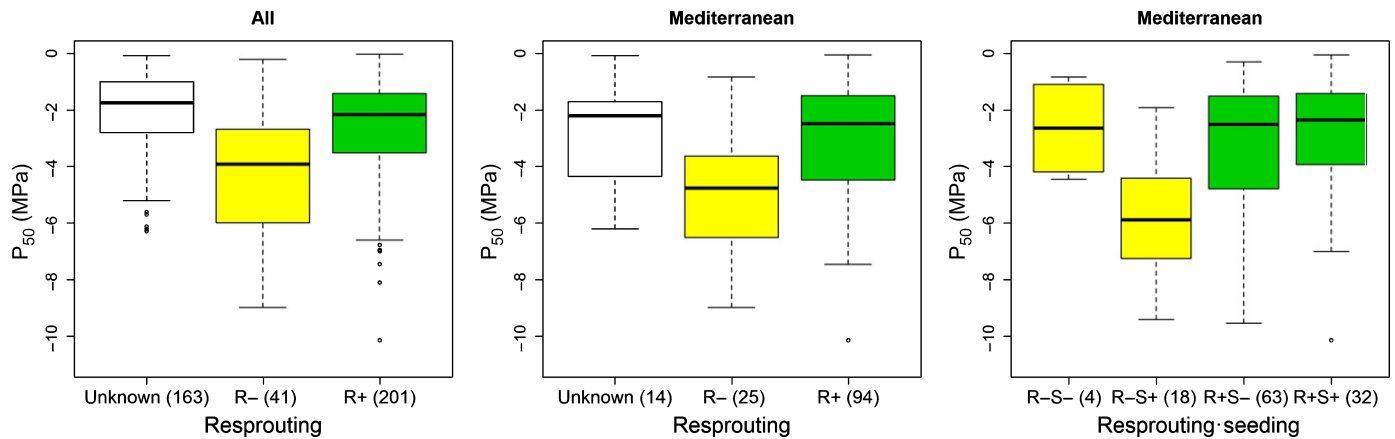
Fig. 1 Relationship between resistance to xylem cavitation (P_{50}, MPa) and resprouting ability in angiosperm species from different biomes (left) and for a subset including Mediterranean species only (centre). The third figure (right) shows the combination of two postfire traits for the Mediterranean species: resprouting (R+/R−, i.e. yes/no) and postfire seeding (S+/S−, i.e. yes/no); number of species considered in each case are in brackets (from bibliographic references, see Supporting Information Table S1 for details). Resistance to xylem cavitation is expressed as the water potential (MPa) at which a plant loses 50% of hydraulic conductivity (see Notes S1 for more details and Notes S2 for statistics). Boxplots show the median (horizontal line), the quartiles (boxes), the 1.5-times the interquartile range (whiskers), and extreme values (dots).

and the Mediterranean basin (Hernández *et al.*, 2011; Vilagrosa *et al.*, 2014) support the pattern of greater tolerance in nonresprouters. Some support has also been found in the Mediterranean-climate regions of South Africa (Pratt *et al.*, 2012). Additionally, there are other traits that segregate out according to resprouting ability that also support this pattern. For example, Mediterranean-climate nonresprouters generally have more structurally robust leaves (i.e. lower specific leaf area), greater xylem tissue density with lower water storage capacity, lower leaf area to xylem area of shoots (particularly for evergreen taxa), and higher vessel implosion resistance (Notes S3). All of this suggests that, in these ecosystems, there is a stronger environmental pressure for developing dehydration tolerance mechanisms in nonresprouters than in resprouters. In this sense, it has been hypothesized that these mechanisms are due to the different regeneration niche of the two resprouting life histories (Pausas & Keeley, 2014): many species recruit seedlings just after fire (i.e. postfire seeders, many of them are nonresprouters; Box 1), and thus, the seasonally dry open-canopy environment has selected for dehydration tolerance; by contrast, obligate resprouters tend to successfully recruit seedlings in more shaded conditions. In support of this, seedlings of Mediterranean nonresprouters typically have much greater survival in postfire open canopy conditions than seedlings of co-occurring resprouter species (e.g. Thomas & Davis, 1989).

In order to fully understand species response to drought, it is useful to frame the response in the context of different drought regimes (McDowell *et al.*, 2008). In this framework, nonresprouters generally fit into a classification of tissue-dehydration tolerators (Box 2); that is, they are more likely to resist droughts of low to moderate intensity and may be able to do so over a long period, particularly if their shallow roots allow them to respond to small pulses of rain. In fact, nonresprouters generally have traits associated with greater levels of productivity when water is available (Notes S3), which is an important part of the suite of traits defining the functional strategy of this life-history type. In Mediterranean-

climate landscapes worldwide, there is field evidence suggesting that nonresprouters tend to predominate in sites that stay dry for longer (e.g. equator-facing slopes), whereas resprouters predominate in sites with more reliable water supply throughout the year (Keeley *et al.*, 2012). Examples of this pattern can be found in California (Meentemeyer & Moody, 2002), in the Mediterranean Basin (Pausas *et al.*, 1999) and in Australia (Clarke & Knox, 2002; Pausas & Bradstock, 2007).

By contrast, for droughts of the highest intensity, nonresprouters are predicted to succumb to catastrophic hydraulic failure and suffer the greatest mortality because their shallow roots do not allow them to maintain tissue hydration and they frequently reach negative water potentials that exceed cavitation thresholds (see Fig. 2). A recent study conducted during an intense record drought in California, found that it was the nonresprouters that suffered the greatest mortality among established adult plants. In addition, the species with the greatest cavitation resistance (i.e. most negative P_{50}) were the ones that had the greatest mortality (Paddock *et al.*, 2013; Fig. 3). Other than the lack of resprouting ability, the characteristics shared by the species most vulnerable to short-term, high-intensity drought were shallow rooting habit and an inability to minimize tissue dehydration, presumably due to lack of stomatal control, leaf shedding or low levels of capacitance. Combined, these data illustrate the susceptibility of nonresprouters relative to resprouters in mature stands during high-intensity droughts, and reinforce the hypothesis that resistance to cavitation (e.g. P_{50}) is not necessarily a good indicator of drought survival.

Overall there is a clear pattern in Mediterranean-type environments suggesting that nonresprouters and resprouters have different mechanisms to deal with water deficit. To say that nonresprouters are more vulnerable to drought as recently suggested (Zeppel *et al.*, 2015) is incomplete because it ignores the existence of different drought resistance mechanisms and the differential responses of nonresprouters and resprouters to different

Box 2 Drought resistance strategies

Plants with different regulatory strategies with respect to water status are hypothesized to be differentially affected by drought regime, which include drought intensity and duration (McDowell *et al.*, 2008). At one end of a continuum are species that dehydrate as the available moisture declines (**dehydration tolerators**). These species generally have shallow roots, they often suffer important water potential oscillations (weak stomatal control, i.e. anisohydric regulation; Box 1), and they lack sufficient water stores to avoid dehydration. The anisohydric regulation allows continued gas exchange during drought; and a shallow rooting habit enables a rapid response to pulses of moisture, but at the expense of greater tissue dehydration (Brodribb *et al.*, 2014). Thus, these species maintain dehydration tolerance mechanisms such as high resistance to xylem cavitation and mechanically strong lignified tissues (high wood density and low specific leaf area) with low water storage capacity. At the opposite end of the spectrum are species that tightly regulate their water status within a narrow range (**dehydration avoiders**). This is accomplished by strict stomatal control and low water potential oscillations (isohydric regulation; Box 1) or leaf shedding as available moisture declines, and these species typically access stable water reservoirs with extensive roots or have high tissue water storage capacity. Studies in both adults and seedlings suggest that mediterranean resprouters tend to correspond to dehydration avoiders while mediterranean nonresprouters correspond to dehydration tolerators (Notes S3). Note that there are nonresprouters with a strong dehydration tolerance that also have mechanisms to partially avoid tissue dehydration, such as *Cistus* species that drop their leaves under extreme drought conditions (Werner *et al.*, 1999).

Short-term droughts of the highest intensity are hypothesized to be most lethal to dehydration-tolerant species over short timescales (see Fig. 2). This is because shallow soil moisture may reach low levels causing tissues to dehydrate below a critical threshold that leads to catastrophic xylem dysfunction (Davis *et al.*, 2002; Hoffmann *et al.*, 2011; Paddock *et al.*, 2013). By contrast, longer term and lower intensity droughts that do not deplete shallow soil water may be resisted by dehydration-tolerant species. For dehydration avoiding species, a protracted drought of a sufficient intensity could lead to mortality due to carbon/energy deficits that may arise due to protracted stomatal closure (isohydric regulation), reduced canopy photosynthesis due to leaf shedding and ultimately the inability to maintain immune responses or meet respiratory demands of an extensive root system (Plaut *et al.*, 2012) (see Fig. 2). During the resprouting process, resprouters may be vulnerable to drought mortality caused either by carbohydrate depletion and/or hydraulic failure (Fig. 2, right); this is because stored carbohydrate reserves must maintain heterotropic root function as well as rapid shoot elongation, and postfire shoot recovery is also associated with greater susceptibility to hydraulic failure (Fig. 5; see section 'Vulnerability to drought during resprouting').
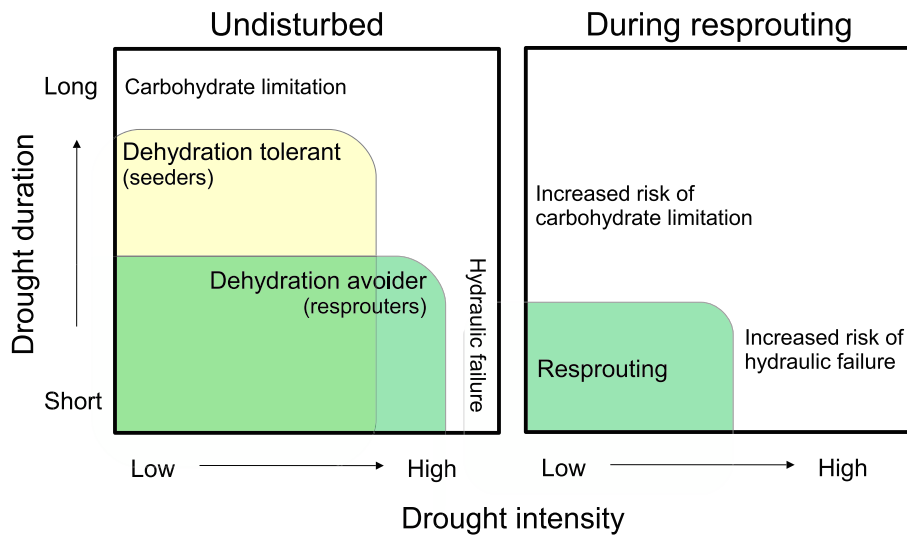

Fig. 2 Conceptual model depicting two key aspects of drought, the duration and intensity, and how they link with species that tolerate dehydration and those that avoid dehydration. Coloured areas are the safety zones for each type of species; blank regions correspond to the risky drought conditions – the risk of carbohydrate limitation (under a long drought) and the risk of hydraulic failure (under an intense drought). In Mediterranean conditions, nonresprouters (seeders) are generally dehydration-tolerant, whereas obligate resprouters are dehydration avoiders (left panel). During the process of resprouting, plants are more vulnerable to drought mortality caused by both carbohydrate depletion and/or hydraulic failure (smaller safe zone; right panel).

drought regimes. It would be useful to test for physiological differences between resprouting abilities in other ecosystems to evaluate the generality beyond Mediterranean-type climate regions. This effort could provide a robust niche-based framework for predicting drought response at a broad scale.

Vulnerability to drought during resprouting

During post-disturbance resprouting, plants mobilize stored resources to grow new shoots (Moreira *et al.*, 2012), and this could jeopardize their tolerance to drought stress (O'Brien *et al.*,

2014), especially if rapidly expanding tissues are ontogenetically sensitive to dehydration (Saruwatari & Davis, 1989). Thus, resprouts are likely to be more susceptible to drought injury than nondisturbed adults. This has been shown for chaparral resprouting species subject to an extreme drought during the postfire recovery period, where resprouts of burned plants had higher water-stress induced cavitation, higher depletion of carbohydrate reserves and higher mortality than unburned plants of the same species (Pratt *et al.*, 2014). A manipulative
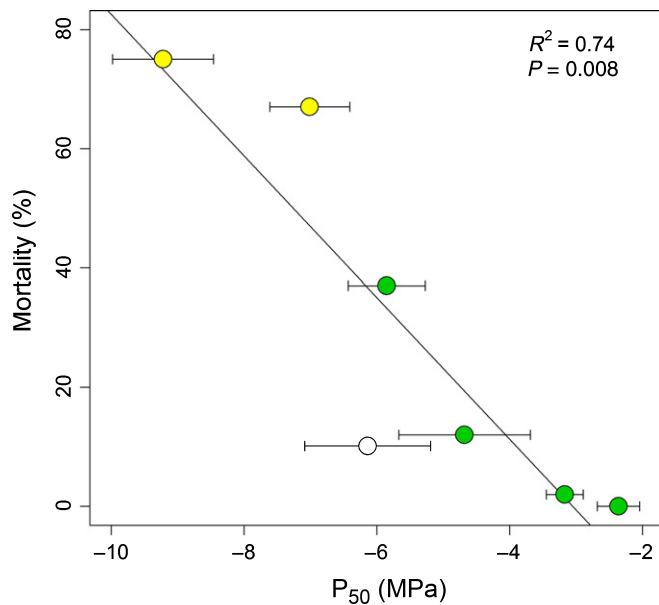
Fig. 3 Mortality during an intense drought is related to cavitation resistance (P_{50}) in seven Mediterranean species of the Californian chaparral. P_{50} is the water potential at 50% loss of hydraulic conductivity (more negative values correspond to greater levels of cavitation resistance). The figure shows that species with greater cavitation resistance exhibited greater mortality during an intense drought. Green symbols, evergreen resprouters; yellow symbols, evergreen nonresprouters; white symbol, to a drought-deciduous species. The line indicates the linear regression; adjusted R^2 and the *P*-value of this regression are also shown (data from Paddock *et al.*, 2013).

experiment with a common resprouting chaparral shrub, *Adenostoma fasciculatum* (chamise; R+S+; Fig. 4), also demonstrates the impact that drought conditions can have on resprouting: watering treatment increased postfire survival during the first dry season whereas an experimental drought treatment resulted in a two-fold increase in postfire mortality (i.e. *c.* 75% mortality) compared to watered plants (Fig. 4b).

There are at least two reasons why resprouting individuals are more sensitive to drought. First, resprouting shoots generally have higher stomatal conductance and a xylem that is more vulnerable to cavitation, compared to undisturbed plants (Fig. 5; Ramirez *et al.*, 2012; Pratt *et al.*, 2014). And second, if substantial aboveground biomass is lost during the disturbance, then considerable carbohydrates have to be mobilized from underground stores to grow new shoots (Moreira *et al.*, 2012). At the same time, root function must be sustained by mobilizing carbohydrates until significant shoot growth generates a surplus of photosynthate. If during this process CO_2 uptake is limited by stomatal restriction due to drought, then carbohydrates could be depleted leading to mortality (McDowell *et al.*, 2008; Pratt *et al.*, 2014).

Functional syndromes and modelling vegetation dynamics

The use of a single disturbance-related trait, such as resprouting, to generalize the response to disturbance at the global scale may be too simplistic. One of the reasons is that in different environments, resprouting is associated with a different set of traits (including other disturbance-related traits), and thus resprouters and nonresprouters may not respond in the same way in all biomes (Pausas, 2001). For instance, in Mediterranean fire-prone ecosystems, nonresprouters tend to form a persistent seedbank in the soil or in the canopy (seeder species, R−S+; Box 1; Pausas *et al.*, 2004; Keeley *et al.*, 2012). These species regenerate very well after fire by recruiting new individuals, and their population size often increases abruptly after fire, even under a drought (Pratt *et al.*, 2014). Nonresprouting seeders recruit in open postfire conditions (Pausas
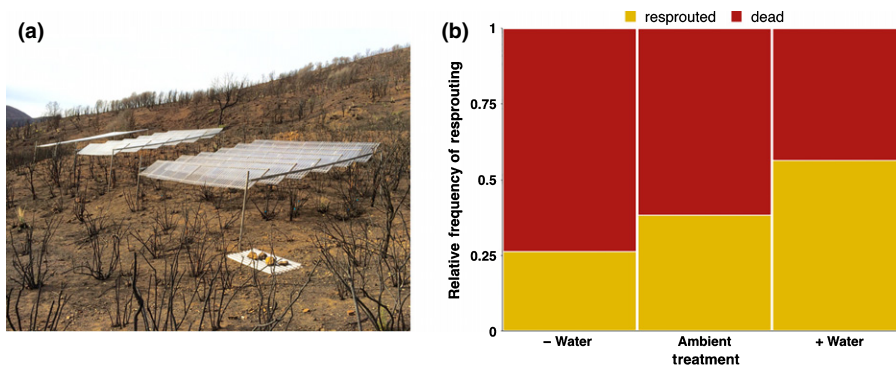

Fig. 4 (a) Postfire rainout shelter experiment in Santa Monica Mountains, southern California (USA). Flat roofed shelters (− water treatment, far left) excluded 100% of wet season precipitation. Shelters with angled roof panels (ambient and + water treatments; center and right) allowed ambient rainfall to fall on the plots. In addition, water was added to one of the treatments (+ water treatment; right) in simulated rainfall events that mimicked an extension of the rainy season. A total of nine 5 × 5 m plots and *n* = 294 chamise shrubs (*Adenostoma fasciculatum*) were included in the experiment. (b) Results of the watering treatment effect on postfire resprouting of chamise expressed as the relative frequency of shrubs that resprouted (yellow) and died (red) after fire. The amount of water available during the first dry season after a fire significantly affected the number of plants that survived and resprouted (χ^2 = 18.43, df = 2, *P* < 0.001). Note that the ambient treatment likely has lower than usual resprouting survival because the study was conducted during a natural drought.
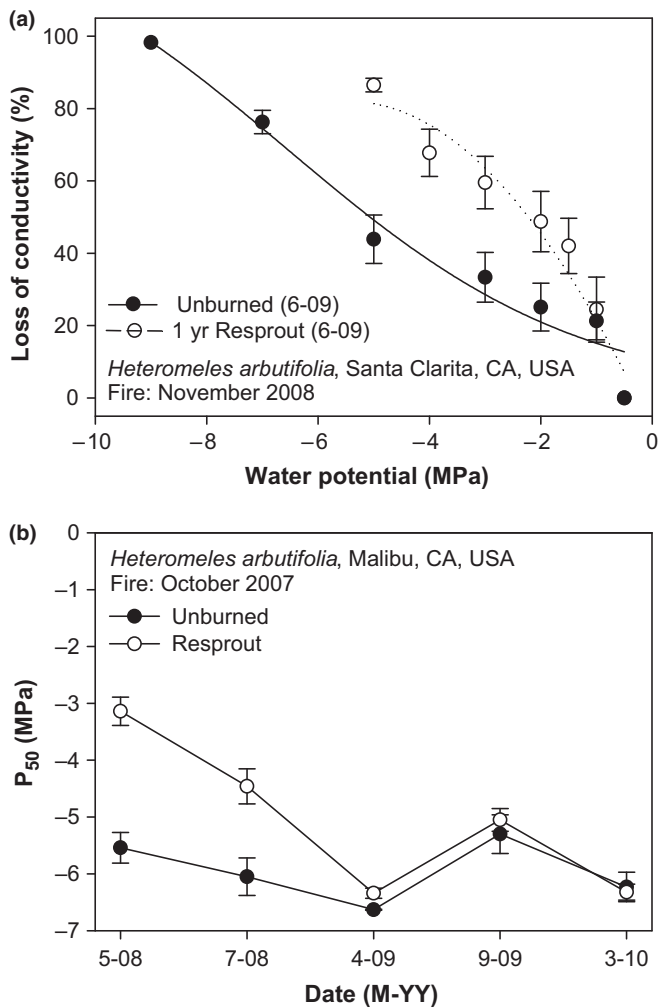
Fig. 5 The vulnerability to water-stress induced cavitation differ between resprouting plants and those that are not currently recovering from disturbance in the chaparral shrub species *Heteromeles arbutifolia* (Rosaceae). (a) Shift in the cavitation resistance of resprouting stems 1 yr postfire compared to adjacent unburned plants measured at the same time and same site (A. L. Jacobsen *et al.*, unpublished; same pattern described for this species at a different site in Ramirez *et al.*, 2012). (b) This shift in vulnerability may persist until 2 yr postfire (data from Kaneakua, 2011). Each point represents a mean of samples from ≥ 6 individuals ± 1 SE. M-YY, month-year.

Fig. 6 Proportion of species with low (< 25% of the individuals), moderate and high (> 75% of individuals) postfire resprouting in 111 tropical plant species from Central/South America and northern Australia (Supporting Information Notes S4). There is an important proportion of species with intermediate resprouting capacity.

& Keeley, 2014) and are the most resistant to cavitation (see R−S+; Fig. 1c); they are those that conform most clearly to the dehydration-tolerant strategy (Box 2).

These trait correlations are contingent on biogeographic history and thus are ecosystem-dependent. For instance, in many savanna woodlands, nonresprouting species do not tend to form a seedbank but are often associated with having a very thick protective bark; in such ecosystems the bark protects the vital tissues of the plant (Pausas, 2015a) and trees are not damaged by fire (understorey-fire ecosystems). In other cases, some nonresprouters have widely dispersed seeds, and even though local populations may not regenerate well after fire there may be recruitment postfire from neighbour populations (metapopulation dynamics; e.g. some Asteraceae). Yet other nonresprouters may lack the ability to
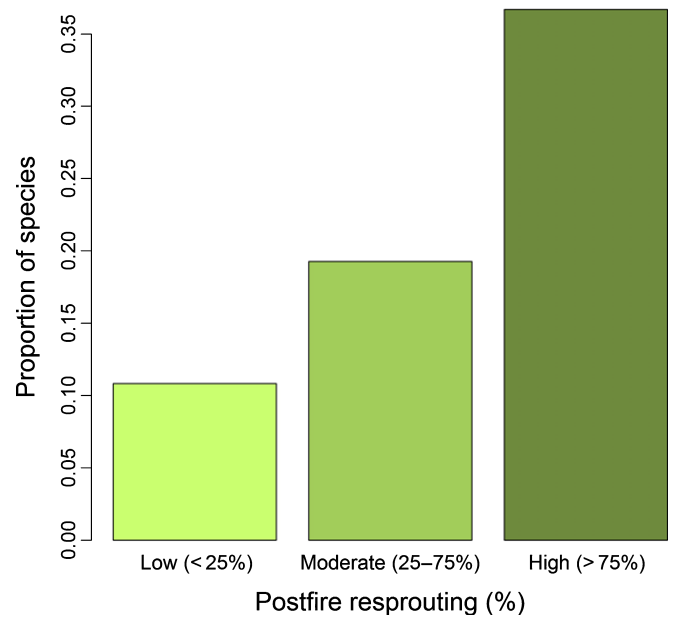
accumulate a seedbank and to disperse efficiently, and thus they recover slowly and they may experience local extinction after recurrent fires (e.g. Bowman *et al.*, 2014). Consequently, to estimate post-disturbance regeneration at the global scale, a multi-trait approach (i.e. functional types or syndromes) is more appropriate (Pausas, 2001). Predicting the dominance of resprouting along disturbance gradients (e.g. Bellingham & Sparrow, 2000) may have predictive value at relatively small scales (e.g. within a biome), but will necessarily lack generality (e.g. among biomes) if the correlated traits are not considered. Even within the same biome there may be biogeographic and physical differences that explain divergences in trait correlations and syndromes. Examples of this within-biome trait divergence can be found in multi-continental biomes including the Mediterranean (Pausas *et al.*, 2006), the tropical savanna (Dantas & Pausas, 2013) and the boreal biome (Rogers *et al.*, 2015), or when there is a strong shift in community structure that acts as a tipping point in the selective regime (as in the savanna–forest mosaics (Dantas *et al.*, 2013) or the Mediterranean chaparral–conifererous forest boundaries (Keeley *et al.*, 2012)). Consequently, trait combinations need to be considered for predicting vegetation responses at larger scales.

Many of the traits and trait combinations relevant for post-disturbance dynamics were included in early vegetation dynamic models working at smaller scales (e.g. Shugart & Noble, 1981; Pausas, 1999) and only recently have these traits been included in some global vegetation dynamic models. A step forward in global modelling was recently presented by Kelley *et al.* (2014) who included resprouting, together with bark thickness, for predicting vegetation and carbon dynamics in Australia. However, there are several reasons to expect that their model would behave poorly at the

global scale. This includes their overestimation of resprouting capacity (they considered some nonresprouting species to be resprouters; Notes S1) and their assumption that resprouters have a thicker bark than nonresprouters (Fig. 4 in Kelley *et al.*, 2014). This assumption is only valid for trees with epicormic (stem) resprouting; there are many species with basal resprouting and thin bark (Pausas, 2015a), and also many eucalypts with epicormic resprouting have a relatively thin bark because their protection mechanism is based on sinking their buds deeply into the trunk wood (Burrows, 2002). Finally, they also included in their recruitment module of the model that the recruitment of resprouters was 10% that of the nonresprouters, which is unlikely to be general. For instance, in Mediterranean ecosystems, recruitment of nonresprouting seeders is much higher than resprouters in the postfire year, but much lower in the years between fires. In non-Mediterranean ecosystems, the difference in recruitment between resprouters and nonresprouters is probably quite different as postfire seeders are a unique syndrome of the Mediterranean biome.

In summary, recent incorporations of disturbance-related traits such as resprouting in global vegetation models is a significant innovation; however, there is still need for improvement. Given the different carbon allocation patterns in resprouters and nonresprouters, the incorporation of these traits may have implications in the predicted carbon budget. Global models typically include climate-based functional types as their aim is to predict climatic-related changes. However, given the overwhelming evidence that disturbance regimes are also changing, the incorporation of disturbance-based functional types (e.g. Pausas, 2015a,b) is urgently needed. Developing models that accurately include plant disturbance responses at the global scale is certainly a challenge for next-generation global dynamic models.

Concluding remarks: beyond binary responses

Postfire resprouting of species is often considered as a binary trait in many species, especially in Mediterranean species where the frequency distribution of postfire resprouting tends to follow a binomial pattern (Pausas *et al.*, 2004; Vesk *et al.*, 2004). This is because in Mediterranean climates, fires tend to be of very high intensity, and intermediate responses may be evolutionarily unstable (Pausas & Keeley, 2014). However, in many ecosystems fires are typically less intense because they are more frequent (savannas), because the environment is wetter (tropical or mountain forests) or because fuels are low (arid systems). In such ecosystems, the proportion of resprouted individuals may range widely without showing a clear binomial distribution (e.g. Vesk & Westoby, 2004; Fig. 6). The causes of such variation are difficult to generalize and there is a clear need to improve our knowledge of resprouting behaviour outside the Mediterranean biome. For instance, of the *c.* 500 species for which P_{50} values were compiled in Notes S1, we were able to assign the resprouting ability to 90% of the Mediterranean species but to < 50% of the non-Mediterranean ones. Understanding resprouting in other biomes means going beyond binary responses and trying to understand resprouting variability. The dichotomy of resprouting vs nonresprouting species may explain a high proportion of variance in Mediterranean

ecosystems but probably little variance at the global scale. In addition, because fire intensities vary with vegetation type and climate, it may be difficult to compare resprouting across biomes. That is, a plant that resprouts after a fire in a tropical ecosystem could fail to resprout if subjected to a Mediterranean high-intensity fire. Consequently, the effect of disturbance on resprouting requires standardization (e.g. by disturbance severity) in order to successfully compile a global resprouting database.

An additional layer of complexity is that resprouting, as a functional trait, is a morphologically and anatomically diverse trait. Plants may resprout from buds located in a variety of organs such as stems, roots, root crown, rhizomes, lignotubers or bulbs (Clarke *et al.*, 2013) and these may be related to a variety of evolutionary pressures. Given that resprouting is an ancestral trait in plants (Pausas & Keeley, 2014), it is also likely that the adaptive importance of resprouting has changed over evolutionary time. For instance, resprouting from a lignotuber is a trait tightly linked to fire-prone ecosystems and likely to evolve as a response to fire (Keeley *et al.*, 2011); however, resprouting from rhizomes, despite conferring fitness benefits to plants living in fire-prone ecosystems, is also common in many plants from nonfire-prone ecosystems, and thus could be a response to a range of disturbance pressures. In addition, disentangling disturbances is not always easy; for instance, the contention that resprouting of Hawaiian trees reflects an adaptation to drought because it increases along a gradient of increasing aridity (e.g. Busby *et al.*, 2010) is confounded by the fact that fires in the Hawaiian Islands likewise increase along the same gradient during ENSO events (Chu *et al.*, 2002). Disaggregating resprouting in the context of multiple types of resprouting, and disentangling the proportion of trait variance that is explained by each selective pressure (disturbance) is not an easy task, but the compilation of global databases together with time-calibrated phylogenies may provide a fruitful pathway.

In conclusion, there are a number of issues and cautions that need to be considered before using resprouting ability to predict vegetation responses across disturbance types and biomes. There are marked differences in resprouting, depending on the disturbance type, and fire is often the most severe disturbance. The relationship between postfire resprouting and drought resistance is well established for the Mediterranean biome (Box 2; Fig. 1), although more work is needed in Mediterranean ecosystems of the Southern Hemisphere. Preliminary results in other biomes are not yet conclusive (Fig. 1; Notes S2), and classifying the resprouting ability as binary in those biomes becomes more complex (Fig. 6). There is a lack of physiological studies on resprouting outside the Mediterranean biome that unambiguously use this trait as a surrogate for drought response and mortality at the global scale. Modelling exercises need to consider the different responses of the species depending on the drought regime (specifically, duration and intensity; Box 2); they also need to consider that correlations between resprouting and other disturbance response traits vary with biome and continent, and thus the success of a species in response to a disturbance most likely results from a related set of traits. Studies of longer term droughts aimed at different resprouting types are generally lacking, but recent protracted droughts in California are facilitating ongoing natural experiments.

Acknowledgements

References

Ackerly DD. 2004. Functional strategies of chaparral shubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* 74: 25–44.

Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.

Bowman DMJS, MacDermott HJ, Nichols SC, Murphy BP. 2014. A grass–fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and Evolution* 4: 4185–4194.

Brodribb TJ, McAdam SAM, Jordan GJ, Martins SCV. 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences, USA* 111: 14 489–14 493.

Burrows GE. 2002. Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae) – implications for fire resistance and recovery. *New Phytologist* 153: 111–131.

Busby PE, Vitousek P, Dirzo R. 2010. Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. *Biotropica* 42: 80–86.

Chu P-S, Yan W, Fujioka F. 2002. Fire-climate relationships and long-lead seasonal wildfire prediction for Hawaii. *International Journal of Wildland Fire* 11: 25–31.

Clarke PJ, Knox JE. 2002. Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Australian Journal of Botany* 50: 53–62.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.

Dantas VL, Batalha MA, Pausas JG. 2013. Fire drives functional thresholds on the savanna–forest transition. *Ecology* 94: 2454–2463.

Dantas VL, Pausas JG. 2013. The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* 101: 1265–1272.

Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker MC, Adams GC. 2002. Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *American Journal of Botany* 89: 820–828.

Fernandes PM, Vega JA, Jimenez E, Rigolot E. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256: 246–255.

Gill AM. 1981. Adaptive response of Australian vascular plant species to fires. In: Groves RH, Noble IR, eds. *Fire and the Australian biota*. Canberra, ACT, Australia: Australian Academy of Sciences, 243–271.

Hanson CT, North MP. 2006. Post-fire epicormic branching in Sierra Nevada *Abies concolor* (white fir). *International Journal of Wildland Fire* 15: 31–35.

Hernández EI, Pausas JG, Vilagrosa A. 2011. Leaf physiological traits in relation to resprouter ability in the Mediterranean Basin. *Plant Ecology* 212: 1959–1966.

Hoffmann WA, Marchin RM, Abit P, Lau OL. 2011. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology* 17: 2731–2742.

Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007. Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* 77: 99–115.

Kaneakua IN. 2011. *Comparison between stem hydraulic properties and mechanical strength of pre-fire adults to post-fire resprouts of the chaparral shrub* Heteromeles arbutifolia. Unpublished thesis. Malibu, CA, USA: Pepperdine University.

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012. *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge, UK: Cambridge University Press.

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.

Kelley DI, Harrison SP, Prentice IC. 2014. Improved simulation of fire–vegetation interactions in the Land surface Processes and eXchanges dynamic global vegetation model (LPX-Mv1). *Geoscientific Model Development Discussions* 7: 931–1000.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.

Meentemeyer RK, Moody A. 2002. Distribution of plant life history types in California chaparral: the role of topographically-determined drought severity. *Journal of Vegetation Science* 13: 67–78.

Michaletz ST, Johnson EA, Tyree MT. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 254–263.

Moreira B, Tormo J, Pausas JG. 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. *Oikos* 121: 1577–1584.

Nguyen-Xuan T, Bergeron Y, Simard D, Fyles JW, Paré D. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research* 30: 1353–1364.

O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4: 710–714.

Paddock W, Davis SD, Pratt RB, Jacobsen A, Tobin MF, López-Portillo J, Ewers FW. 2013. Factors determining mortality of adult chaparral shrubs in an extreme drought year in California. *Aliso* 31: 49–57.

Pate JS, Froend RH, Bowen BJ, Hansen A, Kuo J. 1990. Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of SW Australia. *Annals of Botany* 65: 585–601.

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A *et al.* 2009. Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90: 1420.

Pausas JG. 1999. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *Journal of Vegetation Science* 10: 717–722.

Pausas JG. 2001. Resprouting vs seeding – a Mediterranean perspective. *Oikos* 94: 193–194.

Pausas JG. 2015a. Bark thickness and fire regime. *Functional Ecology* 29: 315–327.

Pausas JG. 2015b. Evolutionary fire ecology: lessons learned from pines. *Trends in Plant Science* 20: 318–324.

Pausas JG, Bradstock RA. 2007. Fire persistence traits of plants along a productivity and disturbance gradient in Mediterranean shrublands of SE Australia. *Global Ecology and Biogeography* 16: 330–340.

Pausas JG, Bradstock RA, Keith DA, Keeley JE. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085–1100.

Pausas JG, Carbó E, Caturla RN, Gil JM, Vallejo R. 1999. Post-fire regeneration patterns in the eastern Iberian Peninsula. *Acta Oecologica* 20: 499–508.

Pausas JG, Keeley JE. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65.

Pausas JG, Keeley JE, Verdú M. 2006. Inferring differential evolutionary processes of plant persistence traits in Northern Hemisphere Mediterranean fire-prone ecosystems. *Journal of Ecology* 94: 31–39.

Plaut JA, Yepez EA, Hill J, Pangle R, Sperry JS, Pockman WT, McDowell NG. 2012. Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell & Environment* **35**: 1601–1617.

Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007a. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* **174**: 787–798.

Pratt RB, Jacobsen AL, Golgotiu KA, Sperry JS, Ewers FW, Davis SD. 2007b. Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecological Monographs* **77**: 239–253.

Pratt RB, Jacobsen AL, Jacobs SM, Esler KJ. 2012. Xylem transport safety and efficiency differ among fynbos shrub life history types and between two sites differing in mean rainfall. *International Journal of Plant Sciences* **173**: 474–483.

Pratt RB, Jacobsen AL, Ramirez AR, Helms AM, Traugh CA, Tobin MF, Heffner MS, Davis SD. 2014. Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences. *Global Change Biology* **20**: 893–907.

Ramirez AR, Pratt RB, Jacobsen AL, Davis SD. 2012. Exotic deer diminish post-fire resilience of native shrub communities on Santa Catalina Island, southern California. *Plant Ecology* **213**: 1037–1047.

Rogers BM, Soja AJ, Goulden ML, Randerson JT. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* **8**: 228–234.

Saruwatari MW, Davis SD. 1989. Tissue water relations of three chaparral shrub species after wildfire. *Oecologia* **80**: 303–308.

Schwilk DW, Ackerly DD. 2005. Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothus* (Rhamnaceae). *American Journal of Botany* **92**: 404–410.

Shugart HH, Noble IR. 1981. A computer model of succession and fire response of the high-altitude Eucalyptus forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* **6**: 149–164.

Te Beest M, Mpandza NJ, Olff H. 2015. Fire and simulated herbivory have antagonistic effects on resistance of savanna grasslands to alien shrub invasion. *Journal of Vegetation Science* **26**: 114–122.

Thomas CM, Davis SD. 1989. Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* **80**: 309–320.

Vesk P, Westoby M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* **92**: 310–320.

Vesk PA, Warton DI, Westoby M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* **107**: 72–89.

Vilagrosa A, Hernández EI, Luis VC, Cochard H, Pausas JG. 2014. Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. *New Phytologist* **201**: 1277–1288.

Werner C, Correia O, Beyschlag W. 1999. Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. *Acta Oecologica* **20**: 15–23.

Zeppel MJB, Harrison SP, Adams HD, Kelley DI, Li G, Tissue DT, Dawson TE, Fensham R, Medlyn BE, Palmer A et al. 2015. Drought and resprouting plants. *New Phytologist* **206**: 583–589.

Supporting Information

Additional supporting information may be found in the online version of this article.

Notes S1 Reanalysis of the global P_{50} in relation to resprouting ability.

Notes S2 Statistical comparison of P_{50} values between resprouting life histories.

Notes S3 Functional differences between resprouting life histories.

Notes S4 References for Fig. 6.

Table S1 Global P_{50}-resprouting database

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