# Evolutionary Ecological Drivers of External Tree Bark Macromorphology in Temperate Ecosystems

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**Abstract**

The study of bark morphology reveals significant although not absolute relationships between bark types, tree species, and their environmental conditions. This paper aims to review the inter- and intraspecific ecological and evolutionary drivers that seem to have shaped the macromorphological features of bark, especially in temperate forest ecosystems and especially in Europe. Extensive literature research shows that various factors influence bark thickness, structure, color, and morphology, including solar radiation, climate, adaptation to various disturbance regimes, site conditions and biotic factors, reflecting together long-term selective pressures during evolution. Bark's simultaneous multiple functions and its ontogenetic changes often complicate the identification of the individual selective agents of the adaptive mechanisms and morphologies. An evolutionary perspective can clarify why certain bark types are common in specific environments, how some traits persist as secondary functions, or why diverse bark forms coexist not only in the same site, but also in various ontogenetic stages and positions of the same individuals. Intraspecific variation shaped by both genetic and environmental influences often results in phenotypic plasticity, enhancing species' environmental and age/size related adaptability. We suggest that further research examine current and historical climate, site, and biotic conditions to understand their influence on bark structure and morphology.

**Keywords** Bark adaptive ecology · Bark evolutionary ecology · Evolution · Functional bark ecology · Dendrology

## Introduction

The study of bark morphology of woody species has received very limited attention compared to that given to their wood, and the forces shaping the diversity of bark types remain only partly understood. Previous research mostly focused

on the factors leading to either thin and smooth, versus thick and fissured bark types, with particular emphasis on the constraints enabling the adaptive evolution of thin versus thick bark and their various ecological roles (Paine et al., 2010). In the beginning, these investigations included geographic distinctions, exploring differences between the usually smooth-barked trees of tropical rainforests (Richards, 1996), and the thick, fissured-barked trees common in Europe, as reviewed by Roth (1981). The functional roles of other bark types were rarely examined, leaving significant gaps in our knowledge (Shtein et al., 2023). Due to the lack of consensus in some of the bark morphology terminology (e.g., Trockenbrodt, 1990), we follow the terminology and definitions proposed by Junikka (1994).

During shoot development, the epidermis and the cortex together form the primary bark (Fahn, 1990; Evert, 2006). As the shoot matures, secondary growth begins in both gymnosperms and woody angiosperms, resulting among other things in the formation of the periderm. The cork cambium (i.e., phellogen), which gives rise to the periderm, produces small amounts of phelloderm (parenchymatous) cells toward the inside and phellem cells (often suberized cork cells) toward the outside, together forming the primary periderm (Fahn, 1990; Serra et al., 2022). In the secondary plant body, the bark is defined by all the tissues found outside of the vascular cambium (Fahn, 1990; Angyalossy et al., 2016). Lenticels of the primary periderm function as small openings that maintain gas exchange for living tissues despite the basic barrier properties of the periderm (Rosner & Morris, 2022).

As wood thickens, the expanding trunk induces dilatation in the outer live bark layers. Because of this, in some species, the primary periderm stretches while still allowing lenticels to remain visible for extended periods on smooth-barked trees (Srivastava, 1964). The appearance of the bark is influenced by a combination of the cellular arrangements (Chattaway, 1953, 1955), and the thickness of the cork layer. For instance, thin-walled cells in a thin cork layer create smooth barks (Roth, 1981).

Dead plant tissues outside the phellogen can absorb and release water vapor or even water in daily or seasonal cycles, possibly generating some stress in the primary periderm. This can lead to cracking, particularly along weaker areas such as lenticels (Braun, 1955; Rosner & Morris, 2022). In trees such as *Quercus suber* L. (cork oak) only a first phellogen is formed and it may function for centuries (Lopes et al., 2020). In most woody species, once the primary periderm ruptures, a new phellogen forms within the old phloem, producing additional periderm layers. The external layers of active periderms die, and repeated cycles of this process result in a fissured bark. The successive layers of periderm and dead phloem tissues trapped between them form the rhytidome. Secondary lenticels may also emerge in subsequent periderms within the rhytidome (Rosner & Morris, 2022). Bark portions of various sizes and shapes may detach from the trunk, leaving scars.

Bark thickness can be genetically determined and either thickens continuously with increasing girth, or exhibit a curvilinear pattern, where bark thickening slows and approaches a plateau as trees age (Gill, 1995). Numerous histological factors influence the properties of the outermost layer, producing various bark types. These include the shape and size of periderm layers: e.g., branched periderm systems (scales), parallel periderm systems (ringed bark) (Roth, 1981), the

structure of the dead bark between cork layers (Srivastava, 1964), and fiber content (fiberless: scales; fiber-rich: tessellated bark) (Chattaway, 1953, 1955; Braun, 1955; Evert, 2006).

Bark development and appearance is determined by the interaction of genetic and environmental factors (Fig. 1). When certain bark properties are examined at a given time, they may appear determined, but it may change with the passing years. Some bark adaptations to environmental factors became (seemingly) fixed during evolution, stabilizing within certain ranges of niche axes. However, because some woody species are broadly tolerant and thrive under varied conditions within wider niche boundaries or types, they also exhibit high adaptability in bark structure and morphology, which implies phenotypic plasticity (Dimitri, 1968; Roth, 1981; Lev-Yadun & Aloni, 1990; Richardson et al., 2015). Thus, it is crucial to distinguish the drivers of inter- and intraspecific external bark appearance to distinguish between "fixed" adaptations from phenotypic plasticity. For this purpose, it is worth reviewing the various driving forces. A recent review (Shtein et al., 2023) examined the current state of research on bark's micro- and macromorphology, mainly focusing on histological and methodological aspects, and mentioning only briefly the evolutionary ecological context.

This review aims to summarize the inter- and intraspecific ecological forces shaping the macromorphological traits of smooth and fissured bark types. We also provide prospectives for further research.
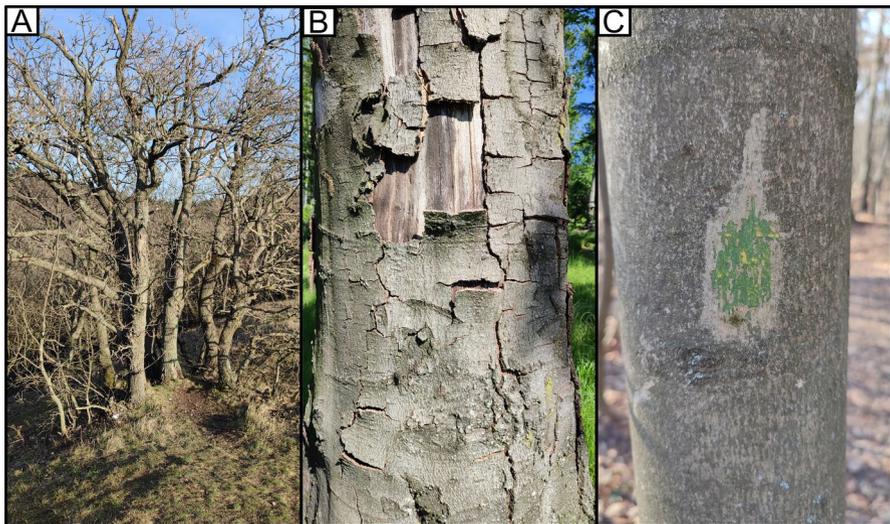


**Fig. 1** The effects of sunlight on bark. **A** Open woodlands typically have trees with fissured bark for sunlight protection (*Quercus pubescens* in a downy-oak shrubland, Hungary). **B** If smooth-barked trees are suddenly exposed to strong sunlight, sunscald can occur (*Fagus sylvatica* in a beech woodland, on the edge of a newly opened gap, Hungary). **C** Beneath the thin, smooth bark surface is a layer of chlorophyll-containing green tissue, which is appearing on the surface because of scratching even in old age (*Fraxinus ornus* in a closed termophilous downy oak woodland, Hungary)

# Drivers of Interspecific Variation of Smooth and Fissured Bark

## Solar Radiation

Different bark types have distinct thermal and physiological properties that are crucial for resilience to disturbances (Nicolai, 1995). Excessive solar radiation is harmful to trees because it overheats and damages bark tissues, reduces their protective function, degrades wood quality, and creates entry points for pathogens, ultimately weakening the tree (Litzow & Pellett, 1983). Nicolai (1995) hypothesized a relationship between forest stand openness and the development of bark types, based on studies of Central European, North American, and African forests. According to this hypothesis, thick barks are impenetrable to solar radiation, while thin and smooth barks allow sun radiation to penetrate. Consequently, smooth-barked trees are predominantly found in closed-canopy forests. In canopy gaps caused by disturbances, shading from young, subdominant, or thick and fissured-barked trees may protect the trunks of the smooth-barked species from strong sun irradiation. However, when such shading is insufficient, smooth-barked trees exposed to intense solar radiation may suffer from sunscalds, particularly along the more sun-exposed gap edges (Nicolai, 1986, 1995). These observations suggest that smooth-barked species primarily inhabit forests with high canopy closure, while fissured, thick-barked species dominate open woodlands, where their thick barks shield them from solar radiation (Fig. 1A). However, developing a thick bark requires substantial resource investment and time. Trees with a smooth bark (e.g., *Fagus* spp.) allocate more energy to competition over light by height growth than on bark thickening. In darker, closed-canopy forests where bark photosynthesis must be maximized, bark thickening is reduced, leaving smooth-barked species with less protection against solar radiation (Huberman, 1943) but with better options for bark photosynthesis. In open habitats, smooth-barked trees may adapt to high sun irradiation by producing shading lateral branches or benefit from shading provided by other woody species.

Bark color is another important factor with respect to solar radiation, although its functional significance is less well known (Shtein et al., 2023). White, reflective bark surfaces reduce heat absorption by reflecting red wavelengths, which defends from overheating. White-barked species often play a pioneering role in successions (Nicolai, 1995). In contrast, green, yellow, and grey barks only moderately absorb heat, while black and brown barks absorb the most. These differences become critical when air temperatures approach freezing. Darker bark can warm a winter frozen cambium above the freezing point, but rapid freezing and thawing due to fluctuating conditions (repetitive shading by clouds) may cause sunscald or other winter cambial, xylem, phloem and outer bark damages. A reflective bark, resistant to red wavelengths, offers a better protection against such winter damages (Harvey, 1923a). This phenomenon was demonstrated experimentally by applying various paints to the bark (Karels & Boonstra, 2003). Bark thickness also influences the wood temperature: bark of at least 2.5 cm thickness significantly reduces heat penetration (Harvey, 1923b). In other parts of the

globe, heat damage to the bark can also occur in summer, involving prolonged exposure to strong sun irradiation and temperatures up to above 50 °C (Fig. 1B).

The adaptive significance of the relationship between geography and bark coloration concerning winter cambial scalding was criticized by Lev-Yadun (2019). While this explanation is probably not wrong, it does not capture the full range of functions of white barks all over the geography of this phenomenon. Moreover, as discussed in Lev-Yadun (2019), Harvey (1923a) studied trees at 47°46'N, Nicolai (1986) studied trees at 50°48'N, and Karels and Boonstra (2003) mostly at 48°N and only some poplar trees at 61°N. In North America, the white-barked *Betula papyrifera* Marshall (paper birch) and *Populus tremuloides* Michx. (quaking aspen) can be found in latitudes as high as 68°N (north of the arctic circle), and in Scandinavia, white-barked *Betula pendula* Roth (silver birch) and *B. pubescens* Ehrh. (hairy birch) can be found up to 66–69°N. Thus, the cambial and bark temperatures measured by Harvey (1923a), Nicolai (1986), and by Karels and Boonstra (2003) do not represent the really cold, much less sun-irradiated, and snowier ecologies of these common, white-barked taxa. Therefore, Lev-Yadun (2019) posited that the hypothesis of avoiding winter cambial heating and consequent freezing and scalding is only partly supported, for instance because of the common occurrence of dark bark in thin *Betula* branches, additional explanations for the evolution of white barks (that will be given in the relevant section of this review) are needed. In temperate regions of middle latitudes, the risk of heating a frozen cambium during winter is much greater than in higher latitudes. It is so because of (1) the higher angle of the sun in relation to the horizon at lower latitudes; (2) the longer daily hours of sun irradiation during winter; (3) and the initial higher internal trunk and branch winter temperatures (although still within the freezing range), resulting from milder winters, allow the cambium to thaw more easily during frozen but sunny winter days. Moreover, if heating by sun irradiation during the frozen winter and consequent cambial scalding was a great problem, more winter deciduous trees of lower but still temperate latitudes or in high mountains of mid-latitudes should have more white-barked tree species and tree individuals than trees of higher latitudes, but it is not so. In these mid-latitudes, most of the tree taxa and individual trees do not have white bark, but rather grey and brown barks (Zoltán & Korda, 2025). In any case, while the damage of cambial scalding during winter is an important commercial problem, because of lowering timber quality, its direct influence on tree fitness may be very small. However secondary infections following sunscald may gradually weaken the tree, potentially leading to its death (Litzow & Pellett, 1983). If indeed the lowering of fitness following cambial scalding, which according to Lev-Yadun (2019) was never measured systematically, is very small, the initial selection for white bark was probably not related to defense from cambial scalding.

The photosynthetic activity of the bark (which was first observed in the late nineteenth century (Ross, 1887)) also plays a crucial role in the morphological evolution of the trunk. The chlorophyll content of the young shoots can be retained in older branches and trunks to some extent (Fig. 1C), but it gradually decreases as additional periderms are formed and cover it and block light penetration. When temperatures rise above freezing in the early spring, smooth, thin barks can resume photosynthesis immediately, sometimes surpassing the beginning of the photosynthesis

capacity of the young leaves (Pearson & Lawrence, 1958; Glass & Granet, 1978). In *Populus tremuloides*, the smooth, thin bark exhibits higher chlorophyll content on the sunlit side than on the shaded one. At lower altitudes, its periderms are whitish, reflecting sunlight, while at higher elevations, they are yellowish-brown and more translucent, allowing light penetration for photosynthesis and probably also serving tissue warming. This capability is advantageous for *P. tremuloides* in plant communities dominated by evergreen coniferous species, where early spring bark photosynthesis may have greater importance (Glass & Granet, 1978). In lower regions, reflective periderms provide protection from sunscald (Covington, 1975). Some genera (*Populus* spp., *Prunus* spp.) maintain chloroplasts in their cortex, phloem, and phelloderm even in maturity (Srivastava, 1964). Others, such as *Rosa* spp., *Rubus* spp., *Genista* spp., and *Ulex* spp., exhibit a green bark with significant chlorophyll content throughout their lifespan (Pfanz & Aschan, 2001).

## Resistance to Fire

Studying the relationships between fire regimes and bark properties is a central and very large topic in bark function, ecology, and evolution. Because of the huge amount of published material on this subject, we will not discuss it in full. Three primary fire-adaptive strategies exist (Schubert et al., 2016): (1) a persistence strategy, relying on a thick bark to protect the trunk; (2) a regeneration strategy, utilizing carbohydrate reserves stored in roots and shoots, along with many supressed buds for post-fire regrowth; (3) and post-fire seed dispersal from serotinous cones and fruit (Lamont et al., 2020). These strategies are evident even in young trees (Jackson et al., 1999). High-intensity fires generally favour the vegetative regeneration and post-fire seed dispersal strategies, while low-intensity fires with various return intervals tend to select for thick barks (Schwilk et al., 2013; Pausas, 2015), especially when the fire return interval is shorter than the lifespan of the trees (Pausas, 2017). However, different strategies often coexist within the same habitat. Some trees, such as certain *Eucalyptus* spp., which shed oil-rich bark fragments and leaves, actively contribute to fire initiation and spread (Morris & Jansen, 2016), or conifer species characterized by shed needle accumulation that facilitates fire as a reproductive aid (Schoennagel et al., 2003).

Thick bark is frequently assumed to be the major determinant of fire survival if a species has a persistence strategy. A global analysis across various fire regimes showed that outer and total bark thickness are among the most important factors explaining the fire regime properties (dry season precipitation, fire return interval, etc.), second only to stem diameter (Rosell, 2016), which in many cases is associated with bark thickness because of allometry. In young trees, relative bark thickness is particularly significant (Lawes et al., 2011a, b), and its effectiveness depends on the ratio of bark thickness to stem diameter (Lawes et al., 2013). Trees in fire-prone ecosystems typically have thicker barks than those in other disturbance regimes (Schafer et al., 2015; Schubert et al., 2016), and the variability in bark thickness among taxa is largely explained by fire regime properties (Pausas, 2017).

Fire resistance is probably influenced by additional factors. Due to fire-induced charring, the bark's thickness may decrease, which also affects the subsequent resilience of the tree. According to some authors, bark density also plays a crucial role, because a thick, low-density bark can effectively insulate the cambium from lethal temperatures (Schafer et al., 2015; Nolan et al., 2020). Bark's moisture content is another key factor (Lawes et al., 2011a, b), which is related to the ratio of inner bark to total bark thickness (Loram-Lourenço et al., 2020). In some cases, a thin, smooth, and moisture-rich bark can also resist fire, as seen in *Eucalyptus* species (Gill, 1995).

According to some authors, fire resistance is determined by several bark properties together, including thickness, thermal conductivity and capacity, density, moisture content, and temperature of combustion (Spalt & Reifsnyder, 1962). Certain species develop a thicker bark only near the trunk base (dual or two-toned bark) to enhance fire protection, a trait observed in the temperate species (*Betula pendula* and *Pinus sylvestri*s L. (Scots pine) (Lev-Yadun, 2019)) and also in a tree species of semi-arid habitats (*Eucalyptus miniata* A. Cunn. ex Schauer. (Darwin woollybutt) (Lawes et al., 2021)), zones with occasional fire occurrence (Pausas, 2015). On the savannas of hot regions, where shoots can also frequently be affected by fire, their thicker bark also contributes to protection (Rosell et al., 2015).

Recent studies suggested that in addition to biophysical traits, bark development is influenced by other factors (Rosell, 2019). While a thick bark offers protection against fire, it may have evolved for multiple purposes, such as defense against herbivores and pathogens, though whether such protection increases with bark thickness is not well-studied (Pausas, 2015). Trade-offs have also been observed, such as between photosynthetic thin barks, and fire-resistant thick barks (Cernusak & Hutley, 2011). Overall, bark thickness plays a pivotal defensive role in fire-affected ecosystems, but further research is needed to clarify the full range of anatomical, physiological, and biophysical mechanisms driving that adaptation.

## Climate and Site Conditions

According to the climate adaptation hypothesis, the thick bark is an adaptation to climatic extremes, such as freezing, drought and strong sun irradiation. A thick bark may protect trees from freezing (Payette et al., 2010) and reduce water loss (Rosell & Olson, 2014; Richardson et al., 2015). However, in more humid, tropical conditions, these functions are less critical, and smooth-barked trees are more common (Roth, 1981; Richards, 1996).

Recent studies have observed that tree species in boreal and mountain tree-line forests often have thin barks (Pausas, 2015). This contrasts with the climate hypothesis, which was based on a dataset predominantly comprising temperate species (Roth, 1981). Pausas critiqued the hypothesis but ultimately suggested it should not be entirely dismissed, emphasizing the need for further research into bark's role in water regulation and fire regimes. While boreal species tend to have thin barks, this does not necessarily contradict the climate adaptation hypothesis. Alternative strategies might provide cold resistance in these species instead of bark thickening.

However, we suggest that because of the short stature of trees in boreal and mountain tree lines forests, the thin bark may simply reflect the allometric relations between bark thickness and tree size.

Hypotheses have also been formulated regarding species in less extreme climatic conditions. Trees with a fissured bark may suffer greater damage from lightning strikes since lightning follows the shortest path of least resistance to the ground. In smooth-barked trees, under wet conditions lightning typically travels along the bark's outer surface, whereas in fissured-barked trees, it can also pass through the wood (Dolwin, 1985). The sudden boiling of water within the trunk can lead to explosion or to severe damage to the cambium and other tissues. But in many cases, even trees with a smooth bark are also struck by lightning, because of other reasons (solitary tree, hollow/cracked trunk, etc.). While lightning strikes are relatively rare and can be fatal, their selective influence likely operates strongly only locally, in areas with high strike frequencies, such as high mountains.

Site conditions may also significantly influence bark morphology. Lenticel distribution and density may also play a role. Trees in dry environments often have a thick bark, which causes the lenticels of the first periderm to disappear, either in order to reduce water loss or as a developmental constraint, whereas trees growing in oxygen-poor conditions (flood tolerance), exhibit a thin, smooth bark with numerous lenticels that facilitate gas exchange (Rosner & Morris, 2022). This hypothesis is supported by our field observations. For example, *Populus* spp. and *Salix* spp. growing in habitats with excess water develop numerous deep, rhomboid, densely-arranged lenticels, while *Alnus glutinosa* (L.) Gaertn. (common alder) produces an even greater number of smaller lenticels. These species also develop a fissured bark in old age but retain their young smooth bark for a long time, compared to species with fissured bark that occur in drier habitats (Fig. 2C–D). This phenomenon
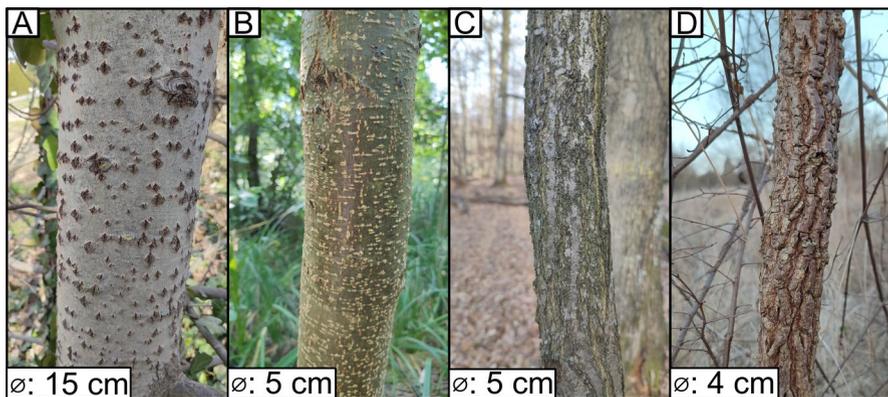


**Fig. 2** The effects of habitat conditions on the bark. **A, B** Tree species from wetter habitats (*Populus alba* in a riverine willow-poplar woodland, Hungary – **A**; *Alnus glutinosa* in a riverine ash-alder woodland, Hungary – **B**) have a smooth bark and high lenticel density. **C** Tree species from drier habitats usually have fissured bark and small, barely noticeable lenticels (*Quercus petraea* in a Turkey oak—sessile oak woodland, Hungary). **D** Some species have adapted to dry and sunny conditions with increased cork growth (*Ulmus minor* in a thermophilous woodland fringe, Hungary)

is probably related to another hypothesis, that trees growing in nutrient-poor soils may develop a thicker bark, potentially for nutrient storage (Roth, 1981; Richardson et al., 2015). One form of adaptation to very dry conditions is the formation of a thick cork. In some species (*Quercus suber*, *Ulmus minor* Mill. (field elm), etc.) this can cover entire young branches and trunks (Fig. 2D). For trees developing more biomass in nutrient-rich habitats, mechanical support by the bark, especially when the shoots are still young and thin (Niklas, 1999; Morris & Jansen, 2016), is also a potentially important aspect.

The development of bark types was shaped by species-specific life-history strategies. Among pioneer tree species, intense intraspecific competition is common, as they often colonize disturbed sites in high densities. Under such conditions, the fastest-height-growing individuals tend to outcompete the rest (King, 1981). This pattern aligns with findings that saplings in canopy gaps tend to allocate more biomass to stem growth, enhancing height and competitive ability, while shade-tolerant, slower-growing species prioritize foliage production (King, 1991). Thinner stems—often a result of rapid competitive height growth—are typically associated with smoother barks. As trees mature and reach the upper canopy, height growth slows down, while stem thickening accelerates significantly. When comparing the shade-intolerant *Populus tremuloides* with *Acer saccharum* Marshall (sugar maple), the latter has a higher mechanical stability and greater resistance to wind damage (King, 1986).

## Biotic Interactions

Bark also provides defense against various biotic factors. Smooth barks reduce the ability of epiphytes (Morris & Jansen, 2016) and pests (Ferrenberg & Mitton, 2014) to establish there. This "slippery hypothesis" is particularly relevant in tropical forests, where pathogen and vascular epiphyte densities are high. Conversely, deeply fissured bark facilitates pest colonization. Although many smooth barks generally become fissured with progressing tree age and size, even small patches of smooth bark can offer advantages by preventing colonization (Ferrenberg & Mitton, 2014). However, this hypothesis requires a rapid bark turnover by shedding (Roth, 1981).

While considering the smaller number of vascular epiphytes in European forests, this hypothesis has a twist in the temperate zone. According to our field observations, rich epiphytic communities can also develop on smooth-barked trees, which are mostly composed of algae, moss, and lichen species. Bark turnover in the case of the powdery shedding of the outer periderm layer is usually not fast or efficient enough to remove them, but their population could be regulated by biotic interactions (Fig. 3A). For example, *Carpinus betulus* L. (European hornbeam) or *Fagus sylvatica* L. (European beech) often carry on the bark algal species such as *Chlorella* spp., *Chlorococcum* spp. (Pfanz & Aschan, 2001), and lichens such as *Phlyctis argena* (Ach.) Flot. The continuous renewal of bark's surface of species with a shedding bark always provide new colonizable surfaces for bark-dwelling species (Fig. 3B). In the case of species with a fissured bark, mosses often colonize it in high density (Fig. 3C) and even compete with each
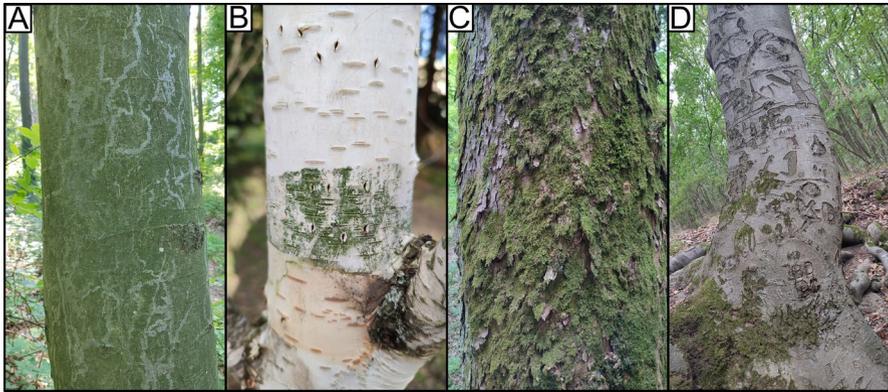
**Fig. 3** Epiphytes and bark types. **A** Biotic interactions (e.g., algae consumption by snails) help to clear smooth barks of epiphytes if bark's turnover is slow (*Fagus sylvatica* in a beech woodland, Hungary). **B** If the smooth bark develops a mechanism to remove epiphytes, it produces a thin, papery exfoliating bark (*Betula utilis* in an urban forest, Budapest, Hungary). **C** In the case of thick, fissured, peeling bark, mosses are most often dominant (*Acer pseudoplatanus* in a ravine forest, Slovakia). **D** Mosses tend to establish more easily on bark surfaces that have become cracked due to aging or intentional scratching by animals and by humans (*F. sylvatica* in a closed acidofrequent oak woodland, Hungary)

other. Rain washes the accumulated nutrient substances from trees and dissolves some of them (stemflow), which is a less studied part of the nutrient cycles (Voigt, 1960; Grundmann et al., 2024). The stemflow composition is also influenced by the morphological properties of the bark. Fissured bark has a larger surface area per trunk length unit, so more substances are dissolved than from a smooth bark. Therefore, a fissured bark provides a larger habitat for specialised organisms. Our field observations support that a non-smooth bark surface is favourable for intensive moss colonization. A good example of this is mosses establishing in the cracks (scar tissues) of tree species that generally have a smooth bark but develop injuries spontaneously or due to various biotic and abiotic factors as they age (Fig. 3D).

Lichen hyphae can physically penetrate substrates causes loss of cohesion in the material (Cozzolino et al., 2022). In species where the bark separates and sheds due to their genetics (in tiles, plates or scales), the higher amounts of metabolic products (lichen acids – Paukov et al. (2022)) may promote bark disintegration, causing the detachment of its outer layers. This facilitation can help to develop microhabitats important for specialist species more quickly (e.g., *Hymenochaete carpatica* Pilát – inner side of *Acer pseudoplatanus* L. bark plates – Kutszegi and Papp (2016)).

Since the global woody surface area is approximately equal to the global land surface area (Gauci et al., 2024), the understanding of bark-epiphyte relationships is extremely important. Based on the above, it can be assumed that (1) epiphytes living on smooth-barked trees do not form such a large amount of biomass that they completely block bark photosynthesis and induce selection for more efficient bark turnover; (2) if a thin bark is an adaptation, it may develop a papery, thin, exfoliating bark, which repeatedly clears large surface areas; (3) biotic

interactions may also control the excessive colonization of epiphytes; (4) non-smooth bark species have a higher density of mosses with a larger biomass.

Bark thickness and rigidity also play defensive roles by preventing bark stripping by herbivores and by protecting internal tissues (Franceschi et al., 2005). Young shoots may feature thorns and spines to deter herbivory (Cooper and Owen-Smith, 1986; Tomlinson et al., 2025), and these may also exhibit aposematic coloration (Lev-Yadun, 2001; Caro and Ruxton, 2019). As trees age, the color of prickles, thorns, and spines fades while thickness, rigidness, and the accumulation of defensive secondary metabolites of the bark provide sufficient defense (Lev-Yadun & Ne'eman, 2006).

Several hypotheses suggested an anti-herbivory function of bark colors, which can effectively be better expressed in the case of a smooth, thin bark. The first one, was that certain bark colors may not match the colors of invertebrate herbivores and by this undermine their camouflage (Lev-Yadun et al., 2004; Lev-Yadun, 2016). This may either cause them to refrain from occupying such barks and thus not to move there towards the leaves, or else, if they do occupy such barks, it may expose them to predators and parasitoids (Lev-Yadun et al., 2004). The second hypothesis (Lev-Yadun, 2019) focused on the white barks of several *Betula* and *Populus* species that grow in high latitudes. Lev-Yadun (2019) suggested that in addition to undermining herbivorous insect camouflage, white barks can defend from herbivory by several other methods: (1) camouflaging trees against extinct Tertiary and Pleistocene megafauna and against current smaller mammals that consume trunks and barks during snowy winters, and possibly also by countershading under dense fog conditions; (2) being a visual aposematic (warning) signal when combined with chemical defense or low palatability; (3) reducing bark heating in spring, summer and autumn in order to prevent herbivorous arthropods from warming, and thus reducing their activity, especially in the morning; (4) and helping predators to spot insects' movements because of the darker horizontal lenticels common in white barks.

Ireland and Ruxton (2022) tested one of Lev-Yadun's (2019) hypotheses, i.e., that a toxic white bark may be aposematic in birch (*Betula pendula*) trees growing in Scotland, and found that indeed a long list of mammalian herbivores refrain from stripping and eating its bark. They concluded that the conspicuous white coloration of birch bark may act as an aposematic visual signal to deter bark-stripping mammals. Betulin is responsible for the white bark coloration of *Betula* spp., and together with other secondary metabolites, it also exerts toxic or detrimental effects on herbivores (Palo, 1984). In addition, *Betula* spp. has developed various mechanical defenses against herbivory: the outer layer of the bark detaches more easily than the inner layer (Ireland & Ruxton, 2022), and the bark tends to peel off in a ring-like, horizontal stripes (Fig. 3B), whereas herbivores typically attempt to strip barks axially, in a vertical direction (Lutz, 1956).

In snowy environments, a light-colored bark may also act as camouflage during winter, after the leaves have been shed, however, dark bark areas that appear in older trees (Lev-Yadun, 2019) can reveal the trees (Ireland & Ruxton, 2022), although this effect is likely limited to close range and fogless hours and days.

## Evolutionary Context

The fossil record provides some valuable insights into the evolution of bark morphology. Environmental and ecological adaptations can also be traced by comparing modern and ancient bark structures.

Studies of the Late Triassic tree *Araucarioxylon arizonicum* Knowlton revealed a fissured bark, suggesting the early adaptation of trees to seasonal stresses such as freezing and drought (Ash & Savidge, 2004). Another study summarized what environmental effects (lightning strikes, hailstorms, floods, fires, and intense sunlight) caused deformations in fossilized bark (Luthardt et al., 2018). Such events may not only have caused physical damage to the bark, but also the climatic and local conditions allow us to infer what may have influenced the evolution of bark structure. Triassic fire scars suggest that a thick bark may have already been an adaptation to survive frequent fires (Byers et al., 2014), and that trees survived the fire due to their thick bark. Thus, fire could have appeared as a driving force for selecting for thick bark long ago.

Late Permian fossil trunks from fluvial sediments (e.g., *Melaleuca* spp.) suggest that a thick, spongy bark evolved as an adaptation to conditions such as periodic flooding a long time ago (Fielding & Alexander, 2001). This raises a new possible function for spongy barks. The very thick spongy bark of *Sequoia* spp. is commonly thought to provide thermal insulation (Berrill et al., 2020; Thoreau, 1909) and mechanical protection (Bold et al., 2020). However, based on the above fossil evidence, an additional function (aeration) may also be attributed to the evolution of spongy barks.

The evolutionary context should not be neglected when examining the formation of the bark of extant species. The original natural vegetation and ecosystems that prevailed before the accumulated environmental damages by modern humans, differed significantly from today's conditions. The megaherbivores in northern parts of Asia, Europe, and North America and those of South America, may have caused great selection pressures, as their extinction at the end of the Pleistocene caused the transformation of ecosystems (Gill et al., 2009), and the expansion of various species (e.g., *Betula pendula* – Doughty et al., 2010).

## Intraspecific Variation

### Genetic Diversity

The morphological bark diversity within and among species is often categorized using taxonomic methods. We present some notable examples from European smooth-barked species:

- *Fagus sylvatica* var. *quercoides* Pers. (stone beech) (Fig. 4A): A rarely occurring European beech variant with an oak-like fissured bark (Joemann, 2010), valued for its resistance to sunscald (Majer, 1966), which may be important in the context of the current global warming (Selimović et al., 2013).

**Fig. 4** Intraspecific differences in barks. **A** An example of genetic diversity is stone beech (*Fagus sylvatica* var. *quercoides* in an urban forest, Göttingen, Germany), which has shallow fissured bark. **B** Beech (*F. sylvatica* in an urban forest, Budapest, Hungary) bark is frequently scratched by vandals, causing permanent physical damage to the bark. **C** The periderm of beech (*F. sylvatica* in a beech woodland, Hungary) bark colonized by pathogens often begins to split, resulting in a fissured bark. **D** Curly birch (*Betula pendula* var. *carelica* in an arboretum, Zvolen, Slovakia) with indented growth-rings caused an irregular trunk

- *Carpinus betulus* var. *Tuzsonii* Kárp.: A variant typical of various habitats found around Budapest, Hungary, characterized by its cylindrical trunk and deeply fissured bark (Kárpáti, 1937).
- *Alnus incana* var. *incana* f. *Kaiseri* J. Murr: This form has a smooth, shiny, reddish-brown bark, distinct from the usual grey bark of *A. incana* (Soó, 1970).

Below are several additional examples where different bark varieties of commonly fissured bark species occur:

- *Betula pendula* var. *pendula* f. *rimosa* Lindq. and f. *laevis* Lindq.: The former exhibits a deeply fissured bark at the base of its trunk, while the latter has a smooth bark (Soó, 1970).
- *Betula pendula* var. *carelica* (Merckl.) Hämet-Ahti (curly birch) (Fig. 4D): Due to the special formation of indented growth-rings (Lev-Yadun et al., 2023; Novitskaya, 1998), the trunk is not a regular cylinder, its bark is thick and is more prone to cracking.
- *Acer campestre* var. *acuminatilobum* J. Papp (Matra ancient maple): This taxon is characterized by pubescent shoots, and its bark peels off in strings, revealing reddish-brown inner layers. It is now often treated as a separate (*Acer acuminatilobum* J. Papp) (Bartha, 2012) or hybrid species (*Acer × bornmuelleri* Borbás nothosubsp. *acuminatilobum* (J. Papp) Kerényi-Nagy) (Kerényi-Nagy, 2019).

Considering their morphological diversity, it is worth using eucalypts as a demonstration. Eucalypts, particularly those belonging to the subgenus *Symphyomyrtus*, show significant morphological bark diversity despite unclear phylogenetic

relationships due to their frequent hybridization (Júnior & Garcia, 2021). Despite close genetic relationships, eucalypts' bark displays high morphological variability and unique traits. Even among the geographic races of *Eucalyptus globulus* Labill. (blue gum) genetic differences in bark morphology and thickness were found, which complicates preserving its genetic diversity (Barbour et al., 2009). This consideration becomes important in the context of hybridization, as the bark characteristics of most *Eucalyptus* hybrids are generally intermediates between those of their parent species (Pryor et al., 1956).

Nowadays, instead of taxonomic distinctions, morphotypes are usually described. Some species demonstrate exceptionally high variability. *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) bark has been classified into 14 types based on fissure patterns and bark roughness (Ross & Krahmer, 1971). *Fagus grandifolia* Ehrh. (American beech) can develop three (smooth, shallowly-, and deeply fissured bark (Ostrofsky & Blanchard, 1984)), while *Acer saccharum* exhibits four bark-morphology types (Sajdak, 1968).

## Abiotic Influences

Abiotic factors such as climate and site conditions significantly affect bark development. Within species, trees in cold or dry climates often have thicker bark than those growing under warmer, more humid conditions (Richardson et al., 2015). Steep, shallow-soil sites, strong winds, or intense sunlight can cause cracking in smooth-barked trees (Bartha, 2024).

Trees exposed to substantial sunlight may affect the initiation and inhibition of phellogen in a polar manner, which can lead to differences in cork development between sun-exposed and shaded sides of the bark, potentially contributing to differential protective properties of the bark (Douliot, 1889; de Zeeuw, 1941; Borger & Kozlowski, 1972; Lev-Yadun & Aloni, 1990). This process is hormonally regulated (induced by ethylene and supressed by auxin), as revealed by Lev-Yadun and Aloni (1990). In the case of *F. sylvatica*, the bark on the sunlit side of the trunk can be 6–8% thicker than on the shaded one (Dimitri, 1968). Based on this, if a beech tree is exposed to constant sunlight from a young age, it can adapt to it. However, if it is adapted to shade, and is suddenly exposed to significant sunlight because of various disturbances to the forest, sunscald may occur (Fig. 1A). Similarly, in European oaks (*Quercus* spp.), bark thickness increases under sunny conditions, even within the same stand or on opposite sides of a single tree (Roth, 1981). One form of adaptation to sun exposure is the formation of winged cork. In some species this is not always expressed. For example, in *Ulmus minor* and *Acer campestre* L. (field maple), it is almost always expressed only in individuals exposed to direct sunlight.

Tree trunks can be damaged by a variety of mechanical injuries. These can be superficial (Figs. 3D and 4B), but more serious injuries can even alter the growth-ring formation, resulting among other responses in indented growth-rings that are sometimes visible as depressions on the outer surface of the bark (Lev-Yadun et al., 2024). This can be caused by pathogens, herbivores, fire, rockfall, or anthropogenic impacts (Lev-Yadun et al., 2023, and citations therein). In habitats where a tree is

exposed to such impacts, it is adaptive to either regenerate effectively (*Tilia* spp. preference of rocky steep slopes (Zukal et al., 2020)) or develop a thick, protective bark.

Lenticels may also play a role during sudden stress events (Rosner & Morris, 2022). While their openness to the environment can potentially act as infection gateways, pathogens are surprisingly infrequent in lenticels, though the reasons remain unclear. Mechanical perturbations, such as bending due to disturbance, can induce bark thickening on the stressed side and increase the size and number of lenticels, likely to prevent cracking. A thick bark can contribute to significant mechanical support, even in branches 3 m long (Rosell & Olson, 2014).

## Biotic Influences

Internal bark layers can be deformed by insect (Langenfeld-Heyser et al., 2006) and fungal attacks (Ross & Krahmer, 1971), causing the bark to be more prone to cracking (Fig. 4C). Trees in harsh habitats may face increased vulnerability due to their lower vitality (Kunca et al., 2000). Fungal spores may enter through lenticels, wounds, or insect galleries, while repeated mechanical damage (e.g., bark stripping) can disrupt the existing periderm and induce the formation of wound periderm. Secondary fungal infections often cause thickened bark in such cases (Kaufert, 1937).

Morphotypes within species exhibit differences in growth potential, as shown for *Betula alleghaniensis* Britton (yellow birch) and *Acer saccharum* (Gauthier & Guillemette, 2018). This has forestry implications, enabling quick selection without a detailed genetic analysis. A manual developed for forestry purposes in Canada states that when the usually smooth-barked trees are less vigorous they develop fissured or tessellated bark, while deeply-fissured trees with horizontal cracks or soft plates also indicate reduced vitality (OMNR, 2004).

*Populus tremuloides* has a thin, smooth bark but it can develop a rough, fissured bark as a response to fungal pathogens, especially those targeting the outer cortex. The growing mycelium ruptures the periderm, causing the tree to produce successive periderm layers, and eventually, after years of infection, to form a thick, fissured bark (Kaufert, 1937). The smooth-barked individuals of *Betula alleghaniensis* grow better than fissured ones (Clausen & Godman, 1969), and *Pseudotsuga menziesii* may develop fissured bark when fungal infections distort new bark layers (Ross & Krahmer, 1971). *Fagus sylvatica* var. *quercoides* is sometimes difficult to distinguish from trees with pathological bark thickening. However, when inherited, this trait is expressed early, often on branches, whereas pathological thickening is typically localized near the base of the trunk or appears in patches (Bartha, 2024).

Bark thickness might be influenced by the structure of forest stands. In deciduous species, growth conditions and species traits that favour either fast or slow growth also influence trunk and crown architecture (King, 2001). Supressed trees with slower growth and thin curved stems often require enhanced mechanical stability to support the load of asymmetrical crowns. Given that bark thickness plays a significant role in mechanical reinforcement in thin stems (Niklas, 1999), variation in bark structure is expected to parallel these growth patterns. As a result of slower

growth, various tree species tend to have thicker bark (Stängle et al., 2017). Trees grow more slowly in uneven-aged forests (Hynynen et al., 2019), therefore, thicker bark can develop in structurally diverse stands. In the case of *Sequoia sempervirens* (D. Don) Endl. (coastal redwood), this relationship has been directly demonstrated (Berrill et al., 2020). We think that this observation highlights the need to investigate the causes of bark diversity not only at increasingly finer levels (histological, cytological, genetical) but also at higher levels of organization, such as ecological systems. Furthermore, this relationship may reflect the importance of forest management practices. However, our understanding of this connection remains limited, necessitating further research.

## Synthesis of the Driving Forces

Bark morphology is shaped by numerous factors, reflecting genotype- or species-level adaptations to environmental and biotic influences. Site conditions, disturbance regimes, potential herbivores and pathogens all act as selective agents. Bark morphology reflects the integration of the dominant selective forces during a species' evolution, although combinations of drivers may lead to similar outcomes via different pathways. Since trees with several bark types occur in one habitat (taking into account age, thickness, and genetic variability), it can be concluded that a wide spectrum of ecological strategies, as reflected by bark morphology, can coexist.

Most studies have attempted to explain bark types through their individual functional roles; however, bark fulfils multiple functions simultaneously. The multifunctionality of bark complicates identifying clear adaptive mechanisms. For instance, thick barks may offer mechanical protection, insulation, or water and nutrient storage, but these functions may either conflict or be synergistic. Understanding the process of prioritization of bark functions likely depends on the specific selective pressures by the ecological environment, necessitating further research.

We suggest that further research should consider the original natural vegetation, paleoecology and the extinct megaherbivores as adaptive drivers. Evolutionary contexts can help distinguish between current correlations between the selective pressures and the inherited ancient adaptations, e.g., thick bark may simultaneously protect against fire and serve water storage, but determining the primary adaptive functions requires understanding its evolutionary/environmental history. Evolutionary perspectives may also clarify why certain bark types evolved across different environments (convergent evolution) or why traits persisted as fulfilling secondary functions. For example, pure white-barked trees are found only in temperate and especially boreal forests, which suggests that its function is not solely to protect against sunscald (Lev-Yadun, 2019). For instance, *Quercus suber* and *Phellodendron amurense* Rupr. (Amur cork tree) have a similar thick, corky bark, evolving under different site conditions and genetic backgrounds. Exploring the relationships between fossils and modern bark structures may enhance the understanding of ecological strategies and responses to environmental changes. This perspective would be useful for predicting climate change impacts. Understanding how bark types

enabled species to survive past climatic extremes can help forecast which species might adapt to future conditions.

Phenotypic plasticity allows for some adaptability of the individual tree or organ. Within tolerable (but not optimal) conditions, different appearances may emerge. Some of these morphological variations were classified into taxonomic categories (which possibly should be revised) that are now often considered as morphotypes. However, sudden changes (abiotic stress) or biotic damage can also induce the formation of atypical bark types. Distinguishing genetic and environmental effects on bark structure and morphology is challenging, but heritability testing, which is not easy in trees with a long generation time and long ontogeny, can help in distinguishing between them.

With all these driving forces in mind (Tables 1 and 2), we propose to consider the development of bark characteristics of individual taxa. We will provide some examples in the next section.

## Examples for Adaptation Mechanisms

When examining the adaptation of certain taxa, it can be beneficial to focus especially not only on the morphology, but also on the typical, most common sites and habitats. Due to the recent large-scale human impact and habitat modifications, species with a wider ecological tolerance or those whose fierce competitors or herbivores disappeared, can occur in habitats (and urban environments) where they would not occur naturally. Many occurrences of these species are atypical, even extreme, in which the species is probably not in an optimal situation, but after settling in some way, they are able to survive and even reproduce, but these do not always reflect their millennia-long adaptations.

### Smooth Bark in Mesic Habitats—European Beech (*Fagus sylvatica*)

*F. sylvatica* is a long-lived tree species native to Europe, growing in temperate, mesic forests. Its bark is smooth and grey even in old age, and its primary periderm can remain active for more than 200 years (Spohn & Spohn, 2020). The outermost layer of the bark flakes off as powder and its lenticels appear as small protrusions on the trunk. One of the most studied and best understood dynamics is of beech forests (Standovár & Kenderes, 2003). In the gap dynamics typical of Central European closed forests, gap opening and closing cycles usually occur before an individual beech tree reaches the upper canopy level. The shade tolerance of beech plays an important role in filling forest gaps, as this is commonly preceded by decades of suppression (Trotsiuk et al., 2012).

The species is associated with closed stands, therefore the utilization of all available light for photosynthesis is vital to their survival. Since there are also deciduous primeval forests dominated by beech (Sabatini et al., 2018), it can be assumed that the species is not susceptible to winter sunscald. In winter, sunlight passes through the leafless canopies, which aids bark photosynthesis and does not damage the bark

**Table 1** Collection of interspecific eco-evolutionary drivers of smooth and fissured bark development

| Interspecific driver | Smooth, thin bark | Thick, fissured bark | References |
|---|---|---|---|
| High-intensity fires | ✓ | ✓ | Gill (1995), Schwilk et al. (2013), Pausas (2015, 2017), Schafer et al. (2015), Schubert et al. (2016) |
| Low-intensity fires | ✗ | ✓ | Schwilk et al. (2013), Pausas (2015, 2017) |
| Storms (lightning) | ✓ | ✗ | Dolwin (1985) |
| Storms (wind) | ✗ | ✓ | Niklas (1999), Morris and Jansen (2016) |
| Floods | ✗ | ✓ | Fielding and Alexander (2001), Kramer et al. (2008) |
| Rockfalls | ✗ | ✓ | Bold et al. (2020) |
| Climatic extremities | ✗ | ✓ | Ash and Savidge (2004), Payette et al. (2010), Rosell and Olson (2014), Richardson et al. (2015) |
| Habitat extremities | ✗ | ✓ | Roth (1981), Niklas (1999), Rosell and Olson (2014), Richardson et al. (2015) |
| High elevations | ✓ | ✗ | Covington (1975), Glass and Granet (1978), Pausas (2015) |
| Open woodlands | ✗ | ✓ | Harvey (1923b), Huberman (1943), Nicolai (1986, 1995) |
| Wet habitats | ✓ | ✗ | Rosner and Morris (2022) |
| High pathogen and epiphyte pressure | ✓ | ✗ | Ferrenberg and Mitton (2014) |
| High ungulate pressure | ✓ | ✓ | Franceschi et al. (2005), Ireland and Ruxton (2022) |
| High (extinct) megaherbivore pressure | ✓ | ✓ | Lev-Yadun (2019) |
| Strong competition for light | ✓ | ✗ | King (1981, 1986, 1991) |

**Table 2** Collection of intraspecific eco-evolutionary drivers of smooth and fissured bark development

| Intraspecific driver | Smooth, thin bark | Thick, fissured bark | References |
|---|---|---|---|
| Habitat extremities | × | ✓ | Douliot (1889), De Zeeuw (1941), Dimitri (1968), Borger and Kozlowski (1972), Roth (1981), Lev-Yadun and Aloni (1990), Bartha (2024) |
| Mechanical injuries | × | ✓ | Bollschweiler et al. (2011), Lev-Yadun et al. (2023, 2024), Rosell and Olson (2014) |
| Bad condition | × | ✓ | Kaufert (1937), Ross and Krahmer (1971), Langenfeld-Heyser et al. (2006), Gauthier and Guillemette (2018) |
| Supressed trees | × | ✓ | Niklas (1999), King (2001), Stängle et al. (2017) |

or the cambium. However, in the summer, marginal gap individuals may suddenly be exposed to direct sunlight, which can cause sunscald (Nagel & Svoboda, 2008). This means that summer sunscald rather than a winter one is problematic for beech trees. In beech forests, the disturbance regime is mostly driven by storms. We consider the selection of the lightning strike hypothesis (Dolwin, 1985) to be less likely a driving evolutionary force, but in this sense, the adaptive role of the smooth bark can also be partially supported by it.

In the case of epiphytes, our experience suggests that algae and lichens tend to settle on trees with smooth barks, in a thin layer that cannot inhibit photosynthesis significantly or is controlled biotically. Bark-stripping affects beech trees (Kuiters et al., 2006; Kurek et al., 2019). Since the beginning of the twentieth century, ungulate populations in Europe have been increasing to the point that there are now local (Carpio et al., 2021) or even regional (Zoltán et al., 2024) overabundance. Tree species with their long generation time have not yet been able to adapt to such a large-scale ungulate pressure. The extinct megaherbivores consumed a completely different diet and composition (Pringle, 2020), therefore their selection pressure on trees was completely different.

## Smooth Barks in Dry, and Fissured Barks in Mesic and Wet Habitats—Ash Species (*Fraxinus* spp.)

The European ash (*Fraxinus excelsior* L.) occurs in mesic forests, and the manna ash (*Fraxinus ornus* L.) occurs in dry forests, and in shrublands. The narrow-leaved ash (*Fraxinus angustifolia* Vahl) and the green ash (*Fraxinus pennsylvanica* Marshall) are gallery forest species. *Fraxinus ornus* is predominantly a small tree species, with a smooth grey bark even in old age. The bark of *F. excelsior* remains smooth for a long time, and it begins to crack only in old age. By contrast, the barks of *F. angustifolia* and *F. pennsylvanica* begin to crack at a young age (Zoltán & Korda, 2025).

*Fraxinus excelsior* lives in similar environmental conditions to *F. sylvatica*. Similar adaptive responses can be observed for a while. The bark starts to crack above a DBH of 25–30 cm (Zoltán & Korda, 2025), until then, in closed stands, the bark is photosynthesizing. Some studies have found that ungulates prefer bark stripping of ash trees over beech trees (Vospernik, 2006), especially in the diameter classes between 12–36 cm (Fehér et al., 2016). The current high bark peeling intensity is probably still a recent phenomenon, but the preference of herbivores is a trait inherited from their ancestors. The fissures in the bark remain shallow for a long time, forming a so-called "ski trail" (Mikolas, 2017). This means that the top of the ridges remains flat, smooth and shiny for a long time, so the tree can both maintain a photosynthetic bark and suppress epiphyte colonization.

*Fraxinus ornus* is a tree species of dry forests with incomplete canopy closure. In our opinion, its smooth bark is probably the result of rarely reaching a large trunk diameter due to poor habitat conditions. With a relatively large trunk thickness, the bark of this tree can also start to crack shallowly (Zoltán & Korda, 2025), but such specimens are rarely found. In shrub forests, it usually does not stand as a solitary tree but is found in groups of several other individuals of tree and shrub species that

shade each other, thus protecting the trunk from overheating and sunscald. In such habitats, the disturbance regime was presumably dominated by fire. Taking this into account, *F. ornus* holds the post-fire regeneration strategy, as its bark is thin and does not protect against fire. The tree produces many easily spreading samara fruit every year that can colonize areas opened by fires. It may be worthwhile to carry out comparative phylogenetic studies within the Oleaceae clade based on bark morphology to clarify the genetic determination or contribution of their bark types.

*Fraxinus angustifolia* and *F. pennsylvanica* are both floodplain-associated tree species. Their barks begin to crack at a very young age, already even at 3 cm in diameter (Zoltán & Korda, 2025). Ungulates appear in resource-rich habitats such as floodplains at higher densities and more intensive habitat use (Churski et al., 2017), which can be explained by the high primary production of these areas (Hanberry et al., 2015). This may have been a strong driver that forced the trees to quickly develop a thick bark. Furthermore, the periodic flooding of these areas can cause mechanical damage to the trunks (Bollschweiler et al., 2011).

## Fissured Barks in Dry Habitats—Oaks (*Quercus* spp.)

In the case of *Quercus* spp., thick, fissured bark is often a characteristic trait (*Q. petraea* (Matt.) Liebl. – sessile oak, *Q. cerris* L. – Turkey oak, *Q. pubescens* Willd. – downy oak, *Q. suber*) (Zoltán & Korda, 2025). These species usually occur in dry habitats. Under such conditions, with their thick bark they protect themselves against both fires (persistent strategy) and herbivores. According to the wood-pasture hypothesis, the original natural vegetation of Central and Western Europe was a park-like open forest, which was maintained by the grazing of large herbivores that are now extinct (Vera, 2000). According to this hypothesis, oaks germinate among thorny shrubs (nurse plants) that protect them from grazing. Their fast bark thickening fits this model. As the young oaks grow above the shrubs, they produce thin shoots, and then the trunks and barks begin to thicken. After the shrubs shaded by the oaks die, the thick bark alone can protect the trees from herbivores. There are criticisms of the wood-pasture hypothesis (Birks, 2005; Hodder et al., 2005), but the megaherbivores likely played a role in shaping forest structure and composition (Mitchell, 2005). The development of species-specific bark characteristics supports the hypothesis. Furthermore, the hypothesis suggests that the high light availability resulting from incomplete canopy closure (Jackson et al., 1999), together with fire dynamics (Roth, 1981), could have jointly contributed to the development of thick barks in these oaks.

## Fissured Barks in Wet Habitats—Poplars (*Populus* spp.)

The *Populus* species (*P. alba* L. – white poplar, *P. nigra* L. – black poplar, *P. deltoides* W. Bartram ex Marshall – eastern cottonwood, and cultur varietas) live in a variety of habitats, but mostly in mesic and gallery forests. Their bark becomes fissured at least partially along the stem base (Zoltán & Korda, 2025). In the case of species with a thicker, fissured bark living in floodplains (especially *Populus* and

*Salix*), much greater resistance to flooding has been shown (Kramer et al., 2008), which may indicate an important selection pressure for a thick bark in these species.

*Populus alba* is characterized by dual bark. It is considered a defense mechanism against fire (Lev-Yadun, 2019; Lawes et al., 2021), but due to its occurrence in disturbance regimes not dominated by fire dynamics, it may also fulfil different functions. This bark type may also protect against periodic flooding and ungulate damage. Due to the maintenance of a large number and deep, diamond-shaped lenticels in the upper part of the trunk, gas exchange is ensured even during prolonged flooding. To maintain this lenticel-rich, smooth bark also on the upper side of the trunk, the development of thick bark appears to be delayed until a larger stem diameter is reached (Fig. 2A). Thus, selection likely favoured late bark thickening to prevent fissuring of the upper trunk while preserving its functional properties.

In the case of *P. nigra*, the bark is already fissured when the trees are young and remains so throughout the trunk. The fissures mostly develop along the lenticels (Rosner & Morris, 2022), so the development of a thick bark does not mean complete insulation, but only a different strategy of aeration. Its hybrids with *P. deltoides* are even bred specifically to have a fissured bark in order to resist the effects of game damage (Hirka et al., 2025).

## Conclusions

The examples presented and discussed here indicate that the discussed driving forces that seem to select for various bark types can at least partly explain bark characteristics within different habitats and taxa, as well as the co-existence of different bark types within the same habitat. It is important to emphasize that micromorphological, histological and physiological properties all have an impact on the development of the various bark types (Shtein et al., 2023). However, the determining driving forces are not unequivocal. Some taxa show great similarity globally (e.g., smooth bark of *Fagus* spp. (Shen, 1992)), but some show high morphological bark diversity (e.g., *Fraxinus* spp.). We suggest that in further research carried out comparative phylogenetic studies, during which the bark types of representative species can be compared with the phylogenetic tree. Determining bark types is not a trivial task either. We have recently published a database on the qualitative bark macroscopic morphology of 115 Central European tree, shrub, and liana species (Zoltán & Korda, 2025), and we are currently working on developing further quantitative traits. In the meantime, it is worth considering, exploring, publishing, and discussing the adaptation mechanisms of as many species as possible, so that more data is available. We have provided some examples here, but the mechanisms determining bark evolution of other species require much more research.

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contributed to the study's conceptual development, enriched it with his suggestions, and thoroughly reviewed the final version of the manuscript.

**Data Availability**  No datasets were generated or analysed during the current study.

**Declarations**

**Competing Interests**  The authors have no competing interests to declare that are relevant to the content of this article.

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