The effects of exurbanization on the food and habitat of Pileated Woodpeckers (*Dryocopus pileatus*)

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ABSTRACT.—*Dryocopus pileatus* (Pileated Woodpeckers) are the largest woodpeckers in the United States. They require large trees for roosting, nesting, and feeding that must be dead or dying for ease of excavation and presence of the woodpeckers’ main prey of ants and beetle larvae. Because of these specific habitat requirements, Pileated Woodpeckers have often been used as an indicator species for mature forests. However, their status in exurban areas, or places of low-density rural development beyond the suburban fringe, is poorly known. Because exurbanization covers a large and growing portion of the eastern U.S., I decided to use the Cumberland Plateau in southeast Tennessee to examine how exurban development affects the habitat and presence of Pileated Woodpeckers. From previous literature I made the assumption that Pileated Woodpeckers would prefer habitat with larger diameter trees, a larger volume of more decayed dead wood, and a greater abundance of food (ants and beetle larvae). By using proportion impervious cover as a proxy for exurbanization, I hypothesized that as exurbanization increased, the following habitat characteristics preferred by Pileated Woodpeckers would decrease: (1) average tree diameter and number of large trees, (2) volume and rot class of standing dead and fallen dead trees, and (3) ant and beetle larva abundance in the soil and leaf litter. Concurrently, I hypothesized that along with these habitat characteristics, the likelihood of Pileated Woodpecker presence would decrease with increasing exurbanization. I conducted the study in Sewanee, Tennessee, U.S.A., establishing 30 stratified random sample points evenly divided between exurban and forested areas. At each point I assessed Pileated Woodpecker presence through visual and vocal surveys; habitat structure through
measures of downed and standing dead wood and standing live trees; and food availability through presence of ants and beetle larvae in soil cores and pitfall traps.

I found no difference in the amount of dead wood, degree of decay of dead wood, ant and beetle larva abundance, nor presence of Pileated Woodpeckers as exurbanization increased. These data suggest that some exurban areas may provide suitable habitat for Pileated Woodpeckers. But tree diameter was found to increase with increasing exurbanization. Such statistically insignificant results suggest that more studies are needed to examine the breeding success and survival rates of Pileated Woodpeckers in exurban and forested areas to determine if exurban areas truly are suitable long-term habitat and not just ecological traps. Because the mature forest characteristics that Pileated Woodpeckers prefer can be found in exurban areas, it is possible that other species requiring these characteristics could also find suitable habitat in exurban areas. This could apply most specifically to those secondary cavity-nesting species such as the northern flying squirrel, owls, and bats that use old Pileated Woodpecker nesting cavities. More studies should be conducted to further explore the effects of exurbanization on these secondary cavity-nesters as well as other species that are thought of as indicating mature forests.
INTRODUCTION

Exurbanization And Biodiversity.—Exurban development, or low-density rural residential development in areas of native vegetation, has been the fastest growing form of land use since the 1950s. Since mid-century, a five-fold increase in this land use type has occurred and by the year 2005 exurbanization encompassed 25% of the lower 48 states (Hansen et al. 2005). Between 1994 and 1997, 80% of houses in the U.S.A. were constructed in non-metropolitan areas (Maestas et al. 2001). This type of development can occur either just beyond the suburban fringe or in rural areas that have natural appeal to home buyers and are not associated with metropolitan areas (Hansen et al. 2005). The developments beyond the suburban fringe exist so that people who work in cities can have easy access to their jobs and city life while living a rural home life. Exurban development more distant from cities has been on the rise in the southeastern US and usually borders national parks, outdoor recreation facilities, public rivers and lakes, agricultural lands, and small towns offering just enough anthropocentric amenities to allow comfortable living (Riebsame et al. 1996, McGranahan 1999, Rasker and Hansen 2000, Maestas et al. 2001).

Exurbanization has been understudied (as compared to urbanization) in proportion to its increasing influence on the landscape and consequentially to biodiversity (Miller and Hobbs 2002, Hansen et al. 2005). Maestas et al. (2001) conducted a study in the Mountain West of the U.S.A. and compared biodiversity in public protected areas, private-land livestock ranches, and exurban developments (one house per 14-20 acres). They found exurbanization to be positively associated with human-adapted wildlife and nonnative plant species. Donovan and Thompson (2001) have suggested that exurban
areas could be ecological traps where the land provides suitable habitat but results in reduced survival and reproduction. General patterns have been found of increasing diversity and richness at intermediate levels of development and decreasing richness of forest species with increasing urbanization (Blair and Launer 1997, Blair 1999, and Germaine and Wakeling 2001). Exurban environments may lead to higher densities of small to mid-sized predators such as cats that could detrimentally effect local “prey” populations (Churcher and Lawton 1987, Baker et al. 2005, Coleman et al. 1997, Crooks and Solue 1999). These studies of cat predation have also revealed detrimental competition with native predators such as falcons and coyotes for prey. Exurban areas also bring roads into native habitat. Trombulak and Frissell (2000) reviewed literature on the effect of roads on biodiversity and found that roads can lead to animal behavior modification by way of altering home range, movement patterns, reproductive success, escape response, and physiological state. Roads were also found to facilitate the dispersal of exotic species by altering native habitats, stressing native species, and creating movement corridors. Leu et al. (2008) found roads and human-caused fires to be great facilitators of exotic plant species. They found human-caused fires to maintain a positive feedback loop with disturbance leading to exotic plants that then lead to a vastly altered fire regime and habitats that were no longer suitable for fauna adapted to habitats resulting from natural fire regimes.

Fraterrigo and Wiens (2005) examined bird communities in the north-central Colorado Rocky Mountains across an exurban gradient. They found bird abundance to be greater in exurban areas due to an increase in habitat heterogeneity, but in the case of cavity nesters and species that forage in downed wood, a decline was seen with increased
building density. Urbanization has been found to accommodate omnivorous, granivorous, and cavity nesting species (Chace and Walsh 2006). Beissinger and Osborne (1982) conducted a study in Ohio comparing bird communities in a mature beech-maple forest to the nearby college town of Oxford and found the residential areas to have a lower species richness and a proportionally higher number of invasive individuals than forested areas. Oxford was dominated by ground gleaners and the mature forest was equally divided between ground gleaners, foliage gleaners, and bark drillers. Conducting a study of 34 Tucson, Arizona neighborhoods placed along a gradient of volume of exotic/native vegetation, Mills et al. (1989) found territorial native bird species, native species richness, and overall species diversity to be strongly associated with volume of native vegetation. Exotic and non-territorial native bird species were correlated with volume of exotic vegetation. Also, vegetation volume was found to be a greater determinant of bird community composition than was housing density. Kluza et al. (2000) compared bird communities between forests with varying housing densities in rural western Massachusetts. Forests with moderate housing density had lower abundances of neotropical migrants and forest-interior species. Ground/shrub nesting birds were greater in forests with low housing density. Blewett and Marzluff (2005) studied the occurrence of, and relationships between, snags and cavity-nesting birds in Seattle, Washington. They found species richness and species evenness of cavity nesting bird species was highest in suburban landscapes highly intermixed with forest cover. Snags were more abundant in the forested parts of the forest/urban matrix and hardly any snags at all remained in the built up areas.
Pileated Woodpecker Habitat Requirements.—Pileated Woodpeckers 
(Dryocopus pileatus) are the largest woodpeckers found in the United States besides the possibly extinct Ivory-billed Woodpecker (Campephilus principalis). Their main food source of carpenter ants and beetle larvae lives in rotting dead and dying snags or fallen wood. Because of their large size, they require large trees for roosting, nesting, and feeding that must be dead or dying for ease of excavation and presence of ants and beetle larvae. Pileated Woodpeckers are seen as mature forest indicators because of this need for large diameter trees (Bull et al. 1995). Bull and Holthausen (1993) followed twenty-three Pileated Woodpeckers fitted with radio transmitters for 5-10 months in Northeastern Oregon. These tagged Woodpeckers foraged 38% of the time on downed wood, 38% on dead trees, 18% on live trees, and 6% on stumps. Hartwig et al. (2006) located cavity trees used by Pileated Woodpeckers in coastal western hemlock and coastal Douglas-fir forest types on southeastern Vancouver Island. Trees that Pileated Woodpeckers used for foraging were larger, more decayed, and had less bark remaining than those not used. Foraging occurred generally in areas with greater snag (dead trees ≥ 1m in height) and “defective” (broken tops, scars, decay or damage) tree basal areas and more coarse woody debris. Flemming et al. (1999), studying the excavation foraging habitat of Pileated Woodpeckers in Canada, found that foraging trees were about 28 cm in diameter and were more decayed than the average tree randomly available in the habitat. Bull et al. (2007) studied two different sites in Ohio that were heavily affected by spruce budworm and Douglas-fir bark beetle outbreaks leading to a sudden increase in snag and log density and thus an abundance of wood-dwelling arthropods. This increase in arthropods resulted in Pileated Woodpeckers remaining in the area even with a decrease
of available nesting trees. Lemaitre and Villard (2005) examined Pileated Woodpecker foraging substrate in an intensively managed forest in northwestern New Brunswick, Canada. Diameter of trees and snags was the most significant predictor of Pileated Woodpecker use of substrate for foraging, which they suggested was a consequence of carpenter ant nesting selection. Trees greater than 35 cm diameter (snags specifically) were the most preferred.

The importance of large nesting/roosting trees for these birds has also been noted. Hartwig et al. (2004), as part of their study mentioned previously, found active nest trees had an average diameter of 82 cm and 91% bark remaining. They also noted that nests were found significantly more often in mature and old forest structural stages, and in moderately disturbed areas. Aubry and Raley (2002) found nesting trees to have a diameter of 65-154 cm and roosting trees 155-309 cm. Renken and Wiggers (1993), working in Missouri, found a positive linear relationship between Pileated abundance and percent cover with trees greater than or equal to 30cm in diameter and density of snags greater than or equal to 54 cm in diameter.

Pileated Woodpeckers are considered keystone habitat modifiers because of their excavation into large trees and should thus be maintained in an area to provide continuous habitat renewal for other species such as secondary-cavity nesters (Aubry and Raley 2002, Bonar 2000). Secondary cavity-nesters require cavities for nesting, but do not have the ability to make these cavities themselves. With their large size and powerful excavation abilities, Pileated Woodpeckers create usable habitat when excavating nest and roost cavities, when simply foraging, and even when beginning and abandoning a cavity opening. Over 20 secondary cavity-nesting species of the Pacific Northwest have
been documented nesting or roosting in old Pileated Woodpecker excavations (table 1 in Aubry and Raley 2002). Several of these 20 species are candidate species or species of concern in the western U.S. including the silver-haired bat, American marten, northern flying squirrel, Bufflehead, and Flammulated Owl (Oregon Fish and Wildlife Office 2009, Sutter et al. 2005, Washington Department of Fish and Wildlife 2008 PHS, Washington Department of Fish and Wildlife 2008 SOC). Candidate species are those for which the Fish and Wildlife Service of a particular state has sufficient biological information to support listing as endangered or threatened. Species of concern are those for which conservation status is of concern, but for which more information is needed (Oregon Fish and Wildlife Office 2009).

Aubry and Raley (2002) noted the following species as secondary-cavity nesters that utilize vacated Pileated Woodpecker cavities in the western US and Canada: Wood Duck, Bufflehead, American Kestrel, Hairy Woodpecker, Boreal Owl, Big brown bat, Northern flying squirrel, Bushy-tailed woodrat, and more. Thirteen out of the 24 species identified by Aubry and Raley (2002) as secondary cavity-nesters that take advantage of Pileated Woodpecker excavations are found in the Southeast U.S. as well as the Pacific Northwest (Cornell 2007, North American Mammals accessed 2009).

The Effects of Exurbanization on Pileated Woodpeckers.---Mellen et al. (1992) used radio telemetry to study habitat use of Pileated Woodpeckers in coastal western Oregon. They noted that although Pileated Woodpeckers did nest and roost in mature and old-growth forests, they foraged in immature forests. Giese and Cuthbert (2003) examined the relationships between forest context and woodpecker nest tree selection in oak forests of southeastern Minnesota and western Wisconsin. They found that the
diameter and decay status of potential nesting trees was more important than the overall surrounding forest or habitat whether agricultural or forested. Blewett and Marzluff (2005) investigated presence of and relationships between snags and cavity-nesting birds in rapidly urbanizing Seattle, Washington. They found Pileated Woodpeckers in suburban landscapes with comparatively higher percentages of forest. Breeding was also successful in these habitats. Snags were abundant and more decayed in forested parts of suburban areas. Blewett and Marzluff (2005) also speculate that large expanses of forest surrounding urban areas provide sources for Pileated Woodpeckers since the density/productivity of these birds was found to have a strong positive association with forest percentage in the landscape. Because of their large home ranges, Pileated Woodpeckers would be able to commute between a forested nest site and an urban feeding site.

Little research has been done on forests of the Eastern U.S. in regards to Pileated Woodpeckers because few large tracts of contiguous mature forests still exist here (McComb and Muller 1983). But, from what has been found by Mellen et al. (1992) and Giese and Cuthbert (2003), large tracts of contiguous mature forests are not required for Pileated Woodpecker populations.

I used the Cumberland Plateau in southeast Tennessee to examine how exurban development affects the habitat and therefore presence of Pileated Woodpeckers. By using proportion impervious cover as a proxy for exurbanization, I hypothesized that as exurbanization increased, the following habitat characteristics preferred by Pileated Woodpeckers would decrease: (1) average tree diameter and number of large trees, (2) volume and rot class of standing dead and fallen dead trees, and (3) ant and beetle larva
abundance in the soil and leaf litter. Concurrently I hypothesized that along with these habitat characteristics, the likelihood of Pileated Woodpecker presence would decrease with increasing exurbanization.

METHODS

Study Area.---The study area was located on the Cumberland Plateau in southeastern Tennessee, USA. This area is characterized by oak-hickory forests interspersed with residential housing and small townships. The Plateau is formed by a nutrient-poor sandstone cap that ends abruptly at an escarpment. All of our study area was on the Plateau, more than 100 m from the escarpment, and within the 13,000 acre Domain of the University of the South.

Site Selection.---Exurban and forested areas were defined spatially using Manifold System 8.0 GIS Software (CDA International, Carson City, NV). Eleven exurban and eleven forested sample points were selected at random that were at least 400 m apart and at least 100 m from the plateau edge. Four additional exurban and forested sample points were selected and t-tests were performed to test whether exurban and forested sample points differed in terms of average distance to stream and average distance to plateau edge. There was no evidence of differences in distance to stream or distance to plateau edge between exurban and forested areas.

Pileated Woodpecker sampling.---To measure presence versus absence, call counts were conducted at each point using playback of Pileated Woodpecker calls (Walton and Lawson 2002) for 1 minute followed by silence for 3 minutes, playback for
1, silence for 3, playback for 1, and silence for 1. Pileated Woodpecker calls were also listened for when doing all other data collection.

This sampling was conducted from May 27 to June 5 2008 between 5:00 am and 8:30 am. No sampling was conducted during rain or when wind was above 3 on the Beaufort scale.

Vegetation sampling.---To quantify live and dead trees, four transects were run at each point, one in each cardinal direction. Each transect was 100m in length with a total length of 400m per point. All standing trees within 0.75m of the transect line on either side with diameter >10 cm had diameter measured at breast height or 1.37 m (DBH). All dead wood >10 cm, standing within 0.75 m of the line or fallen across the line, was put into a rot class. These rot classes included A for newly fallen with no decay, B for very slight decay still retaining tree shape and either no branches or no bark, C for no bark, no branches, and some decay causing loss of tree shape, and D for rotting through and falling apart. Standing dead wood had DBH measured and height visually estimated to obtain volume while fallen dead wood had mid-diameter and length measured to obtain volume. This sampling was conducted between November 2007 and August 2008.

Insect sampling.---Potential food availability was estimated by quantifying ants and beetle larvae found in soil cores and pitfall traps at each point. Soil core sampling was conducted from June 24 to July 22 2008 and pitfall sampling was conducted from July 2 to July 24 2008.

Soil cores were obtained by driving a 4-inch deep, 2-inch diameter garden borer as deep into the soil as possible or until flush with the soil. The resulting cone of soil was placed into a sieve with the following four grate divisions: >4 mm, 2-4 mm, and <2 mm.
The soil was shaken for 30 seconds and then each of the resulting three layers was searched for ants and beetle larvae, from top layer to bottom layer, for 60 seconds, 90 seconds, and 120 seconds respectively.

Pitfall traps were constructed by burying 270-mL waxed paper-cups (filled with 120-mL water and 0.2 ounces of unscented liquid soap) flush with the soil in the holes dug for soil cores. Traps were buried 5 and 10m away from each point in the four cardinal directions. They remained in the soil to collect ants and grubs for 43-48 hours. Water collected was poured through filter paper and all insects were then transferred into 95% alcohol so that ants and grubs could be quantified at a later time.

**Exurban to Forest Gradient Quantification.**---Using Manifold System 8.0 GIS Software (CDA International, Carson City, NV), buffers with a diameter of 200 m were drawn around each point. All canopy cover and impervious cover within 200 m of each sample point was mapped at a scale of 1:1700. Canopy cover was mapped from National Agriculture Imagery Program digital orthoimagery derived from aerial photographs taken in September of 2008 of the Cumberland Plateau (1m pixel resolution) and included all contiguous forest patches and individual trees in open spaces. Impervious cover was mapped from high-resolution orthoimagery derived from aerial photographs taken in March 2008 (6 inch pixel resolution) of Franklin County, TN for the Franklin County GIS User's Group (a collaboration between the University of the South and local municipal agencies and utilities) and included all asphalt, concentrated/compacted gravel, and buildings. Proportions of both overall canopy cover and impervious cover were calculated for each sample point within these 400,000π m² areas.
Statistical Analysis.---Using linear regression, the following were all calculated as a function of both proportion canopy cover and proportion impervious surface: tree diameter, volume of dead wood, rot class, and abundance of ants and beetle larvae. Logistic regression was used to calculate presence/absence of Pileated Woodpeckers as a function of both proportion canopy cover and proportion impervious cover.

RESULTS

Pileated Woodpecker presence did not change with proportion canopy cover or proportion impervious cover (Fig. 1, $R^2 < 0.01$, $P = 0.931$; Fig. 2, $R^2 = 0.01$, $P = 0.584$).

The mean tree diameter at each sample point decreased as proportion canopy cover increased and increased as proportion impervious cover increased. A strong relationship between mean tree diameter and both proportion canopy cover and proportion impervious cover was shown with linear regression (Fig. 3, $R^2 = 0.226$, $P = 0.008$; Fig. 4, $R^2 = 0.350$, $P = 0.001$). The number of larger diameter trees decreased as proportion canopy cover increased and increased as proportion impervious cover increased. A strong relationship between number of large diameter trees and both proportion canopy cover and proportion impervious cover was shown with linear regression (Fig. 5, $R^2 = 0.043$, $P < 0.0001$; Fig. 6, $R^2 = 0.052$, $P = 0.000$). No relationship was shown by linear regression between volume of dead wood in m³ and either proportion of canopy cover or impervious cover (Fig. 7; Fig. 8, $R^2 < 0.001$, $P = 0.911$; Fig. 9, $R^2 = 0.001$, $P = 0.852$). No relationship was shown by linear regression between rot class of dead wood and either proportion of canopy cover or impervious cover (Fig. 10, $R^2 < 0.001$, $P = 0.947$; Fig. 11, $R^2 < 0.001$, $P = 0.996$).
Neither ants in pitfall traps ($R^2 = 0.031, P = 0.353; R^2 = 0.035, P = 0.325$), beetle larvae in pitfall traps ($R^2 = 0.043, P = 0.269; R^2 = 0.023, P = 0.420$), ants in soil cores ($R^2 = 0.017, P = 0.487; R^2 = 0.028, P = 0.376$), nor beetle larvae in soil cores ($R^2 = 0.034, P = 0.332; R^2 = 0.026, P = 0.393$) changed with either proportion canopy cover or proportion impervious cover. Total ants and beetle larvae in pitfall traps and soil cores combined did not change with either proportion canopy cover or proportion impervious cover (Fig. 12, $R^2 = 0.045, P = 0.259$; Fig. 13, $R^2 = 0.050, P = 0.233$).

DISCUSSION

I originally hypothesized that with increasing exurbanization, the following habitat characteristics would decrease: (1) mean tree diameter and number of large diameter trees, (2) volume and rot class of standing dead and fallen dead trees, and (3) abundance of ants and beetle larvae in the soil and leaf litter. And that concurrently with these habitat characteristics, the likelihood of Pileated Woodpecker presence would decrease with increasing exurbanization.

Tree diameter was significantly different along a gradient of exurbanization. Mean tree diameter was negatively associated with canopy cover, meaning that with more canopy cover in an area, mean tree diameter was smaller. Mean tree diameter was positively associated with impervious cover, meaning that with more impervious cover in an area or with a greater degree of exurbanization, mean tree diameter was larger. When every measure of diameter was plotted above the corresponding canopy or impervious cover proportion, the same relationships were supported. This data supports a trend of trees having greater diameters in exurban areas. Histograms showing tree diameter size
class distributions in the original two groupings of exurban and forested areas reveal a greater number of large diameter trees in exurban areas. On average, exurban areas contained 4.4 trees per sample that were greater than 50 cm in diameter and forested areas contained 1.6 trees per sample that were greater than 50 cm in diameter. Therefore the trend for exurban areas to have larger trees than forested areas was not a consequence of the removal of small trees from exurban areas, but reflects a trend for exurban areas to have more large trees. This may be an indication of the human tendency to maintain large, old, ornamental trees for aesthetic pleasure, the lack of smaller surrounding trees to compete with these large trees for growth space, and the lack of logging activity in exurban areas. This abundance of large trees in exurban areas does raise the question though of what happens when these trees get really old and must be cut down for safety reasons. As the histograms also show, there are not as many smaller trees in exurban areas as in forested areas to act as an eventual replacement class.

No significant relationship was found between volume of dead wood and canopy or impervious cover. The same result was true for rot class. This supports a similarity between exurban and mature forest habitats in regards to forageable substrate. In other words, wood suitable for ant and beetle larva inhabitance can be found anywhere on the gradient and thus food availability would most likely not be affected by exurbanization. This assumption is supported by the lack of a significant relationship between ant and grub abundance and canopy or impervious cover.

Corresponding to the above results of no significant differences between food and habitat (except for tree diameter) along the exurban gradient is the presence of Pileated Woodpeckers along the gradient. No relationship was found between presence of
Pileated Woodpeckers and canopy or impervious cover. These results suggest that some exurban areas can provide suitable habitat for Pileated Woodpeckers and therefore are not detrimental to the species. With more large diameter trees found in exurban areas and all other factors equal, one would expect this habitat to actually be more suitable for nesting and roosting. The only problem would be the one mentioned previously of the distant future when these large old trees that are now great for nesting, fall and become only usable for foraging. This would lead to exurban areas being ecological traps for actual habitation. But as far as utilizing exurban areas, Pileated Woodpeckers can easily forage in exurban areas while living in forested areas thus making the combination of both land use types quite suitable (Giese and Cuthbert 2003, Blewett and Marzluff 2005).

The ability of Pileated Woodpeckers to live in exurban areas could also support exurban areas as suitable habitat for secondary cavity-nesters that use old Pileated Woodpecker nest cavities. Further studies should be conducted to develop a list specifically of southeastern secondary-cavity nesters dependent on Pileated Woodpeckers since most previous studies have focused on the northwest United States and Canada. In addition, at least the following four of those on the Aubry and Raley (2002) list are state-listed in the southeast: Northern Saw-whet Owl, red squirrel, northern flying squirrel, fisher (South Carolina Department of Natural Resources 2006, Withers 2009). With a further study of southeastern secondary cavity-nesters, more listed species might be found and thus present more reasons to support conservation of Pileated Woodpeckers and their habitat.

To fully determine whether exurban areas can be a good long-term substitute for mature forests for Pileated Woodpeckers and not just ecological traps, studies on the
survival and breeding success of Pileated Woodpeckers between these two land cover
types should be completed. Because the mature forest characteristics that Pileated
Woodpeckers prefer can be found in exurban areas, it is possible that other species
requiring these characteristics could also find suitable habitat in exurban areas. More
studies should be done that test the habitats along an exurban gradient for other mature
forest indicator species.
FIG. 1. Presence (1) and absence (0) of Pileated Woodpeckers along a gradient of proportion of canopy cover at each of 30 sample points (Logistic Regression; slope = -0.174, P = 0.931).

FIG. 2. Presence (1) and absence (0) of Pileated Woodpeckers along a gradient of proportion of impervious cover for each of 30 sample points (Logistic Regression; slope = -2.352, P = 0.584).
FIG. 3. Mean tree diameter in cm along a gradient of proportion of canopy cover ($R^2 = 0.226$, $P = 0.008$). Mean tree diameter is the mean of all tree diameters measured at each of 30 sample points.

FIG. 4. Mean tree diameter in cm along a gradient of proportion of impervious cover for each of 30 sample points ($R^2 = 0.350$, $P = 0.001$). Mean tree diameter is the mean of all tree diameters measured at each of 30 sample points.
FIG. 5. Diameter measurements for each individual tree along a gradient of proportion of canopy cover at each of 30 sample points (R² = 0.043, P < 0.001).

FIG. 6. Diameter measurements for each individual tree along a gradient of proportion of impervious cover at each of 30 sample points (R² = 0.052, P < 0.001).
FIG. 7. Frequency distributions of tree diameter size classes in (a) exurban areas and (b) forested areas. A greater number of large trees can be found in exurban areas than in forested areas.
FIG. 8. Total volume of dead wood in cm³ along a gradient of proportion of canopy cover at each of 28 sample points ($R^2 = 0.000$, $P = 0.911$).

FIG. 9. Total volume of dead wood in cm³ along a gradient of proportion of impervious cover at each of 28 sample points ($R^2 = 0.001$, $P = 0.852$).
FIG. 10. Mean rot class of downed wood along a gradient of proportion of canopy cover at each of 28 sample points ($R^2 < 0.001$, $P = 0.947$). Rot classes were translated into numbers as follows: A = 1, B = 2, C = 3, and D = 4.

FIG. 11. Mean rot class of downed wood along a gradient of proportion of impervious cover for each of 28 sample points ($R^2 < 0.001$, $P = 0.996$). Rot classes were translated into numbers as follows: A = 1, B = 2, C = 3, and D = 4.
FIG. 12. Total ants and beetle larvae along a gradient of proportion of canopy cover for each of 30 sample points ($R^2 = 0.045$, $P = 0.259$). Total ants and beetle larvae is the sum of ants in pitfall traps and soil cores and beetle larvae in pitfall traps and soil cores.

FIG. 13. Total ants and beetle larvae along a gradient of proportion of impervious cover for each of 30 sample points ($R^2 = 0.050$, $P = 0.233$). Total ants and beetle larvae is the sum of ants in pitfall traps and soil cores and grubs in pitfall traps and soil cores.
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