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Seasonality, Distribution, and Diversity of Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae and Geotrupidae: Geotrupinae) in Great Smoky Mountains National Park, USA

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Abstract

Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae and Geotrupidae: Geotrupinae) communities provide crucial ecosystem services in a diverse range of habitats. As part of their breeding activities, dung beetles remove portions of a dung source and bury them under the soil. This behavior adds nutrients to the soil, aerates the soil, and disperses seeds. Dung beetle species are numerous in forest, prairie, savanna, and pasture ecosystems across the globe, but dung beetle communities vary across elevational gradients and habitat types. A variety of dung beetle species are native to the southeast region of the USA, yet we have limited knowledge of the life history and community assemblage of these species. Previous research on southeastern dung beetles has focused primarily on censusing the species inhabiting agricultural pasture land; bioinventories of dung beetle communities in the Appalachian Mountain regions are thus incomplete. To fill this knowledge gap, a census of dung beetles was performed in the Great Smoky Mountains National Park (North Carolina and Tennessee, USA), quantifying differences in abundance and distribution across season, habitat type, and elevation. Using pitfall traps baited with cattle dung for 24-h periods, dung beetles were collected and identified from six plots once every two weeks during April through September 2017. This research determined that communities of dung beetles varied both temporally and geographically. Low-elevation communities were more diverse than high-elevation communities, and high-elevation communities were dominated by non-native species. Population abundance peaked in late summer at both low and high elevations.

Keywords: All Taxa Biodiversity Inventory, Appalachian Mountains, bioinventory, introduced species, Scarabaeoidea

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Introduction

Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae and Geotrupidae: Geotrupinae) communities provide crucial ecosystem services in a diverse range of habitats. As part of their breeding activities, dung beetles remove portions of a dung source and bury them under the soil for oviposition, and this dung is the sole food source for larvae during development (Halffter and Edmonds 1982). This behavior increases the amount of dung buried underground, which adds nutrients to the soil, aerates the soil, disperses seeds, and decreases survival of vertebrate pests (Nichols *et al.* 2008). Dung beetle species are numerous in forest, prairie, savanna, and pasture ecosystems across the globe, but species distributions change across space, and thus the composition of dung beetle communities varies across elevation and latitude (Andresen 2005; Hanski and Cambefort 1991; Jay-Robert *et al.* 2008; Simmons and Ridsdill-Smith 2011; Verdú *et al.* 2007). A variety of dung beetle species are native to the southeast region of the United States. Yet, we currently have limited knowledge of the life history and community assemblage of these species because previous research has focused primarily on agricultural pasture land (Bertone *et al.* 2005; Kaufman and Wood 2012). Thus, bioinventories of dung beetles in the Appalachian Mountains are rare and incomplete.

Documenting community assemblage of dung beetles is important for understanding the ecosystem services provided by beetles (Dangles *et al.* 2012). Dung beetles are split into three guilds based on breeding behavior. Rolling dung beetles (telecoprids) remove and roll dung away from the dung pat to a suitable site before laying a single egg within the dung mass and burying it in a shallow hole below ground (Halffter and Edmonds 1982). Tunneling dung beetles (paracoprids) dig a tunnel beneath the dung source, pack dung into a brood mass in the tunnels, lay a single egg within the brood mass, and then backfill the tunnel (Halffter and Edmonds 1982). Dwelling dung beetles (endocoprids) lay eggs in a brood mass that they shape within the dung pat, and thus dwellers do not place dung beneath the soil surface (Halffter and Edmonds 1982). The composition of the different functional guilds within a community significantly affects the rate of dung burial (Dangles *et al.* 2012). Furthermore, the dung burial rate and depth depend on the dung beetle's size (Dangles *et al.* 2012; Gregory *et al.* 2015; Mamantov and Sheldon 2021). Determining the makeup of dung beetle communities across the Appalachian Mountains can thus provide insight into ecosystem services across the region's different elevations and habitat types.

Dung beetle communities in the Appalachians include native species as well as non-native species that were introduced to the region throughout the 20th century. During the 1960s–1970s, non-native dung beetles were intentionally introduced on agricultural land across the United States to increase the rate of dung removal (Fincher and Woodruff 1975; Floate *et al.* 2017; Hoebeke and Beucke 1997; Pokhrel *et al.* 2021). Since introduction, these species have spread to unintended areas and are likely competing with native species for access to dung resources and breeding space (Howden and Howden 2001; Howden and Scholtz 1986; Ridsdill-Smith 1993; Young 2007). These types of biological invasions are recognized as one of the major threats to biodiversity across the globe (Elton 1958; Simberloff 2013). Because historic dung beetle inventories in the Appalachian Mountains are lacking, little is known about how introduced dung beetle species affect native dung beetle species and community assemblage.

A census of dung beetle communities was performed to provide a biological inventory of the location, timing of activity, and abundance of native and introduced species in the temperate forests of the Appalachian Mountains within Great Smoky Mountains National Park (GSMNP), North Carolina and Tennessee, USA. The research was conducted to discover: 1) how dung beetle communities in GSMNP vary across habitat and elevation; 2) how dung beetle populations in GSMNP vary seasonally; and 3) how the abundance of introduced dung beetle species varies across habitat and elevation. To address these questions, dung beetles were collected every other week during April–October 2017 at six sites in GSMNP varying in elevation and habitat type.

Materials and Methods

Study Sites

Dung beetles were trapped at six All Taxa Biodiversity Inventory (ATBI) plots in GSMNP (Permit #GRSM-2017-SCI-2004) (Fig. 1). The ATBI plots are a project organized by Discover Life in America in conjunction with the National Park Service that works to inventory species and maintain species databases for the Smoky Mountains (https://dlia.org; Nichols and Langdon 2007). The 1-ha ATBI plots were established in 1998 and have been monitored for various taxa since their conception (Nichols and Langdon 2007). Six ATBI plots were chosen for this study, spanning different elevations and habitat types (Jenkins 2007): (1) Cataloochee ATBI—high-elevation old-growth forest (1,382 m; 35.586°, −83.081°, Haywood County, NC); (2) Purchase Knob ATBI—high-elevation forest edge (1,524 m; 35.586°, −83.073°, Haywood County, NC); (3) Indian Gap ATBI—high-elevation beech gap forest (1,672 m; 35.611°, −83.444°, Sevier County, TN); (4) Cades Cove ATBI—low-elevation meadow (522 m; 35.592°, −83.838°, Blount County, TN); (5) Tremont ATBI—low-elevation early successional forest (549 m; 35.686°, −83.499°, Blount County, TN); (6) Twin Creeks ATBI—low-elevation early successional forest (594 m; 35.638°, −83.499°, Sevier County, TN) (Fig. 1, Table 1).

Trapping

Dung beetles were trapped once every two weeks, 14 April–27 September 2017, to census throughout the entirety of the beetles' active period. Due to bear activity that impacted baited traps and site access, there was some variation in trapping periods among sites (Table 1). Five pitfall traps were set within a 100-m radius circle within each plot. Traps were at least 25 m apart. Pitfall traps consisted of a buried 900-g plastic container with a funnel entrance filled with ~3 cm of field soil. Traps were baited with cattle dung that was wrapped in cotton fabric and suspended from a metal frame over the pitfall. Cattle dung was sterilized by autoclaving to prevent transfer of microorganisms into the park. The traps were covered with a white Styrofoam plate, which served as a rain cover. Traps were left open for 24 ± 4 h in order to collect both diurnal and nocturnal beetles. Captured beetles were sorted, identified, and released at the collection site. Voucher specimens were collected for each species and deposited at the Twin Creeks Science and Education Center, part of the National Park System.

Data Analysis

The VEGAN package in R v3.6.3 (Oksanen *et al.* 2016; R Core Team 2020) was used to examine how dung beetle communities vary across habitat and elevation. Shannon's diversity index (H) and species evenness (E) were calculated for each ATBI plot to make comparisons among habitats and between high-elevation and low-elevation sites. Abundance was calculated across the active season to compare seasonality among species and between high- and low-elevation sites. Abundance of introduced versus native species was examined at high- and low-elevation sites.

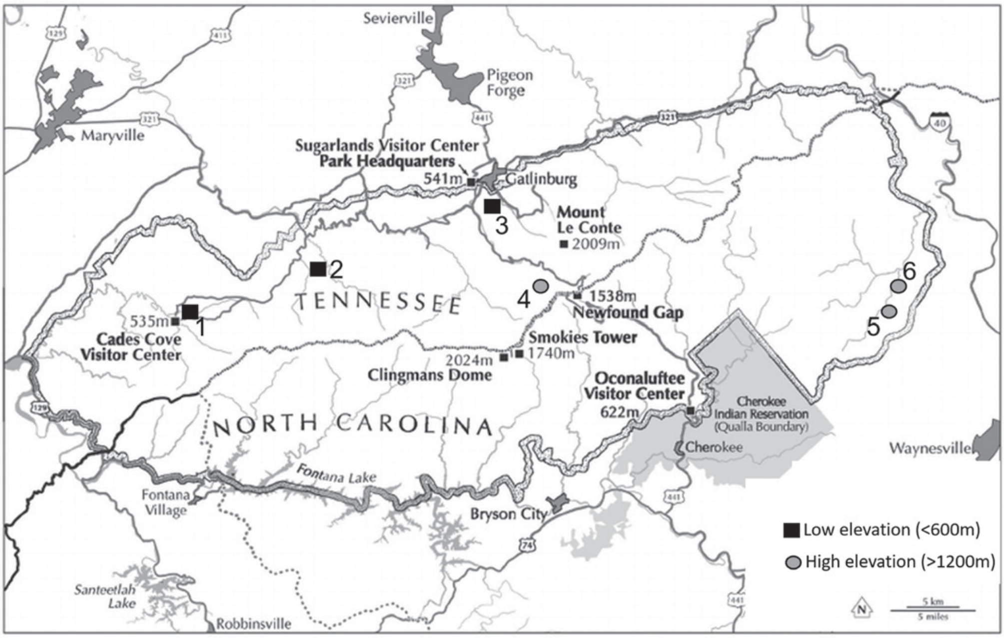

Fig. 1. Location of the six All Taxa Biodiversity Inventory (ATBI) plots. High-elevation (> 1,200 m) plots are labeled with a gray circle and low-elevation (< 600 m) are labeled with a black square. The numbers indicate the following plots: 1) Cades Cove, 2) Tremont, 3) Twin Creeks, 4) Indian Gap, 5) Cataloochee, and 6) Purchase Knob. Map modified from Miegrot *et al.* (2001).

Table 1. Location, description, and diversity results at each study site used during this research.

Site	Latitude	Longitude	Elevation (m)	Habitat Type	Species Richness (*S*)	Species Evenness (*E*)	Species Diversity (*H*)	Trapping Dates in 2017
Purchase Knob	35.586	−83.073	1,494 (high)	oak forest edge	2	0.11	0.08	April 14; May 13, 24; June 13, 27; July 10, 24; August 7
Cataloochee	35.586	−83.081	1,382 (high)	red oak forest	3	0.39	0.43	April 14; May 13, 24; June 13, 27; July 10, 24; August 7
Indian Gap	35.611	−83.444	1,672 (high)	beech gap forest	2	0.31	0.22	May 24; June 13, 27; July 10, 24; August 7
Cades Cove	35.592	−83.838	522 (low)	old field / meadow	5	0.97	1.57	May 24; June 13, 27; July 10, 24; August 7, 28; September 26
Twin Creeks	35.638	−83.699	549 (low)	Appalachian hardwood forest	5	0.86	1.38	June 13, 27; July 10, 24; August 7, 28; September 26
Tremont	35.686	−83.499	594 (low)	Appalachian hardwood forest	6	0.78	1.40	June 13, 27; July 10, 24; August 7, 28; September 26

Results

In total, 403 dung beetle specimens within nine species and six genera, including one dwelling species, one rolling species, and seven tunneling species (Table 2), were collected. Seven of the nine species are native to the Appalachian region, and two species are introduced from Eurasia (Table 2).

Abundance, Location, and Seasonal Activity of Dung Beetle Species

Geotrupidae: Geotrupinae

Geotrupes blackburnii (Fabricius, 1781)

In total, 39 individuals of *G. blackburnii* (Geotrupini) were collected in forested plots at both low and high elevations (Table 2), though the species was more abundant at high elevation. *Geotrupes blackburnii* is a mid-sized (10–13 mm), black earth-boring scarab beetle that is abundant across much of eastern North America (Guarnieri and Harpootlian 2013). Earth-boring beetles feed on dung and decaying matter and thus are attracted to fungi, dung, and carrion, though they prefer fungi as a food resource (Fincher *et al.* 1970; Howden 1955; Simons *et al.* 2018). *Geotrupes* beetles, unlike true dung beetles, do not provision offspring with dung. Instead, *Geotrupes* beetles construct burrows underground and provision offspring with plant litter. The developing larvae feed on the decaying litter (Scholtz *et al.* 2009). *Geotrupes blackburnii* was active during June through August, with peak abundance during late July (Fig. 2).

Geotrupes splendidus (Fabricius, 1775)

In total, 14 *G. splendidus* were collected in forested plots at low elevations (Table 2). *Geotrupes splendidus* is a mid-sized (13–15 mm) earth-boring scarab beetle distributed across eastern North America. *Geotrupes splendidus* is usually metallic green in color but has also been observed in hues ranging from black to copper and even purple (Guarnieri and Harpootlian 2013). The beetles collected in the study sites ranged across this color spectrum, from lustrous dark brown to a brighter green color to a purplish hue. Like *G. blackburnii*, *G. splendidus* feeds on decaying plant litter, fungi, dung, and carrion. *Geotrupes splendidus* was active during June through September, with a peak in mid-July (Fig. 2). Because they were still abundant during the last survey in late September, their activity likely extends into the fall.

Scarabaeidae: Aphodiinae

Aphodius fimetarius (Linnaeus, 1758)

In total, 223 individuals of *A. fimetarius* (Aphodiini) were collected in high-elevation, forested sites (Table 2). *Aphodius fimetarius* is a small (5–9 mm) dwelling dung beetle with a distinctive bicolored orange and black pattern. Originally from Eurasia, *A. fimetarius* is now widely distributed across Asia, Europe, northern Africa, Australia, and North America and can be found throughout the continental United States (Miraldo *et al.* 2014). Though it is thought to prefer cattle dung and open pastures (Gordon 1983), specimens were collected

Table 2. Species, number of specimens, and location of dung beetles collected.

Species	Status	Guild	Study Site	Elevation	Number
Aphodius fimetarius	non-native	dweller	Cataloochee	high	140
			Indian Gap	high	17
			Purchase Knob	high	66
Onthophagus taurus	non-native	tunneler	Cataloochee	high	4
			Cades Cove	low	6
			Purchase Knob	high	1
			Tremont	low	1
			Twin Creeks	low	22
Onthophagus hecate	native	tunneler	Cades Cove	low	10
Onthophagus orpheus	native	tunneler	Tremont	low	11
			Twin Creeks	low	8
Phanaeus vindex	native	tunneler	Cades Cove	low	8
Copris fricator	native	tunneler	Cades Cove	low	5
			Tremont	low	26
Canthon chalcites	native	roller	Cades Cove	low	11
			Tremont	low	11
			Twin Creeks	low	3
Geotrupes blackburnii	native	N/A	Cataloochee	high	15
			Indian Gap	high	1
			Twin Creeks	low	22
			Tremont	low	1
Geotrupes splendidus	native	N/A	Tremont	low	8
			Twin Creeks	low	6

from forested and forest edge habitats. Individuals were active during April through August, with a peak during early August (Table 2, Fig. 2). *Aphodius fimetarius* is now thought to be a species complex comprised of *A. fimetarius* and *Aphodius pedellus* (De Geer), which can be distinguished genetically (Miraldo *et al.* 2014). Specimens collected during this study appear to be *A. fimetarius*, based on the rounded head shape of the specimens (Miraldo *et al.* 2014), but genetic tests would be necessary to confirm the identification.

Scarabaeidae: Scarabaeinae

Canthon chalcites (Haldeman, 1843)

In total, 25 *C. chalcites* (Deltochilini) were collected in low-elevation sites, including hardwood forests and grasslands (Table 2). *Canthon chalcites* is a large (13–21 mm) rolling dung beetle that occurs throughout the eastern United States. *Canthon chalcites* can be either black or copper in color (Nemes and Price 2015), but all specimens collected during this research were copper colored. The species has been collected from dung, rotting fruit, and roadkill (Nemes and Price 2015). Seasonally, *C. chalcites* was active during June through late September and most abundant during mid-July (Fig. 2).

Copris fricator (Fabricius, 1787)

In total, 31 *C. fricator* (Coprini) were collected in forested and pasture ecosystems at low elevations (Table 2). *Copris fricator* is a mid-sized (10–18 mm), black tunneling dung beetle found in the eastern United States into Canada. Major males have a large, single horn on the center of their head and minor males have either a small horn or no horn present. Females have a rounded tubercle in the center of their head (Nemes and Price 2015). *Copris fricator* beetles show biparental care and bury brood balls below the dung pat (Scholtz *et al.* 2009). The species was active during late July to September and showed peak abundance in early August (Fig. 2).

Onthophagus hecate (Panzer, 1794)

In total, 10 *O. hecate* (Onthophagini) were collected in the Cades Cove meadow site (Table 2). *Onthophagus hecate* is a small (5–9 mm) tunneling dung beetle widely distributed across most of the United States, except the Pacific Coast. Individuals of the species are matte black and have major males with a forked horn projecting forward from the pronotum. Minor males have a reduced pronotal horn

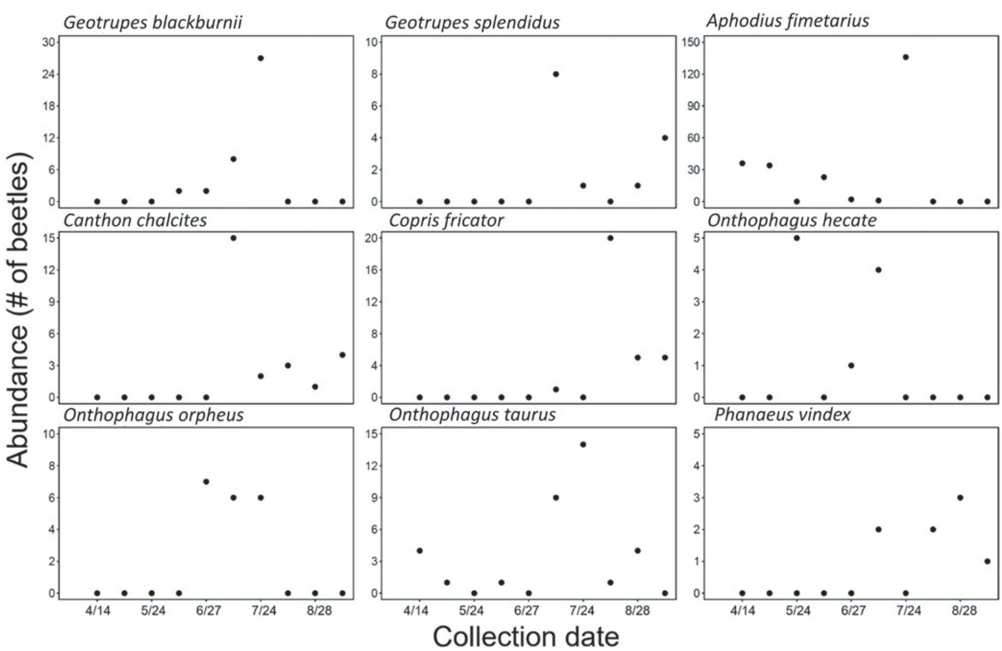

Fig. 2. Seasonality and abundance for nine dung beetle species trapped in Great Smoky Mountains National Park during mid-April to late September 2017. Species varied in their seasonality and length of active period. The number of individuals trapped per species varies; for some species, very few individuals were recovered throughout the study so their observed seasonal distribution is likely to be less representative of the species' true active period than the species with increased sample size.

or pronotal ridge, and females have a pronotal ridge. *Onthophagus hecate* is most often found in open pastures but also occurs in forested areas. *Onthphagus hecate* is one of the most common North American dung beetle species due to its wide geographic range, broad habitat preference, and high abundance (Howden and Cartwright 1963; Nemes and Price 2015). *Onthophagus hecate* prefers dung but also feeds on fungi, carrion, and decaying plant matter (Nemes and Price 2015). *Onthophagus hecate* buries oblong brood balls (approximately 1.0–2.5 g) around 3–10 cm below the dung pat (Mamantov and Sheldon 2021). In the GSMNP, the species was active during May through August, with peaks in abundance in mid-May and early July (Fig. 2).

Onthophagus orpheus (Panzer, 1794)

In total, 19 *O. orpheus* were collected in low elevation, forested sties (Table 2). *Onthophagus orpheus* is a small (5–9 mm) tunneling dung beetle that can be metallic green in color, purplish brown, reddish, or copper, but all specimens collected in this study had copper coloration. Similar to *O. hecate*, major males have a forked horn projecting forward from the pronotum, minor males have a reduced pronotal horn or pronotal ridge, and females have a pronotal ridge. *Onthophagus orpheus* is distributed across the eastern United States with a preference for old-growth forested habitats (Price 2004). The species has been found feeding on mammalian dung and carrion (Howden and Cartwright 1963; Nemes and Price 2015). *Onthophagus orpheus* was active during mid-June until early August with no clear peak in abundance (Fig. 2).

Onthophagus taurus (Schreber, 1759)

In total, 34 *O. taurus* were collected in forested and meadow habitats at both high and low elevation, but beetles were more abundant at low-elevation sites (Table 2). *Onthophagus taurus* is a small (8–11 mm), non-native tunneling dung beetle that is widely distributed across most of the United States, Central America, and Australia with lustrous dark brown to black coloration (Floate *et al.* 2017). Major males have two long, curved horns projecting outwards from the center of the head, minor males have short, often straight horns, and females have a ridge along the head. *Onthophagus taurus* is native to the Mediterranean region, but during the 20th century, *O. taurus* was introduced multiple times into much of the USA. *Onthophagus taurus* was first recorded in 1974 on cattle pastures in northwestern Florida, central and southwestern Georgia, and southeastern Alabama (Fincher and Woodruff 1975). During the 1980s, the species was intentionally introduced by the US Department of Agriculture onto cattle pastures in California, Texas, and Georgia to decrease dung build-up; at the same time, the New Jersey Department of Agriculture also released *O. taurus* beetles into pastures in the northern United States. *Onthophagus taurus* prefers open habitats and feeds primarily on cow and horse dung (Howden and Cartwright 1963; Nemes and Price 2015), burying

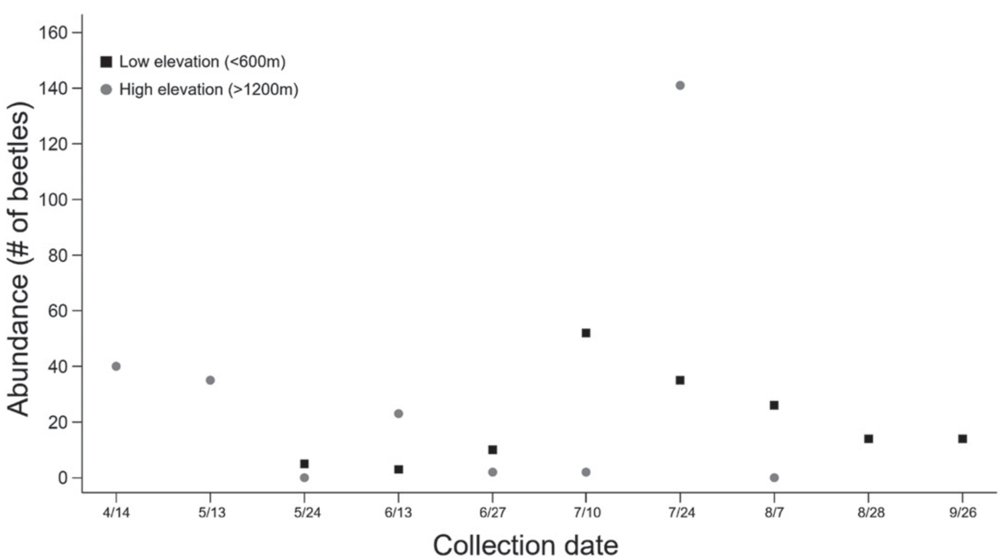

Fig. 3. Seasonality and abundance of all dung beetles trapped at either high- (> 1,200 m, black line) or low-elevation (< 600 m, gray line) sites in Great Smoky Mountains National Park during 2017. Note that the high-elevation pattern is driven by one species, *Aphodius fimetarius.*

oblong brood balls (approximately 2.0–4.5 g) in clumps around 5–18 cm below the dung pat (Mamantov and Sheldon 2021). *Onthophagus taurus* was active throughout the entire sampling period during May to September, with a peak in early to mid-August (Fig. 2).

Phanaeus vindex (Macleay, 1819)

In total, eight *P. vindex* (Phanaeini) were collected from the Cades Cove meadow site (Table 2). *Phanaeus vindex* is a mid-sized (11–22 mm) tunneling dung beetle distributed across much of the southern United States. *Phanaeus vindex* has distinctive rainbow coloration with a coppery-red pronotum, and shiny green elytra. Major males have a large horn protruding from the center of the head, minor males have a short horn, and females are hornless. Due to its larger size, *P. vindex* tends to bury brood balls deeper than other co-occurring species (Gregory *et al.* 2015; Hanski and Cambefort 1991). The species prefers open fields and large mammal dung and carrion. *Phaneaus vindex* was active during June through late September, with a peak in late August (Fig. 2).

Dung Beetle Community Structure at Different Elevations

Community structure varied between low and high elevation sites (Fig. 4). Nine species were trapped at low-elevation sites, but only three at high-elevation sites. Low-elevation sites yielded rolling and tunneling Scarabaeinae and two *Geotrupes* species. Shannon's diversity index was 1.99 for low-elevation communities (Tremont: S = 6, H = 1.40; Twin Creeks: S = 5, H = 1.38; Cades Cove: S = 5, H = 1.57). Low-elevation sites had an even species distribution (E = 0.96), and individuals of introduced species made up 18% of total dung beetle abundance. In contrast, the ecological community at high-elevation sites consisted of a dwelling Aphodiinae, a tunneling Scarabaeinae, and one *Geotrupes* species. For high-elevation communities, Shannon's diversity index was only 0.34 (Cataloochee: S = 3, H = 0.43; Indian Gap: S = 2, H = 0.22; Purchase Knob: S = 2, H = 0.08). At the high-elevation sites, dung beetle communities were dominated by the non-native dweller *A. fimetarius*, which meant the sites showed low evenness (E = 0.31), and 95% of the recovered dung beetles were individuals of introduced species.

Discussion

During this research, 403 dung beetle specimens were collected, representing six species of Scarabaeinae, one species of Aphodiinae, and two species of Geotrupinae attracted to cow dung. Fewer species were collected at the sample sites in GSMNP than are typically recovered from cattle pastures in

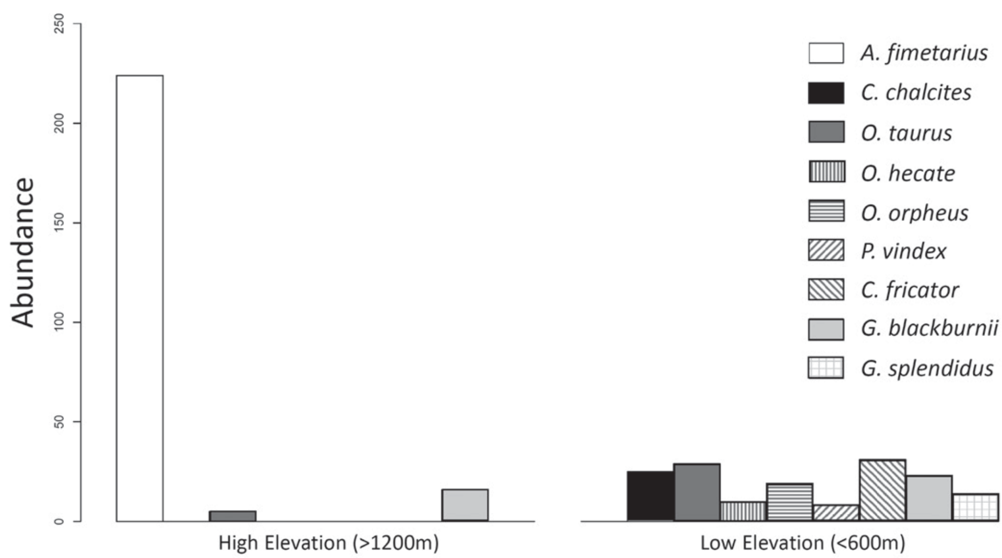

Fig. 4. Abundance of dung beetles in high- (> 1,200 m) versus low-elevation (< 600 m) communities in Great Smoky Mountains National Park during 2017. Bar height indicates the total number of individuals collected across the breeding season. Bar color indicates species guild: dwellers (white), rollers (black), tunnelers (dark gray), and earth-boring beetles (light gray). Bar shading varies by species.

the southeastern United States; at least 41 species of dung beetles have been collected from pastures in North Carolina and Tennessee (Bertone *et al.* 2005; Bezanson and Floate 2019). Furthermore, on pastures with grazing livestock, thousands of dung beetles can be collected in a single season (Bertone *et al.* 2005; Fiene *et al.* 2011; Fincher *et al.* 1986). The lower abundance and species richness recovered in GSMNP is likely due to dung availability. In the park, large herbivore dung is limited to deer and elk, both which produce pelleted dung unlike the large, wet dung mounds that these species prefer for breeding. Beetles have been recovered from bear dung in GSMNP, but this resource is much less abundant than dung mounds on pastureland because bear density varies across the landscape and over the course of the beetle breeding season. Furthermore, bears prefer habitat in mid elevations (600–1,000 m), while our sites were either below 600 m or above 1,000 m (Van Manen 1994). There are a number of cattle, horse, and bison farms just outside GSMNP in both Tennessee and North Carolina, including pasture land within eight kilometers from the park borders; therefore, collection sites near the border of the park may attract beetles who primarily breed on dung on pasture land, rather than dung found within the park itself. For this research, cattle dung that had been autoclaved was used in order to prevent the spread of microorganisms into the park, but these bacteria are responsible for producing many of the volatile chemicals dung beetles use to locate food sources (Tribe and Burger 2011). The bait provided in this study may not have attracted as many beetles as non-sterilized dung and if this study had been completed with other dung types or unsterilized cattle dung, more beetles and perhaps different species may have been recovered.

This research demonstrated that low-elevation communities were more diverse than high-elevation communities, which were dominated by the non-native dweller *A. fimetarius*. Low-elevation communities varied by habitat type as some species were only collected on open meadow land in Cades Cove (Table 2). Species at high-elevation sites experience cooler, more variable temperatures than species at low-elevation sites, meaning these beetles should have a broader thermal tolerance at higher elevations (Gaston and Chown 1999; Janzen 1967). This could limit the elevational range of many species collected at low elevations (Sheldon and Tewksbury 2014; Verdú *et al.* 2007). Furthermore, resource availability may change across elevation since mammalian density varies across the park.

While most species peaked in activity in late summer, seasonality varied among species (Fig. 2) and between the high- and low-elevation sites (Fig. 3). At high-elevation sites there were two peaks in dung beetle activity, one during April and the other during late July, which was driven by the seasonality of *A. fimetarius*. At low-elevation sites there was a single peak in activity in late July. Species varied in the length of their active period, with both introduced species (*O. taurus* and *A. fimetarius*) active for longer periods than the native species (Fig. 2), which may be due to broader thermal tolerances often observed in invasive species (Kelley 2014; Simberloff 2013; Zerebecki and Sorte 2011). The longer active period could also be due to differences in life history. *Aphodius fimetarius* overwinters in the adult life stage, leading to an early spring peak in adults, which then breed, producing a late summer peak of the new generation of adults (Floate and Gill 1998; Gordon and Skelley 2007). Many of the native species overwinter as pupae, emerging later in the season, leading to a single peak of activity (Floate and Gill 1998; Gordon and Skelley 2007).

The Twin Creeks ATBI site was impacted by the Gatlinburg wildfires during 2016. These wildfires burned approximately 11,000 acres in the northern part of GSMNP (Miller *et al.* 2017), which occurred approximately six months before this study began. The site experienced moderate burning and had several downed and charred trees. Fire can impact dung beetle communities by changing plant community structure (Louzada *et al.* 2010). More specifically, by reducing forest canopy, fire creates open habitats preferred by some dung beetle species. Open habitat also allows the odor from baits to disperse more widely. Fire affects plant resources available to the mammalian herbivores and omnivores whose dung is preferred by many dung beetle species. The study design did not provide a large enough sample to compare burned and unburned forests. However, it is interesting to note that the dung beetle communities of Tremont and Twin Creeks were similar in species richness and evenness, but one species, *Copris fricator*, was found only in the unburned site. Furthermore, the abundance of *O. taurus* was highest in the burned site, suggesting that fire disturbance was favorable to this non-native species. Habitat disturbance is thought to promote biological invasion (Buckley *et al.* 2007; Simberloff 2013), which could explain this observation, but further research investigating burned and unburned sites with sufficient replication would be required to understand the impact of fire on dung beetle communities in GSMNP.

One purpose of this research was to document the spread of introduced beetles from pasture land into natural systems. Because dung beetles provide numerous ecosystem services (Beynon *et al.* 2015), dung beetles have been introduced into US pasture land over the past century, both accidently and through intentional introduction programs (Fincher and Woodruff 1975; Floate *et al.* 2017; Hoebeke and Beucke 1997; Pokhrel 2021). A number of introduced species have been recorded on pasture land in the southeastern US, including the tunnelers *O. taurus*, *Digitonthophagus gazella* (Fabricius, 1787), and *Euonticellus intermedius* (Reiche, 1849), and the dwellers *Colobopterus erraticus* (Linnaeus, 1758) (formerly *Aphodius erraticus*), *A. fimetarius*, *Chilothorax distinctus* (Müller, 1776) (formerly *A. distinctus*), *Calamosternus granarius* (Linnaeus, 1767) (formerly *A. granarius*), and *Labarrus pseudolividus* (Balthasar, 1941) (formerly *A. pseudolividus*) (Bezanson and Floate 2019). Of these species, two (*O. taurus* and *A. fimetarius*) have expanded their introduced range beyond managed pastures and into high and low elevation forested habitats in GSMNP even though these species are thought to prefer open grassland habitats. The impact of non-native dung beetles on native communities, particularly in forested or non-pasture habitats, is unknown, but it is likely that these species compete for access to dung resources with native species. In high-elevation sites, the non-native *A. fimetarius* was the most commonly trapped species, which is likely due to the lack of large mammalian dung necessary to support other guilds of dung beetles. On pasture lands in the southeast, individuals of *O. taurus* often inundate dung beetle communities. For example, Bertone *et al.* (2005) found that on North Carolina cattle pastures *O. taurus* made up approximately 45–85% of the dung beetle community. In the forested sites, only 34 *O. taurus* were collected across the breeding season (Table 2), suggesting that its effect on native communities in wooded sites may be less than on pastures. At Twin Creeks, where *O. taurus* was recovered in the greatest numbers, these beetles made up approximately 35% of the community, indicating they may have a detrimental effect on the native community and should be monitored.

Dung beetles provide ecosystem services in the USA that exceed several hundred million dollars annually (Beynon *et al.* 2015; Fincher 1981; Losey and Vaughan 2006; Nichols *et al.* 2008). They are crucial members of ecological communities across a variety of habitat types; however, the services they provide vary in part due to community structure. Large-bodied beetles process more dung and bury dung deeper than their smaller-bodied counterparts, which influences nutrient cycling and seed dispersal (Dangles *et al.* 2012; Gregory *et al.* 2015; Simmons and Ridsdill-Smith 2011). However, small-bodied beetles often arrive and occupy pats in greater numbers than large-bodied beetles, which can increase the rate of dung removal (Simmons and Ridsdill-Smith 2011). Furthermore, tunnelers and rollers are more effective at providing services than dwellers because they move dung away from the dung pat and bury it. In contrast, dwellers simply manipulate dung within the pat. Understanding the makeup of dung beetle communities is thus of great importance, and this survey suggests that in GSMNP, dung beetle communities, and the ecosystem services provided, vary across habitat type and elevation.

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