REVIEW PAPER

Insect ecology and veteran trees

Jakub Horák¹

Received: 14 June 2016 / Accepted: 16 January 2017 / Published online: 2 February 2017 © Springer International Publishing Switzerland 2017

Abstract Insect and veteran trees are important parts of ecosystems and are usually included in ecological studies of forest management. The loss of veteran trees in woodlands and open landscapes would lead to the loss of saproxylic organisms-an important part of biodiversity. Hence, the persistence of many specialized insects depends on the presence of veteran trees scattered in woodlands (e.g. ancient wood pastures, game parks or protected areas), cities, towns and villages (e.g. avenues, parks or chateau parks) or open landscapes (e.g. fishpond dams, solitary trees or fruit orchards). Veteran tree conditions could be fairly well described by three components-diameter, age and microhabitats present. The problem is that diameter belongs to the most studied characteristics, while age and microhabitats, which can be quite complicated to measure, are much less studied. This paper illustrates that, due to this unbalanced use of indicators of veteran-tree conditions, we are still missing some important information on saproxylic species ecology-and sometimes only large trees might be studied, rather than real veterans. Although we already know that veteran trees are essential habitat for a range of saproxylic organisms, there are still gaps in our knowledge of the specific conditions that veteran trees provide. It is vital that these are quantified and understood so that this information can be used to conserve veteran trees and their associated species.

⊠ Jakub Horák jakub.sruby@gmail.com

Introduction

Insects are driven by many environmental factors and, in turn, insects can influence their environment. Many species of insects are important pollinators, often mentioned as keystone species-which are necessary for ecosystem functioning and, moreover, for future crop production and quality (Klatt et al. 2014). Some organisms are recognized in conservation biology as umbrella species; habitat management for such species thus protects and shelters a range of others who require similar conditions (Gouix et al. 2015; Foit et al. 2016). Some umbrella species have high potential to strongly modify their environment and increase its biodiversity value, as do ecosystem engineers (Lill and Marquis 2003; Hilszczanski et al. 2016). Even if the majority of insects are, in general, not as popular with people as orchids, big trees, passerine birds or carnivores, there are still numerous conspicuous species that can be used as flagships (Schlegel and Rup 2010).

Nevertheless, one surely cannot say which group of insects is the most popular—and it does not matter whether it is taxonomic, guild, functional or any other group. However, a review of papers in scientific journals published within the last decade reveals that one of the most popular groups is insects that are dependent on dead wood—especially in forest ecosystems (e.g. Grove 2002). They are mostly called saproxylic and, of course not surprisingly, the most important taxonomic group is beetles (Speight 1989; Stockland et al. 2012). If we compared them with the other groups, their popularity in the last years could be compared with butterflies in grasslands. Saproxylic insects can reveal



¹ Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 1176 165 21 Prague, Czech Republic

much new and important information for basic science and applied research and should be used to help forest and landscape managers design optimum management programs for forest ecosystems (Bouget et al. 2013; Horak et al. 2014; Kirby 2015). One of the most important factors in the retention of saproxylic species in an area is the presence of veteran trees (Alexander 2008). However, veteran trees remain under threat by felling, leading to problems with spatiotemporal continuity at the landscape level (Miklín and Čížek 2014).

Information on the location of the most important aggregations of veteran trees has improved in recent years, typically these include ancient forests, game parks, avenues or fishpond dams, fruit orchards or chateau parks that were not previously identified as being important sites for veteran trees (Figs. 1, 2). Whilst this information has improved our knowledge of where to find veteran trees, our knowledge of the specific conditions that veteran trees provide that are essential for saproxylic species is still wanting (Alexander 2008). We still, as yet, need to identify and quantify the most important characteristics which are responsible for high biodiversity values of saproxylics associated with particular veteran trees. Of course, veteran trees do not live in isolation and changes to their local surroundings (e.g. the felling of avenues of old trees and their replacement with new stock) are likely to have an influence on their colonization by insects. Saproxylic species have moderate dispersal abilities (Jackson and Fahrig 2015) and can be influenced by land-use



Fig. 1 Big oak (*Quercus* spp.) trees as potential veterans on a former fishpond dam—now growing inside the forest together with smaller trees of Norway spruce, European ash (*Fraxinus excelsior*) and black alder (*Alnus glutinosa*). Oaks are probably as old as the fishpond which is illustrated on maps from 1839 (III. Austrian-Hungarian Military Mapping) and the trees are recognizable by their large crowns, compared to surrounding trees, on aerial photographs from 1954 (e.g. kontaminace.cenia.cz)



Fig. 2 Abandoned traditional fruit orchard, as formerly common agro-forestry habitat in Europe, here dominated by cherry trees (*Prunus avium*). The passive trunk tree trap in front trapped the false click beetle *Dromaeolus barnabita*, a saproxylic beetle species that is mentioned as an indicator of primeval forest conditions and had approximately five localities of known occurrence in the Czech Republic in 2010 (Dušánek and Mertlik 2010). This tree had less than 40 cm of DBH, but had some dead twigs and branches, and some were attacked by bark beetles (*Scolytus mali* and *S. rugulosus*). Other trapped important saproxylic species were the handsome fungus beetle *Symbiotes gibberosus*, skin beetle *Megatoma undata* and rose chafer *Protaetia marmorata*

changes within the surrounding 0.5 km, although changes occurring closer to the trees may be particularly important (Horak 2014). Stand-level characteristics, such as the density (total number) of veteran trees (Ranius 2006) and structural characteristics of patches such as the distance to the nearest veteran tree (Buse et al. 2007) are also important. Although we are beginning to get a feel for the macro- to meso-scale issues affecting saproxylics, it is at the tree level that data is most needed (Horak and Pavlicek 2013). For example, whilst many studies have been carried out that examine the impact of tree diameter, the impact of tree age is understudied and the role of microhabitats are somewhere in between (e.g. Irmler et al. 1996). Clearly it is important to establish what the most important characteristic of individual trees is in terms of their relationship with saproxylic insects; and here it is worth remembering that veteran trees are living, and not dead (Lonsdale 2013).

Most literature sources describe veteran trees as old (without giving a lower age limit), with a large diameter, and comment on the number and range of microhabitats (e.g. hollows, dead limbs or fruiting bodies of fungi). One can conclude from this that the tree diameter is much easier to establish than the age, and that microhabitats, often hidden in the crown, are not easily sampled or categorized (Winter and Möller 2008).

Continuing, in a roundabout way: one of the most important patterns in biogeography is the species-area relationship, which in general says that the number of species increases with increasing area of suitable habitat (e.g. Gaston 2000). This rule is clearly reflected in the response of grassland insect taxa to habitat area (e.g. Horák 2016). But what is the appropriate equivalent parameter to area for saproxylic insects; is it, for example, the amount of dead wood in the surroundings? If yes, exactly what do we mean by surroundings, what would be the appropriate size area to assess? Nevertheless, the amount of dead wood in a given area has little to do with the characteristics of a living veteran tree and its specialist microhabitats, but is rather a measure of patch quality (Horák et al. 2016). Alternatively, the diameter of a particular tree could be the most important parameter and there are several studies that use this successfully (e.g. Buse et al. 2016). Most of the studies using the diameter of a tree use the 'diameter at the breast height' (DBH)-i.e. the measurement is taken at 1.3 m above ground. Nevertheless, this might be one of the potential pitfalls-because some veterans can have more than one stem, especially very old stumps in coppices. Furthermore, not all veteran trees have a regular shape of circumference of the stem. One of the options is to use the total volume of the tree, but we can mostly use only forest standards that are suitable for trees growing in dense forest conifer plantations. Thus, in this case, when diameter still is, and in the future probably will be, one of the most used characteristics of veteran trees, there is a strong need for studies that are able to shed more light into the connection of diameter with age and microhabitats (Irmler et al. 1996; Horak and Pavlicek 2013; Altman et al. 2016). An example that could bring more attention to the use of diameter as the reflection of the age of the tree is the fact that some forest trees grow slowly-so, a 525 year-old Norway spruce (Picea abies) named Stožecký smrk in Šumava (Czech Republic) had a 0.13 m diameter at the age of 130 years and the 409 year-old European beech had a diameter of a 0.66 m (Čada 2014).

Regarding the interconnection of DBH and microhabitats, there is evidence that as pedunculate oak increases in age, so does DBH (*Quercus robur*) and so does the number of hollows (Ranius et al. 2009). On the other hand, hollows are only one part to the mosaic of microhabitats in veteran trees (Winter and Möller 2008). Most of the known published results would lead to the conclusion that a large diameter means the increased age of the tree and high number of microhabitats—but what if it is not the full story (Figs. 2, 3, 4)? Probably not, but based on a search within scientific journals, we can find disproportionately more between studies based on the relationship of insects with the diameter (or circumference) compared with those using the age of the tree—because measuring the age of the tree



Fig. 3 Lower part of the stem of a pedunculate oak, which was felled from the fishpond dam. Despite its huge diameter, this tree was only a little over 100 years old



Fig. 4 Uprooted Devils' oak. Despite its size and possible age, which ranked this tree among the most monumental trees in the region, this oak bears virtually no microhabitats

is expensive and in the case of very old trees, that are rotten inside, often impossible (Altman et al. 2016). It is also nearly impossible to gain permission for this kind of study in protected areas of nature conservation interest. Nevertheless, where it is possible to identify the age of trees, it would be worth exploring the impact of tree age on the value of veteran trees for saproxylic insects (e.g. in commercial forests).

Everybody, who has ever collected tree-level data and has used statistics for their evaluation regarding insect diversity, knows that the inclusion of microhabitats is quite complicated. This can be done in a number of ways, and one of them is the use of microhabitat-specific

 Table 1 An outline of possibilities of measurement of veteran tree characteristics in prevailing forest management types in most of Europe

Forest management type	DBH	Microhabitats	Age
Agro-forestry	Easy	Easy	Easy
Coppice	Hard	Moderate	Hard
Coppice with standards	Moderate	Easy	Moderate
High forest	Easy	Easy	Easy
High forest with green tree retention	Moderate	Easy	Moderate
Hands-off forests	Easy	Moderate	Moderate
Wood pastures	Easy	Easy	Moderate

Note that DBH is the diameter at breast height

categorization—e.g. the number of hollows or the percentage of stem without bark. The problem is that each categorical variable worsens the parsimony in statistical analysis (e.g. loss of degrees of freedom, imbalance of categories or an artificial increase in explained variance). We can also use the number of microhabitats in a particular tree at a continuous scale, but in this case we lose the information about microhabitat diversity. Thus, studies combining these approaches in different habitats are needed.

Finally, there are at least three options to best describe veteran tree conditions regarding the fascinating saproxylic insect diversity. While the diameter can be measured relatively easily, age and microhabitats are quite difficult to evaluate and may sometimes only be estimates. Even if diameter bears many potential pitfalls it will probably be the most used surrogate for veteran tree conditions in saproxylic insect ecology. Nevertheless, the use of two other measures (age and microhabitat diversity) with a high potential for improvement in our knowledge of the relationship between insects and veteran trees is highly recommended in future studies (Table 1).

Conclusions

Veteran trees can be described by more parameters than just diameter, but the others cannot be measured as easily. Thus, if we study the impact of veteran trees on insect diversity, we need to carefully pay attention to what characteristics at the tree level were used and how to correctly interpret them. It is clear that we still do not know much about the true relationship of insects with the age of a particular tree—especially because large does not necessarily mean old (Fig. 3). Furthermore, trees with a large diameter and old age do not always provide microhabitats that are suitable for saproxylic insects (Fig. 4). It is vital that veteran trees are quantified and understood so that this information can be used to conserve them and their associates. Acknowledgements This study was supported by the grant NAZV KUS QJ1520197 ENvironmental REsistance of stable FOrest stands fulfilling the non-wood-producing roles and the Internal Grant Agency (IGA no. B03/16), Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague.

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