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Review

Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management

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ABSTRACT

Studies on the vertical distribution patterns of arthropods in temperate deciduous forests reveal highly stratified (i.e., unevenly vertically distributed) communities. These patterns are determined by multiple factors acting simultaneously, including: (1) time (forest age, season, time of day); (2) forest structure (height, vertical foliage complexity, plant surface textures, tree cavities); (3) plant community composition (plant diversity, invasive species); (4) climatic gradients (light exposure, temperature, wind speed, humidity); (5) resource availability (foliage, sugars, wood, epiphytes, carrion, dung, prey, hosts, mates); (6) inter-specific interactions (predation, interference, competition) and (7) logistics (dispersal abilities, proximity to emergence sites, open flight zones). Several recommendations can be made with respect to incorporating canopy habitats and resources into management plans in order to maintain diverse forest arthropod communities. Efforts should be made to maintain diverse plant communities, for instance, including eliminating or controlling invasive plant competitors. Protecting large diameter trees and snags is also important, especially for a wide variety of canopy arthropod taxa associated with standing or suspended dead wood, tree cavities and epiphytes. Finally, it is essential to ensure adequate spatial and temporal continuity in the availability of these and other key resources. Although how to best achieve this last objective remains an active area of research, it may be preferable to retain clusters of trees as opposed to isolated individuals.

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1. Overview

Although the importance of biodiversity to the stability, resilience and productivity of forests is now widely recognized (Loreau et al., 2002; Hooper et al., 2005; Peuttmann et al., 2009), most forest-dwelling species remain either undiscovered (May, 1988; Stork, 1988), unknown ecologically (Spence et al., 2008), or of undetermined conservation status (Wilcove and Master, 2005). Because a large proportion of these organisms reside in the forest canopy (defined as, “all aboveground plant structures and the interstitial spaces between them, which collectively form the interface between the soil and the atmosphere”), canopy research is essential for acquiring the holistic perspective needed to optimize conservation and management strategies (Moffett, 2000; Moffett, 2001; Didham and Fagan, 2004). Temperate deciduous forests are among the most widespread and altered forests in the world, having been exploited intensively throughout their range to meet the demands of agriculture, industry and human settlement (Röhrig and Ulrich, 1991). Yet their canopies (and associated organisms) have historically received less attention than those of tropical rainforests. This is perhaps due to the belief that they are less stratified (i.e., unevenly vertically distributed) (Lowman et al., 1993; Basset et al., 2003) and support a smaller proportion of highly specialized species restricted to the canopy. Structurally, there is little doubt that temperate deciduous forests are less vertically complex and these differences probably do equate to a lower proportion of canopy-restricted specialists. For example, differences in the light regime, particularly the angle of incidence, along the latitudinal gradient may play a central role in determining the possible number of vegetative strata (Terborgh, 1985; Tanabe et al., 2001) and this, in turn, is likely to influence the stratification of other organisms (Smith, 1973; Tanabe et al., 2001; Tanabe, 2002). The dramatic seasonality characteristic of temperate deciduous forests (i.e., the loss of foliage, cold winter temperatures, etc.) is also likely to limit the proportion of species truly restricted to the canopy, as many must return to the ground to overwinter (Elton, 1966). It is clear from a growing body of literature, however, that a large number of species in temperate deciduous forests depend on canopy habitats, even if relatively few of them are restricted there. While studies have shown many arthropod orders become less abundant, species rich or diverse with height above the forest floor (e.g., Nielsen, 1987; Preisser et al., 1998; Hollier, 2007; Hacker and Müller, 2008; Hirao et al., 2009), the highly stratified nature of these communities (and the importance of arboreal habitats and resources) becomes obvious with increasing taxonomic resolution (in addition to examples given below, see Davidson, 1930; Snow, 1955; Anderson and DeFoliart, 1961; Dobson, 1974; Tanner and Turner, 1974; Kiszewski and Cupp, 1986; Saure and Kielhorn, 1993; Mora et al., 1999; Anderson et al., 2004; Russell and Hunter, 2005; Leksono et al., 2005a; Darbro and Harrington, 2006; Leksono et al., 2006; Andreadis and Armstrong, 2007; Hirao et al., 2007; Savage et al., 2008; Gossner, 2009; Černý et al., in press). The primary objectives of this article are to (1) demonstrate that arthropod communities are highly dependent on canopy habitats, (2) review the primary factors influencing vertical stratification and (3) discuss implications for conservation-oriented management.

2. Time

Time is one of the greatest sources of variability with respect to arthropod vertical distribution (Didham and Springate, 2003) and this is especially true in temperate deciduous forests. First, forest canopies deepen and become increasingly structurally complex (see Section 3) as succession proceeds and trees age. The canopies of old forests contain a greater variety of habitats and resources than those of young forests (Brokaw and Lent, 1999; Ishii et al., 2004b) and support more diverse arthropod faunas (Jeffries et al., 2006; Floren and Schmidl, 2008; Horstmann and Floren, 2008). Between-forest comparisons made without regard to differences in forest age, such as those between primary tropical rainforests and predominately secondary temperate deciduous forests (e.g., Lowman et al., 1993), should therefore be avoided. Second, the seasonal changes characteristic of temperate deciduous forests are more dramatic than those of any other forest type (Röhrig and Ulrich, 1991), with important implications for the vertical distributions of arthropods. With some important exceptions (e.g., Gibson, 1947; Park et al., 1950; Paviour-Smith and Elbourn, 1993; Nickel, 2008; Ulyshen, in press), many species are thought to move to the forest floor with the onset of cold temperatures (e.g., Yamazaki, 2010), with migration in the reverse direction occurring the following spring (Weese, 1924; Adams, 1941). Less obvious seasonal changes such as host tree phenology (e.g., flowering, see Section 6.2) are also very important in affecting vertical distribution patterns (Didham and Springate, 2003). Finally, many arthropods exhibit distinct daily activity patterns and their vertical distribution patterns change accordingly (Adams, 1941; Novak et al., 1981; Costa and Crossley, 1991).

3. Forest structure

The physical framework upon which epiphytic (see Section 6.4) and faunal communities develop and across which vertical gradients establish is of central importance in determining the vertical distribution patterns of arthropods. Particularly important structural attributes include forest height, vertical foliage complexity, plant surface textures and tree cavities, as outlined below.

3.1. Forest height

Among the many factors influencing forest height are age, site quality, tree composition and altitude (Aber, 1979). Although arthropod species–volume relationships have not been explored in forests, increases in canopy volume per unit area with forest height likely enhance canopy arthropod diversity. Furthermore, ecologically meaningful vertical gradients are more likely to establish in tall than in short forests (Brokaw and Lent, 1999).

3.2. Vertical foliage complexity

Foliage becomes less concentrated high in the canopy and more evenly distributed vertically (i.e., diverse, see MacArthur and MacArthur, 1961) as forests age (Aber, 1979; Yang et al., 1999; Nadkarni et al., 2004) and tree species richness increases (Yang et al., 1999; Ishii et al., 2004a), thereby enhancing habitat heterogeneity and promoting microhabitat segregation within arthropod communities (Tanabe, 2002). Moreover, intra-crown leaf area index decreases as trees age, with important implications for within-canopy gradients (Nock et al., 2008). A distinct midstory is sometimes present (Parker et al., 1989), but only when there is adequate spacing (i.e., crown shyness) between adjacent overstory trees (Terborgh, 1985). Because midstory trees tend to reach

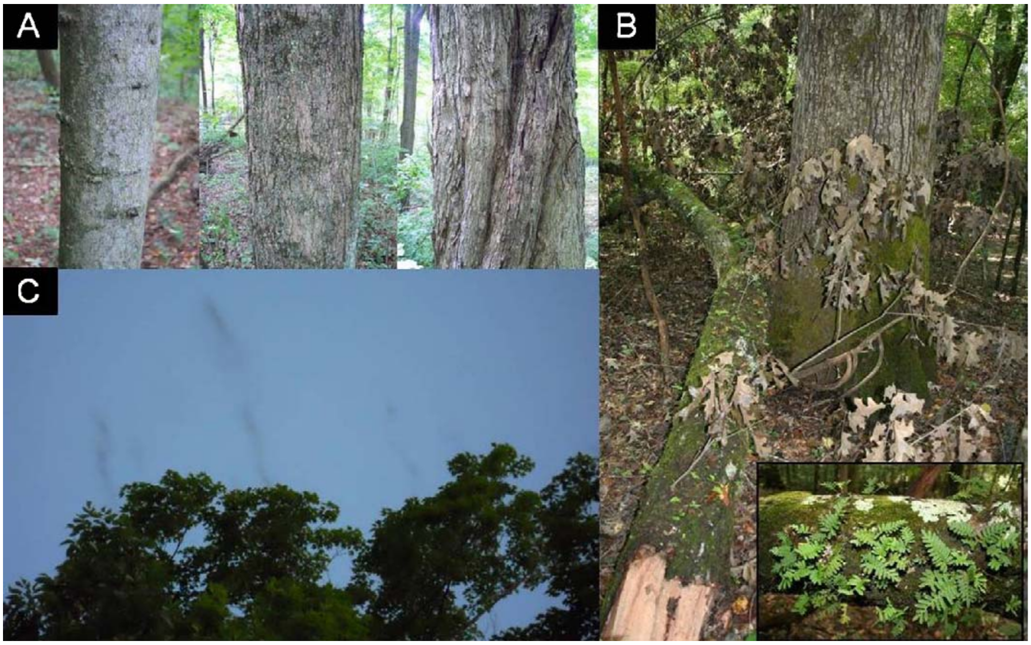

Fig. 1. (A) Bark roughness increases with tree age and size as demonstrated by these *Acer saccharum* from Ohio, U.S.A. (approximate diameters from left to right were 6, 30 and 100 cm). (B) Epiphytes on a mature oak in Mississippi, U.S.A. The broken branch to the left was attached to the tree approximately 15 m above the ground. It supported thick mats of bryophytes, lichens and the fern *Pleopeltis polypodioides* (L.) Andrews and Windham (inset). (C) Flies swarming above the forest canopy at dusk in New York, U.S.A.

the same maximum height regardless of species or age (Terborgh, 1985), forests with midstories have a highly layered appearance and these layers are likely to influence the dispersal heights of arthropods by creating flight paths (Smith, 1973). Similar midstory layers can develop temporarily following flushes of seedling production resulting from a disturbance event or from aggregations of suppressed saplings (Smith, 1973) or shade tolerant species developing beneath an early successional canopy, although these are generally less uniform in height. Many arthropod taxa are less numerous in the relatively open and less-vegetated trunk zone than in the upper canopy or near the forest floor (Toda, 1977; Schroeder et al., 2009). Forests become more horizontally complex with age as well, with mature forests consisting of a mosaic of treefall gaps at various stages of succession (Brokaw and Lent, 1999; Tanabe, 2002). These and other open spaces greatly influence the vertical distribution patterns of arthropods (and their predators), particularly those capable of flight (Didham and Fagan, 2004).

3.3. *Plant surface textures*

The textures of plant surfaces often vary with height above the ground and can affect how many arthropods are distributed vertically. For example, tree bark provides or supports important habitats (i.e., epiphytes, see section 6.4) for a specialized fauna (Nicolai, 1986, 1993; Walter, 2004; Szinetár and Horváth, 2005; Pinzón and Spence, 2010). In central Europe, Nicolai (1986) found that rough-barked tree species had about twice the diversity and evenness of arthropods as smooth-barked tree species, including a number of species dependent on rough bark. Because tree bark inevitably becomes rougher and more epiphyte-laden with age (Fig. 1A), old trees provide more canopy habitats than young trees (Elton, 1966; Fritz, 2009) and are no doubt of greater importance to bark dwelling arthropods.

Similarly, the leaf surfaces of many plant species support a variety of structures of relevance to minute arthropods, including raised veins, hairs, rolled margins, etc. (Walter, 1996). Of particular interest are leaf domatia, "discrete pits, pockets, tufts of hair or combinations thereof, generally on the underside of the leaf" (Willson, 1991) that have no known function in plants other than providing shelter for beneficial predatory or mycophagous mites (mites harmful to the plants rarely inhabit leaf domatia) (Walter, 1996). By maintaining higher mite densities (Walter and O'Dowd, 1992), plants with leaf domatia gain extra protection from herbivorous mites and reduced pathogenic fungal loads while the mites secure shelters for hiding, oviposition and molting (Willson, 1991; Walter, 1996; O'Dowd and Pemberton, 1998; Norton et al., 2000, 2001). This mutualistic association occurs in forests throughout the world (e.g., Walter and O'Dowd, 1995) but appears particularly common in temperate deciduous forests of the northern hemisphere (O'Dowd and Pemberton, 1998). In the United States, for instance, Willson (1991) found leaf domatia to be present on 48% of the trees, shrubs and vines examined. An additional 23% of species had raised hairy veins that also sheltered mites of potential benefit to plants. Similarly, in Korea, O'Dowd and Pemberton (1998) found leaf domatia to be present on half of all woody species examined. The authors found domatia-bearing species to be well represented in the canopy, subcanopy and shrub layers but not in the herbaceous layer and suggest that leaf domatia play a key role in determining the distribution and abundance of mites in forest canopies.

3.4. *Tree cavities*

Tree cavities, both dry and water-filled, provide critical habitats for wildlife in forests worldwide (McComb and Lindenmayer, 1999) and become much more common as trees age (Fan et al., 2003). These structures range in size from small galleries created by wood-boring insects to entirely hollow trunks. They can be found throughout the canopy (Kitching, 1971) but generally decline in size with height, with important implications for arthropod occurrence. For example, only ant species with small nest space requirements can be found nesting high in the canopy (Seifert, 2008). It is interesting to note that ants, when present, significantly reduce the abundance and diversity of cavity-dwelling arthropods (Park et al., 1950).

Arthropods associated with dry tree cavities include those associated with decaying wood, ectoparasites of cavity-dwelling vertebrates, nesting bees, wasps and ants, etc. (Park et al., 1950; Park and Auerbach, 1954; Elton, 1966; Choate, 1987; Speight, 1989). Some of these species appear to be largely or entirely restricted to tree cavities (Park et al., 1950) and are of particular conservation concern (Floren and Schmidl, 2008; Sverdrup-Thygeson et al., 2010). For instance, nearly 90% of all cavity-dwelling beetle species in Germany are threatened (Floren and Schmidl, 2008). Little attention has been given to the vertical distribution patterns of this fauna. Several studies from Europe, however, have shown many species (e.g., elaterids, tenebrionids, scarabaeids) to be more abundant in elevated cavities than in those closer to the ground (Martin, 1989; Ranius, 2002), with richness increasing with height (Ranius, 2002). These patterns may be due to differences in microclimate affecting wood decay, reduced predation risk or to a higher incidence of bird nests in elevated cavities (Ranius, 2002). Sobek et al. (2009a) found cavity-nesting wasps, bees and their parasitoids to exhibit a similar preference for elevated cavities in Germany. In contrast, Park et al. (1950) found the abundance and diversity of pselaphine staphylinids to decline with cavity height.

As for arthropods utilizing water-filled cavities, the North American mosquito *Aedes hendersoni* Cockerell breeds almost exclusively in elevated tree holes (Scholl and DeFoliart, 1977; Sinsko and Grimstad, 1977; Copeland and Craig, 1990b), presumably to avoid competition with a related species concentrated near the ground (Copeland and Craig, 1990b). The cold tolerance of a particular species may also affect its distribution because the water within elevated tree cavities gets colder than in basal cavities during the winter (Copeland and Craig, 1990a).

4. Plant community composition

Plant diversity is an important determinant of arthropod vertical distribution, with species poor forests supporting fewer arthropods in the canopy than species rich forests (Sobek et al., 2009b). In addition, arthropod communities appear to be more concentrated near the ground in forests consisting of few tree species (e.g., Nielsen, 1987) than in more diverse forests (e.g., Ulyshen and Hanula, 2007; Pucci, 2008). The addition or removal of a single species of plant may have far reaching consequences for arthropod stratification. This is particularly true for invasive species. For example, Ulyshen et al. (2010a) studied how experimental removals of an invasive shrub affected the vertical distribution patterns of flying beetles. Few beetles were captured near the ground where the shrub was present but where it had been removed the vertical distribution patterns were similar to those observed in uninvaded forests.

5. Climatic gradients

In general, conditions in the canopy are much more variable, even over short periods of time, than those near the forest floor (Shaw, 2004) and the tolerance ranges and preferences of arthropods (or their hosts) are important in determining their vertical distribution patterns (Gruppe et al., 2008). Light exposure, temperature and wind speed decrease steadily from the treetops to the forest floor whereas humidity exhibits the opposite pattern (Geiger, 1950; Elton, 1966; Baldocchi and Meyers, 1988; Parker, 1995; Tal et al., 2008). These patterns are most noticeable in closed interior forests, especially mature forests dominated by shade tolerant trees (Canham et al., 1994), during the daylight hours of the growing season. At night, during the dormant season, or near disturbances, these gradients often reverse, weaken or disappear (Baldocchi and Meyers, 1988; Parker, 1995; Tal et al., 2008). These fluctuations in climate are more moderate in tree cavities and other sheltered canopy habitats (Park and Auerbach, 1954). Gall-forming arthropods are often concentrated in the upper canopies of forests (Ribiero and Basset, 2007), including temperate deciduous forests (Ejlersen, 1978; Kampichler and Teschner, 2002; Thomas et al., 2010), presumably due to reduced parasitism and fungal disease in these sun-exposed xeric environments (Fernandes and Price, 1992). Seifert (2008) discussed the importance of thermophily, cold-hardiness and desiccation resistance to canopy-dwelling ants in Germany. Nielsen (1987) suggested wind speed influenced the vertical distribution patterns of flies in Denmark, causing them to be less numerous in the relatively windy trunk zone. Finally, many taxa move up or down within the canopy (sometimes on a daily basis, see Section 2) to thermoregulate (May, 1979). According to Dixon (1970), for example, sycamore aphids move downward within the tree crown as summer approaches to avoid extreme temperatures in the upper canopy.

6. Resource availability

Resource availability is one of the most important determinants of arthropod vertical distribution. It is important to note that because the larval and adult stages of many holometabolous taxa require different habitats or resources, their vertical distribution patterns often differ as well. Many saproxylic insects (e.g., Cerambycidae and Buprestidae) species, for example, inhabit wood near the forest floor as larvae but utilize resources high in the canopy as adults (Wermelinger et al., 2007; Schmidl and Bussler, 2008). Similarly, some mosquitoes are more abundant high in the canopy when seeking blood meals, but descend to the forest floor to lay eggs (Anderson et al., 2006). Particularly important resource categories include foliage, sugars, wood (and associated fungi), epiphytes, carrion and dung, prey and hosts, and mates.

6.1. Foliage

Foliage is not distributed evenly (see Section 3.2), with many individual plant species (e.g., herbs, midstory trees, etc.) being restricted to a narrow range of heights (Parker et al., 1989; Parker and Brown, 2000). Foliage quality changes vertically as well, especially as the season progresses (Murakami and Wada, 1997; Murakami et al., 2005), with sun-exposed leaves in the upper canopy being thicker, tougher, smaller, drier and better chemically defended than those closer to the forest floor (Murakami and Wada, 1997; Shaw, 2004; Murakami et al., 2005). The nutrient content of foliage also changes with height (Rowe and Potter, 1996, and references therein; Fortin and Mauffette, 2002), but not consistently (e.g., Ellsworth and Reich, 1993). Some herbivorous arthropod taxa may respond to the seasonal decline in foliage palatability high in the canopy by migrating downward in mid-season to pursue higher quality resources (Murakami and Wada, 1997). Given these considerations, it is perhaps not surprising that herbivore density and damage generally decline with height (Nielsen and Ejlersen, 1977; Phillipson and Thompson, 1983; Holmes and Schultz, 1988; Reynolds and Crossley, 1997; Thomas et al., 2010). Some studies, however, have shown the opposite pattern (Rowe and Potter, 1996; Horchler and Morawetz, 2008) or no change at all (Le Corff and Marquis, 1999). While it is not uncommon for herbivorous insects to be unevenly distributed vertically (Nielsen and Ejlersen, 1977; Fowler, 1985; Wagner et al., 1995; Rowe and Potter, 1996; Le Corff and Marquis, 1999; Leksono et al., 2005b; Ulyshen and Hanula, 2007; Francese et al., 2008), the mechanisms underlying these patterns are not fully understood. In many cases, as discussed elsewhere, the abundance or quality of host resources appear to be less important than other factors (e.g., proximity to overwintering sites (Section 8), sun exposure (Section 5), etc.) in determining these patterns (e.g., Nielsen and Ejlersen, 1977; Rowe and Potter, 1996; Brown et al., 1997; Thomas et al., 2010). Finally, it should be mentioned that the outer layer of foliage often extends uninterrupted from the upper canopy to the ground at forest edges, bringing species normally restricted largely to the tree tops in close proximity to the forest floor (Toda, 1987, 1992; Wermelinger et al., 2007).

6.2. Sugars

A variety of sugar resources are available to arthropods in temperate deciduous forests, including floral nectar, extrafloral nectaries, fruit, sap flows and honeydew. The availability and relative importance of these resources vary with height above the ground and with season. For example, floral nectar is more readily available in the understory because most tree genera are wind-pollinated in contrast to tropical forests where animals are more important (Murawski, 1995). It should be noted, however, that wind-pollinated flowers provide an important source of pollen for a variety of canopy arthropods (Elton, 1966). The availability of floral nectar and pollen at any height within the forest is short-lived as almost all trees and most understory plants bloom early in the year before or during leaf expansion (Heinrich, 1976; Schemske et al., 1978). With few exceptions (Kudo et al., 2008), late-season flowering plants are confined to canopy gaps, forest edges and other disturbed areas receiving direct sunlight (Heinrich, 1976). In contrast, some sugar sources remain readily available to forest arthropods throughout the season. Sap flows, for instance, commonly develop on trees (especially old trees) in response to injury and are important resources for many arthropods (Elton, 1966, and references therein; Yoshimoto et al., 2005; Yamazaki, 2007). These are frequently colonized by fungi and other microbes and are breeding habitats for some insects (Elton, 1966). Although no efforts have been made to determine how sap flows are distributed within the canopies of temperate deciduous forests, the vertical distribution of certain sap-feeding insects (e.g., cetoniine scarabs, certain drosophilid flies) suggest they may be more common high in the canopy (Basden, 1953; Shorrocks, 1975; Toda, 1977, 1987; Beppu, 1980, 1984; Tanabe, 2002; Ulyshen and Hanula, 2007). Honeydew, the waste product of aphids and other sap-sucking insects (e.g., Nickel, 2008), is perhaps the most important non-floral sugar source. While many ants collect it directly from the insects themselves and regularly enter the canopy by climbing trunks or other plant parts in pursuit of this resource (Seifert, 2008), many other arthropods, belonging to at least 50 families according to one study, collect it from the surfaces on which it falls (Elton, 1966, and references therein). For example, bees feed on honeydew, sap and other sugar sources in the absence of flowers (Elton, 1966) and the importance of honeydew to the longevity and fitness of hymenopteran parasitoids has been particularly well documented. Honeydew is probably more readily available high in the forest canopy (Moran and Southwood, 1982; Wardhaugh et al., 2006; Nickel, 2008), likely influencing the distributions of associated arthropods. For example, Ulyshen et al. (2010b) found bees to be much more abundant high in the canopy than near the forest floor in the United States, especially in mid-summer when flowers were absent from the canopy and scarce near the ground.

6.3. Wood

One fifth or more of all forest-dwelling arthropod species are saproxylic (Elton, 1966; Grove, 2002), meaning they are directly or indirectly dependent on dead or dying wood (Speight, 1989). Although all dead wood eventually falls to the ground, much of it begins in the canopy in the form of standing dead trees (i.e., snags), dead branches and twigs, and rotting heart wood (Fonte and Schowalter, 2004). For instance, in Sweden, Nordén et al. (2004) found snags made up about 22% of the total dead wood volume and another 6% was attributed to dead branches attached to living trees. While these resources support fewer saproxylic arthropod species than wood on the forest floor (Larkin and Elbourn, 1964; Roling and Kearby, 1975; Jonsell and Weslien, 2003; Hammond et al., 2004; Gibb et al., 2006; Franc, 2007; Hjältén et al., 2007; McGeoch et al., 2007; Jomura et al., 2008; Ulyshen and Hanula, 2009; Vodka et al., 2009), community composition changes considerably with vertical position, with many species preferring standing or suspended wood (Paviour-Smith and Elbourn, 1993; Jonsell et al., 1998; Sverdrup-Thygeson and Ims, 2002; Hedgren and Schroeder, 2004; Hammond et al., 2004; Kappes and Topp, 2004; Ødegaard, 2004; Schlaghamerský, 2004; Franc, 2007; Ulyshen and Hanula, 2009, in press; Vodka et al., 2009; Ulyshen et al., in press; Bouget et al., 2011). Many arthropods, particularly beetles, are known to be attracted to dark vertical silhouettes in the trunk zone and more readily attack upright dead, dying or weakened trees than fallen trees. Franc (2007) found this to be particularly true for wood-boring beetle species attacking oaks in Sweden, whereas fungivores were generally more common on downed trees. Species occupying the same snag often exhibit vertical stratification (Ulyshen and Hanula, 2009) and many species known to infest branches and twigs are more common in the crowns of overstory trees (Sippola et al., 2002; Vance et al., 2003; Schlaghamerský, 2004; Ulyshen and Hanula, 2007, 2009; Bouget et al., 2011). Furthermore, certain wood-boring pests of living trees initially attack the crown and move downward as tree vigor declines (Cote and Allen, 1980; Haack and Benjamin, 1982; Cappaert et al., 2005; Haack et al., 2006).

The conditions in standing or suspended dead wood differ greatly from those in dead wood on the forest floor, with important implications for the vertical distribution patterns of the arthropod fauna. For instance, the change in moisture availability from the damp forest floor to the relatively desiccated uppermost branches is important in governing fungal community composition. The canopy fungal community in a German forest was dominated by species with small fruiting bodies growing close to the substrate and often on the less desiccated undersides of branches (Unterseher et al., 2005). As fungal composition affects the arthropod community, with many species specific to particular kinds of fungi (Jonsell et al., 2001, 2005; Johansson et al., 2006), these differences are likely to affect arthropod community composition in forest canopies. In addition, many arthropod species favor sun-exposed wood (Jonsell et al., 1998; Bouget and Duelli, 2004; Lindhe et al., 2005; Vodka et al., 2009) and these habitats are, with the exception of canopy gaps, forest edges and other open areas, naturally more common in the forest canopy than near the ground.

Young forests typically have less volume and variety of dead wood than mature forests and have comparatively simple canopies. For example, they lack the large-diameter snags characteristic of mature forests. While the density and longevity of snags vary among forest types and tree species, they are common features in all mature forests and provide important habitats to a wide variety of species, as described above. Young forests also lack the large "veteran" trees characteristic of mature forests (Grove, 2002). These living but declining trees provide warm, sunlit crowns full of dead and dying limbs and rot-holes (Schmidl and Bussler, 2008). Because they are still living, these trees, unlike snags, provide continuous resources and are critical to the long-term persistence of saproxylic arthropod communities in the canopy (Schmidl and Bussler, 2008).

Consequently, measures that provide snags and large-diameter living trees will greatly enhance conditions for saproxylic faunas in the canopies of managed and regenerating forests. Studies from the boreal forests of Europe show that even intensively managed forests can support high diversities of saproxylic beetles (including, in some cases, more threatened species than in old-growth forests) if snags (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002) or large-diameter trees are created or retained. Some countries such as Sweden encourage conservation of saproxylic species by creating 4–5 m tall stumps from living trees during harvest (Jonsell et al., 2004). Research from North America suggests this practice may be improved by retaining entire trees (perhaps through girdling) in order to provide habitats for canopy specialists dependent on resources in the crown (Ulyshen and Hanula, 2009).

6.4. Epiphytes

Lichens, mosses, ferns and other epiphytes often grow on the main trunks or branches of trees in temperate deciduous forests (Fig. 1B). In addition, epiphytic fungi or “sooty molds” often grow on leaves covered by honeydew excreted by sap-sucking insects. It has long been known that epiphytes are not distributed evenly in the canopies of these forests (Billings and Drew, 1938; Hale, 1952, 1965; Elton, 1966; Stubbs, 1989; Fritz, 2009). In an old-growth Wisconsin forest, for example, Hale (1952) recorded epiphytes along the entire lengths of 10 wind-thrown trees belonging to seven species. Bryophytes were found mainly near the bases of the trees with about half of the species restricted there. In contrast, lichen species richness increased with height, peaking at 20 m. Individual lichen species, however, exhibited unique distribution patterns, with some preferring the base, some the mid-bole and others the crown. Fritz (2009) reported similar stratification of epiphytes associated with beech trees in Sweden.

Vertical stratification of epiphytes can be attributed to multiple causes. Many species, particularly those associated with mature forests, are concentrated near the bases of trees due to shade and moisture requirements (Asplund et al., 2010). The distributions of other species are determined by bark roughness with some preferring rough bark near the base of a tree and others preferring the younger, smoother bark of the crown. Grazing pressure from gastropods is strongest near the ground where it affects the distribution patterns of epiphytes on *Fraxinus excelsior* in Norway (Asplund et al., 2010). The species most susceptible to grazing from gastropods can colonize bark with lower pH. As pH is higher near the soil where gastropods are most abundant and gastropods are intolerant of low pH, this adaptation likely represents a grazing-avoidance strategy (Asplund et al., 2010). Finally, many species associated with mature forests are poor dispersers (Selva, 1994; Kuusinen, 1996), making colonization high on the trunk a rare event (Asplund et al., 2010).

Numerous studies have shown that epiphytes provide food, shelter, hunting grounds and camouflage for diverse terrestrial (arthropods, gastropods, etc.) and aquatic (rotifers, nematodes, tardigrades, etc.) invertebrate faunas (Gerson, 1973; Seyd and Seaward, 1984; Meininger et al., 1985; Henderson and Hackett, 1986; Nicolai, 1986; Stubbs, 1989; Prinzing and Wirtz, 1997). The vertical distributions of these organisms depend on their specific epiphyte associations and other habitat requirements. Species most prone to desiccation are likely restricted to the base of trees where moisture levels are relatively high. For example, Billings and Drew (1938) found bark under bryophyte mats at the base of old-growth *Liriodendron tulipifera* L. in Tennessee to contain almost six times as much water as bare bark approximately 2 m high on the trunk. In Maine, Miller et al. (2008) sampled arthropods from epiphytes growing at three heights (0–2, 2–4, 4–6 m) on *Acer rubrum* L. trunks. While most collembolans were concentrated in the dense bryophyte mats located near the bases of the trees, others were more uniformly distributed and one morphospecies was more strongly associated with a species of epiphyte commonly found higher on the trunks where there is greater light exposure. In addition, many families of Diptera were more abundant higher on the trunk. Root et al. (2007a) sampled the branches of twelve large-diameter *Acer saccharum* trees for epiphytic lichens and associated mites in three old-growth forests and three reserve shelterwood stands in New York. Three of the 24 mite taxa collected were new to science, demonstrating the potential diversity yet to be discovered. Foliose lichen supported more mites than crustose lichen or bare bark, and mite communities differed between the two forest types. Although vertical stratification patterns were not investigated in that study, other researchers have shown that many mite species are restricted to trees (Aoki, 1973).

Epiphyte communities develop slowly on temperate deciduous trees, becoming more diverse with time and often exhibiting predictable patterns of succession (Elton, 1966; Selva, 1994; Kuusinen, 1996; Root et al., 2007b). In southern Belgium, for example, André (1985) noted the succession of epiphytic lichens begins with crustose lichens followed by foliose lichens and finally fruticose lichens. Similarly, Root et al. (2007b) found that *A. saccharum* trees of different sizes support distinct epiphyte communities in New York. Recent work by Fritz (2009) demonstrates the importance of old trees in maintaining diverse epiphyte communities. Epiphyte communities and associated arthropods can be negatively impacted by forest management, resulting in less vertical complexity in altered stands. For example, gap harvests in Maine decreased the abundance of epiphytic bryophytes, Collembola, spiders and total arthropods on the bark of *Acer rubrum* (Miller et al., 2007). The harvests had the greatest effect on epiphytes and arthropods at the bases of trees, perhaps because these organisms have higher shade and humidity requirements than those occurring higher in the canopy. Epiphytes with poor dispersal capabilities require mature tree continuity and are often absent from managed forests (Selva, 1994; Kuusinen, 1996) so Root et al. (2007b) recommend retaining mature trees at the time of harvest to maintain source populations. Furthermore, retaining groups of mature trees as opposed to isolated individuals will likely help maintain many species sensitive to microclimatic extremes (Miller et al., 2007; Root et al., 2007b).

6.5. Carrion and dung

Although information on the vertical distribution patterns of carrion and dung is lacking, it seems probable that these resources are available to some extent throughout the forest canopy. For example, a large proportion of all forest vertebrate species utilize tree cavities (McComb and Lindenmayer, 1999) (see Section 3.4) and these shelters can be found at almost any height above the ground. Obvious sources of carrion in tree cavities include sick and injured individuals and abandoned young. While most arthropods associated with carrion and dung appear to be concentrated near the forest floor (Ulyshen and Hanula, 2007), there are some interesting exceptions. For example, the North American burying beetle *Nicrophorus pustulatus* Herschel was recently found to be more abundant high in the canopy than near the forest floor using carrion-baited traps (Ulyshen et al., 2007; leGros and Beresford, 2010). The species may utilize carrion in tree cavities to avoid competitive interactions near the forest floor (Ulyshen et al., 2007), but this has not been tested.

6.6. Prey and hosts

Approximately half of all arthropod species inhabiting temperate deciduous forest canopies are predators or parasitoids (Moran and Southwood, 1982). Although these organisms are generally less restricted in their vertical distribution patterns than their prey (Elton, 1966), they often exhibit a high degree of stratification as well. For species with strong dispersal abilities, these patterns are probably determined largely by the availability of resources.

Host tracking, for example, is thought to be particularly important in determining the vertical distribution patterns of blood-seeking mosquitoes and other biting flies, with bird and mammal specialists being more abundant high in the canopy and near the forest floor, respectively (Love and Smith, 1958; Main et al., 1966; Service, 1971; Mitchell and Rockett, 1979; Rockett and Somers, 1983; Lundström et al., 1996; Farajollahi et al., 2006; Swanson and Adler, 2010; Russell and Hunter, 2010). Similarly, predatory wasps, even ground-nesting species, are many times more abundant in the upper canopy than near the forest floor (Vance et al., 2007; Sobek et al., 2009a, M.D.U. unpublished data), possibly due to differences in the availability of prey and honeydew. The vertical distribution of parasitoids, many of which are more abundant high in the canopy, is also thought to be determined largely by the availability of hosts (especially highly host-specific species) and honeydew, although preferred dispersal heights and bark thickness may also be important (Pucci, 2008; Sobek et al., 2009a; Ulyshen et al., in press). In addition, Ulyshen and Hanula (2007) found coccinellid beetles to be more abundant and species rich in the upper canopy than near the forest floor, presumably due to the abundance of aphids and other sap-sucking Hemiptera high above the ground. Furthermore, it should be noted that many animal species carry loads of parasitic, phoretic and commensal arthropods (Walter and Behan-Pelletier, 1999; Redborg and Redborg, 2000; Walter, 2004) which contribute greatly to biodiversity in the canopy.

6.7. *Mates*

Mate seeking probably affects the vertical distribution patterns of many species but this has only been documented for swarming or otherwise conspicuous taxa. For example, many fly species are known to form mating swarms above prominent landmarks, including treetops (Downes, 1969) (Fig. 1C). Furthermore, Turner (1990) studied the flight heights of papilionid butterflies patrolling for mates on a forested hilltop in the southeastern United States. Most species were concentrated near the forest floor (i.e., <3 m), but one species flew almost exclusively 6 m or more above the ground. Certain siricid wasps also mate in the tops of trees, although this behavior is best documented from species associated with conifers (Morgan, 1968). Finally, the males of many arthropod species, as Schal (1982) demonstrated for tropical cockroaches, may enhance their abilities to locate pheromone-emitting females by situating themselves higher vertically.

7. Interactions

Three inter-specific interactions likely to influence the vertical distribution of arthropods are predation, interference and competition. Whereas many predatory and parasitic arthropod (e.g., wasps, certain parasitoids, coccinellid beetles, Neuroptera, etc.) and vertebrate (e.g., birds) taxa become more abundant with height above the forest floor (Hollier and Belshaw, 1993; Ulyshen and Hanula, 2007; Vance et al., 2007; Pucci, 2008; Sobek et al., 2009a; Ulyshen et al., in press), many others (e.g., ants, spiders, other parasitoids, carabid beetles (excluding Lebiini), staphylinid beetles, mammals) exhibit the opposite pattern (Ulyshen and Hanula, 2007; Vance et al., 2007; Pucci, 2008; Seifert, 2008; Larrivée and Buddle, 2009). This uneven distribution in predation pressure should play an important part in determining how prey species are vertically arranged, but few have quantified the contributions of such top-down forces. In Japan, Murakami (2002) studied how the foraging patterns of four bird species changed as Lepidoptera larvae moved from the upper canopy to the forest floor. Only one bird species followed the larvae downward, with the other species remaining in the upper canopy. These results suggest that arthropods can reduce predation risk to some extent by moving vertically within the canopy. Equally few studies have attempted to document the role of interference among arthropods in determining their vertical distribution patterns, although Turner (1990) suggested that *Papilio glaucus* L. patrols for mates high above the forest floor in order to avoid energy-wasting interactions with other butterfly species concentrated near the ground. Although it is easy to envision how past competitive interactions may have resulted in observed vertical stratification patterns (Askew, 1962; Copeland and Craig, 1990b; Redborg and Redborg, 2000; Ulyshen et al., 2007; Seifert, 2008), this is difficult to demonstrate experimentally (Connell, 1980).

8. Logistics

The difficulty, risk and energetic cost of entering the canopy are probably more important than other factors in determining the vertical distribution of many less mobile taxa. For instance, only 69 of the 173 ant species occurring in Central Europe are known to nest or forage for arthropod prey or honeydew in the canopy (Seifert, 2008). Of those, 14 are truly adapted for life in the canopy, being capable of nesting in the small spaces available (i.e., within wood) high above the ground (Seifert, 2008). Ant species with slow walking speeds, a poorly developed visual system and small crop storage capacities are particularly less likely to forage in the upper reaches of forests (Seifert, 2008). Proximity to emergence sites may also be important. For example, after eliminating a number of other possible explanations, Brown et al. (1997) concluded that the most likely explanation for why the leaf-mining moth *Cameraria hamadryadella* Clemens occurs at higher densities on foliage in the lower crown of oak trees is that female moths run out of eggs before they reach the upper crown. The same explanation was given by Nielsen and Ejlersen (1977) to account for a similarly distributed weevil species in Denmark. Finally, it should be mentioned that many arthropods disperse at particular heights and may favor open flight zones (Smith, 1973; Fierke and Stephen, 2007).

9. Conclusions

It can be concluded that (1) the canopies of temperate deciduous forests provide critical habitats and resources for a large fraction of arthropods even though few taxa are restricted there; (2) most canopy-dwelling taxa are unevenly distributed vertically as determined by multiple factors acting simultaneously, and (3) the structurally complex canopies of old forests support more species than the relatively simple canopies of young forests. Based on the literature reviewed above, three broad recommendations can be made for improving conditions for arthropods in temperate deciduous forests canopies. First, maintaining diverse plant communities is critically important, including eliminating or controlling invasive plant competitors (Section 4). Second, protecting large diameter trees and snags is necessary to provide for the wide variety of canopy arthropod taxa associated with standing or suspended dead wood, tree cavities and epiphytes (Sections 6.3, 3.4 and 6.4, respectively). Third, it is essential to ensure adequate spatial and temporal continuity in the availability of these and other important resources. How to best achieve this last objective remains an active area of research and will no doubt vary depending on the taxa of interest (Pommerening and Murphy, 2004). In many cases, however, it may be preferable to retain clusters of trees as opposed to isolated individuals (Section 6.4). While achieving these goals should greatly benefit forest canopy arthropods in general, additional interventions will likely be required for many individual taxa of conservation concern.

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