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Unearthing belowground bud banks in fire-prone ecosystems

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Summary

Despite long-time awareness of the importance of the location of buds in plant biology, research on belowground bud banks has been scant. Terms such as lignotuber, xylopodium and sobole, all referring to belowground bud-bearing structures, are used inconsistently in the literature. Because soil efficiently insulates meristems from the heat of fire, concealing buds below ground provides fitness benefits in fire-prone ecosystems. Thus, in these ecosystems, there is a remarkable diversity of bud-bearing structures. There are at least six locations where belowground buds are stored: roots, root crown, rhizomes, woody burls, fleshy swellings and belowground caudexes. These support many morphologically distinct organs. Given their history and function, these organs may be divided into three groups: those that originated in the early history of plants and that currently are widespread (bud-bearing roots and root crowns); those that also originated early and have spread mainly among ferns and monocots (nonwoody rhizomes and a wide range of fleshy underground swellings); and those that originated later in history and are strictly tied to fire-prone ecosystems (woody rhizomes, lignotubers and xylopodia). Recognizing the diversity of belowground bud banks is the starting point for understanding the many evolutionary pathways available for responding to severe recurrent disturbances.

Burying buds

Many plants are able to survive recurrent disturbance by resprouting. How plants resprout after disturbance depends on the number and location of the dormant buds and on the type of storage organ. These traits vary widely among plants, depending on the phylogenetic context of the species and disturbance regime in which it evolved (Klimešová & Klimeš, 2007; Clarke *et al.*, 2013; Fidelis *et al.*, 2014). For example, fire produces heat that can easily kill surface buds and poorly insulated meristems that are not affected by other disturbances; thus, fires tend to be a relatively severe and nonspecific disturbance (Pausas *et al.*, 2016). Consequently, in ecosystems where fires are frequent, plants must protect their buds from fire heat or perish. One way to protect them is by growing a thick insulating bark (Pausas, 2015, 2017). Another is to locate the buds below ground, as soil is an excellent heat insulator (Auld & Bradstock, 1996). In fire-prone ecosystems, there is a diversity of ways by which plants successfully conceal their buds below ground that enable them to survive and resprout vigorously after fire.

Despite a long-time appreciation of the importance and variability of the location of the bud bank in the ability of plants to recover from seasonal stresses or fitful disturbances (Lindman, 1900; Jepson, 1916; Raunkiaer, 1934; Tansley, 1946), research on belowground bud banks has been scant. Belowground organs may store buds, carbon, water and nutrients, and thus have a key function in food webs and ecosystem processes. Recent research highlights the importance of belowground traits in surviving disturbance (Bardgett *et al.*, 2014; Laliberté, 2017) but it does not explicitly recognize the diversity of belowground structures and their abundance in many ecosystems. One problem retarding progress in the field is a lack of consensus on the correct terminology for different bud-storage structures. For instance, terms such as lignotuber, xylopodium, caudexes and soboles are used inconsistently in the literature and are not even mentioned in current terminology resources for plant biology (Garnier *et al.*, 2017). Other terms such as burls, underground trees and rootstocks are too generally applied to convey exactly what structures are involved. This limits the potential for sharing and integrating data in broad-scale analyses. It also limits our understanding of the evolution of these structures in different ecosystems and lineages as they are clearly nonhomologous (i.e. having different evolutionary origins).

Here we review the different locations of the belowground bud bank (BBB) in plants of fire-prone ecosystems with the aim to demonstrate their diversity and to clarify their terminology, origin and function. Many of these BBB organs are shared with nonfire-prone ecosystems and may have evolved initially as responses to other disturbances, or also perform other functions, such as lateral spread and colonization, yet they have adaptive value in recovering from fire (Keeley *et al.*, 2011) as they protect buds from fire heat. Fire-prone ecosystems also harbour unique belowground structures, and thus are the most appropriate ecosystems for exploring belowground organs. Understanding the array of BBBs, and their origin and function, should provide insights into the diversity of adaptive-response options in disturbance-prone ecosystems, and also promote more productive, coordinated research on this topic.

A plethora of belowground bud banks

We recognize six plant locations that support belowground buds in fire-prone ecosystems: roots, root crown, rhizomes, basal burls, fleshy swellings and belowground caudexes. These six major morphological types cover many distinct organs with different origins and characteristics and most can be further subdivided on finer grounds as well (Table 1). Below we provide a detailed description of these structures (also see Supporting Information Notes S2 and S3), supported by a key to their identification (Box 1; Fig. 1), an initial world-wide database for BBBs (> 2000 species; Notes S1; Table S1), and a list of the types of carbon reserves that they store (Table S2). Then, in the next section we provide an evolutionary framework based on published phylogenies (also see Table S3).

Roots

Many plants have lateral roots growing near the soil surface with adventitious buds that produce vertical stems (root suckers or sprouts). Root suckering has been described in many angiosperm families (mainly dicots), in a few ferns and in some conifers (Klimešová & Klimeš, 2003), in a wide range of ecosystems (Table S1). Suckers can develop from 'additional' buds (with an endogenous origin and connected to the primary xylem by a bud trace; Bosela & Ewers, 1997; Jones & Raynal, 1986) and/or

Table 1 Main features of the belowground bud bank (BBB) in plants from fire-prone ecosystems

Bud location	Origin	Bud bank size	Bud protection	Growth form	Ecosystem type	Seasonal stems	Colonization ability
Root	Root	Mod-high	Mod-high	Most types	Any	No	Moderate (clonal)
Root crown	Stem	Moderate	Low-mod	Most types	Any	No	No
Basal burls (woody)							
Lignotuber	Stem (cot. node)	High	Mod-high	Shrub, mallee	Medit., warm temperate, savanna	No	No*
Xylopodium	Hypocotyl (+ root + stem)	Low-mod	Moderate	Shrub, suffrutex, forb	Savanna	(Yes)	No*
Rhizomes							
Non-woody rhizome	Stem	Moderate	Mod-high	Herb	Any	Yes	High (clonal)
Woody rhizome	Stem	Moderate	Mod-high	Shrubs, suffrutex	Savanna, medit., warm temperate	(Yes)	Mod-high (clonal)
Rhizophore	Stem	Low-mod	Mod-high	Herb	Savanna	(Yes)	Low/variable (clonal)
Fleshy swellings							
Bulb	Stem (+ leaf)	Low	High	Herb (geophyte)	Any	Yes	Low
Corm	Stem	Low	High	Herb (geophyte)	Any	Yes	Low
Root tuber	Root	Low	Mod-high	Herb (geophyte)	Any	Yes	No-low
Stem tuber	Stem	Low-mod	Low-high	Herb (geophyte)	Any	Yes	No-mod (clonal)
Belowground caudex	Stem	Low	Mod-high	Palm-like rosette	Medit., warm temperate, grassland	No	No

For each BBB, the characteristics considered are: **origin** of the bud-supporting tissues; **bud bank size** (for the genet: low: < 10 buds, moderate: 10–100, high: > 100; this is correlated with the number of resprouting stems, an easier parameter to observe: low: 1, moderate: 2–20, high: > 20); **bud protection** (low: most buds above ground or at the soil surface, moderate: most buds < 1 cm below ground, high: most buds > 1 cm below ground; bark thickness, bud scales and leaf bases may also contribute to protection); **growth form** (herb: perennial forb or graminoid, suffrutex: subshrub with short-lived shoots from a woody base); **seasonal** aboveground biomass (Yes: annual stems, No: perennial stems, (Yes): sometimes annual); **colonization ability** (ability to increase the spatial extent relative to crown cover: low: not beyond the crown, moderate: not more than twice the crown, high: more than twice the crown). Clonal here refers to genets consisting of ramets that do not physically separate from the parent. Examples of species with the different BBB types are given in Supporting Information Table S1. Mod, moderate; cot., cotyledonary; Medit, Mediterranean ecosystems; Savanna includes tropical and subtropical grasslands.
*Unless combined with woody rhizomes or stolons.

Box 1 Key to identify major belowground bud bank structures for resprouting after disturbance

Emphasis is given to morphological traits to facilitate identification rather than anatomical or ontogenetic details that are confined to the text. For completeness, the key also includes a related structure that is not fully below ground (i.e. stolons). Letters in parentheses after the belowground bud bank (BBB) name refer to illustrations in Fig. 1; also see Fig. 2.

1. Woody bud support
   1. Swollen bud bank
      1. Produces a few stems apically, often joined to tuberous roots. Buds are restricted to the upper part; xylem is not contorted and often lacks reserves. Typically of small shrubs – **xylopodium** (Xy)
      2. Produces many stems scattered or around the edge with associated roots woody. Buds are located over the entire structure; xylem is contorted and stores starch. Typically of large shrubs – **lignotuber** (Li)
   2. Non-swollen bud bank, although sometimes horizontal knots present (among rhizomes)
      1. Produces a few vertical (aerial) stems (coppices) at or above the root collar – **root crown** (RC)
      2. Produces a few stems that arise horizontally or vertically, unrelated to root collar
         1. Horizontal stem (with nodes) attached to a burl, root crown or other horizontal stems that produces vertical suckers – **woody rhizome** (WR)
         2. Lateral root (no nodes) attached to base of burl, root crown or to other roots that produces vertical suckers – **bud-bearing root** (Ro)
2. Non-woody (or soft-wooded) bud support
   1. Swollen bud bank (swelling localized compared with aerial stems)
      1. Single storage structure, vertically oriented
         1. Reaches ± ground level and produces one or a few stems, usually globose but sometimes elongated; sometimes large and soft-wooded – **taproot tuber** (TT)
         2. Below ground level and produces a single stem or leafy rosette
            1. Globose, with fleshy scale leaves around stem core – **bulb** (Bu)
            2. Flattened, with dry scale leaves around swollen stem core – **corm** (Co)
      2. Multiple storage structures underground, vertically to horizontally oriented
         1. Stem origin; nodes present from which several vertical stems, culms or roots may arise
            1. No adventitious roots (until separated from mother plant); localized swelling – **stem tuber** (ST)
            2. Adventitious roots produced by underground stems
               1. Underground stems only – **nonwoody (fleshy) rhizome** (FR)
               2. Downward-facing stem that supports vertical (aerial) stems; sometimes linked to stem tubers – **rhizophore** (Rh)
         2. Root origin; nodes absent so can only produce 1–2 vertical stems from base; usually multiple units – (adventitious) **root tuber** (RT)
   2. Non-swollen, stems usually uniform
      1. Multiple thin stems, horizontal, semi-vertical or procumbent; adventitious roots
         1. Stem system below ground, with **m**onopodial or **s**ympodial branches terminating in culms – **nonwoody (fibrous) rhizome** (NRm, NRs)
         2. Aerial procumbent stems with belowground knots, leaf rosettes and adventitious roots – **stolon/layer** (St)
      2. Solitary thick stem, vertical, with the apex at ca. ground level; secondary or adventitious roots, may eventually rise above ground – **belowground caudex** (Ca)

'reparative' buds (formed in response to physical injury, dieback or senescence of the root or crown and identified by the absence of a bud trace; Bosela & Ewers, 1997; Hayashi *et al.*, 2001; Hayashi & Appezzato-da-Glória, 2009).

Root suckering is strongly associated with lateral spreading, where the ramets remain connected to the parent plant (Jones & Raynal, 1986; Wiehle *et al.*, 2009). Root suckering is an effective resprouting mechanism in response to disturbances, including fire (Lamont, 1988; Hoffmann & Solbrig, 2003; Rodrigues *et al.*, 2004), as the lateral buds are typically well insulated from fires by the soil (Kennard *et al.*, 2002; Hoffmann & Solbrig, 2003). Buds can be quite abundant; for instance, 50–90 root buds were recorded on 3-yr-old saplings of *Populus tremuloides* (Landhäusser *et al.*, 2006). For adult plants, up to 30 buds (*Fagus grandifolia*) and > 200 buds (*Populus tremuloides*) per 10–25 cm root-segment have been counted (Schier & Zasada, 1973; Jones & Raynal, 1986). Species that produce root suckers also often resprout from other bud-bearing structures such as root crowns or lignotubers (Table S1). A prominent example of a root suckering plant is 'Pando', a genet of *P. tremuloides* in central Utah at an estimated age of 80 000 yr, with an intricate root system that covers 80 ha; it is probably the largest, heaviest and oldest living organism known (Mitton & Grant, 1996). In most species, sucker growth is supported by starch stored in the roots, although some species store fructans (Table S2).

Root crowns

Many woody plants resprout from buds located at the root–shoot transition zone, called the root crown or root collar. Resprouting from the root crown is the most widespread postdisturbance regeneration mechanism (Table S1). It is the most common bud bank among trees (Del Tredici, 2001), including some conifers, and has also been described in shrubs and perennial herbs (Table S1; Fig. 2a). Root-crown resprouting does not facilitate lateral spreading and colonization (Table 1), and therefore it is functionally restricted to *in situ* persistence after disturbances. In some species, root crowns may become

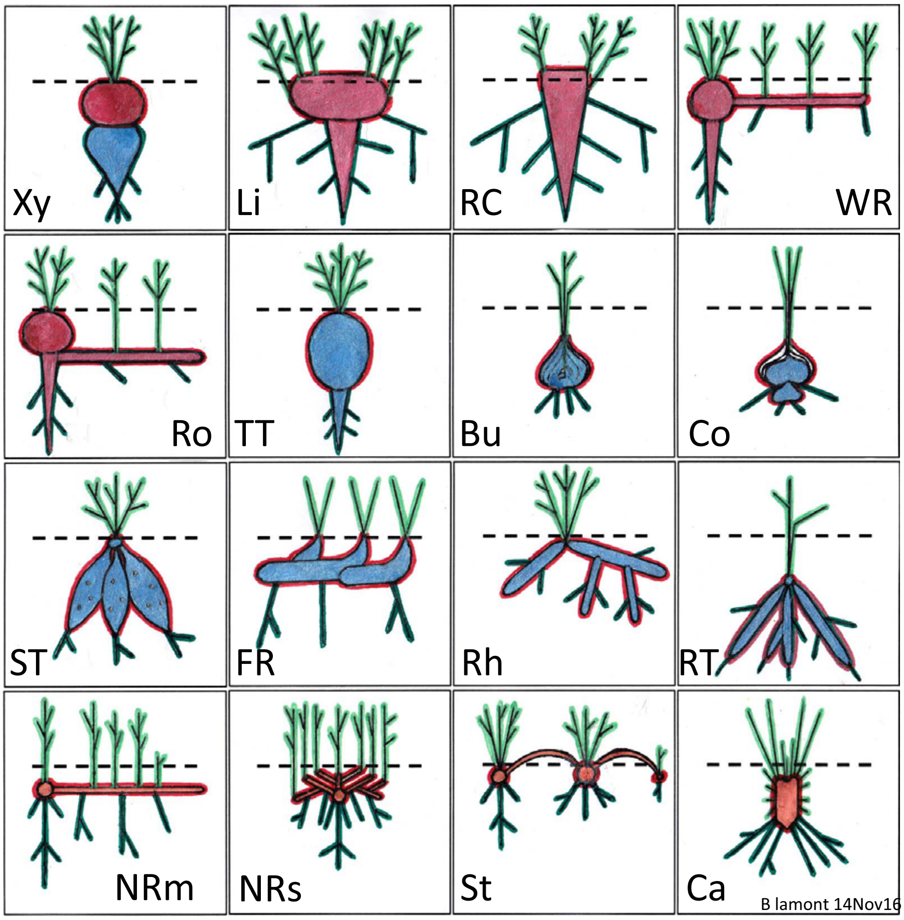

Fig. 1 Stylized diagrams of 16 belowground bud bank (BBB) structures that enable plants to resprout following fire (highlighted in red), as outlined in Box 1. Also see Fig. 2 for some illustrative examples. Broken horizontal line indicates position of soil surface. Pink, structures characterized by woody tissues; blue, fleshy tissues; orange, neither woody nor fleshy (usually highly sclerified primary tissues, fibrous or 'wiry'). Shoots highlighted in apple green: stems with leaves, branched; leaves only, unbranched. Roots highlighted in olive green: triangular-shaped roots indicate a primary system, while those arising directly from the bud-storing structures are adventitious. From top left to bottom right: Xy, xylopodium (in red) joined to tuberous root (in blue); Li, lignotuber; RC, root crown; WR, woody rhizome, arising (here) from a burl; Ro, bud-bearing lateral root arising (here) from a burl (note that the root is not necessarily woody); TT, taproot tuber; Bu, bulb; Co, corm, with previous year's corm still present; ST, stem tuber; FR, nonwoody fleshy rhizome; Rh, rhizophore (note buds are only supported by the oldest rhizophores); RT, adventitious root tuber; NRm, nonwoody fibrous rhizome with a monopodial arrangement leading to expansive clone; NRs, nonwoody fibrous rhizome with sympodial arrangement leading to a caespitose habit; St, stolons that produce new ramets following fire (note that it is not a BBB); belowground caudex (Ca). Drawings by B. B. Lamont.

dense and thick after many recurrent resprouting events to resemble a basal burl (*thickened root crown* in Table S1; Notes S1; also see *Basal burls* below).

The bud bank of the root crown originates from dormant buds located at the cotyledonary region that produce clusters of a few buds (Kauppi *et al.*, 1987; Pascual *et al.*, 2002). As the plant develops, the bud bank increases by accumulating axillary buds on basal branches growing from these initial buds (Kauppi *et al.*, 1987). For instance, the bud bank increases from 42 buds in 4-yr-old pine saplings to several hundred in mature plants (e.g. *Pinus rigida*; Little & Somes, 1956). At the seedling stage, root-crown resprouters with hypogeal germination show higher fire survival than those species with epigeal germination, because their cotyledonary nodes remain below ground (Pascual *et al.*, 2002; Brose & Van Lear, 2004; Fisher, 2008). Some species are able to move the bud bank closer to the soil surface or even below ground by the root or hypocotyl contracting or by bending of the seedling axis (Stevenson, 1980; Fisher, 2008); this may increase postfire survival of juveniles (Lilly *et al.*, 2012). Eventual weak resprouting from the root crown after frequent severe fires can be explained by the relatively small bud bank size and its limited insulation by the soil. The storage reserve that fuels root–crown resprouting is typically starch in the roots, although fructans are present in species physiologically active at low temperatures, particularly among herbs (Table S2).

Basal burls

Plants that store axillary buds in the root crown are common in fire-prone ecosystems. However, the number of buds in the root crown may be too limited for long-lived plants if fire recurrence is high. In such cases, storing a large number of buds at or below ground may be beneficial. Thus, many woody plants have acquired basal burls (swollen woody structures) in which there is a disproportionately

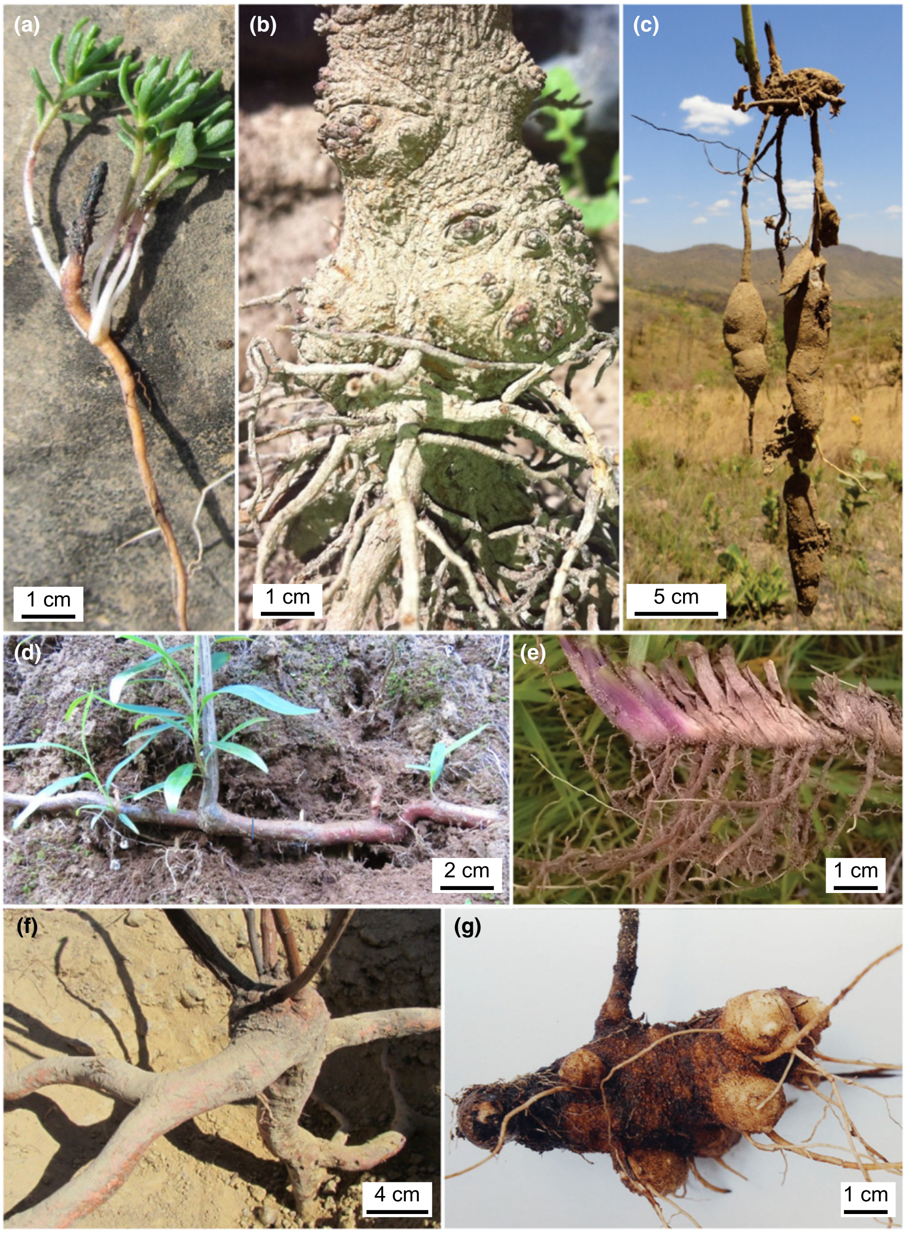

Fig. 2 Examples of selected belowground bud banks (BBBs). (a) Postfire root crown resprouting (*Coris monspeliensis*, Mediterranean Basin). (b) Lignotuber of a juvenile plant (*Cryptocaria alba*, central Chile). (c) Xylopodium with tuberous roots (*Aldama grandiflora*, Brazilian savanna). (d) Bud-bearing root with suckers (*Embothrium coccineum*, Chilean temperate rainforest). (e) Nonwoody rhizome of a grass species (Brazilian savanna). (f) Woody rhizome connected to a knot (*Mimosa leiocephala*, Brazilian savanna). (g) Rhizophore of *Chrysolaena* (*Vernonia*) *platensis*, Brazilian savanna. Photos by J. G. Pausas (a), S. Paula (b, d), B. Appezzato-da-Glória (c, e, g) and T. Zupo (f).

high concentration of renewal buds. Two types of basal burls are recognized: lignotubers and xylopodia; they essentially only occur in fire-prone ecosystems. The term 'burl' has a more general meaning; it is often used for woody swellings induced by pathogens or injury, typically produced above ground, and not necessarily linked to a bud bank (James, 1984). However, in the ecology literature, the use of 'basal burl' is now well established for swollen woody structures at the base or below ground with an accumulation of buds used for resprouting after disturbance (Keeley *et al.*, 2012). Some early researchers referred to it as a root-crown (Jepson, 1916) or 'rootstock' (which includes both lignotubers and thickened root crowns; Bowen & Pate, 1993; Rebelo, 2001). Typically, plants start to accumulate buds and generate the basal burl from the seedling stage (i.e. basal burls are ontogenetically fixed; Paula *et al.*, 2016). Among some root-crown resprouters, multiple resprouting events or particular (stressful) conditions may result in thickening of the root-crown to resemble a basal burl (termed '*basal burls of secondary origin*' in Rizzini & Heringer, 1961; Keeley *et al.*, 2012; and '*thickened root crown*' in the BBB database, Table S1; Notes S1); in many cases, only by looking at undisturbed young plants is it possible to distinguish between basal burls and thickened root-crowns.

Lignotuber These swollen woody structures are located at the transition between the stem base and root crown of woody shrubs, mallees and small trees, and are formed from stem tissues. Lignotubers were initially described in *Eucalyptus* (Kerr, 1925) but are now known in many phylogenetically distant families, including gymnosperms and angiosperms (Table S1). The bud bank initially develops at the cotyledonary axils, with accessory buds around the primary bud proliferating to form bud clusters on swellings that gradually coalesce to form a massive bud bank (Del

Tredici, 1998; Mibus & Sedgley, 2000; Paula *et al.*, 2016). In some species, adventitious buds also develop exogenously at the base of the cotyledons (Molinas & Verdaguer, 1993; Mibus & Sedgley, 2000) or endogenously within the lignotuber tissues (Chattaway, 1958; Graham *et al.*, 1998). In some large species, the lignotuber might be suppressed or inconspicuous when the juvenile develops in the absence of disturbance, and adults resprout epicormically; but if severely burnt, the lignotuber may become functional (Kerr, 1925; Abbott & Loneragan, 1984; Burrows, 2013). Bud-bearing burls on other parts of the plant have sometimes been termed lignotubers (e.g. layered branches in *Sequoia sempervirens*, Del Tredici, 1998; woody rhizomes of *Podocarpus* spp., Ladd & Enright, 2011); we prefer the term burls for these structures and limit the term lignotuber to those basal structures originating in the cotyledonary region.

Lignotubers are typically 15–50 cm wide (in adults) but may reach *c.* 100 cm (*Banksia attenuata*; Lamont *et al.*, 2011) or more in large trees. They are partially or totally buried (Clarke *et al.*, 2013; Paula *et al.*, 2016), and contain numerous dormant buds over the entire lignotuber surface; therefore, buds may be located deep in the soil (up to 20 cm; Beadle, 1940). The number of buds in the lignotuber ranges from several hundred (e.g. *Erica* species; Riba, 1998; S. Paula & J. G. Pausas, unpublished) to several thousand (e.g. *Eucalyptus* species; Wildy & Pate, 2002). The large size of the bud bank and its high degree of protection make lignotubers especially adaptive where high-intensity fires are frequent, and thus they are common in Mediterranean fire-prone ecosystems (Keeley *et al.*, 2012; Paula *et al.*, 2016), although they also occur in fire-prone temperate forests and tropical savannas in Australia (Table S1). In addition, it is known that lignotuber occurrence is a phylogenetically labile trait (Bond & Midgley, 2003; He *et al.*, 2011); even intraspecific variability has been reported and linked to fire-proneness (Lamont & Markey, 1995; Schwilk & Ackerly, 2005; Verdaguer & Ojeda, 2005). Overall, these data indicate that lignotubers should only be selected for when they are the key to postdisturbance survival, as in fire-prone ecosystems. Lignotubers store starch, in addition to buds (Table S2); however, most of the starch sustaining resprouting is stored in the root system (Smith *et al.*, 2018).

Xylopodium (plural: xylopodia) These are basal woody burls that originate from the hypocotyl and sometimes the upper part of the main root; as development proceeds, the bases of the branches may lignify and contribute to the structure of the xylopodium (Appezzato-da-Glória & Cury, 2011). Xylopodia are typically smaller than lignotubers (e.g. 2–5 cm wide). The buds are axillary or adventitious originating from the cambium of the xylopodium; they are usually located on the upper part of the xylopodium, i.e. close to the soil surface (Lopes-Mattos *et al.*, 2013; da Silva *et al.*, 2014). They may be supported by a taproot tuber (Fig. 1) or by a few swollen lateral or adventitious roots (tuberous roots; Fig. 2c). Owing to the small size of the xylopodium and the restricted location of the buds on this organ, the number of buds is fewer (*c.* 150 recorded in *Eupatorium ligulaefolium*; Fidelis *et al.*, 2010), and their xylem is not as contorted as in lignotubers (Appezzato-da-Glória *et al.*, 2008; Lopes-Mattos *et al.*, 2013; da Silva *et al.*, 2014). Some species store fructans or starch in the xylopodium (Table S2); however, in most cases the xylopodium lacks reserves and these are instead associated with the tuberous roots where carbohydrates are stored (Table S2; Fig. 2c).

Xylopodia were recognized long ago in Brazilian grasslands (Warming, 1893; Lindman, 1900) and are common in South America, especially among Fabaceae and Asteraceae (Table S1). There is a tendency to call all basal burls observed on that continent as xylopodia; however, anatomical studies show that some burls in the Brazilian savannas are better described as lignotubers (e.g. *Styrax camporum* Appezzato-da-Glória, 2015). While Maurin *et al.* (2014) placed the geoxyles that they studied in south–central Africa under the general umbrella of xylopodia, our literature search indicated that they are more likely to be lignotubers, woody rhizomes and/or taproot tubers (Lamont *et al.*, 2017). In general terms, lignotubers are associated with larger woody shrubs and mallees occurring under high-intensity fire regimes, whereas xylopodia tend to occur among smaller shrubs and forbs, often with seasonal stems, under frequent low-intensity fires in grasslands and savannas; however, without a detailed inspection it is often difficult to ascertain the actual type of basal burl.

Rhizomes

Many plants have subterranean stems that grow horizontally (or semivertically) from a parent plant without a defined limit. Each 'segment' is typically called a 'rhizome' and may support aerial shoots and adventitious roots. Some authors (Appezzato-da-Glória, 2015) have proposed that the term rhizome be restricted to belowground stems with no secondary growth (Holm, 1929), and instead use the term 'sobole' for those with secondary growth. However, most of the literature uses 'rhizome' in a general way for perennial, belowground horizontal stems independent of their woodiness (Bell, 2008) that we accept here. In addition, 'sobole' has been used not only for woody rhizomes (Rizzini & Heringer, 1966; Alonso & Machado, 2007) but also for slender and nonwoody stems among monocots (Bell, 2008; Saxena, 2010). We propose that the term sobole be restricted to (and consider it synonymous with) woody rhizomes, in contrast to nonwoody rhizomes (that may be fleshy or dry and wiry). Rhizomes may arise at depth (hypogeogenous) or be initiated at the soil surface and then pulled beneath the soil by contractile roots (epigeogenous) (Klimešová & Klimeš, 2007); the latter are more characteristic of nonfire-prone ecosystems. Rhizophores that grow downwards and give rise to roots are also included under the umbrella of rhizomes (*sensu lato*). The main functions of rhizomes are lateral spreading, vegetative reproduction and increased ability to survive shoot loss. Many rhizomatous species are highly successful in fire-prone ecosystems, ranging from fleshy herbs to evergreen trees.

Nonwoody rhizomes (rhizomes *sensu stricto*) These are herbaceous stems that spread laterally below ground; they lack secondary growth and produce aboveground leaves or shoots. These rhizomes were first described in ferns, and then applied to many monocots and some basal herbaceous eudicots (Holm, 1929; Raunkiaer, 1934; Table S1); currently, the term is applied to nonwoody belowground stems in any plant. Nonwoody rhizomes show a unipolar stem branching system consisting of one axis stem with buds (covered by cataphylls) generating aerial leaves or shoots and adventitious roots. Typically these rhizomes originate from the apex of the seedling epicotyl (plumule), and subsequent rhizomes arise from axillary buds on the parent rhizome. Some nonwoody rhizomes are fleshy while others are dry and stiff (Box 1); typical examples of the former are *Moraea* (Iridaceae), with fire-simulated flowering (Lamont & Downes, 2011), and of the latter are Poales (graminoids) that are strongly linked to disturbances such as surface fire and grazing. The reserve component stored in the rhizome is quite variable among taxa (Table S2).

Rhizophore This term originally described the leafless axillary branch arising from stolons of the lycopod *Selaginella* that produces roots from its apex on entering the soil (Lu & Jernstedt, 1996); it is also used for the leafless stems with positive geotropism in the mangrove *Rhizophora mangle* (Menezes, 2006). As now used for species in fire-prone environments, it refers to nonwoody rhizomes, slightly fleshy and leafless, that originate from a bipolar branching system, that is, with aerial shoots and subterranean shoots growing downwards that produce roots; they lack a primary root system (Menezes, 2007). A classic example of a rhizophore system is *Chrysolaena obovata* (= *Vernonia herbacea*, Asteraceae) in the Brazilian savannas (Table S1). Rhizophores often become locally swollen and remarkably complex as in *Dioscorea alata* (Table S1); these tuberculized rhizophores are basically stem tubers attached to rhizophores. The length of rhizophores is highly variable, and they can develop from axillary cotyledonary buds (Rocha & De Menezes, 1997; Hayashi & Appezzato-da-Glória, 2005), belowground buds of the cauline axis (Martins *et al.*, 2011) or from a thickened hypocotyl (Menezes, 2007). Rhizophores occur in monocots and dicots in tropical savannas (Table S1), although more research is needed to properly understand the structure of this organ as well as its geographical and taxonomic distribution. Buds supported by rhizophores are often deeply buried and are thus well protected from fire (Overbeck & Pfadenhauer, 2007). Sometimes the rhizophore also permits vegetative reproduction when the tuberculized part splits from the parent plant (Rocha & De Menezes, 1997). Carbon reserves are stored in the rhizophore and/or the roots (Table S2).

Woody rhizome (= sobole) These are long woody stems that grow horizontally under the soil surface and produce new aerial stems (ramets) from buds located along the rhizome or from the knots connecting them (Fig. 2f). Woody rhizomes were first described in Brazilian savannas (Warming, 1893), and later recorded among eucalypts in Australia's fire-prone ecosystems, and among oaks in temperate and Mediterranean ecosystems (Table S1). They originate from the cotyledonary axil in hypogeous species and at the base of an enlarged hypocotyl in epigeous ones (Alonso & Machado, 2007). Subsequent woody rhizomes arise from axillary buds on the parent rhizome or the connecting knot. They are typically located 5–50 cm below ground and bear many dormant buds, most of which are concentrated in the connecting knots (Tiedemann *et al.*, 1987). Plants with woody rhizomes resprout profusely after fires, and colonize space vegetatively (Table 1); they are characteristic of

Box 2 Geoxyles, underground trees and woody clumps

Burtt Davy (1922) noted that *suffrutices* are plants with annual stems from a perennial woody crown or underground system. Lindman (1914), cited in Du Rietz (1931), suggested the term *geoxyles* for a plant growth form with large woody underground structures and with an aboveground biomass of only a few years' duration. White (1977) later defined *geoxylic suffrutice* as plants with deciduous or short-lived shoots with a massive underground structure. These early authors also noted that, in many cases, geoxylic suffrutices are congeneric to trees, and thus White used the term 'underground forest' in the title of his paper. Since then, other researchers have used the term *underground trees* to refer to geoxylic suffrutices (e.g. Maurin *et al.*, 2014). These two terms have been used mainly in reference to savanna ecosystems (White, 1977; Pennington & Hughes, 2014) and it is in the tropics where they are most diverse. A notable example is *Jacaranda decurrens*, a short neotropical plant that may spread more than 20 m due to woody rhizomes that elongates after each fire and can live for over 3000 yr (Alves *et al.*, 2013).

Here we propose to generalize the term geoxyle to any plant that resprouts after disturbance from buds located on prominent woody underground structures (woody rhizomes, xylopodia or lignotubers; Lamont *et al.*, 2017), independent of their phylogenetic context; almost all geoxyles occur in fire-prone ecosystems and resprout vigorously after fire, and in fact, fire is the main reason the shoots are short-lived. Thus, we propose that there are not just suffrutescent geoxyles, but also chamaephyte geoxyles and phanerophyte geoxyles. For instance, there are some shrubby oaks in fire-prone ecosystems of the Northern Hemisphere (e.g. *Quercus gambelli*, *Q. lusitanica*, *Q. coccifera*) that can be classified as (nano-)phanerophytic geoxyles as they have a network of woody rhizomes that can form broad carpets of a single genet. Plants that arise from a single lignotuber (e.g. Paula *et al.*, 2016) or xylopodium are also placed under geoxyles, including mallee trees in Australia (mega-phanerophytic geoxyles). Our concept of geoxyles includes many of the species that form *woody clumps* as described by Lacey & Johnston (1990). While most geoxyles have woody rhizomes or basal burls, there are some species producing large tree-like clumps thanks to a massive root system that generates many root suckers that form tall erect stems after fire (some *Populus* species form clonal trees of several hectares; Mitton & Grant, 1996); these may also be treated as geoxyles.

Consequently, there are three general categories of underground resprouters: (**1) geoxyles**: woody resprouters with large woody underground parts (xylopodia, lignotubers, woody rhizomes) that bear a few to many concealed buds – they often produce perennial stems but there are also many with ephemeral shoots (suffrutescent geoxyles); (**2) geophytes**: resprouters with nonwoody underground parts that bear a few concealed buds (bulbs, corms, nonwoody rhizomes, stem/root tubers, belowground caudex) that usually possess annual stems; and (**3)** other **basal resprouters** without any specialized BBB structure – woody or nonwoody plants that resprout from unmodified roots or from the root crown. A fourth group of resprouters not considered here are the aerial resprouters (**aeroxyles**), whose main stems survive fire and recover from aboveground buds; this group includes epicormic resprouters (Pausas & Keeley, 2017) and palm-like plants with apical resprouting.

many geoxylic species (Box 2). For instance, *Quercus coccifera* and *Q. lusitanica* in the Mediterranean Basin are highly resilient to recurrent fires (Malanson & Trabaud, 1988; Ojeda *et al.*, 1996); they may form carpets of stems with an intricate rhizome system, where it is impossible to distinguish genetic individuals. *Banksia candolleana*, with new rhizomes that extend radially 5–10 cm after each fire, is estimated to reach an age exceeding 1000 yr (Merwin *et al.*, 2012). The largest known genet of *Jacaranda decurrens* has a circular crown 22 m in diameter (although only 50 cm tall) and occupies 380 m^2 thanks to its woody rhizomes, and has an estimated age of 3800 yr (Alves *et al.*, 2013).

Fleshy underground swellings

Many perennial herbaceous plants have swollen underground structures with one or a few buds. They are more related to carbohydrate, water and mineral-nutrient storage for assisting seasonal dynamics than to the accumulation of buds. However, the buds are well protected by the soil due to their geophytic habit and are especially adaptive in fire-prone ecosystems with highly seasonal climates (Table 1). Depending on the origin and morphology of these structures, they have different names, including bulb, corms, stem tubers, adventitious root tubers and taproot tubers (all of which are described in Notes S2; see also Box 1). The type of stored carbohydrate compound is variable (Table S2). Plants with these fleshy swellings are common in fire-prone ecosystems, and they resprout quickly after fire, sometimes with spectacular postfire flowering (Lamont & Downes, 2011; He *et al.*, 2016a). Mediterranean ecosystems are rich in these species (Pate & Dixon, 1982; Parsons & Hopper, 2003), especially the Cape region (Procheş *et al.*, 2006), where bulbs and tubers were consumed by early hominids (Dominy *et al.*, 2008) and they are now widely used in horticulture. There are many geophytic species that only flower or germinate after fire (Le Maitre & Brown, 1992; Keeley, 1993), and this pyrogenic flowering has been used to trace back the origin of fire-prone ecosystems in the Cape region (Bytebier *et al.*, 2011; He *et al.*, 2016a). Taproot tubers are more common in savannas and semiarid ecosystems than in Mediterranean regions. Some bulbous, cormous and tuberous plants have contractile secondary roots that pull down the perennating organ (Pütz, 1998), thus increasing insulation by the soil.

Belowground caudex

Some species with a single stem surrounded by persistent dead leaves or leaf bases, as in grasstrees (*Xanthorrhoea*, *Kingia*), aloes, palms, cycads and Velloziaceae, have an undivided (monopodial) trunk called a caudex. In some cases the caudex may spend many years below ground level, with their buds protected from heat by the soil and their compact young leaves, before they emerge. Despite only having one (apical) bud, they are reliable postfire resprouters. Grasstree caudexes may lie 30 cm below ground, and may remain underground for up to 60 yr (Lamont & Downes, 1979; P. Curtis, pers. comm.). The cycad caudex may arise from a depth of 80 cm (Lamont, 1984), dragged down by its contractile taproot, and might never emerge from the soil. Belowground caudexes are common in Australian temperate regions and rare in Brazilian savannas (Table S1).

The evolution of belowground bud banks in fire-prone ecosystems

Fire-prone ecosystems are rich in species with BBBs, as the protection of the buds by the soil provides fitness benefits in the presence of frequent fires (Flinn & Wein, 1977; Schimmel & Granstrom, 1996; Vesk *et al.*, 2004). Some structures may have been selected for by recurrent fire, as with many lignotubers, woody rhizomes and xylopodia (Maurin *et al.*, 2014; Paula *et al.*, 2016; Lamont *et al.*, 2017). Others have come from lineages that had traits for lateral spreading (colonization) or for seasonal dynamics that were later conserved in fire-prone communities thanks to their capacity to withstand recurrent fires (fleshy underground swellings, bud-bearing roots). The sequence of these two processes is not easy to identify as both may have occurred simultaneously or certainly contemporaneously, or alternated in different periods (Keeley *et al.*, 2011). There is increasing evidence that many fire-adaptive traits arose as a direct response to fire rather than seasonality that developed later (Lamont & He, 2017; Lamont *et al.*, 2017). Basal resprouting may have been selected for by a range of disturbances in early ecosystems that included floods, strong winds, drought, grazing and fires, and thus it can be considered an ancient and widespread functional trait (Pausas & Keeley, 2014). However, as we have shown above, there is a diversity of organs that provide this same functionality, and different organs may have evolved under different ecological and biogeographic settings (convergent evolution). There are few fossils indicative of BBBs and few phylogenetic analyses that include information on the type of BBB (Table S3, Fig. 3). However, even with this limited information, we can detect some trends in the evolution of BBBs that is tied to the long existence of disturbances in terrestrial ecosystems. Note that lineage ages we provide below have some uncertainty (Fig. 3).

An early origin

Well-developed nonwoody rhizomes have been observed in Paleozoic fossils (Tiffney & Niklas, 1985; Retallack, 1999) and they are present in many extant ferns from lineages that can be traced back to the Paleozoic (350–250 Ma; Equisetaceae, Ophioglossaceae) and early Mesozoic (Polypod ferns; Pryer *et al.*, 2004). Given the abundance of fires in some Paleozoic periods such as the Carboniferous, when atmospheric oxygen levels where high (Pausas & Keeley, 2009), the presence of rhizomes might have provided a clear advantage for these plants. In fact, the extinction of ferns at the Permo-Triassic boundary was greater among nonrhizomatous species (Tiffney & Niklas, 1985). Similarly, the expansion of angiosperms in a gymnosperm-dominated world may have been helped by low-intensity fires that favored weedy rhizomatous angiosperms during the Cretaceous (Feild & Arens, 2005; Bond & Scott, 2010). Our phylogenetic compilation for some angiosperm lineages indicates that rhizomes of monocots have at least a Cretaceous origin (for fossil evidence, see Doyle, 1973). Several Southern Hemisphere plant families of monocots

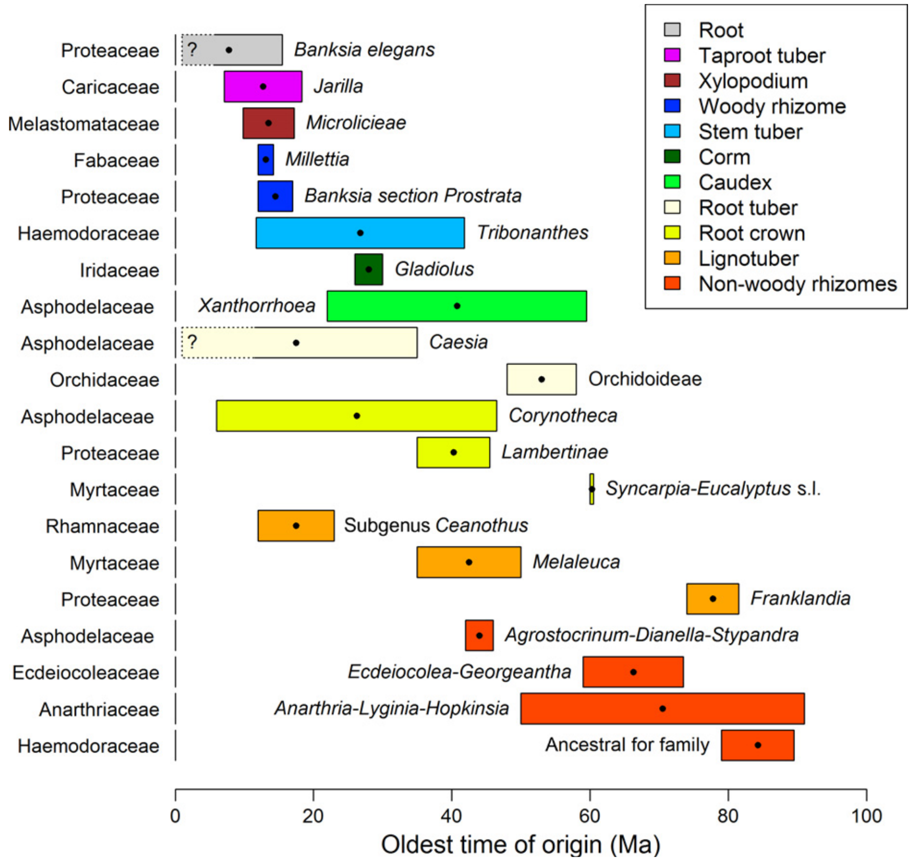

Fig. 3 Oldest time of origin for different belowground bud bank (BBB) organs (different colours) in selected angiosperm families (the lineage used for the dating is included next to the bar). The bar represents the range of ages between the crown age and the stem age of the lineage extracted from published molecular phylogenies (see Supporting Information Table S3); the specific origin of the trait for the given lineage should be somewhere at or between these ages, and a conservative estimate would be the midpoint (the black dot). A question mark (?) in the crown age indicates that the phylogeny used for the lineage had one species only, and thus the crown age is unknown. Note that the oldest time for each belowground structure should be taken as a minimum as other yet to be studied lineages could be considerably older. Ma, million years ago.

with nonwoody rhizomes, including Anarthriaceae and Haemodoraceae, both with pyrogenic flowering (He *et al*., 2016a), and Ecdeiocoleaceae, with pyrogenic germination, are the oldest fire-prone angiosperm clades detected so far (Fig. 3). In summary, having a nonwoody rhizome (or the geophytic habit) is likely to be an ancestral trait among many land plants, especially among monocots.

The evolutionary history of geophytes with fleshy swellings is poorly known. There is evidence of an underground storage organ wrapped by swollen leaf bases, and rhizomes bearing tubers among Cretaceous angiosperms (Krassilov & Volynets, 2008; Srivastava & Krassilov, 2012). Geophytic monocots occur in all ecosystems (including those not subject to recurrent fires; Table S1); they are also well represented in many fire-prone ecosystems, where many species have become fire-dependent (e.g. with fire-stimulated flowering; Keeley, 1993; Bytebier *et al*., 2011). Terrestrial orchids almost universally have adventitious root tubers and date from at least 60 Ma. Arising + 40 Ma, the Orchideae possesses fire-stimulated flowering as an ancestral trait, indicating that its fire history must be even longer (Lamont & He, 2017). *Caesia* (Xanthorrhoeaceae), with adventitious root tubers, can be traced to *c*. 40 Ma (Fig. 3). *Tribonanthes* (Haemodoraceae), confined to seasonally wet heath in south-west Australia, possesses stem tubers and dates from the mid-Eocene (Fig. 3). In summary, our analysis suggests that geophytes are likely to be of Mesozoic origin, with their evolution escalating during the Cenozoic.

With an origin > 250 Ma, cycads are the oldest extant seed plants with the ability to resprout after fire from below the ground surface (belowground caudex), and given that all current cycads resprout, it is likely that this ability is ancestral in the group; however, the diversification of this group is much more recent (Nagalingum *et al*., 2011) and thus the origin of their resprouting ability is difficult to trace. The best-known flowering-plant group with a caudex is *Xanthorrhoea*, although some (younger) species are rhizomatous. This highly fire-prone grasstree genus with pyrogenic flowering is estimated to have evolved 60–40 Ma (Crisp *et al*., 2014). Fossil evidence suggests that Triassic conifers (early Podocarpaceae; 250–230 Ma) were already able to produce root suckers (Decombeix *et al*., 2011) similar to many extant conifers representative of old lineages (Podocarpaceae, Araucariaceae, Mesozoic origin; Table S1). Root suckering is currently widespread in many angiosperm lineages in most ecosystems worldwide, although little research is available (Table S1; see Klimešová *et al*., 2017 for temperate ecosystems) and thus our phylogenetic compilation is poor in this regard (Fig. 3).

Another BBB that is likely to be of Mesozoic origin is the root crown. Despite poor knowledge of root-crown resprouting, it is clearly present in many species, including a few conifers (Table S1). In addition, most epicormically resprouting species may also resprout from the base (root crown, lignotuber) at least when young, and thus it is likely that epicormic resprouting is derived from basal resprouting ancestors. If so, and given widespread resprouting ability among conifers (94 species in 41 genera among all six extant families; He *et al*., 2016b), root-crown resprouting is likely to be of Mesozoic origin. For angiosperms, the widespread presence of epicormic, root-crown and lignotuber resprouting among Myrtaceae suggests an age for the root crown bud bank is more than 60 Ma (Fig. 3). In support, the origin of the genome of *Eucalyptus grandis* has recently traced to 110 Ma (Myburg *et al.*, 2014).

The rise of geoxyles

With increased fire activity during the Cenozoic, and especially since the Late Miocene (Bond, 2015), the ancestral (Paleozoic and Mesozoic) traits were the raw material on which fire-driven selection could act, and have shaped the efficient postfire resprouting structures characteristic of the geoxylic growth form (Box 2). The transition from root-crown resprouting to the formation of basal burls (lignotubers, xylopodia) may be an example of this process, as the former is widely distributed in many ecosystems while the latter is almost completely restricted to fire-prone ecosystems. The oldest lignotuberous genus detected so far is *Franklandia* (Proteaceae; Fig. 3) that probably arose 80 Ma from rainforest ancestors (He *et al.*, 2016c). *Eucalyptus* (Myrtaceae), which evolved 60 Ma (Fig. 3; Table S3) and dominates much of the Australian nonarid flora, predominantly resprouts epicormically but most juvenile plants pass through a lignotuberous phase (Burrows, 2013; Table S1). Mallees, which can be considered large shrubs with lignotubers, appear to be a development associated with increasing fire-proneness in the Miocene and therefore represent a reversion to the juvenile condition (M. Crisp., pers. comm.). *Ceanothus* (Rhamnaceae) in California is of particular interest as the genus split at 23 Ma into a nonresprouting section (subgenus *Cerastes*) and a lignotuberous section (subgenus *Ceanothus*) (Fig. 3; Keeley *et al.*, 2012; Onstein *et al.*, 2015). The condition of the parent stem is unknown but it is likely that it was not fire-prone before 43 Ma. The *Protea* ancestor arose 28 Ma in the Cape region (South Africa) and was a nonresprouter, with the lignotuberous form first arising 18.7 Ma (Lamont *et al.*, 2013). Invasion of the savanna grasslands by proteas was delayed until 12.5 Ma, and diversification began 5 Ma later again, when a lignotuberous subclade evolved from a nonresprouting ancestor that was adapted to the much more frequent fires there (Lamont *et al.*, 2017).

Similarly, the origins of xylopodia and woody rhizomes in South America match the age of the origin of flammable savannas in that region, and evolved from rainforest ancestors: species/lineages with xylopodia there have arisen independently many times in the huge *Mimosa* genus (Fabaceae) (Simon *et al.*, 2009), averaging 4 Ma with a maximum age of origin for one lineage of 9.1 Ma and two species separating just 18 000 yr ago (calculated considering the stem as origin for the lineage in Simon *et al.*, 2009). By contrast, the Microlicieae tribe of Melastomataceae arose at 17.2 Ma and began to diversify at 9.9 Ma with the most recent speciation event at 0.67 Ma among five genera. It is instructive to compare these data with the equivalent growth form (subshrub geoxyles) in a matched environment (tropical grasslands) in southern Africa: a mean of 3.6 Ma with a maximum at 15.2 Ma and a minimum at 0.3 Ma (data for 22 families collated from Maurin *et al.*, 2014; see Lamont *et al.*, 2017). Thus, even though the African species are probably lignotuberous-rhizomatous (Table S1; Lamont *et al.*, 2017), this evidence of their coincident origins can be attributed to the rise of highly fire-prone, tropical grasslands worldwide *c.* 10 Ma (Pennington & Hughes, 2014).

Concluding remarks

Burying buds is a strategy for the persistence of individuals in disturbance-prone ecosystems. Because soil is an efficient insulator of meristems from the heat of fire, this strategy provides fitness benefits in fire-prone ecosystems. Consequently, there is a high diversity of BBB organs that allow plants to successfully resprout after any fire that they are likely to experience; yet they are morphologically and anatomically diverse and have distinct evolutionary histories (analogous). Thus, there is much functional convergence among BBBs. Considering their history and function (but not their anatomical structures), this diversity of BBBs may be divided in three groups. (1) Those that originated in the early history of plants (Paleozoic and Mesozoic) and are currently widespread in many species, mainly woody dicots in different

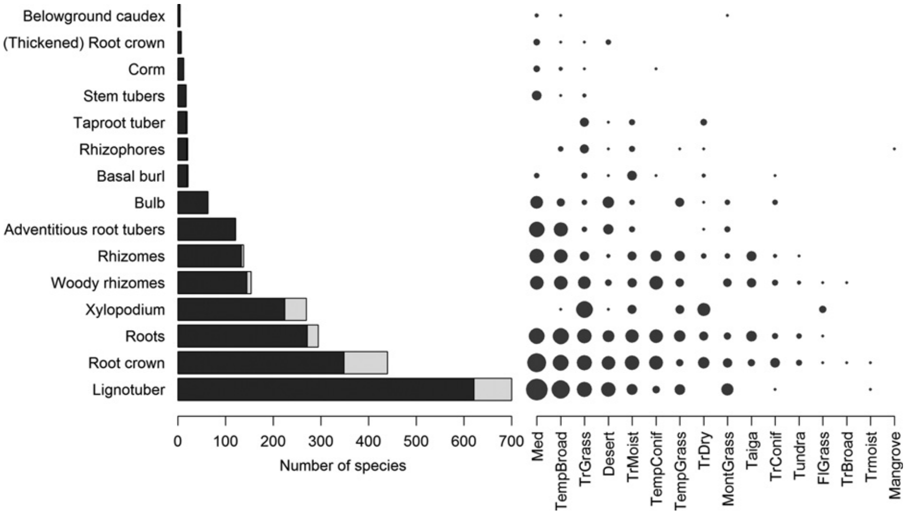

Fig. 4 Summary of the belowground bud bank (BBB) database (Table S1). Number of species in the database for each BBB type and biome. In light grey (bar plot on the left) are the species with uncertain information (indicated by a question mark in the database; Supporting Information Table S1). Size of the circles (right) is proportional to the number of species in the database for each biome and BBB type. Data from Table S1; for details see Notes S1.

lineages and environments; they act as a resprouting source after a range of disturbances, not just fire. These include bud-bearing roots and root crowns. (2) Those that also originated early in the evolution of vascular plants and have spread mainly among monocots and ferns. They are characteristic of the geophyte and graminoid growth forms occurring in many ecosystems, often tied to seasonal stresses; they have been highly successful under recurrent fire regimes. They also include nonwoody rhizomes and a diversity of fleshy underground swellings. (3) Those that originated later in history (throughout the Cenozoic) and are strongly tied to fire-prone ecosystems. They are characteristic of the geoxyle growth form (Box 2) and include woody rhizomes, lignotubers and xylopodia. While all BBBs are common in fire-prone ecosystems and their evolution may have been fine-tuned by varying fire regimes, the third group is the one that is most likely to have been strongly selected for by fire, and thus provides a clear case of convergent evolution for postfire resprouting.

The study of BBBs is still in its infancy. This review is intended to set the scene for understanding BBBs at the global scale. Our database (Fig. 4; Table S1; Notes S1) is the first global compilation of the diversity of BBBs; it is focused on (but not exclusive of) species from fire-prone habitats, and we have prioritized quality rather than quantity of data. It needs to be enlarged as we continuously learn about this topic. Understanding BBBs for a large number of species should provide clues to the diversity of forms that plants have evolved as a response to particular disturbance regimes and the timing of their appearance helps us to understand the key drivers of the Earth's biodiversity. BBBs also provide key information in understanding responses to future disturbance regime changes. Given that BBB organs often store and use carbon resources (carbohydrates), they are also a key to ecosystem food webs and function, including acting as an important sink for carbon dioxide. Research on BBBs should be multidisciplinary, including resprouting experiments to reveal their fitness benefits as well as morpho-anatomical analyses, together with phylogenetic approaches. Recognizing the diversity of BBBs provides a basis for understanding the many evolutionary pathways available to plants for responding to severe recurrent disturbances. We hope this review will provide a turning point for new BBB research.

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Author contributions

J.G.P. designed the research; J.G.P., B.B.L. and S.P. wrote the first version of the manuscript; S.P., assisted by all other authors, compiled the data. J.G.P., B.B.L., S.P., B.A-d-G. and A.F. contributed to the final writing and presentation of the data.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 Global BBB database

Table S2 Carbon reserve compounds in selected BBB species

Table S3 Time of the origin of BBB for selected lineages

Notes S1 Description of the BBB database.

Notes S2 Types of fleshy underground swellings.

Notes S3 Some special cases.

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