



Conservation and Biodiversity

Assessing the Old-Growth Dependency of Two Saproxylic Beetle Species in the Southern Appalachian Mountains

Clayton R. Traylor,^{1,4,✉} Michael S. Caterino,^{2,✉} Michael D. Ulyshen,³ Michael L. Ferro,² and Joseph V. McHugh¹

¹Department of Entomology, University of Georgia, 120 Cedar Street, Athens, GA 30602, USA, ²Department of Plant and Environmental Sciences, Clemson University, 277 Poole Agricultural Center, Clemson, SC 29634, USA, ³Southern Research Station, USDA Forest Service, 320 Green Street, Athens, GA 30602, USA, and ⁴Corresponding author, e-mail: clayton.r.traylor@gmail.com

Subject Editor: Jeffrey Lozier

Received 17 February, 2022; Editorial decision 27 April, 2022

Abstract

The southern Appalachian Mountains were intensively logged during the early 1900s, leaving little remaining old-growth forest. Much of the region is now second-growth forest, which may not be suitable to specialist saproxylic species. Moreover, if suitable habitat exists, poorly dispersing species may not be able to colonize it. To investigate this, we assessed the distribution and old-growth dependency of two low-mobility saproxylic beetles in Great Smoky Mountains National Park. Using both field surveys and community science data, we found *Megalodacne heros* (Say 1823) (Coleoptera: Erotylidae) to be limited to lower elevations regardless of disturbance history, while *Phellogopsis obcordata* (Kirby 1837) (Coleoptera: Zopheridae) was restricted to inside or near old-growth forests. Although trees were generally smaller in second-growth, we detected no habitat limitation for *P. obcordata*: fungal hosts were present in second-growth areas and the beetle was present on trees as small as 11 cm in diameter. This suggests its distribution is shaped by its low dispersal capability and need for temporal continuity of deadwood habitat, therefore qualifying it as an indicator species. For *P. obcordata*, old-growth acted as refugia during landscape-wide, anthropogenic disturbances in the early 1900s, though we can draw no conclusions about *M. heros* from our dataset. The difference in sensitivity to human disturbance displayed between species may be linked to their relative dispersal abilities: *P. obcordata* is entirely flightless while *M. heros* is capable of some flight. This study highlights the value of using saproxylic invertebrates with limited dispersal ability for assessing impacts from anthropogenic forest disturbances.

Key words: fungus beetles, iNaturalist, land-use history, forest continuity, citizen science

In North America, 99% of temperate deciduous forests have been intensively cleared or disturbed by anthropogenic activity (Reich and Frelich 2002). These disturbances often homogenize forests in age, resulting in altered forest composition and structure (Bormann and Likens 1979, Fralish et al. 1991, Fan et al. 2003, Chazdon 2014), with legacies persisting for several decades or more (Chazdon 2003, Tuttle et al. 2016, Holmes and Matlack 2017). Forest-dwelling organisms respond in a variety of ways to these changes, and while some taxonomic or functional groups benefit from disturbance, others are harmed (Paillet et al. 2010). Particularly vulnerable to anthropogenic disturbance are saproxylic species (Grove 2002, Paillet et al. 2010), which depend on deadwood or associated resources for all or part of their lives (Speight 1989, Ulyshen and Šobotník 2018). Because anthropogenic activities typically remove or reduce

deadwood in forests, these species may be disproportionately harmed relative to other organisms (Martikainen et al. 2000, Stenbacka et al. 2010), and some saproxylics require habitats free of human impact (Lachat and Müller 2018).

Old-growth forests, spared from intensive anthropogenic disturbance, hold a diverse and unique community of saproxylic species (Grove 2002). Also referred to as ‘primary’ or ‘virgin’, old-growth forests are characterized by uneven aged stands, extremely large trees, and high volumes of deadwood (Tyrrell et al. 1998). These characteristics are intrinsically linked to saproxylic beetle communities, whose diversity depends on the amount and diversity of deadwood (Økland et al. 1996, Brin et al. 2011, Seibold et al. 2016) and the presence of tree microhabitats (e.g., tree-hollows, Müller et al. 2014). Moreover, old-growth forests

provide a continual supply of deadwood through time, which is more important for the presence of some species than current deadwood amounts (Sverdrup-Thygeson et al. 2014). This is especially true for low-mobility saproxylic species (Nordén et al. 2014), some of which are restricted to old-growth forests due to their inability to disperse to otherwise suitable younger forests (Brunet and Isacsson 2009, Buse 2012).

Intensive logging between 1900 and 1920 stripped the southern Appalachian Mountains of more than 83% of its forest (Wilson 1908). Despite this, the region holds the majority of remaining old-growth forest in the southeastern United States (Yarnell 1998, Conner and Hartsell 2002, Trani 2002). Much of the logged area was left to regrow (Wilson 1908) and the landscape today is dominated by second-growth forests (Yarnell 1998). Thus, a major difference in age exists between forests that were never logged and those that regenerated. Other land uses also occurred in the mountains (Pyle 1988, Yarnell 1998), which have additional ramifications for today's forest structure and composition in this region (Kincaid and Parker 2008, Tuttle and White 2016). Importantly, deadwood resources are especially disparate between second-growth and old-growth Appalachian forests (Webster and Jenkins 2005).

As second-growth forests persist and accumulate deadwood resources, there is evidence that saproxylic communities may recover (Paillet et al. 2010, Vandekerckhove et al. 2011; Janssen et al. 2016, 2017). However, old-growth specialists may be incapable of successfully colonizing second-growth forests until specific habitat requirements are met (e.g., Busse et al. 2022). Moreover, dispersal ability could preclude recolonization of suitable habitat (Nilsson and Baranowski 1997, Brunet and Isacsson 2009, Buse 2012, Brin et al. 2016). In other words, even if suitable habitat does exist in second-growth forests, poorly-dispersing species may not be able to colonize it. Therefore, we can gain insight on how second-growth forests are recovering by investigating the distribution of poorly dispersing saproxylic species in relation to land-use history and current habitat suitability.

Here, we evaluate the distributions of two saproxylic beetles, *Phelopsis obcordata* (Kirby 1837) (Coleoptera: Zopheridae) and *Megalodacne heros* (Say 1823) (Coleoptera: Erotylidae), in relation to land-use history (old-growth vs various second-growth), habitat suitability (fungal host presence, tree size, and stand basal area), and elevation (which may be a constraining distributional factor) in the southern Appalachian Mountains (Fig. 1). Although their ecology and habitat requirements are not well known, both species are large and have limited dispersal capabilities, and *P. obcordata* is suggested to be an old-growth specialist (Steiner 1992). Using both field searches and community science data within Great Smoky Mountains National Park (GSMNP), USA, we ask the following questions:

1. Are the species and their fungal hosts restricted to old-growth forests?
2. Does forest structure (tree size and basal area, potential indicators of habitat quality) differ among disturbance histories?
3. Is the occurrence of these species and their hosts best predicted by forest structure, disturbance history, and/or elevation?

The answers to these questions will clarify whether these beetles are limited to old-growth forests or if they have recolonized or persisted in second-growth forests, and if their habitat requirements or dispersal limitations are responsible for their distribution. Furthermore, our study aims to add to existing knowledge of the natural history of these species.

Materials and Methods

Study Species

Our first target species is a zopherid beetle, *P. obcordata* (Fig. 2A), which is thought to be restricted to old-growth forest (Steiner 1992). This species has been reported to undergo larval development within the infested wood and fruiting bodies of *Fomitopsis betulina* (Bull.) Cui et al. (2016) (Polyporales: Fomitopsidaceae) growing on *Betula* spp. L. (Fagales: Betulaceae) (Steiner 1992, 1999), although habits of the larvae are poorly known. Adults are brachypterous and entirely flightless (Foley and Ivie 2008). Adults are reported to feed on *F. betulina* and other fungi, but the full scope of habitat requirements remains unknown (Steiner 1992, 1999). Its range extends from eastern Canada to northern Georgia (USA), though in the southernmost portion it is limited to high elevation forests in the Appalachian Mountains (Steiner 1992, Foley and Ivie 2008).

The erotylid *M. heros*, our second target species (Fig. 3A), is fully winged, but is thought to fly infrequently (Park and Sejba 1935) and may be incapable of flight during certain times of the year when many individuals have degenerated wing musculature (McHugh et al. 1997). Found throughout eastern North America, *M. heros* is considered less common than its congener, *Megalodacne fasciata* F. (1777) (Blatchley 1910, Boyle 1956). Adults of *M. heros* aggregate and feed on two related species of fungi, *Ganoderma applanatum* (Pers.) Pat. (1887) (Polyporales: Ganodermataceae) growing on hardwood trees and *Ganoderma tsugae* Murrill (1902) growing on *Tsuga* spp. (Endl.) Carrière (Pinales: Pinaceae), in which the larvae also develop (McHugh et al. 1997; Fig. 3B). Adult activity is believed to be mostly nocturnal, and adults hide during the day (Park et al. 1931, Park and Sejba 1935, McHugh et al. 1997).

Study Area

Our primary study area was Great Smoky Mountains National Park (GSMNP), located in western North Carolina (portions of Haywood and Swain counties), and easternmost Tennessee (portions of Blount, Cocke, and Sevier counties), USA (Fig. 1). Established in 1934, GSMNP comprises forested mountainous terrain which varies extensively in elevation (267–2,024 m) and disturbance history. The intensity and type of anthropogenic disturbance occurring post-European colonization has been mapped within the park (Pyle 1988). In order of most to least intense, these disturbance histories are:

- Settlement: concentrated areas of human population (roughly 9% of the park area), that are typically located on the periphery of the park (except for areas such as Cades Cove and the Oconaluftee River valley) and at lower elevations (except for the Cataloochee area).
- Heavily logged: large logging operations that are defined by the use of mechanized tree removal methods (railroads, skidders and loaders, band sawmills). These operations rarely considered tree species and often clear-cut over half of a watershed at a time, well into high elevations (over 40% of the park area).
- Diffuse disturbance: the most generalized category (combining both diffuse categories from Pyle (1988)), consisting of low-density settlement (sporadic farms) with small fires and livestock grazing, and small nonmechanized logging (combined, 21% of the park area). Generally, these areas were surrounded by a forest matrix, some of which may have been selectively logged, leaving behind mature trees.
- Undisturbed forest: areas that have no documentation of anthropogenic disturbance post-European colonization (20% of the park area). While much of this area might be considered old-growth (also referred to as virgin or primary forest),

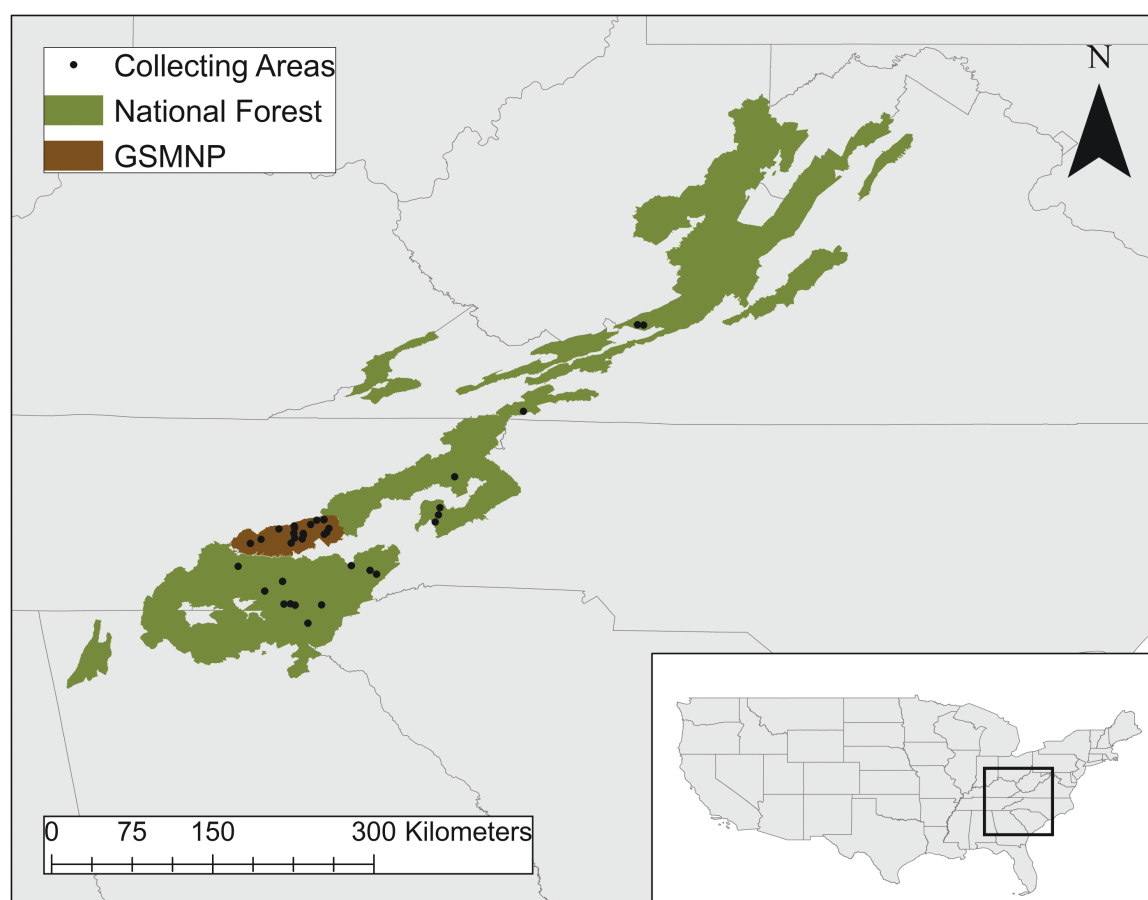


Fig. 1. Map of the southern Appalachian Mountains in the southeastern United States, showing collecting areas within National Forests and Great Smoky Mountains National Park (GSMNP). Inset shows the region within the United States.

other disturbances such as large-scale blow-downs, the loss of American chestnut, or invasive insects have likely played a role in shaping forest composition and age structure. Additionally, these areas were likely influenced to some degree by Indigenous peoples prior to European colonization (Yarnell 1998, Munoz et al. 2014).

Field Work

During May through July 2019, we hiked established trails in undisturbed forest sections of GSMNP to find *M. heros* and *P. obcordata*. Trails and undisturbed areas were found using GSMNP GIS layers (National Park Service 2015, 2018). We checked known hosts (*Fomitopsis* spp. and *Ganoderma* spp.) and other polypore fungi for adult beetles, as well as on surfaces and beneath the bark of logs and trees where fungi were present. We also looked at other infrequently encountered habitats, such as freshly cut logs oozing sap, and found some beetles on the ground by chance. When either species was found, we recorded the precise location and performed a rapid habitat assessment protocol. First, the tree genera, diameter (either DBH for standing trees or the width of the downed log where the beetle was found), and decay stage (according to Spetich et al. 1999) were measured and recorded. When a polypore fungus was present, we identified it if possible and ranked the maturity and decay stage as well (Graves 1960). Finally, the surrounding stand basal area was calculated using the MSU basal area gauge (Mississippi State University Extension, Starkville, MS), separated into hardwood and

softwood components. While the MSU basal area gauge is held at a constant 63.5 cm away from the eye, trees larger than the window (at approximately 1.37 m aboveground) are scored 1, while those smaller than the window are scored as 0. Trees roughly the same size as the window are scored as 0.5. All values are summed and multiplied by 10 for a basal area estimate in ft/acre. We searched for and collected between 8 and 12 beetle specimens of each species per area, but recorded tree and stand measurements even for specimens that were not collected (except for *M. heros* in several areas where they were very common, see Results). At the end of hiking within an area, a general tree community was listed based on where we found beetles present. Field work was primarily completed during the day, but on a few occasions, we visited field sites with known populations of both beetle species at night. We also searched for beetles using the same methods in areas outside of GSMNP, including Chattahoochee National Forest (NF) (Georgia: Rabun, Towns, and Union counties), Nantahala and Pisgah NF (North Carolina: Avery, Buncombe, Cherokee, Clay, Graham, Haywood, Jackson, Macon, Mitchell, Swain, Transylvania, and Yancey counties), George Washington and Jefferson National Forests (Virginia: Grayson and Smyth counties), and Mountain Lake Biological Station (Virginia: Giles County) (see Fig. 1). We recorded the same information at these locations as well.

During June and July, 2021, we targeted areas in GSMNP that had been heavily logged, densely settled, or had light logging or other diffuse human disturbances prior to national park establishment (Pyle 1988). These areas were targeted in order to determine beetle presence and compare habitat characteristics between

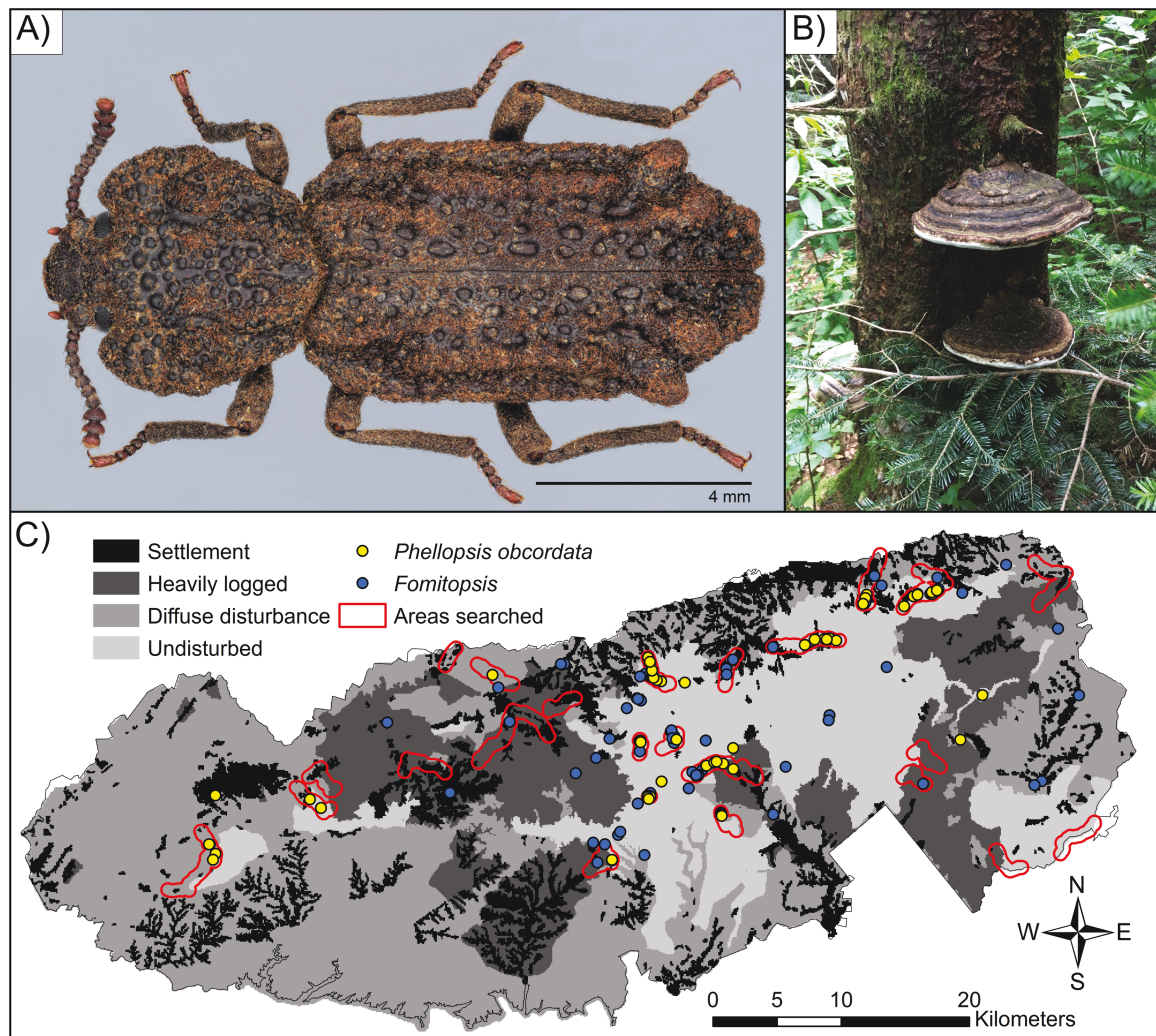


Fig. 2. (A) *Phellopsis obcordata*, dorsal habitus. (B) *Fomitopsis ochracea*, newly recorded host. (C) Records of *P. obcordata* and *Fomitopsis* spp. within Great Smoky Mountains National Park with historic land uses. Outlined areas on the map indicate areas searched during this study in 2019 and 2021. All records outside and some records inside of the areas searched are from iNaturalist and previous literature.

disturbed and undisturbed areas. In order to make fair comparisons, we targeted northern hardwood, coniferous northern hardwood, and high elevation spruce-fir areas where we would expect to find at least one of our target species (see Results). In these areas, we attempted to follow the 2019 sampling protocol with a few modifications. First, the habitat assessment protocol was undertaken whether target taxa were present or not. To do this, we hiked established trails with a timer and stopped every 5 min to sample the surrounding area (except when it ended in a nontarget area or some sort of clearing). The tree we sampled at each point preferably belonged to a species on which one of the fungal hosts was known to grow and a species that we sampled in 2019 (viz., species of *Betula*, *Tsuga*, *Picea* A. Dietr. (Pinales: Pinaceae), and *Acer* L. (Sapindales: Sapindaceae) in some northern hardwood areas; see Results). Second, we intentionally did not sample small trees (<15 cm DBH) so that the average tree size sampled was not smaller in these areas due to bias. We recorded the same measurements as previously, though most of the living trees had no fungi present. On some occasions we found both beetles and host fungi present (though not always together) in disturbed and undisturbed areas (i.e., when hiking through undisturbed areas to disturbed areas). When this occurred, we recorded the field measurements as in 2019

but did not collect the beetle specimens, then reset the timer. As in 2019, in an attempt to cover more ground, we did not record field measurements for all *M. heros* occurrences if the species was common in an area. During 2021, further localities without the full assessment protocol were collected by MSC while performing field work for another project.

Acquiring Recent Distribution Data

In order to better assess the distribution of target taxa and their fungal hosts, we used data from iNaturalist (www.inaturalist.org). Briefly, this website allows users to upload ‘observations’ of taxa (generally photographs), with the date and location (with error estimates) of the observation. Anyone with access to the internet and a camera can become users of iNaturalist, allowing for new observations to be added by nearly anyone—scientists, nature enthusiasts, or other curious people. Observations can then be identified by the uploader and other users. Often, iNaturalist also suggests a potential identification, for which the uploader can choose to use or disregard. While this can be a wonderful tool, there are pitfalls and biases which must be avoided and addressed. For example, whenever an observation gains the same species level identification by two or more users (unless there is another conflicting identification), it

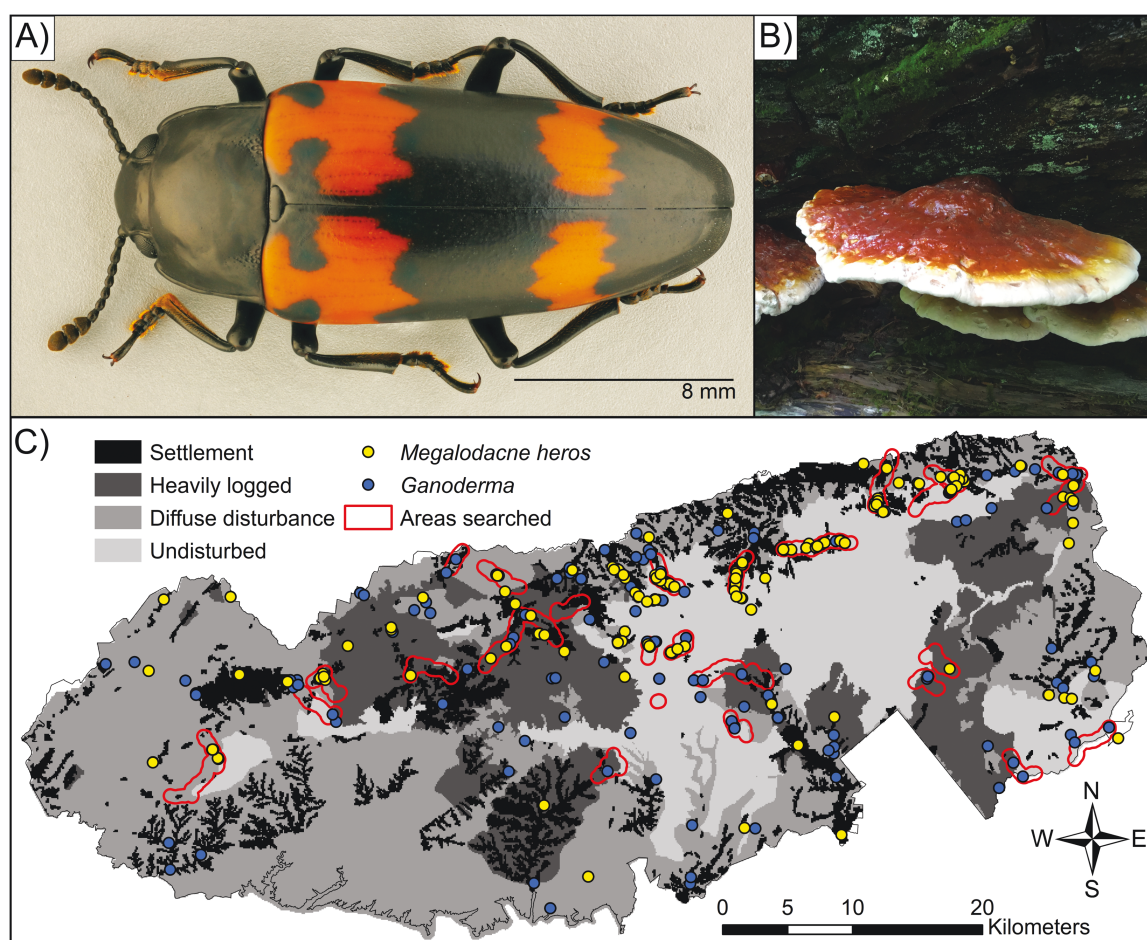


Fig. 3. (A) *Megalodacne heros*, dorsal habitus. (B) *Ganoderma tsugae*. (C) Records of *M. heros* and host *Ganoderma* spp. within Great Smoky Mountains National Park with historic land uses. Outlined areas on the map indicate areas searched during this study in 2019 and 2021. All records outside and some records inside of the areas searched are from iNaturalist.

becomes ‘research grade’, meaning that the online community has reached a consensus about the observation. However, identifications are not usually confirmed by experts, meaning that ‘research grade’ observations can still be misidentified. Furthermore, observations are more likely to occur in popular areas (i.e., close to Gatlinburg or on highly trafficked trails in GSMNP) and large or flamboyant species are more likely to be observed than small or drab species (i.e., *M. heros* would be more likely to be observed than *P. obcordata* due to coloration). Sometimes, the same individual might be observed by multiple users, potentially inflating the abundance of the taxa. Finally, accuracy data and location for each observation is dependent on the diligence and honesty of iNaturalist users. Aware of these pitfalls, we attempted to use iNaturalist observations to increase the number of localities for our target species and their hosts.

Locality records within GSMNP were acquired from iNaturalist for both beetle species and their host fungi. To do this, we inspected all ‘Coleoptera’ and ‘Polypore fungi’ records within the park which were uploaded before 25 January 2022, flagging observations of both beetle species as well as all records of *Fomitopsis* spp. and *Ganoderma* spp. of fungi. *Fomitopsis* spp. observations were commonly misidentified on iNaturalist as *Ganoderma applanatum* or *Fomes fomentarius* (L.) Fr. (1849) (Polyporales: Polyporaceae). When found, we noted such errors and submitted a corrected identification to iNaturalist. Many observations of *G. tsugae* growing on eastern hemlock were also incorrectly identified as *G. sessile* Murrill

(1902) or *G. lucidum* (Curtis) Karst (1881) (which grow on hardwoods, commonly *Quercus* L. (Fagales: Fagaceae), and *G. lucidum* is not known from eastern North America; Loyd et al. 2018); we submitted corrected determinations to iNaturalist for these records as well. Records of correctly identified *G. sessile* were excluded from further analysis as it is not known to host *M. heros*. Furthermore, observations were excluded when they could not be confidently identified to either beetle species or fungal genus or had a positional accuracy > 1,000 m. Therefore, the only species included in the analysis were *P. obcordata*, *M. heros*, *Fomitopsis ochracea* Ryarden and Stokland (2008), *Fomitopsis mounceae* (Sw.) Haight and Nakasone (2019), *F. betulina*, *Fomitopsis* sp. (when we could not be confident in species), *G. tsugae*, *G. applanatum*, and *G. megaloma* (Lév.) Bres. (1912) (see Results for reasoning for complete fungal list). Furthermore, we inspected each iNaturalist observation of host fungus for the presence of its respective beetle species. We also obtained additional records of *P. obcordata* from previous literature (Foley and Ivie 2008). These locality records were then collated with our own from field surveys. Finally, we inspected iNaturalist observations of *M. heros* and *P. obcordata* outside of GSMNP to obtain any new natural history and distributional information.

Data Analysis

Within GSMNP, we extracted disturbance history (National Park Service 2018) and elevation (U.S. Geological Survey 2020)

information for locality records of all species (both beetles and hosts) from both this study, community science observations, and other recent observations. As tree genera differ in growth rate and maximum size, we attempted to standardize for differences in tree size based on the genus. For each genus, we calculated the mean diameter in meters (*Betula* = 0.28, *Picea* = 0.34, *Tsuga* = 0.58), then subtracted the mean from each observation for its respective genus. This provides a measurement of how much larger or smaller any observation is from the mean of its genus. While we sampled *Acer* in some northern hardwood forests, the tree size of these samples was left out of further analysis because we did not sample them from any undisturbed areas and the fungal hosts in this study do not utilize *Acer*. Additionally, we did not include unidentifiable trees/logs ($n = 26$) because of the inability to appropriately standardize. The unidentifiable trees/logs were barkless and/or decomposed to the point that identification was not possible. Basal area was converted to a measure of m²/ha but was not standardized. In instances where we removed tree observations from the analysis, the basal area from these observations was still used. Summary counts of our observations are provided in Table 1.

All statistical procedures were performed in R (R Core Team 2021). We first compared how elevation, basal area, and tree size might differ between disturbance histories. Because our data were unable to meet the normality and equal variance assumptions of ANOVA, we used the Kruskal–Wallis rank sum test on tree diameter, basal area, and elevation. Following this, we used the dunn.test R package (Dinno 2017) for the post hoc Dunn's multiple pairwise comparisons test to determine which disturbance history categories significantly differed after using Bonferroni adjustments.

Next, we performed logistic regression to determine if occurrence of each beetle species and their hosts was influenced by disturbance history, elevation, tree diameter, and basal area. In undisturbed forest, absences occurred whenever we found one species but not the other (Table 1). We considered two aspects of disturbance history, the categories presented by Pyle (1988) and the distance to undisturbed forest. Because elevation differed between the disturbance history categories (see Results) and was highly correlated to distance to undisturbed forest (Pearson coefficient = -0.459 , $P = 3.838 \times 10^{-9}$), we did not include the terms in the same model. For each species, we created three competing models: the first included the disturbance history categories, the second included the distance in meters to undisturbed forest (observations within undisturbed forest being set to 0), and the third included elevation. All models included the local factors (basal area and standardized tree diameter). Distance to undisturbed forest was calculated using the Near function in ArcMap 10.4 (Esri, Redlands, California). Multicollinearity was checked using the *vif* function in the faraway package (Faraway 2016) and spatial autocorrelation using the *Moran.I* function in the ape package (Paradis and Schliep 2019). We report the best model for each species according to the lowest Akaike information criterion (AIC) and an AIC differential of >2 .

Specimen Photography and Deposition

We photographed *P. obcordata* with the automatic 3D image rendering system of the Keyence VHX-7000 digital imaging microscope (Keyence, Itasca, IL). Because of the glossy surfaces of *M. heros*, we instead used a Canon EOS1 digital camera and the Digital Photo Professional software (Canon Inc., Tokyo, Japan) then stacked using Helicon Focus 6 (Helicon Soft Ltd., Kharkiv, Ukraine). We edited both photos with Adobe Photoshop CS4 (Adobe Inc., San Jose, CA). Voucher specimens of beetles will be deposited in the Twin

Creeks Science and Education Center (found in GSMNP), University of Georgia Collection of Arthropods (UGCA), and the Clemson University Arthropod Collection (CUAC) after extraction of DNA.

Results

Distributional Data

Within GSMNP, we extracted additional records of the beetles and their fungal hosts from iNaturalist: 1 locality of *P. obcordata*, 83 of *Fomitopsis* spp., 175 of *M. heros*, and 182 of host *Ganoderma* spp. (Supp Table 1 [online only]). Three records of *P. obcordata* in GSMNP since 2000 were also added to our dataset from Foley and Ivie (2008). From our field work, we found 10 localities where *P. obcordata* was absent but *Fomitopsis* was present and 12 localities where *M. heros* was absent but *Ganoderma* was present. This is an underestimate of beetle absences, particularly in undisturbed areas, as we did not collect this information in 2019.

We found *P. obcordata* to be patchily distributed in the southern Appalachian Mountains. From our field work, we recorded 90 localities of *P. obcordata* from 26 general sites (Appendix 1, Supp Fig. 1 [online only]), from which we collected 178 specimens. Sites covered three general forest types (Tyrell et al. 1998) between 647 and 1,933 m in elevation: 1) Northern hardwood forests, composed of *Betula*, *Acer*, and other hardwoods with $<25\%$ of basal area being coniferous trees, principally *Tsuga*, ranged from 707 to 1,508 m in elevation; 2) Conifer-northern hardwood, similar to northern hardwood but with higher than 25% basal area being coniferous (generally *Tsuga* and *Picea*), ranged from 647 to 1,714 m; and 3) Montane spruce-fir forests, which ranged from 1,617 to 1,933 m in elevation and were composed of *Abies* Mill. (Pinales: Pinaceae), *Picea*, *Betula*, and other less common hardwood trees. Sampled areas do not include the full elevational range of each forest type, and these forest types commonly transition from one to another (Tyrell et al. 1998).

We found *M. heros* to be widely abundant in the southern Appalachian Mountains. As such, we did not record every locality of this species. Within GSMNP, we collected 93 specimens from 38 localities in 14 general sites, which we used to describe their habitat preferences (Appendix 2). In general, *M. heros* occupied conifer-northern hardwood and northern hardwood forests, and elevations with the combined dataset range between 392 and 1,592 m. However, records above 1,300 m were scarce ($n = 4$, or 1.9%). Beetles were also present in other forest types where *Tsuga* was present, such as hardwood-pine mixtures (e.g., Lumber Ridge Trail).

Disturbance history influenced the current distribution of *P. obcordata* and its *Fomitopsis* hosts (Fig. 2C). Both the beetle and fungal hosts were most common in undisturbed forests, but both were present in lower numbers in areas that were settled, diffusely disturbed, and heavily logged (Table 1). In previously disturbed areas, the beetles' presence was generally $<1,000$ m from undisturbed areas, except in three cases: Laurel Falls, Balsam Mountain Trail, and Cades Cove. Both Laurel Falls and Cades Cove observations were based on published accounts by Foley and Ivie (2008). The Laurel Falls and Balsam Mountain Trail localities occurred in diffusely disturbed forests, approximately 4,000 m and 1,500 m from the nearest undisturbed patch, respectively. The Cades Cove locality occurred in a settlement, roughly 3,000 m from the nearest undisturbed forest but only ~ 200 m from the nearest diffusely disturbed forest. Apart from this one previous observation, we found no evidence of *P. obcordata* inhabiting settled or heavily logged areas without undisturbed forests adjacent or nearby ($<1,000$ m), but the *Fomitopsis* hosts did occur in these areas without nearby undisturbed forest. Contrastingly, neither *M. heros* nor its *Ganoderma*

hosts were distributed according to disturbance history (Fig. 3C). Both the beetle and its fungal hosts were distributed in all disturbance types (Table 1), irrespective of distance to undisturbed areas.

Natural History Observations

P. obcordata was most commonly found on *Fomitopsis ochracea* (Fig. 2B; Appendix 1), a newly documented host for the beetle. This fungus was found growing on dead hemlock *Tsuga canadensis* (L.) Carrière and other softwood trees (*Abies* and *Picea*), typically with the crowns and bark still present, and sometimes on fallen or cut logs. However, this perennial species likely persists on these trees after crowns break and the bark falls off, well into later decay stages when the wood becomes soft and blocky. Adult beetles were found regardless of the progression of tree decay, feeding on sporulating or early decaying sporocarps. Furthermore, they were commonly found on or under the bark of trees with fungi or hiding in bark or wood crevices. We found *P. obcordata* less commonly on *F. betulina* growing on birch (*Betula* spp.), though we also encountered this fungus species less often. On *F. betulina*, adults excavate cavities in the spore tissue as described in Steiner (1992), sometimes resulting in tunnels within which we found the beetles hiding. Based on iNaturalist observations, it seems that adult beetles also feed on *F. mounceae*, and this is likely another larval host. When *P. obcordata* was present, tree size ranged from 15 cm to >1 m DBH for *T. canadensis* and 11–34 cm for *Betula* spp.

Our search for *P. obcordata* confirmed that the larvae bore into fungi-infested wood (Steiner 1999). In one instance at Richland Balsam Mountain (Nantahala NF) on 9 July 2019, we removed a *F. ochracea* sporocarp from a moderately decayed softwood stump (*Abies* likely, or *Picea*, based on 1,859 m elevation; bark missing, exterior wood soft) and found one adult of *P. obcordata* in the wood behind the fungus, approximately 2 cm inside of the wood without any apparent openings that would have allowed it to enter from the outside. Next to the beetle there was an obvious oval cavity approximately the same size as the specimen, possibly a pupation chamber, with its length parallel to the wood grain. We furthermore found a pair of mating adults on the exterior wood of this same stump. Mating pairs could be found elsewhere on both fungal sporocarps and on the wood or bark. However, we never witnessed oviposition, so it remains unknown into/onto which substrate the eggs are placed.

Phellopsis obcordata adults were active diurnally from May through September (though they may be active before and after these months based on iNaturalist observations in April and October). At two sites with large populations, we found the species to be much harder to find at night than during the day. At night, more individuals seemed to be hiding in bark crevices and fewer were feeding or copulating out on or near fungus. Gregariousness occurs with this species, with several mating pairs on the same log or even the same fungal fruiting body at once. However, it was also common to find lone individuals on a single log. On two occasions, we found several (10 and 6) adults inside of dry, decayed sporocarps of *G. tsugae*. In both instances, *F. ochracea* was found growing on the same tree. It is unknown whether the beetles were simply hiding in these fungi or eating them. However, we did find the adults to opportunistically feed on *Laetiporus* spp. Murrill 1904 (Polyporales: Fomitopsidaceae) on multiple occasions, as well as two species of unidentified, perennial fungi growing on a lightly decayed *T. canadensis* log, and a heavily decayed softwood. Furthermore, multiple specimens were found near the oozing, fermenting sap at the cut ends of recently felled oak and hemlock logs.

Megalodacne heros displayed gregarious behavior on the sporocarps of *G. tsugae* (most commonly, Fig. 3B), *G. applanatum*, and *G. megaloma*, of which the latter has not been listed as a host in

Table 1. Number of data points used to characterize the tree diameter and basal area of disturbance history categories in Great Smoky Mountains National Park, as well as the number of presences (pres) and absences (abs) for each beetle species and fungal hosts

	Tree species					Basal Area	<i>Phellopsis obcordata</i> pres/abs	<i>Megalodacne heros</i> pres/abs	<i>Fomitopsis</i> hosts pres/abs	<i>Ganoderma</i> hosts pres/abs
	<i>Tsuga</i>	<i>Betula</i>	<i>Picea</i>	<i>Acer</i> or unknown						
Heavy cut	10	23	5	7	45	3/42	2/43	4/41	4/41	
Settlement	20	6	0	4	30	3/27	8/22	5/25	9/21	
Diffuse disturbance	13	1	0	3	17	3/14	6/11	2/15	6/11	
Undisturbed	40	3	2	12	57	38/19	14/43	31/26	13/44	

previous literature (Appendix 2). The new record on *G. megaloma* was made on a fallen buckeye *Aesculus* sp. L. (Sapindales: Sapindaceae) from Coweeta Hydrological Laboratory (Nantahala NF), in a northern hardwood forest approximately 1,301 m in elevation. Typically, adult beetles were present whenever host fungi were sporulating, and they chewed holes and pits on the underside (spore tissue) and top (non-spore tissue) of the fungi. However, they were also found on growing, nonsporulating fungi and decaying host fungi. Adult beetles were also commonly found inside of sporocarps and hiding between cracks in the bark. Hemlock with *G. tsugae* ranged from 35 cm to >1 m DBH, and were typically dead with crown branches and bark still present, or fallen logs with bark still present.

To our surprise, adults of *M. heros* were quite active in the day-time when we most commonly searched for beetles. Diurnal activities included active feeding, aggregating, and copulating on host fungi. Despite their activity, we never observed flight. Based on our own observations and iNaturalist data, peak adult activity appears to be in May and June, with declining activity thereafter. This species was also found walking on the ground between fungi-infested trees and feeding opportunistically on nonhost mushrooms both on the ground and on logs. Opportunistic adult feeding was observed on growing or sporulating individuals of *Laetiporus* spp., *F. ochracea*, and unidentified ephemeral mushrooms.

Comparisons of Disturbance History

Among sites sampled, we found that disturbance history categories differed in elevation (Kruskal–Wallis: $\chi^2(3) = 77.479$, $P = 2.20 \times 10^{-16}$; Fig. 4A). Post hoc Dunn's test identified undisturbed areas to be higher in elevation than diffusely disturbed ($z = 5.367$, $P = 2.40 \times 10^{-7}$) and settled ($z = 7.344$, $P = 6.22 \times 10^{-13}$), but no different than heavily logged ($z = 0.548$, $P = 1.00$). Similarly, heavily logged forests were situated higher in elevation than diffusely disturbed ($z = 4.825$, $P = 4.20 \times 10^{-6}$) and settled ($z = 6.564$, $P = 1.57 \times 10^{-10}$) areas. There were no elevation differences found between diffusely disturbed and settled forests ($z = 0.571$, $P = 1.00$). Notably, our sampling of heavily logged and undisturbed areas occurred over a wider range of elevation than for diffusely disturbed and settled areas (Fig. 4A).

Tree diameter also differed significantly by disturbance history (Kruskal–Wallis: $\chi^2(3) = 24.076$, $P = 2.41 \times 10^{-5}$; Fig. 4B). Post hoc Dunn's test demonstrated that undisturbed areas had larger trees than settled areas ($z = 4.167$, $P = 9.27 \times 10^{-5}$), but no differences were found between undisturbed and diffusely disturbed ($z = 1.241$, $P = 0.643$) or heavily logged forests ($z = 1.614$, $P = 0.320$). Similarly, diffusely disturbed forests held trees larger than settled areas ($z = 4.173$, $P = 9.03 \times 10^{-5}$) as well. There were no significant differences detected between heavily logged and diffusely disturbed ($z = 2.323$, $P = 0.060$) or settled forests ($z = 2.636$, $P = 0.025$). In general, undisturbed and diffusely disturbed forests had a wider range of tree sizes than heavily logged and settled forests, and extremely large trees were present in low amounts in undisturbed areas (Fig. 4B). Contrary to tree diameter, basal area was not found to significantly differ among disturbance history categories (Kruskal–Wallis: $\chi^2(3) = 4.457$, $P = 0.216$; Fig. 4C).

Predicting Beetle and Host Fungi Occurrence

Of the three competing models predicting the occurrence of the focal beetle species and hosts, distance from undisturbed forest was the best model for *P. obcordata*, disturbance history was the best for *Fomitopsis* hosts (though distance to undisturbed had $\Delta\text{AIC} < 2$), and the elevation model was best for *M. heros* and *Ganoderma* hosts

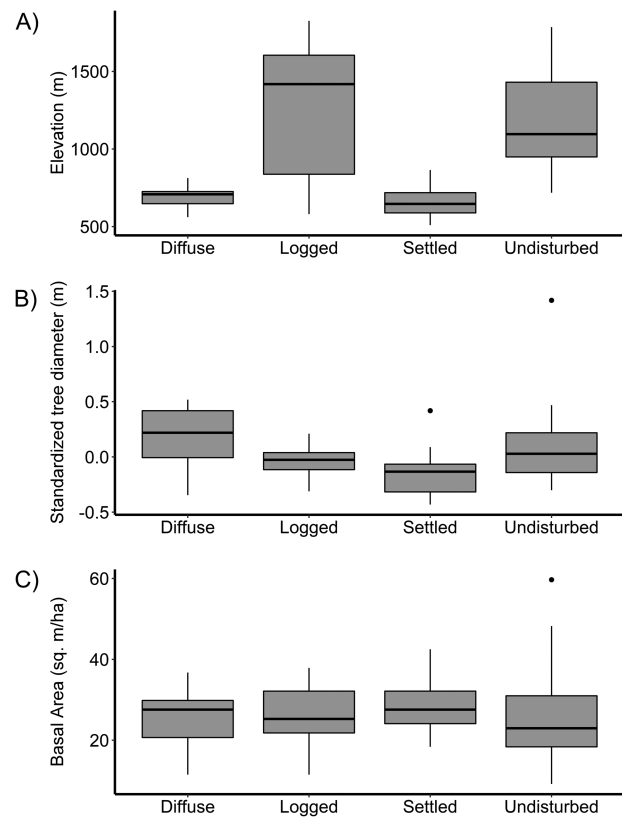


Fig. 4. Boxplots of (A) elevation, (B) tree diameter, and (C) basal area among sampled historic disturbance classes in Great Smoky Mountains National Park.

(Table 2). Because the models for fungal hosts include observations of multiple species, the results are an estimate of host availability rather than species-specific responses. The probability of occurrence significantly decreased for *P. obcordata* with increasing distance from undisturbed forest (Table 3), resulting in a sharp decline in probability from 0 to 700 m (Fig. 5A). For *Fomitopsis* hosts, occurrence was significantly greater in undisturbed forest than in other disturbance categories (Table 4). For *M. heros* and *Ganoderma* hosts, occurrence probability declined with increasing elevation (Tables 3 and 4), with the occurrence of *M. heros* nearly reaching 0 at about 1,500 m (Fig. 5B). From the chosen models, the probability of occurrence of both beetle species and their hosts was not significantly influenced by either the diameter of trees or stand basal area (Tables 3 and 4).

Discussion

Here, we tested the dependency of two low-mobility, saproxylic beetles on old-growth forests in the southern Appalachian Mountains. Our results demonstrate that old-growth forests acted as a refuge for some saproxylic species during the major landscape-wide disturbances occurring after European colonization. As secondary forests grow and accumulate deadwood resources, saproxylic communities are expected to recover (Paillet et al. 2010; Janssen et al. 2016, 2017). Our study documents this process and suggests that differences in dispersal ability are linked to species' sensitivity to human disturbance.

Southern Appalachian forests have undergone extreme change during the last 100 years due to intensive anthropogenic

Table 2. AIC and Δ AIC values from competing models to predict *Phellopsis obcordata*, *Megalodacne heros*, *Fomitopsis* host, and *Ganoderma* host occurrence in Great Smoky Mountains National Park

	<i>Phellopsis obcordata</i>		<i>Megalodacne heros</i>		<i>Fomitopsis</i> hosts		<i>Ganoderma</i> hosts	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Disturbance history categories	114.6	4.0	120.7	7.4	133.5	0.0	135.7	6.4
Distance to undisturbed forest	110.6	0.0	125.1	11.8	135.1	1.6	138.7	9.4
Elevation	148.1	37.5	113.3	0.0	155.3	21.8	129.3	0.0

Lowest AIC (and best model) indicated in bold. All models included tree size and basal area as covariates.

Table 3. Logistic regression results for *Phellopsis obcordata* and *Megalodacne heros*, showing the best occurrence model for each species in Great Smoky Mountains National Park

	<i>Phellopsis obcordata</i>				<i>Megalodacne heros</i>			
	Coef.	SE	<i>z</i>	Pr(> <i>z</i>)	Coef.	SE	<i>z</i>	Pr(> <i>z</i>)
Distance to undisturbed forest (m)	-4.48×10^{-3}	1.39×10^{-3}	-3.229	1.24×10^{-3}	-2.82×10^{-3}	9.60×10^{-4}	-2.936	3.32×10^{-3}
Elevation (m)					1.496	0.921	1.625	0.104
Tree diameter (m)	9.34×10^{-3}	0.893	0.010	0.992	-0.070	0.040	-1.770	0.077
Basal area (m ² /ha)	0.024	0.028	0.856	0.392				

Significant *z*-values indicated with bold.

disturbance, with most of the landscape now comprising second-growth forests (Yarnell 1998). Since the 1930s, second-growth forests in GSMNP have become more similar to undisturbed forests in both structure and composition, but still have not fully aligned with conditions found in undisturbed old-growth (Tuttle and White 2016). Disturbance histories have especially created a legacy in deadwood availability (Webster and Jenkins 2005). Recent work suggests that second-growth forests in the southern Appalachians have similar saproxylic beetle diversity to old-growth, but there are more species strictly associated with old-growth than second-growth (Ferro et al. 2012a). Additionally, unique deadwood habitats, such as highly decayed (i.e., veteris) wood, had higher richness and more associated species in old-growth than secondary forests (Ferro et al. 2012b). Similarly, we found that fungal resources for our species were available in disturbed forests in GSMNP, but some hosts were less common there than in undisturbed forests. This pattern mirrors wood-decaying fungi in European forests (Jonsson and Nordlander 2006, Vandekerckhove et al. 2011). Furthermore, the general absence of *P. obcordata* from second-growth indicates there are still saproxylic invertebrate species missing from second-growth communities. As deadwood microhabitats are more abundant and generally larger in older forests with senescent trees (Lachat and Müller 2018), it is not altogether surprising that saproxylic communities display this pattern 100 years post-disturbance.

In accordance with the extreme disturbances experienced in the early 1900s (Yarnell 1998), *P. obcordata* was infrequently collected after World War II and records were limited to old-growth forests (Foley and Ivie 2008). Congruently, our data suggest that *P. obcordata* is generally restricted to old-growth in the southern Appalachians today, and that its distribution has been shaped by the landscape-wide, anthropogenic disturbances of the early 1900s. While the majority of localities we recorded in GSMNP were inside or near undisturbed forests, there are three observations of *P. obcordata* that are far away from any undisturbed sources and deserve further examination: Laurel Falls Old-Growth, Balsam Mountain Trail, and southwest of Cades Cove. At face value, these localities seem to contradict the species' dependence on undisturbed

forest. But, all three observations occurred in or near to diffusely disturbed areas, where large trees were left to grow and undisturbed forest was interspersed by human-altered areas (Pyle 1988). This suggests that the species was able to persist in some areas of the mountains that were spared from the most severe disturbances. Overall, the distribution of *P. obcordata* highlights its sensitivity to anthropogenic disturbance.

The restricted distribution of *P. obcordata* warrants additional investigation: is dependence on old-growth due to second-growth lacking required habitat (i.e., habitat limitation) or from the inability to disperse to appropriate habitat in second-growth (i.e., dispersal limitation)? Beyond unique microhabitats and large amounts of deadwood (Tyrell et al. 1998, Grove 2002), old-growth forests additionally provide stable forest habitat and deadwood resources through time (Lachat and Müller 2018). For many saproxylic species, dependence on old-growth may be entirely caused by the inability to disperse to new habitat (Jonsson et al. 2001, Jonsell and Nordlander 2002, Buse 2012). Therefore, the temporal continuity of deadwood may be the most important habitat characteristic for the persistence of low-mobility saproxylic species (Sverdrup-Thygeson et al. 2014, Nordén et al. 2014). Consistent with this, we found *P. obcordata* on fungus-infested trees as small as 11 cm DBH, and neither tree size nor basal area was significant predictors in our occurrence model (Table 3). Most importantly, suitable larval habitat, host fungi, were present in second-growth (albeit in lower numbers than old-growth) but the beetles generally were not. While we cannot rule out an affinity for other old-growth characteristics due to our lack of complete forest inventories, it is unlikely that habitat limitation is occurring. Instead, our data suggest that dispersal limitation has shaped the distribution of *P. obcordata*, and that temporal stability of habitat is more important for this species than structural attributes or unique microhabitats found only in old-growth forests. A similar conclusion has been reached for other low-mobility saproxylic beetles restricted to old forests, despite younger forests exhibiting suitable habitat (Brunet and Isacson 2009, Buse 2012).

The limited dispersal ability and sensitivity to anthropogenic disturbance of *P. obcordata* make it a suitable indicator of southern Appalachian forests that have been spared from intensive

disturbance in the past, and thus have a long temporal continuity of deadwood habitat (Siitonen and Saaristo 2000, Jonsson et al. 2001, Jonsell et al. 2002, Müller et al. 2005, Thomas and Hedin 2006, Horák and Adamová 2009, Nieto and Alexander 2010, Belcik et al. 2019). This species is an ideal indicator in this region because it is large, identifiable without a microscope, and its presence and absence can be easily determined by searching on and around sporocarps of *Fomitopsis* hosts. However, this consideration should only be limited to northern hardwood, conifer-northern hardwood, spruce-fir, and their transitional forests in this region as these are the dominant forest types for this species.

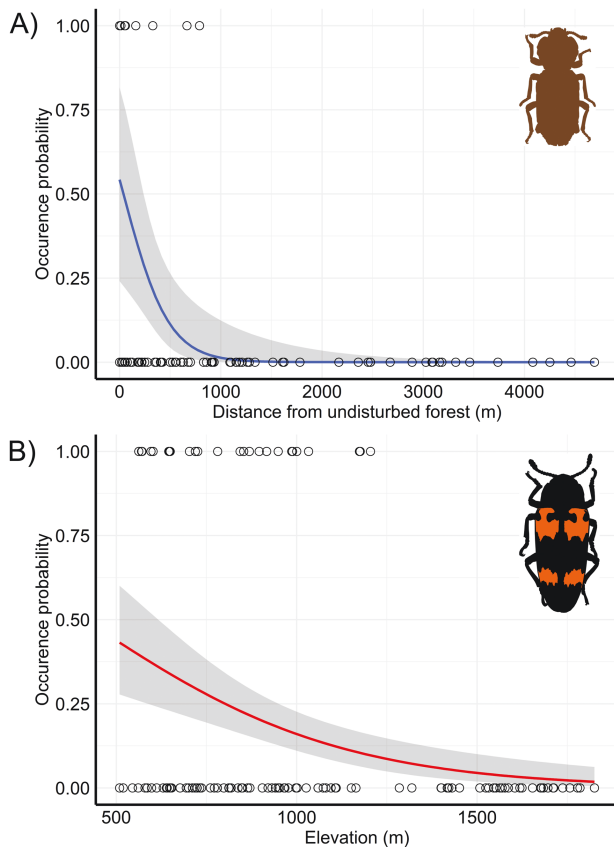


Fig. 5. Probability of occurrence within Great Smoky Mountains National Park of (A) *Phellopsis obcordata* based on distance from the nearest undisturbed forest (0 indicates inside undisturbed areas), and (B) *Megalodacne heros* based on elevation.

By contrast, *M. heros* was distributed throughout GSMNP without an obvious preference for any historical disturbance category. The only limiting factor uncovered in our analysis was high elevation, and records of the species are mostly absent above 1,300 m. Overall low occurrence probabilities in our model may be due to our sampling design for this species, as we prioritized covering more ground rather than recording each locality of this species. However, due to its widespread distribution, it is unlikely that our sampling design erased any association of this species with old-growth forests. Its current distribution also prevents us from knowing if old-growth forests acted as refugia during the turmoil of the early 1900s. Based on general trends of saproxylic diversity reduction in disturbed landscapes (Paillet et al. 2010), this scenario seems entirely plausible, together with nonmontane refugia outside of the park. However, sensitivity to human disturbance is species-specific (Lachat and Müller 2018), and other saproxylic species were able to persist through disturbance in Appalachian forests (Caterino and Langton-Myers 2018). In this case, micro-refugia too small to be mapped by Pyle (1988) may have allowed for numerous taxa to persist in otherwise disturbed areas (Caterino and Langton-Myers 2018, 2019; Caterino et al. 2017). These micro-refugia were likely on steep slopes and nontimber company land, allowing for avoidance of direct, devastating impact (Yarnell 1998). Moreover, although many of the logging operations in the southern Appalachians were described as indiscriminate and large-scale, the overall landscape formed a patch-mosaic of varying disturbance intensity and history (Pyle 1988), making persistence even more plausible. Based on its current distribution, *M. heros* appears to be relatively tolerant of human disturbance and ultimately, we are unable to know if it has recolonized or persisted in disturbed areas. Further genetic analysis may be able to better uncover the history of its distribution and sensitivity to disturbance.

Sensitivity to human disturbance is a species-specific trait for saproxylic insects (Lachat and Müller 2018), with some species disappearing soon after human interference and others able to persist even in highly disturbed areas. These responses are often determined by functional traits. For example, in Germany, large species and those requiring open canopies and large deadwood pieces are the most sensitive to human disturbance (Seibold et al. 2015). For our focal species, *M. heros* was distributed regardless of disturbance history while *P. obcordata* was restricted mainly to old-growth forests. Obvious differences in habitat availability may prohibit some saproxylic species from occurring in second-growth (Lachat and Müller 2018). Yet, both of our species require a similar habitat, fungal fruiting bodies, for reproduction. Despite the potential of some fungal hosts being less abundant in second-growth, they were

Table 4. Logistic regression results for *Fomitopsis* and *Ganoderma* hosts, showing the best occurrence model for each genus in Great Smoky Mountains National Park

	<i>Fomitopsis</i> hosts				<i>Ganoderma</i> hosts			
	Coef.	SE	<i>z</i>	Pr(> <i>z</i>)	Coef.	SE	<i>z</i>	Pr(> <i>z</i>)
Disturbance history: Undisturbed	2.045	0.835	2.449	0.014				
Disturbance history: Logged	−0.548	0.953	−0.575	0.565				
Disturbance history: Settled	0.086	0.965	0.089	0.929				
Elevation (m)					−2.08 × 10 ^{−3}	7.55 × 10 ^{−4}	−2.759	5.79 × 10 ^{−3}
Tree diameter (m)	−0.161	0.921	−0.175	0.861	1.324	0.873	1.517	0.129
Basal area (m ² /ha)	0.037	0.029	1.256	0.209	−0.053	0.035	−1.536	0.124

Significant *z*-values indicated with bold. For the categorical variable Disturbance history, the diffuse disturbance was used as the reference. Results indicate fungal host availability, not species-specific responses.

nonetheless present. Therefore, when habitat limitation is not the case, as in our scenario, differences in dispersal can explain divergent species responses to disturbance (Ranius 2006, Brin et al. 2016). This pattern was reported for two fungus beetles in Europe: *Bolitophagus reticulatus* L. (1767) and *Oplocephala haemorrhoidalis* F. (1787) (Coleoptera: Tenebrionidae). Both species require the same larval habitat of fungal fruiting bodies, but *O. haemorrhoidalis* is restricted to long-continuity forests while *B. reticulatus* is common and insensitive to anthropogenic disturbance (Jonsson et al. 2001). The key difference between the two species is their dispersal ability, with *B. reticulatus* being more able and willing to disperse (Jonsson 2003). In another example, the weak dispersal ability of tree-hollow specialists is thought to prevent the colonization of habitat in second-growth forests while species requiring other larval habitats successfully colonized second-growth (Nilsson and Baranowski 1997). Similarly, dispersal ability produces differences in the successful colonization of wood-decaying fungi among insects, with declining success farther away from old-growth forest experienced only for low-mobility species (Jonsson and Nordlander 2006). Therefore, differences in dispersal ability likely explain the patterns observed here as well. While *P. obcordata* is entirely flightless, *M. heros* is capable of some flight, which lessens its dependence on forest continuity, in theory (Norden et al. 2014).

Ongoing anthropogenic disturbance, such as invasive insect outbreaks, continue to alter southern Appalachian forests today, and have undoubtedly impacted this study. Most notably, Hemlock Woolly Adelgid (*Adelges tsugae*) Annand (1928) (Hemiptera: Adelgidae) has decimated eastern hemlock populations, resulting in large amounts of woody debris in and near streams (Vose 2013). Both *G. tsugae* and *F. ochracea* grow on hemlock, and this disturbance has provided a resource boom in the mountains. Additionally, the die-off of Fraser fir (*Abies fraseri*) (Pursh) Poir (Pinales: Pinaceae) from the Balsam Woolly Adelgid (*Adelges piceae*) Ratzeburg (1844) (Hemiptera: Adelgidae) has created another large resource pool for *F. ochracea* (Rose and Nicolas 2008). Although both beetle species can reproduce in fungi that grow on trees representing other genera and can feed opportunistically as adults, *G. tsugae* and *F. ochracea* were by far the most commonly found fungi in this study overall and comprised the largest number of occurrences for *M. heros* and *P. obcordata*, respectively. Based on our own observations and those by iNaturalist users, *G. tsugae* is more common than *F. ochracea* on dead hemlock, which may also help explain differences in the distributions of *M. heros* and *P. obcordata*. It is likely that increased host availability in the landscape has aided both species in expanding their distributions (as seen in Vandekerckhove et al. 2011, Busse et al. 2022), but particularly for *M. heros*. Indeed, both fungal hosts were present in intensively disturbed areas, and wood-decaying fungi are not typically limited by dispersal (Komonen and Müller 2018). However, whether the expansion of *P. obcordata* into second growth progresses in the long-term will depend on the continued availability of fungal hosts in the region. Due to declining host tree population sizes (Vose 2013), it seems that this major resource pool will only be short lived, and both *M. heros* and *P. obcordata* will have to rely on less common hosts growing on other tree genera. Future monitoring of both species should take place to assess population health after the deceleration of hemlock death.

Understanding a species' biology is the basis of biological inquiry and is necessary for successful conservation. In this work, we document several new insights into the natural history of our study species. Of these, the most important are the additional fungal hosts recorded for each species: *F. ochracea* is a larval host for *P. obcordata* and *G. megaloma* is a presumed larval host for *M. heros*. It is possible

that previous records of *P. obcordata* on *Heterobasidion annosum* (Fr.) Bref. (1888) (Russulales: Bondarzewiaceae) (= *Fomes annosum*) growing on *Abies* (Steiner 1992) were actually *F. ochracea*. But, it is impossible to be certain, especially considering that adults opportunistically feed. While adult beetles may feed on a wide variety of fungi (e.g., Epps and Arnold 2018), larval associations with fungi are expected to exhibit stricter host-specificity (Ashe 1981, 1984), especially in polypore fungi (Birkmoe et al. 2018). Therefore, it seems likely that *Fomitopsis* spp. are the larval hosts for *P. obcordata*, *Ganoderma* spp. are the larval hosts for *M. heros*, and other associations are based on opportunistic feeding by adults. These new host associations will provide better estimates of larval resources. However, it should be noted that not all species of these genera may be larval hosts for the respective beetles. Finally, we found *M. heros* to be diurnally active despite it being regarded as a nocturnal species (Park et al. 1931, Park and Sejba 1935, McHugh et al. 1997). It is possible that the behavior is regional, with populations in the Southern Appalachians being diurnal and those previously studied in the Midwest and Northeast being nocturnal, but further work should look into this behavioral oddity.

Conclusions

Old-growth forests harbor rich saproxylic communities and provide refugia during anthropogenic disturbances in the broader landscape. Furthermore, old-growth enriches second-growth forests throughout the landscape with a 'spillover' of saproxylic species (Gibb et al. 2006, Brunet and Isacson 2009, Olsson et al. 2012, Bouget and Parmain 2016). In the southern Appalachian Mountains, old-growth forests were refugia for *P. obcordata* through the heavy logging of the early 1900s. Today, the distribution of this species is still mostly restricted to undisturbed forests, though it may have begun recolonizing second-growth. The recolonization of second-growth forests by saproxylic organisms relies on deadwood habitat being available and the organisms' ability to disperse to that habitat and reproduce (e.g., Busse et al. 2022). We found only evidence of dispersal limitation for *P. obcordata*, though trees were generally smaller and fungal hosts less common in intensively disturbed areas. While the recolonization of second-growth may be a slow process for this species due to its flightless nature, it may not yet be possible at all for other species which require microhabitats associated with old-growth: large diameter logs, tree-hollows, highly decayed wood, and so on. Therefore, saproxylic communities will benefit from protecting remnant old-growth patches and allowing second-growth forests to mature and functionally connect old-growth in the landscape (Norden et al. 2014).

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

Acknowledgments

We thank A. Deczynski, C. Dukes, F. Etzler, G. Farnsworth, V. Formica (and lab), C. Harden, S. Horn, S. Imus, E. Recuero, E. Stone, A. Traylor, K. Traylor, and P. Wooden for assistance with field work. We are grateful to I. Foley for sharing his museum locality records for *P. obcordata*. Collection in GSMNP was done under permits # GRSM-2019-SCI-2453 and GRSM-2021-SCI-2045. This study was funded by Presidential Early Career Award (PECASE) funds awarded to M.D.U. (USDA Forest Service), NSF DEB-1916263 to M.S.C. (Clemson University), and USDA National Institute of Food and Agriculture Hatch project GEO00886 to J.V.M. (University of Georgia). The authors declare no conflicts of interest.

Author Contributions

All authors aided in planning the study and performing field work. C.R.T. inspected iNaturalist records, analyzed the data, and wrote the first draft. All authors edited and revised subsequent drafts. All authors agreed to the final version of this manuscript.

References Cited

- Ashe, J. S. 1981. Studies of the life history and habits of *Phanerota fasciata* Say (Coleoptera: Staphylinidae: Aleocharinae) with notes on the mushroom as a habitat and descriptions of the immature stages. *Coleopt. Bull.* 35: 83–96.
- Ashe, J. S. 1984. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of described subgenera and major features of evolution. *Quaest. Ent.* 20: 129–349.
- Belcik, M., J. Goczał, and M. Ciach. 2019. Large-scale habitat model reveals a key role of large trees and protected areas in the metapopulation survival of the saproxylic specialist *Cucujus cinnaberinus*. *Biodivers. Conserv.* 28: 3851–3871.
- Birkmore, T., R. M. Jacobsen, A. Sverdrup-Thygeson, and P. H. W. Biedermann. 2018. Insect-fungus interactions in dead wood systems, pp. 377–427. In M. D. Ulyshen (ed.), *Saproxylic insects: diversity, ecology, and conservation*. Springer International Publishing, Cham, Switzerland.
- Blatchley, W. S. 1910. On the Coleoptera known to occur in Indiana. *Indiana Dept. Geol. Nat. Resour. Bull.* 1: 1–1386.
- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forest ecosystem. Springer-Verlag, New York, USA.
- Bouget, C., and G. Parmain. 2016. Effects of landscape design of forest reserves on saproxylic beetle diversity. *Conserv. Biol.* 30: 92–102.
- Boyle, W. W. 1956. A revision of the Erotylidae of American north of Mexico (Coleoptera). *Bull. Am. Mus. Nat. Hist.* 110: 61–172.
- Brin, A., C. Bouget, H. Brustel, and H. Jactel. 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *J. Insect Conserv.* 15: 653–669.
- Brin, A., L. Valladares, S. Ladet, and C. Bouget. 2016. Effects of forest continuity on flying saproxylic beetle assemblages in small woodlots embedded in agricultural landscapes. *Biodivers. Conserv.* 25: 587–602.
- Brunet, J., and G. Isacson. 2009. Restoration of beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution. *Biodivers. Conserv.* 18: 2387–2404.
- Buse, J. 2012. ‘Ghosts of the past’: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J. Insect Conserv.* 16: 93–102.
- Busse, A., L. Cizek, P. Čížková, L. Drag, V. Dvorak, J. Foit, M. Heurich, P. Hubený, J. Kašák, F. Kittler, et al. 2022. Forest dieback in a protected area triggers the return of the primeval forest specialist *Peltis grossa* (Coleoptera, Trogossitidae). *Conserv. Sci. Pract.* 4: e612.
- Caterino, M. S., and S. S. Langton-Myers. 2018. Long-term persistence of flightless weevils (*Eurhoptus pyriformis*) across old- and second-growth forests patches in southern Appalachia. *BMC Evol. Biol.* 18: 165.
- Caterino, M. S., and S. S. Langton-Myers. 2019. Intraspecific diversity and phylogeography in Southern Appalachian *Dasycterus carolinensis* (Coleoptera: Staphylinidae: Dasycterinae). *Insect Syst. Divers.* 3: 8.
- Caterino, M. S., L. M. Vásquez-Vélez, and S. S. Myers. 2017. On the conservation value of second-growth forests for leaf-litter inhabiting beetles. *Insect Syst. Divers.* 1: 20–28.
- Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol.* 6: 51–71.
- Chazdon, R. L. 2014. *Second growth*. The University of Chicago Press, Chicago, USA.
- Conner, R. C., and A. J. Hartsell. 2002. Forest area and conditions (revised), pp. 357–402. In D. N. Wear and J. G. Greis (eds.), *Southern forest resource assessment*. General Technical Report SRS-53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, N.C.
- Dinno, A. 2017. dunn.test: Dunn’s test of multiple comparisons using rank sums. R package version 1.2.5. (<https://cran.r-project.org/web/packages/dunn.test/index.html>).
- Epps, M. J., and E. Arnold. 2018. Quantifying the beetle-macrofungal associations in a temperate biodiversity hotspot. *Mycologia*. 110: 269–285.
- Fan, Z., S. R. Shifley, M. A. Spetich, F. R. Thompson III, and D. R. Larsen. 2003. Distribution of cavity trees in midwestern old-growth and second-growth forests. *Can. J. Forest Res.* 33: 1481–1494.
- Faraway, J. 2016. Faraway: functions and datasets for books by Julian Faraway. R package version 1.0.7. (<https://CRAN.R-project.org/package=faraway>).
- Ferro, M. L., M. L. Gimmel, K. E. Harms, and C. E. Carlton. 2012a. Comparison of Coleoptera emergent from various decay classes of downed woody debris in Great Smoky Mountains National Park, USA. *Insect Mundi*. 0260: 1–80.
- Ferro, M. L., M. L. Gimmel, K. E. Harms, and C. E. Carlton. 2012b. Comparison of Coleoptera communities in leaf-litter and rotten wood in Great Smoky Mountains National Park, USA. *Insect Mundi*. 0259: 1–58.
- Foley, I. A., and M. A. Ivie. 2008. A revision of the genus *Phellopsis* LeConte (Coleoptera: Zopheridae). *Zootaxa*. 1689: 1–28.
- Fralish, J. S., F. B. Cooks, J. L. Chambers, and F. M. Harty. 1991. Comparison of presettlement, second-growth and old-growth forest on six site types in the Illinois Shawnee Hills. *Am. Midl. Nat.* 125: 294–309.
- Gibb, H., J. Hjäältén, J. P. Ball, O. Atlegrim, R. B. Pettersson, J. Hilszczański, T. Johansson, and K. Danell. 2006. Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography*. 29: 191–204.
- Graves, R. C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. *Ann. Entomol. Soc. Am.* 53: 61–78.
- Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* 33: 1–23.
- Holmes, M. A., and G. R. Matlack. 2017. Agricultural history drives structure and tree species composition of second growth forest over 100 years in southeastern Ohio, USA. *J. Veg. Sci.* 28: 736–746.
- Horák, J., and J. Adamová. 2009. Contribution to knowledge of two rare saproxylic beetles (Coleoptera) from Eastern Bohemia (Czech Republic). *Elateridarium*. 3: 7–18.
- Janssen, P., E. Cateau, M. Fuhr, B. Nusillard, H. Brustel, and C. Bouget. 2016. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodivers. Conserv.* 25: 1167–1185.
- Janssen, P., M. Fuhr, E. Cateau, B. Nusillard, and C. Bouget. 2017. Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biol. Conserv.* 205: 1–10.
- Jonsell, M., and G. Nordlander. 2002. Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *Forest Ecol. Manag.* 157: 101–118.
- Jonsson, M. 2003. Colonization ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *Ecol. Entomol.* 28: 159–167.
- Jonsson, M., and G. Nordlander. 2006. Insect colonization of fruiting bodies of the wood-decaying fungus *Fomitopsis pinicola* at different distances from an old-growth forest. *Biodivers. Conserv.* 15: 295–309.
- Jonsson, M., M. Jonsell, and G. Nordlander. 2001. Priorities in conservation biology: a comparison between two polypore-inhabiting beetles. *Ecol. Bull.* 49: 195–204.
- Kincaid, J. A., and A. J. Parker. 2008. Structural characteristics and canopy dynamics of *Tsuga canadensis* in forests of the southern Appalachian mountains, USA. *Plant Ecol.* 199: 265–280.
- Komonen, A., and J. Müller. 2018. Dispersal ecology of deadwood organisms and connectivity conservation. *Conserv. Biol.* 32: 535–545.
- Lachat, T., and J. Müller. 2018. Importance of primary forests for the conservation of saproxylic species, pp. 581–605. In M. D. Ulyshen (ed.), *Saproxylic insects: diversity, ecology, and conservation*. Springer International Publishing, Cham, Switzerland.
- Loyd, A. L., C. W. Barnes, B. W. Held, M. J. Schink, M. E. Smith, J. A. Smith, and R. A. Blanchette. 2018. Elucidating ‘lucidum’: Distinguishing the

- diverse laccate *Ganoderma* species of the United States. PLoS One. 13: e0199738.
- Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. 94: 199–209.
- McHugh, J. V., C. J. Marshall, and F. L. Fawcett. 1997. A study of adult morphology in *Megalodacne heros* (Say) (Coleoptera: Erotylidae). T. Am. Entomol. Soc. 123: 167–223.
- Müller, J., H. Bußler, U. Bense, H. Brustel, G. Flechtner, A. Fowles, M. Kahlen, G. Möller, H. Mühle, J. Schmidl, et al. 2005. Urwald relict species—Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online. 2: 106–113.
- Müller, J., A. Jarzabek-Müller, H. Bussler, and M. M. Gossner. 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Anim. Conserv. 17: 154–162.
- Munoz, S. E., D. J. Mladenoff, S. Schroeder, and J. W. Williams. 2014. Defining the spatial patterns of historical land use associated with the indigenous societies of eastern North America. J. Biogeogr. 41: 2195–2210.
- National Park Service. 2015. GRSM trails. (<https://grsm-nps.opendata.arcgis.com/datasets/nps:grsm-trails/about>).
- National Park Service. 2018. Pyle disturbance history. (<https://grsm-nps.opendata.arcgis.com/datasets/nps:grsm-pyle-disturbance-history/about>).
- Nieto, A., and K. N. A. Alexander. 2010. European red list of saproxylic beetles. Publications Office of the European Union, Luxembourg, Luxembourg.
- Nilsson, S., and R. Baranowski. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography. 20: 491–498.
- Nordén, B., A. Dahlberg, T. E. Brandrud, Ö. Fritz, R. Ejrnaes, and O. Ovaskainen. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Écoscience. 21: 34–45.
- Ökland, B., A. Bakke, S. Hågvar, and T. Kvamme. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers. Conserv. 5: 75–100.
- Olsson, J., T. Johansson, B. G. Jonsson, J. Hjältén, M. Edman, and L. Ericson. 2012. Landscape and substrate properties affect species richness and community composition of saproxylic beetles. Forest Ecol. Manag. 286: 108–120.
- Paillet, Y., L. Bergès, J. Hjältén, P. Ódor, C. Avon, M. Bernhardt-Römermann, R. -J. Bijlsma, L. D. Bruyn, M. Fuhr, U. Grandin, et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24: 101–112.
- Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analysis in R. Bioinformatics. 35: 526–528.
- Park, O., and O. Sejba. 1935. Studies in nocturnal ecology, IV. *Megalodacne heros*. Ecology. 16: 164–172.
- Park, O., J. A. Lockett, and D. J. Myers. 1931. Studies in nocturnal ecology with species reference to climax forest. Ecology. 12: 709–727.
- Pyle, C. 1988. The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. Castanea. 53: 183–196.
- R Core Team. 2021. R: a language and environment for statistical computing. (<https://www.R-project.org/>).
- Ranius, T. 2006. Measuring the dispersal distance of saproxylic insects: a key characteristic for their conservation. Popul. Ecol. 48: 177–188.
- Reich, P. B., and L. Frelich. 2002. Temperate deciduous forests, pp. 565–569. In H. A. Mooney and J. G. Canadell (eds.), The Earth system: biological and ecological dimensions of global environmental change. John Wiley and Sons Ltd., Chichester, England.
- Rose, A. K., and N. S. Nicholas. 2008. Coarse woody debris in a southern Appalachian spruce-fir forest of the Great Smoky Mountains National Park. Nat. Area J. 28: 342–355.
- Siebold, S., R. Brandl, J. Buse, T. Hothorn, J. Schmidl, S. Thorn, and J. Müller. 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv. Biol. 29: 382–390.
- Siebold, S., C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, and J. Müller. 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. J. Appl. Ecol. 53: 934943.
- Siitonen, J., and L. Saaristo. 2000. Habitat requirements and conservation of *Pytho koluwensis*, a beetle species of old-growth boreal forest. Biol. Conserv. 94: 211–220.
- Speight, M. C. D. 1989. Saproxylic insects and their conservation. Strasbourg Council of Europe, France.
- Spetich, M. A., S. R. Shifley, and G. R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in midwestern old-growth forests. Forest Sci. 45: 302–313.
- Steiner, W. E. 1992. ‘Ironclad beetles’, the family Zopheridae, in Maryland: notes on the natural history and distribution of *Phellopsis obcordata* (Kirby). Md. Nat. 35: 25–30.
- Steiner, W. E. 1999. Flightless beetles in Appalachian ‘deserts’: studies on the distribution and localized habitats of some species of Tenebrionidae (Coleoptera), pp. 125–144. In R. P. Eckerlin (ed.), Proceedings of the Appalachian Biogeography Symposium. Virginia Museum of Natural History, Blacksburg, VA, USA.
- Stenbacka, F., J. Hjältén, J. Hilszczański, and M. Dynesius. 2010. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. Ecol. Appl. 20: 2310–2321.
- Sverdrup-Thygeson, A., L. Gustafsson, and J. Kouki. 2014. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodivers. Conserv. 23: 513–535.
- Thomas, S. M., and M. Hedin. 2006. Natural history and distribution of the enigmatic southern Appalachian opilionid, *Fumontana deprehendor* Shear (Laniatores: Triaenonychidae), with an assessment of morphological variation. Zootaxa. 1242: 21–36.
- Trani, M. K. 2002. Terrestrial ecosystems, pp. 3–46. In D. N. Wear and J. G. Greis (eds.), Southern forest resource assessment. General Technical Report SRS-53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, N.C.
- Tuttle, J. P., and P. S. White. 2016. Structural and compositional change in Great Smoky Mountains National Park since protection, 1930s–2000s, pp. 263–294. In C. H. Greenberg and B. S. Collins (eds.), Natural disturbances and historic natural range of variation. Switzerland, Cham, Springer.
- Tyrrell, L. E., G. J. Nowacki, T. R. Crow, D. S. Buckley, E. A. Nauertz, J. N. Niese, J. L. Rollinger, and J. C. Zasada. 1998. Information about old growth for selected forest type groups in the eastern United States. General Technical Report NC-197. U.S. Department of Agriculture, Forest Service, St. Paul, MN, USA.
- Ulyshen, M. D., and J. Šobotník. 2018. An introduction to the diversity, ecology, and conservation of saproxylic insects, pp. 1–50. In M. D. Ulyshen (ed.), Saproxylic insects: diversity, ecology, and conservation. Springer International Publishing, Cham, Switzerland.
- U.S. Geological Survey. 2020. Standard 1/3 arc-second Digital Elevation Model. (https://www.usgs.gov/core-science-systems/ngp/3dep/about-3dep-products-services?qt-science_support_page_related_con=0#qt-science_support_page_related_con).
- Vandekerckhove, K., L. D. Keersmaecker, R. Walley, F. Köhler, L. Crevecoeur, L. Govaere, A. Thomaes, and K. Verheyen. 2011. Reappearance of old-growth elements in lowland woodlands in northern Belgium: do the associated species follow? Silva Fenn. 45: 909–935.
- Vose, J. M., D. N. Wear, A. E. Mayfield III, and C. D. Nelson. 2013. Hemlock woolly adelgid in the southern Appalachians: control strategies, ecological impacts and potential management responses. Forest Ecol. Manag. 291: 209–219.
- Webster, C. R., and M. A. Jenkins. 2005. Coarse woody debris dynamics in the southern Appalachians as affected by topographic position and anthropogenic disturbance history. Forest Ecol. Manag. 217: 319–330.
- Wilson, J. 1908. Report of the Secretary of Agriculture on the Southern Appalachian and White Mountain watersheds. U.S. Government Printing Office, Washington, DC, USA.
- Yarnell, S. L. 1998. The southern Appalachians: a history of the landscape. General Technical Report SRS-18. U.S. Department of Agriculture, Forest Service, Asheville, NC, USA.