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Smooth bark surfaces can defend trees against insect attack: resurrecting a 'slippery' hypothesis

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Summary

1. Smooth bark on trees and shrubs was historically hypothesized to be an anatomical defence against epiphytic vegetation and phytophagous insects. This hypothesis has fallen from favour, yet no clear tests of bark texture as a defence against insects have been published.

2. We tested the smooth bark defence hypothesis using bark beetles specialized in attacking pine trees as model insects, and *Pinus flexilis* (limber pine) – a widespread tree that can have both smooth and rough bark surfaces on the same stem – as the model tree. We investigated the effects of bark texture on the locations of bark beetle attacks on trees with a combination of field surveys and experiments in the Colorado Rocky Mountains, USA.

3. Bark beetle attacks were overwhelmingly located on rough bark surfaces and virtually absent from smooth bark. Increasing proportional coverage by smooth bark was negatively related to bark beetle attacks per square metre of bark surface. Experimental tests of bark beetles' ability to grip smooth versus rough bark revealed that bark beetles have difficulty gripping and quickly fell from smooth bark but not from rough bark.

4. Smooth bark was negatively related to increasing tree size, but our models indicated that even partial coverage by smooth bark on a tree's trunk can significantly reduce total bark beetle attacks – this reduction likely improves tree fitness as bark beetles must aggregate to overcome tree defences.

5. *Synthesis*. Our results indicate that smooth bark on trees can act as an anatomical defence against insects by reducing their ability to grip a tree's surface – even for insects specialized in attacking tree stems. Similar to other forms of anti-insect defence (i.e. secondary chemistry, leaf toughness), smooth bark appears to be influenced by plant ontogeny whereby younger trees have greater defences than older trees. Understanding the adaptive significance of bark texture will require continued field and genetic study. Nevertheless, our results revealed that smooth bark texture increases tree resistance to phytophagous insects calling for the resurrection and vetting of the smooth bark defence hypothesis.

Key-words: anatomical defence, bark beetle, conifer, *Dendroctonus ponderosae*, limber pine, *Pinus flexilis*, plant texture, plant–insect interactions, tree resistance

Introduction

Smooth-textured bark on trees was historically hypothesized to be an anatomical defence against epiphytic vegetation and insect pests (Black & Harper 1979). Smooth bark was thought to make it harder for epiphytes and insects to grip a tree's surface, reducing their ability to remain on a tree's stem and limbs. The smooth bark defence hypothesis was most widely considered in tropical forests where many tree species have smooth bark and plant and insect pests abound. However, the idea fell from favour when no differences in liana infestations were found between smooth- and rough-barked trees (Boom & Mori 1982) and alternative defences against epiphytic vegetation were proposed (Putz 1984). However, to our knowledge, no empirical tests of bark texture effects on the interactions between trees and their phytophagous insect pests have been published.

Bark texture can influence the density, diversity and location of both sessile and mobile organisms on tree bark in temperate forests (Cramer 1975; Stephenson 1989). Habitat suitability for epiphytic lichens and bryophytes increases in relation to increasing bark texture (roughness) in various forest types (Forsyth & Miyata 1984; Holien 1997; Friedel *et al*. 2006). Bark with great texture or roughness has also been shown to host a greater diversity and abundance of micro- and macro-animals, while smooth-barked trees

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harbour far less diversity (Wardle *et al.* 2003). While bark texture has received little consideration as a potential defence against insect pests in any tree species, a number of widespread conifers can have smooth bark (Farjon 1984; Biswas & Johri 1997; see Fig. 1). Conifers are also of particular interest in the context of potential bark texture defences against insects because many conifers are hosts of specialist bark beetles that attack and kill conifers by landing upon and crawling along the tree's stem before chewing deeper into the bark or wood (Wood 1982; Franceschi *et al.* 2005). Interestingly, an association between bark beetle attack locations and bark texture was indicated by a report in the secondary literature where attacks by the bark beetle *Dendroctonus pseudotsugae* (Douglas fir beetle) on *Pseudotsuga menziesii* (var. *menziesii;* coastal Douglas fir) were more common on rough bark than smooth bark (Hedden & Gara 1972). However, the authors of this report did not consider possible mechanisms behind the observed pattern.

As with any type of anti-insect defence, understanding when chemical and physical traits have evolved in response to herbivory vs. other biotic and abiotic pressures (i.e. 'neutral resistance') remains a central challenge in plant defence theory (Edwards 1989; Hanley *et al.* 2007).

Fig. 1. Bark texture of trees varies both within and between species: (a) an example of variable bark texture within lodgepole pines (*P. contorta*) of similar age and in a shared environment, (b) a limber pine (*P. flexilis*) with rough bark texture and attacked by bark beetles (red coloured resin visible from attacks by the mountain pine beetle, MPB), (c) a limber pine with a high proportion of smooth-textured bark and (d) a limber pine with MPB attacks present on rough/crenulated bark, but absent on nearby smooth bark.

Nevertheless, plant resistance to insects is often based on a collection of plant traits that can be collectively viewed as defensive regardless of their primary function (Strauss & Agrawal 1999; Agrawal & Fishbein 2006). While research into tree defences against insects, including defences of conifers against bark beetles, is typically focused on secondary chemistry (e.g. Trapp & Croteau 2001), conifers also have formidable anatomical defences that can influence tree resistance to bark beetles (Baier 1996; Franceschi *et al.* 2005). Importantly, a recent meta-analysis found plant physical traits and structural defences to be far more effective against insects than secondary chemistry on broad scales (Carmona, Lajeunesse & Johnson 2011). Thus, a direct role of bark texture in tree resistance to insects is not only possible, but potentially combines with a suite of physical and chemical traits to form a complex of anti-insect defence over a tree's life span (Boege & Marquis 2005; Agrawal & Fishbein 2006).

As noted by Hanley *et al.* (2007), studies that identify how phytophagous insects interact with structural/anatomical traits are important for understanding not only defence trait evolution, but also how plant–insect interactions might be influenced by climate-induced changes in phenology and ranges. From a practical point of view, investigating the role of bark texture as an anatomical defence against tree-killing insects is both novel and important in the light of climate-induced insect epidemics that have recently killed billions of trees across North America and Europe (Meddens, Hicke & Ferguson 2012; Hlásny & Turčáni 2013). *Dendroctonus ponderosae* (mountain pine beetle), for example, is currently among the most destructive forest pests in the world, having killed millions of hectares of pine trees (*Pinus spp.*) across western North America (Meddens, Hicke & Ferguson 2012). In recent years, we observed stands of *Pinus flexilis* (limber pine) in the Colorado Rocky Mountains, USA, where only trees with large proportions of smooth-textured bark on their stems had survived stand-level infestations of *D. ponderosae*. During our observations, we qualitatively defined smooth-textured bark as those areas with no visible cracks, flakes, crenulations or other surface features that would aid an insect's grip (Fig. 1c). Detailed inspection revealed that trees with predominantly smooth bark surfaces had often been attacked by *D. ponderosae*, but only on rough bark around limb insertions for example (Fig. 1d). These observations inspired us to test the role that bark texture may play in defence against bark beetles.

We predicted that smooth-textured bark hinders the ability of bark beetles to land on or crawl upon a tree's stem and tested two related hypotheses: (i) bark surface texture influences bark beetle attack locations and attack density on pine trees and (ii) bark texture affects bark beetles' ability to grip a tree's surface. We also predicted that smooth-textured bark is more common in younger/smaller trees as reported for bark texture in other tree species (Whitmore 1963; Lev-Yadun & Aloni 1993; Biswas & Johri 1997; Friedel *et al.* 2006) and as also reported for a number of antiherbivore defences in numerous plant species (Boege & Marquis 2005). Thus, we tested a third hypothesis: (iii) bark texture (roughness) increases with increasing tree size (as a correlate of age). To understand the larger potential effects of bark texture on tree–insect interactions, we used our data to estimate bark texture effects on bark beetle attack density (a correlate of attack success as bark beetles must aggregate to kill trees) expected across a range of tree sizes and illustrated this effect in comparison with expected attack densities in the absence of a smooth bark effect.

Materials and methods

STUDY SYSTEM

We used *P. flexilis* (limber pine) as our model tree and *D. ponderosae* (mountain pine beetle) as our model insect. Both species are native to western North America, where they are widespread and ecologically important organisms. *Pinus flexilis* is a five-needled pine (of the subgenus *Strobus*) that can have a mixture of smooth and rough bark on its stem and is found across a large range of latitude and elevation (Biswas & Johri 1997; Schoettle & Rochelle 2000). *Dendroctonus ponderosae* attacks all true pines (*Pinus spp.*) found within its native range and has recently caused extensive mortality in subalpine forests that were historically above its elevational range limit (Mitton & Ferrenberg 2012). During epidemic phases, *D. ponderosae* can attack and kill seemingly healthy trees, overcoming tree defences through the use of aggregation pheromones to increase their attack densities and by vectoring a potentially lethal fungal symbiont that aids in killing host trees (Wood 1982; Raffa & Berryman 1983). Pine trees with high volume of defensive resin (Kane & Kolb 2010; Ferrenberg, Kane & Mitton 2013) or high concentrations of monoterpenes (Sturgeon & Mitton 1986) can escape bark beetle-induced mortality by lowering bark beetle attack densities, indicating that defences which reduce bark beetle attacks can lead to concomitant decreases in tree mortality (Franceschi *et al.* 2005).

HYPOTHESIS 1: BARK TEXTURE AND INSECT ATTACK

We tested our first hypothesis that bark surface texture influences *D. ponderosae* (hereafter referred to as 'bark beetles') attack locations on tree stems using limber pines (hereafter referred to as 'trees') from four bark beetle-infested stands found on U.S. National Forest lands at 40° 04′ 20″ N; 105° 125 30′ 36″ W (2800 m asl) and at the University of Colorado's Mountain Research Station (CU-MRS) at 40° 02′ 09″ N; 105° 32′ 09″ W (3021 m asl), Colorado, USA. Climate and soils common to the forests of this area were described by Duhl *et al.* (2013). Stands were selected using visible evidence of recent bark beetle activity. Trees used to assess bark beetle attack locations met two criteria: (i) the tree had been attacked by at least five bark beetles, which was determined by the presence of bark beetle-caused pitch tubes (Fig. 1b) and (ii) the tree had a significant proportion of both smooth and rough bark surfaces on its main stem (i.e. a minimum proportion of 0·25 to a maximum of 0·75 smooth bark surfaces). We considered bark to be smooth textured when it had no visible cracks, flakes, crenulations or other notable features aside from microtopography – that is, rolling or buckling can still be covered by smooth surfaces (Fig. 1c). Bark patches covered by lichens were considered to be rough textured, as the underlying surfaces were typically rough (Fig. 1d) and lichens added obvious texture to tree surfaces.

We determined proportional coverage by smooth and rough bark on a tree's stem by measuring the amount of smooth and rough bark found along four vertical bark transects, each 2 m in length running along the tree from just above the ground's surface to a height of 2 m and oriented on the tree stem with the cardinal directions. We also measured each tree's diameter at breast height (DBH – 1·37 m above the ground surface). We examined the surface of each tree and recorded whether attacks were seen on rough bark and on smooth bark (i.e. each tree received a 'yes' or 'no' for each surface texture type); these categories were then turned into counts for a 2 × 2 contingency table. We used a Yate's corrected *chi-squared* test to compare the frequencies of trees in the two categories and calculated Cramer's V – a measure of tendency towards an outcome or association with a category within a test's variables (Agresti 1996). Cramer's V ranges from 0 to 1, with a value close to or equal to 1 in our test indicating a strong tendency for attacks to be associated with rough bark and not smooth bark.

We tested the relationship between bark texture and insect attacks per square metre using 44 limber pine trees that were mass-attacked by bark beetles between 2010 and 2012 and that had similar DBH (20 to 25 cm) to control for potential effects of tree size on attack density. To assess bark texture on each of these 44 trees, we affixed a flexible nylon grid (20 × 50 cm = 1000 cm^2) to a limbless area of the trunk between 1 and 2 m above the ground's surface, and used the number of cells covering rough bark vs. smooth bark to calculate proportional coverage of each bark type. We then determined insect attack density by counting the number of bark beetle attacks per the area under the attached grid. Proportion of smooth bark (independent variable) was then related to bark beetle attack density (dependent variable) using linear regression.

HYPOTHESIS 2: INSECTS' ABILITY TO GRIP SMOOTH VS. ROUGH BARK

We tested our second hypothesis that bark beetles' ability to grip tree stems is influenced by bark texture using *P. flexilis* trees located at CU-MRS (described above). To minimize possible effects of tree chemistry on bark beetle behaviour, we tested bark beetle ability to grip bark surfaces by comparing each beetle's performance on smooth and rough bark found on the same tree. To prevent the loss of bark beetles and to eliminate lengthy falls, we attached a paper shelf below each bark patch. We randomly selected 22 individual beetles from approximately 50 bark beetles captured in flight traps earlier in the day (July 2011) and wearing powder-free nitrile-gloves, we placed each beetle into timed trials on both smooth and rough bark (the starting bark texture type was chosen at random). Based on observation of bark beetles' ability to grip the different bark textures during the development of our methods, we chose to run each bark beetle through one trial on rough bark and three trials on smooth bark to create a mean time on smooth bark. The use of multiple trials on smooth bark was intended to ensure that we were measuring a true effect of bark texture and not a fall caused by our handling of bark beetles, which had trouble gripping smooth bark. Each beetle was given time to grip the bark and orient for 5 s before we started a timer to measure the number of seconds until fall. A maximum time of 300 s (5 min) could elapse before trials were ended if the bark beetle had not yet fallen. We statistically verified that different trees (block effect) had no effect on the time trials ($P > 0{\cdot}25$) and then compared each beetle's time on smooth bark to its time on rough bark with a paired *t*-test.

HYPOTHESIS 3: BARK TEXTURE ACROSS TREE SIZE AND HEIGHT

To test our third hypothesis that bark texture is related to tree size and height on a tree's stem, we measured tree DBH – 1·37 m above the ground surface and the coverage of smooth- and rough-textured bark on 151 trees growing in subalpine forests described above for hypothesis 1. Because mountain pine beetles rarely attack tree limbs or upper reaches of tree stems, we focused on calculating the mean coverage of rough- and smooth bark texture on the lower 2 m of each tree's trunk, again using four vertical transects of 2 m length and oriented on the tree stem with the cardinal directions as described above. We sampled trees that were ≥2 m tall and that fell within 10 m of a randomly oriented (random compass vector), 20-m-long transect at each sample point. We used linear regression to relate tree size (DBH; the independent variable) to bark texture (dependent variable) selecting the best-fit regression model as the one with the lowest Akaike Information Criterion (AIC)and Bayesian Information Criterion (BIC) scores, which are assessments of model fit that balance overall fit with the number of terms included (Yang 2005). To test for a tree height effect on bark texture, we compared the proportional coverage of smooth bark on the lowest 1 m of each tree to the next highest 1 m on each stem with paired *t*-tests.

BARK TEXTURE EFFECTS ON INSECT ATTACK DENSITY

To estimate the effect of bark texture on insect attacks, we combined measured effects of both tree size and bark texture on bark beetle attack densities. We first used linear regression to relate tree diameter (DBH) with the number of bark beetle attacks per square metre of bark surface using data collected from 23 rough-barked pine trees recently killed by bark beetles at CU-MRS. We used the resultant regression equation to estimate the number of bark beetle attacks expected across tree size. Our field surveys and experimental trials with mountain pine beetles described above indicated that bark beetles cannot effectively attack smooth bark surfaces. As a result, the proportion of smooth bark on a tree's stem strongly influences bark beetle attack densities. To combine the effect of tree size on bark beetle attack density with an effect of smooth bark on attack density, we next calculated the expected proportion of smooth bark on a tree's lower stem (bottom 2 m) as related to tree size using the linear regression models described above for hypothesis 3. Finally, to estimate the effect of both tree size and bark texture on bark beetle attack densities, we combined our estimates of bark beetle attack density in relation to tree diameter with the equation describing the effect of smooth bark proportional coverage across tree size to create an estimate of 'smooth bark effect' on total bark beetle attacks. While bark beetles are less commonly found attacking trees <10 cm DBH than larger trees, the mechanisms behind this pattern are poorly researched. Thus, we included estimated attack densities for trees ranging from 1 to 40 cm DBH in our model to illustrate the point in tree size and defence when potential bark beetle attacks drop to zero.

Results

HYPOTHESIS 1: BARK TEXTURE AND INSECT ATTACK

We found 52 trees, with a mean DBH ± 1SE of 22·2 ± 1·1 cm, that fit our criteria of having ≥ 5 bark beetle attacks and at least 0·25 to 0·75 proportion smooth bark on the lower 2 m of the tree's main stem. We did not count total attacks on each tree, but given that all trees included in our survey met a minimum threshold of 5 attacks, we examined a minimum of 260 attacks collectively across the 52 trees and found only one bark beetle attack on smooth bark. Thus, 51 trees were categorized as '0' (no attack on smooth bark) and one tree as a '1' (attack on smooth bark), resulting in a highly significant difference via Yate's corrected $X^2 = 96{\cdot}19$ ($P < 0{\cdot}0001$, d.f. = 1) and a Cramer's V = 0·98 (i.e. bark beetle attacks are strongly associated with rough bark and rarely associated with smooth bark). In addition to attack locations on a tree, we also found evidence that bark texture significantly influences bark beetle attack density. As the proportion of smooth bark increased, total bark beetle attacks decreased, resulting in a negative relationship between proportion of smooth bark and attacks per square metre ($R^2_{(1,42)} = 0{\cdot}83$, $P < 0{\cdot}0001$; Fig. 2).

HYPOTHESIS 2: INSECTS' ABILITY TO GRIP SMOOTH BARK VS. ROUGH BARK

In experimental trials, bark beetles were less capable of gripping smooth bark than rough bark (paired $t_{21} = -17{\cdot}5$, $P < 0{\cdot}0001$; Fig. 3). When placed onto rough bark surfaces, 21 of the 22 bark beetles tested (95%) remained on the bark until the 300 s (5 min) trial cut-off time, giving the beetles a mean time of 293·9 s before falling from the tree. All but one of the 22 bark beetles placed onto smooth bark fell from the tree's stem in < 60 s (95%), with a mean time of 43·3 s before falling from the smooth bark (Fig. 3).

HYPOTHESIS 3: BARK TEXTURE ACROSS TREE SIZE AND HEIGHT

We found that smaller trees have a greater proportion of smooth bark on their main stem than larger trees. Specifically, we found a significant negative relationship between tree size (DBH) and the proportion of smooth bark on a tree's stem ($R^2_{(2,149)} = 0{\cdot}76$; $P < 0{\cdot}0001$; Fig. 4) with the best-fit regression model found when DBH was considered as a second-order polynomial term. Regardless of tree size, the proportion of smooth bark texture was significantly greater with increasing height on the tree stem – that is, the lower metre of bark closest to the ground surface had less smooth-surfaced bark coverage (mean proportional coverage of 0·44) than the upper measured metre (mean proportional coverage of 0·57) (paired $t_{151} = 9{\cdot}5$, $P < 0{\cdot}0001$).

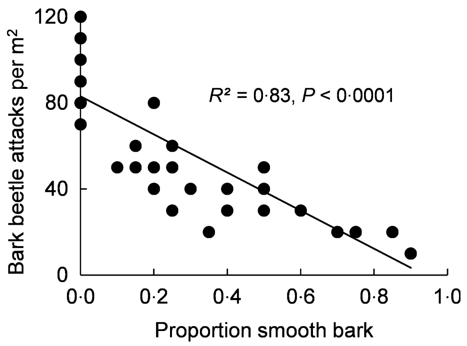

Fig. 2. Increasing proportional coverage of smooth bark on a pine tree's lower stem reduces the density of bark beetle attacks (mountain pine beetle attacks per square metre). The relationship between proportional coverage of smooth bark and bark beetle densities was tested via linear regression on data measured from a 50 × 20 cm grid placed on 43 limber pines between 20 and 25 cm in diameter at breast height in the Colorado Rocky Mountains, USA.

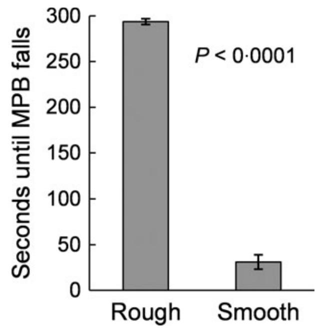

Fig. 3. Time (seconds) until mountain pine beetles (MPB) fell from the surface of rough- vs. smooth-textured bark in paired trials. Trials were stopped at a maximum time of 300 s (5 min) if MPB had not yet fallen. Smooth- and rough bark surfaces were located on the same tree to reduce variation in chemical cues that might influence MPB behaviour. Means (grey bars) and one standard error of the mean are shown; *P* value is from a paired *t*-test.

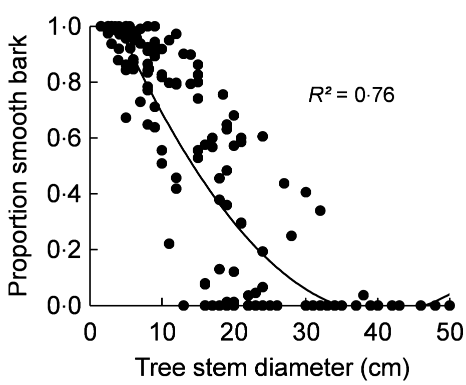

Fig. 4. Proportion of total bark surface that is smooth textured on the lower two metres of limber pine trees as related to tree size (diameter at 1·37 m above the ground surface). Data are from 151 trees sampled in the Colorado Rocky Mountains, USA. The solid line and values of *P and* R^2 are from polynomial regression.

BARK TEXTURE EFFECTS ON INSECT ATTACK DENSITY

Mean attack density measured from 23 pines killed by bark beetles in recent years was 99·1 (SE = 6·6) attacks/m^2, with a minimum of 37·1 and a maximum of 145·0 attacks/m^2 found among all trees. However, bark beetle attacks per square metre were positively related to tree size whereby larger trees have greater attack densities than smaller trees ($R^2_{(1,20)} = 0{\cdot}22$; $P = 0{\cdot}028$; $y = 52{\cdot}4 + 1{\cdot}49 \times$ DBH). Combining estimates of bark beetle attack densities across tree size with estimates of bark beetle attack density in relation to the proportion of smooth bark across tree size revealed the largest total reduction in bark beetle attacks per square metre due to the smooth bark effect was found for intermediate tree sizes (Fig. 5). The largest effect of smooth bark on bark beetle attacks for any sized tree was found for trees 9 cm in diameter, which see a reduction of 65·5 attacks/m^2. All trees measuring ≤ 23 cm in diameter have an estimate reduction in bark beetle attacks ≥ 20·0 attacks/m^2, while all trees ≤ 28 cm in diameter have an estimated reduction of ≥ 10·0 attacks/m^2. Reduction in bark beetle attacks for larger trees ranges from 9·0 attacks/m^2 in trees 28 cm in diameter to 2·1 attacks/m^2 in trees 40 cm in diameter.

Discussion

Tree bark is a first line of defence against insects and pathogens. Bark can contain not only chemical means to combat insect attacks (Krabel & Petercord 2000; Petrakis *et al.* 2011), but also anatomical structures (Franceschi *et al.* 2005). While smooth bark texture was historically hypothesized to be an anti-insect defence that operates by reducing the ability of insects to grip tree stems, no empirical tests of this hypothesis are available in the literature. We found that bark beetle attacks on *P. flexilis* (limber pines) were overwhelmingly located on rough bark and virtually absent on smooth bark (Fig. 1b,d), and that increasing proportions of smooth bark on tree stems led to decreases in bark beetle attack densities (Fig. 2). We also found in experimental trials that bark beetles were less able to grip smooth bark and quickly fell from the smooth bark surfaces, but not from rough bark surfaces (Fig. 3). This result supports the supposition that smooth bark defends

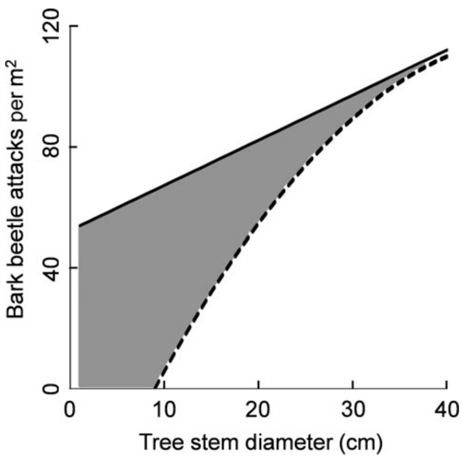

Fig. 5. The interacting effects of smooth bark texture and tree size on the number of mountain pine beetle (MPB) attacks per square metre of bark on limber pine trees (lower two metres of a tree's stem considered here as MPB rarely attack tree tops or limbs). The solid line shows the effect of tree size on MPB attack density; the dashed line shows the possible number of MPB attacks per square metre of bark based on the effect of bark texture and tree size. The shaded area illustrates the difference in total MPB attacks due to an effect of bark texture. While bark beetles rarely attack very small trees (trees < 10 cm in diameter), the mechanisms behind this pattern are poorly described. Thus, the effect of bark texture and tree size across trees of 1–40 cm is shown here to demonstrate the point when bark beetle attacks reach zero.

trees by mechanically 'shedding' attacking insects, and collectively, our results support our first two hypotheses that smooth bark on pines influences the location of insect attacks by reducing an insect's ability to grip the bark. Importantly, in our study, smooth bark on pine trees acted as an anatomical defence against one of the world's most destructive forest pests, the mountain pine beetle (*D. ponderosae*), which are insects specialized in attacking trees by boring through the bark.

We found that even for trees with mixtures of rough and smooth bark, smooth surfaces reduce total bark beetle attacks by ≥ 20 attacks/m^2 of bark surface in trees ≤ 23 cm in diameter (DBH). This is a notable reduction given that our model estimated average starting attack densities (i.e. densities expected in the absence of smooth bark effects) of 89·9 attacks/m^2 across trees 10–40 cm in diameter. Importantly, the estimated attack densities used in our predictive model are within the range of attacks per square metre reported for other mountain pine beetle-infested forests (Clark, Huber & Carroll 2012; Duhl *et al.* 2013) and are similar to the threshold densities reported to bring about pine mortality (Raffa & Berryman 1983). Also, while it is commonly stated or assumed that bark beetles primarily attack only the largest trees in mature forest stands, recent mountain pine beetle epidemics in the U.S. Rocky Mountains have been marked by substantial mortality in small trees. For example, trees <23 cm in diameter account for roughly 50% of bark beetle-induced mortality in numerous stands of lodgepole pine (*Pinus contorta*), a tree that rarely has smooth bark surfaces (Progar *et al.* 2013). The large numbers of attacks on smaller size classes of trees combined with the need for bark beetle aggregation on individual tree stems to overcome tree defences suggest that smooth bark could realistically reduce bark beetle attack density and related tree mortality across the many coniferous tree species with smooth bark traits during or throughout their life spans (Biswas & Johri 1997). It should be noted that the number of insect attacks necessary for overcoming plant defences, in this and other study systems, is influenced by plant physiological status and other abiotic and biotic factors over time (Huberty & Denno 2004; Gaylord *et al.* 2013). Nevertheless, defence mechanisms that reduce total bark beetle attacks have been shown to reduce tree mortality in several coniferous species (Wood 1982; Raffa & Berryman 1983). Also, while defensive resin flow and secondary chemistry can enable conifers to withstand bark beetle attacks (Sturgeon & Mitton 1986; Kane & Kolb 2010; Ferrenberg, Kane & Mitton 2013), these defences are mainly encountered after beetles have already damaged the tree (Franceschi *et al.* 2005). Smooth bark, however, inhibits bark beetle attacks before damage is incurred, which presumably leaves overall tree vigour unaffected, and makes this bark defence highly effective for predominantly smooth trees.

Bark texture has long been considered to be of adaptive significance (Esau 1967; Roth 1981). While we found that smooth bark defends against insect attack, bark texture could enhance tree fitness in other ways. For example, rough-textured bark can increase resistance to fire and drought (Glitzenstein & Harcombe 1979; Pinard & Huffman 1997) and improve a tree's heat balance (Derby & Gates 1966). Meanwhile, smooth bark can increase the volume and nutrient content of water flowing along tree stems after precipitation (Van Stan & Levia 2010). Taken together, these reports indicate that smooth bark could be an adaptation to stresses other than herbivory or insect attack, which would make its contribution to defences a form of 'neutral resistance' (Edwards 1989). Nevertheless, neutral resistance traits (traits that offer defence but are evolved for other purposes) still influence overall plant anti-insect defence. As noted by Strauss & Agrawal (1999), a trait that confers anti-insect defence to a plant must be considered in the study of defences regardless of its adaptive function. It is also important to note that plant surface texture has been previously shown to influence plant–insect interactions in ways that could promote co-evolved relationships. For example, some bees can identify flowers by touch (Kevan & Lane 1985; Erber *et al.* 1998; Scheiner *et al.* 2005; Yoshioka *et al.* 2007) and increased surface texture of flower petals increases pollinator visits (Comba *et al.* 2000). Experiments also indicate that bees avoid smooth, steeply angled flowers because of an inability to grip their surfaces (Whitney, Federle & Glover 2009b & Whitney *et al.* 2009a). Taken collectively, these studies and our results indicate a need for further study of the roles that plant surface textures might play in plant–insect interactions and evolutionary biology.

We found support for our third hypothesis that bark texture is influenced by tree ontogeny, whereby increasing tree size leads to decreasing coverage by smooth bark (Fig. 4) and that surface area of smooth bark tends to increase with increasing height on tree stems. These results suggest an effect of age-related or growth-related factors on bark texture in *P. flexilis*. Similar changes in bark texture with stages of ontogeny have been described for other deciduous (Lev-Yadun & Aloni 1993; Pinard & Huffman 1997; Friedel *et al.* 2006) and coniferous species (Biswas & Johri 1997; Malone & Liang 2010). We found the defence offered by smooth bark against bark beetles is greatest for smaller trees, but is retained into trees that are, respectively, large in size (approximately 30 cm in diameter; Fig. 5) in our study system – a subalpine forest with short growing seasons and slow tree growth (Mitton & Ferrenberg 2012; Duhl *et al.* 2013; Ferrenberg, Kane & Mitton 2013). The greater defence offered by smooth bark on smaller trees is important since younger trees located near mature conspecifics or congeners can have higher probabilities of being attacked by shared pests (Janzen 1970; Peters 2003; Terborgh 2012). Also, coniferous trees such as those studied here often grow in dense, low diversity stands, which can promote the movement of pests and reduce survival of younger/smaller trees (Schupp, Milleron & Russo 2002). Thus, smooth bark surfaces might benefit pines more in early ontogenetic stages – when proportional coverage of stems by smooth bark is greatest – helping them to escape shared insect pests. However, increased resistance against insect attack offered by even small proportions of smooth bark in larger trees (Fig. 5) could have long-term consequences for pine survival as warming temperatures promote insect range expansion (Mitton & Ferrenberg 2012) and as insect-induced mortality continues to exceed drought-induced mortality in high elevation forests (Das *et al.* 2013).

Conclusions

While ours is the first known study of its kind, we have demonstrated that smooth bark can limit attacks by insects on trees – even for insect species specialized in attacking tree stems. The reduction in bark beetle attacks on trees with large proportions of smooth bark appeared to decrease rates of bark beetle-induced mortality – an observation that initially inspired our study but that requires long-term investigation. However, we did not attempt to measure bark texture impacts on rates of mortality because we selected our study sites by locating dead or dying trees, which could lead to an over-sampling of trees susceptible to insect attack, and reduced our ability to determine whether trees had been predisposed to insect attack due to prior stresses such as native root fungi and introduced pathogens that abound in our study region (Kinloch 2003). Our results will hopefully inspire future studies of ways in which bark texture might influence the demography and ecology of trees and forest insects. While the effects of bark texture have been widely considered for lichens (Cramer 1975; Holien 1997), bark effects are overlooked in studies of forest insects. Even when differences in bark texture between trees are clear and variation in secondary chemistry is minimal, differences in the diversity and density of tree bark-associated insects are still often attributed to plant-secondary chemistry (e.g. Petrakis *et al.* 2011). Nevertheless, our results not only indicate that smooth bark defends a widespread and ecologically important pine species from one of the world's most destructive forest insects, but also call for a resurrection of the 'smooth bark as defence' hypothesis.

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References

Agrawal, A.A. & Fishbein, M. (2006) Plant defense syndromes. *Ecology*, **87**, S132–S149.

Agresti, A. (1996) *An Introduction to Categorical Data Analysis*, vol. **135**. Wiley, New York.

Baier, P. (1996) Defence reactions of Norway spruce *(Picea abies* Karst.) to controlled attacks of *Ips typographus* (L.) (Col., Scolytidae) in relation to tree parameters. *Journal of Applied Entomology*, **120**, 587–593.

Biswas, C. & Johri, B.M. (1997) *The Gymnosperms*. Springer Verlag, Berlin.

Black, H.L. & Harper, K.T. (1979) The adaptive value of buttresses to tropical trees: additional hypotheses. *Biotropica*, **11**, 240.

Boege, K. & Marquis, R.J. (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology & Evolution*, **20**, 441–448.

Boom, B.M. & Mori, S.A. (1982) Falsification of two hypotheses on liana exclusion from tropical trees possessing buttresses and smooth bark. *Bulletin of the Torrey Botanical Club*, **109**, 447–450.

Carmona, D., Lajeunesse, M.J. & Johnson, M.T. (2011) Plant traits that predict resistance to herbivores. *Functional Ecology*, **25**, 358–367.

Clark, E.L., Huber, D.P.W. & Carroll, A.L. (2012) The legacy of attack: implications of high phloem resin monoterpene levels in lodgepole pines following mass attack by mountain pine beetle, *Dendroctonus ponderosae* Hopkins. *Environmental Entomology*, **41**, 392–398.

Comba, L., Corbet, S.A., Hunt, H., Outram, S., Parker, J.S. & Glover, B.J. (2000) The role of genes influencing the corolla in pollination of *Antirrhinum majus*. *Plant Cell and Environment*, **23**, 639–647.

Cramer, M.B. (1975) Corticolous lichens of riparian deciduous trees in the central Front Range of Colorado. *Bryologist*, **78**, 44–56.

Das, A.J., Stephenson, N.L., Flint, A., Das, T. & van Mantgem, P.J. (2013) Climatic correlates of tree mortality in water- and energy-limited forests. *PLoS ONE*, **8**, e69917.

Derby, R.W. & Gates, D.M. (1966) The temperature of tree trunks–calculated and observed. *American Journal of Botany*, **53**, 580–587.

Duhl, T.R., Gochis, D., Guenther, A., Ferrenberg, S. & Pendall, E. (2013) Emissions of BVOC from Lodgepole Pine in response to Mountain Pine Beetle attack in high and low mortality forest stands. *Biogeosciences*, **10**, 483–499.

Edwards, P.J. (1989) Insect herbivory and plant defence theory. *Towards a More Exact Ecology* (eds P.J. Grubb & J.B. Whittaker), pp. 275–297. Blackwell, Oxford.

Erber, J., Kierzek, S., Sander, E. & Grandy, K. (1998) Tactile learning in the honeybee. *Journal of Comparative Physiology A*, **183**, 737–744.

Esau, K. (1967) *Plant Anatomy*. John Wiley and Sons, New York, NY, USA.

Farjon, A.. (1984) *Pines: Drawings and Descriptions of the Genus Pinus*. EJ Brill, Leiden, Netherlands.

Ferrenberg, S., Kane, J.M., & Mitton, J.B. (2013) Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia*, DOI.10.1007/s00442-013-2841-2

Forsyth, A. & Miyata, K. (1984) *Tropical Nature*. Charles Scribner's Sons, New York, NY, USA.

Franceschi, V.R., Krokene, P., Christiansen, E. & Krekling, T. (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, **167**, 353–376.

Friedel, A., v. Oheimb, G., Dengler, J. & Härdtle, W. (2006) Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany. *Feddes Repertorium*, **117**, 172–185.

Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yepez, E.A., Macalady, A.K. *et al.* (2013) Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist*, **198**, 567–578.

Glitzenstein, J. & Harcombe, P.A. (1979) Site-specific changes in the bark texture of *Quercus falcata* Michx. (Southern red oak). *American Journal of Botany*, **66**, 668–672.

Hanley, M.E., Lamont, B.B., Fairbanks, M.M. & Rafferty, C.M. (2007) Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 157–178.

Hedden, R.L. & Gara, R.I. (1972) The analysis of the spatial attack pattern of an endemic Douglas-fir beetle population. Internal Report 76 of the U.S. International Biological Program, Coniferous Forest Biome, University of Washington, Seattle, WA, USA.

Hlásny, T. & Turčáni, M. (2013) Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: case study from Central Europe. *Annals of Forest Science*, **70**, 481–491.

Holien, H. (1997) The lichen flora on *Picea abies* in a suboceanic spruce forest area in Central Norway with emphasis on the relationship to site and stand parameters. *Nordic Journal of Botany*, **17**, 55–76.

Huberty, A.F. & Denno, R.F. (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, **85**, 1383–1398.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.

Kane, J. & Kolb, T. (2010) Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia*, **164**, 601–609.

Kevan, P.G. & Lane, M.A. (1985) Flower petal microtexture is a tactile cue for bees. *Proceedings of the National Academy of Sciences, USA*, **82**, 4750–4752.

Kinloch, B.B. (2003) White pine blister rust in North America: past and prognosis. *Phytopathology*, **93**, 1044–1047.

Krabel, D. & Petercord, R. (2000) Genetic diversity and bark physiology of the European beech (*Fagus sylvatica*): a coevolutionary relationship with the beech scale (*Cryptococcus fagisuga*). *Tree Physiology*, **20**, 485–491.

Lev-Yadun, S. & Aloni, R. (1993) Bark structure and mode of canopy regeneration in trees of *Melia azedarach* L. *Trees: Structure and Function*, **7**, 144–147.

Malone, T. & Liang, J. (2010). A bark thickness model for White spruce in Alaska Northern Forests. International Journal of Forestry Research, 2009.

Meddens, A.J., Hicke, J.A. & Ferguson, C.A. (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*, **22**, 1876–1891.

Mitton, J.B. & Ferrenberg, S.M. (2012) Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *American Naturalist*, **179**, E163–E171.

Peters, H.A. (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters*, **6**, 757–765.

Petrakis, P.V., Spanos, K., Feest, A. & Daskalakou, E. (2011) Phenols in leaves and bark of *Fagus sylvatica* as determinants of insect occurrences. *International Journal of Molecular Science*, **12**, 2769–2782.

Pinard, M.A. & Huffman, J. (1997) Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology*, **13**, 727–740.

Progar, R.A., Blackford, D.C., Cluck, D.R., Costello, S., Dunning, L.B., Eager, T. *et al.* (2013) Population densities and tree diameter effects associated with verbenone treatments to reduce mountain pine beetle-caused mortality of lodgepole pine. *Journal of economic entomology*, **106**, 221–228.

Putz, F.E. (1984) How trees avoid and shed lianas. *Biotropica*, **16**, 19–23.

Raffa, K.F. & Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*, **53**, 27–49.

Roth, I. (1981) *Structural Patterns of Tropical Barks. Encyclopedia of Plant Anatomy Vol. IX, Part 3*. Gebruder Borntraeger, Berlin. 609 pages.

Scheiner, R., Kuritz-Kaiser, A., Menzel, R. & Erber, J. (2005) Sensory responsiveness and the effects of equal subjective rewards on tactile learning and memory of honeybees. *Learning and Memory*, **12**, 626–635.

Schoettle, A.W. & Rochelle, S.G. (2000) Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. *American Journal of Botany*, **87**, 1797–1806.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) *Dissemination Limitation and the Origin and Maintenance of Species-Rich Tropical Forests*, pp. 19–33. Ecology, Evolution and Conservation, Seed dispersal and frugivory.

Stephenson, S.L. (1989) Distribution and ecology of myxomycetes in temperate forests. II. patterns of occurrence on bark surface of living trees, leaf litter, and dung. *Mycologia*, **81**, 608–621.

Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*, **14**, 179–185.

Sturgeon, K.B. & Mitton, J.B. (1986) Biochemical diversity of *Pinus ponderosa* Laws. and predation by bark beetles, *Dendroctonus* spp. (Coleoptera: Scolytidae). *Journal of Economic Entomology*, **79**, 1064–1068.

Terborgh, T. (2012) Enemies maintain hyperdiverse tropical forests. *American Naturalist*, **179**, 303–314.

Trapp, S. & Croteau, R. (2001) Defensive resin biosynthesis in conifers. *Annual Review of Plant Physiology and Plant Molecular Biology*, **52**, 689–724.

Van Stan, J.T. & Levia, D.F. (2010) Inter- and intraspecific variation of stemflow production from *Fagus grandifolia* Ehrh. (American beech) and *Liriodendron tulipifera* L. (yellow poplar) in relation to bark microrelief in the eastern United States. *Ecohydrology*, **3**, 11–19.

Wardle, D.A., Yeates, G.W., Barker, G.M., Bellingham, P.J., Bonner, K.I. & Williamson, W.M. (2003) Island biology and ecosystem functioning in epiphytic soil communities. *Science*, **301**, 1717–1720.

Whitmore, T.C. (1963) Studies in systematic bark morphology. IV. The bark of beech, oak and sweet chestnut. *New Phytologist*, **62**, 161–169.

Whitney, H., Federle, W. & Glover, B.J. (2009b) Grip and slip: mechanical interactions between insects and the epidermis of flowers and flower stalks. *Communicative and Integrative Biology*, **2**, 505–508.

Whitney, H., Chittka, L., Bruce, T. & Glover, B.J. (2009a) Conical epidermal cells allow bees to grip flowers and increase foraging efficiency. *Current Biology*, **19**, 1–6.

Wood, D.L. (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Reviews of Entomology*, **27**, 411–446.

Yang, Y. (2005) Can the strengths of AIC and BIC be shared? *Biometrika*, **92**, 937–950.

Yoshioka, Y., Ohashi, K., Konuma, A., Iwata, H., Ohsawa, R. & Ninomiya, S. (2007) Ability of bumblebees to discriminate differences in the shape of artificial flowers of *Primula sieboldii* (Primulaceae). *Annals of Botany*, **90**, 1175–1182.

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