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Effects of forest composition on trophic relationships among mast production and mammals in central hardwood forest

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Oak-dominated forest has declined in the eastern United States as shade-tolerant mesophytic species (e.g., maple [*Acer* spp.]) replace oaks (*Quercus* spp.), sparking concern among ecologists regarding species that consume acorns. Our goal was to describe how increasing mesophication of oak forests may affect consumers in higher trophic levels. We investigated relationships among forest composition, mast production, small-mammal density, and carnivore occurrence in 8 stands representing a gradient of oak–hickory dominance in central hardwood forest in southern Illinois. We live-trapped small mammals for >24,000 trap-nights in June–August 2009–2011 with trapping webs to estimate population density of mice (*Peromyscus* spp.). We collected mast seeds during October–November 2009–2010 and calculated average dry biomass (g/m²) for each species and stand. During winters 2009–2011, we photographed carnivores using baited camera traps. We regressed mast biomass on measures of forest composition and regressed *Peromyscus* density and carnivore occurrence on estimates of mast biomass. *Peromyscus* summer density was not related to percent hard-mast basal area or hard-mast biomass from the previous autumn. Logistic regressions of carnivore occurrence on *Peromyscus* density were not significant. Many other studies have demonstrated links of several species to oak forest and mast production, but the lack of associations that we observed was consistent with recent meta-analyses across latitude. The landscape matrix of oak–hickory forest and alternative soft-mast foods also may act to homogenize *Peromyscus* density across our study sites. Maintenance of stand heterogeneity in the forest landscape will support a wider diversity of species.

Key words: acorns, mesocarnivores, mesophication, *Peromyscus*, *Quercus*, trapping webs

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Recent decades have seen a decline in the distribution of oak-dominated forests in the eastern United States due to reduced oak regeneration (Abrams 1998; Aldrich et al. 2005; Lorimer 1984). Shade-tolerant species, especially red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and American beech (*Fagus grandifolia*), are better competitors in light-limited conditions and are replacing oaks (*Quercus* spp.) in the understories of these forests. Nowacki and Abrams (2008, p.123) label this process mesophication and define it as “a positive feedback cycle...whereby microenvironmental conditions (cool, damp, and shaded conditions; less flammable fuel beds) continually improve for shade-tolerant mesophytic species and deteriorate for shade-intolerant, fire-adapted species.”

Several interacting factors have been hypothesized for the change in oak forest dynamics in eastern North America (McEwan et al. 2011). Fire suppression for much of the 20th century allowed fire-sensitive maples to gain a foothold in the understories of eastern oak forests (Abrams 1992; Lorimer

1984). The removal of livestock grazing pressure also acted to release understory seedlings and increase stem density of shade-tolerant species that can outcompete young oaks in light-limited conditions (Aldrich et al. 2005; Spetich and Parker 1998). Uneven-aged timber harvest techniques may suppress oak regeneration by mimicking gap succession, a disturbance regime common to late-successional forests (McDonald et al. 2008b; Ozier et al. 2006). Insects, disease, and herbivory by deer also have contributed to oak decline (Aldrich et al. 2005; Beals et al. 1960; Oak 2002; Rooney and Waller 2003). Extinction of the passenger pigeon (*Ectopistes migratorius*) removed an important disturbance mechanism that opened the canopy, released oaks in the understory, and may have contributed to dominance of oak–hickory forest in the early 20th century (Albrecht and McCarthy 2006; Ellsworth and



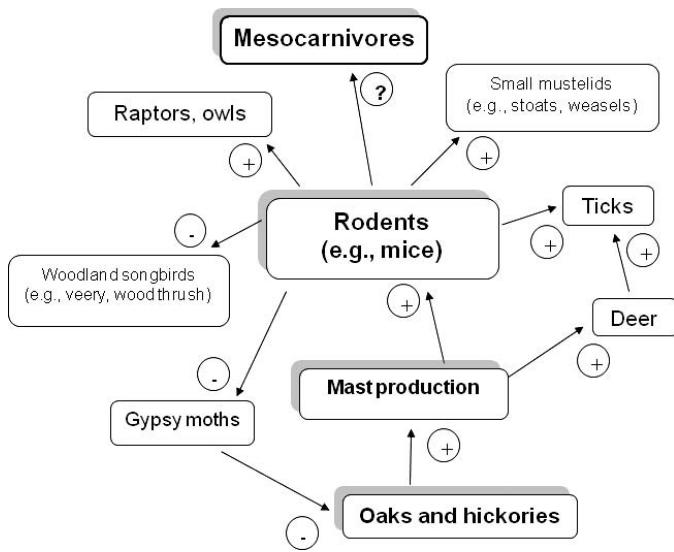


FIG. 1.—Conceptual model of relationships among some species or guilds in oak forests, adapted from Ostfeld et al. (1996). Arrows indicate the direction of influence between units. Plus and minus signs indicate a positive or negative relationship between units, respectively. Bolded, shadowed boxes highlight the elements of interest for this project.

McComb 2003). Finally, climate variation over the past 500 years and land-use dynamics also may have contributed to the species composition shift (McEwan et al. 2011).

Abundant mast production in oak forests can cause interactions and cascading effects through multiple trophic levels, involving primary and secondary consumers, parasites, and disease (Clotfelter et al. 2007; Jones et al. 1998; Ostfeld et al. 1996; Schmidt and Ostfeld 2003; Fig. 1). Therefore, forest compositional changes associated with mesophication may affect a variety of consumers, especially because acorn mast is considered a keystone resource in oak forests (Clotfelter et al. 2007; Ostfeld et al. 1996). Acorns are highly nutritious and decompose slowly (Rodewald 2003), providing an important food source during fall and winter for a variety of mammalian and avian species (DeGange et al. 1989; Eiler et al. 1989; Martin et al. 1961; McShea and Schwede 1993). However, the pulsed nature of acorn production can affect consumers. Many rodent species exhibit population irruptions in the spring and summer following a heavy mast crop in the fall via winter reproduction (King 1983; McShea 2000; McShea and Schwede 1993; Ostfeld et al. 1996; Wang et al. 2009; Wolff 1996). A large acorn crop can increase survival of rodents by improving body condition and reducing vulnerability to predators through reduced foraging time (Ostfeld 2002).

The loss of acorns in the transition of oak forests to maple could potentially cause bottom-up trophic effects on both primary and secondary consumers in the community, yet links between primary and secondary consumers in relation to acorn production has not been widely studied. In the absence of periodic bumper acorn crops, carrying capacity of primary consumers (e.g., mice) may be reduced, lowering abundance or density in some areas. Secondary consumers (e.g., mesocarni-

vores) are highly mobile and should move to areas with enough resources to support them (i.e., areas of high prey density—Chamberlain and Leopold 2000; Litvaitis and Shaw 1980). Occurrence patterns (presence-absence) of mesocarnivores in eastern forest (coyotes [*Canis latrans*], bobcats [*Lynx rufus*], gray foxes [*Urocyon cinereoargenteus*], and red foxes [*Vulpes vulpes*]) probably reflect local prey density sooner than population size, due to high vagility. Shifts in forest composition will likely result in altered occurrence and relative abundance of both groups of consumers along an oak-dominance gradient from drier, fire-adapted communities to mesophytic forest. However, there is a notable lack of data addressing the effects of mesophication on faunal assemblages (Rodewald 2003).

We initiated testing of the hypothesis that increasing mesophication of oak forests affects abundance of primary consumers (i.e., rodents) and occurrence of mesocarnivores through bottom-up trophic processes. Overall, we predicted positive relationships among oak-hickory dominance, mast production, rodent abundance, and mesocarnivore occupancy (Fig. 1). We identified the following objectives to test these predictions across a gradient of oak-hickory dominance in central hardwood forests: quantify variation in mast availability; quantify variation in small-mammal abundance, specifically *Peromyscus* spp. density; quantify occurrence of 4 mesocarnivore species (*C. latrans*, *L. rufus*, *U. cinereoargenteus*, and *V. vulpes*) across the oak-hickory gradient; and investigate relationships among mast availability, primary consumer density, and mesocarnivore occurrence.

MATERIALS AND METHODS

Study area.—We conducted research in 8 forest stands located throughout the Ozark Hills in parts of Shawnee National Forest and Trail of Tears State Forest, centered at approximately 37°30'N and 89°22'W. The Ozark Hills of southern Illinois, primarily located in Jackson and Union counties, compose the easternmost edge of the Missouri Ozark Mountains. Braun (1950) placed the Ozark Hills in the western mesophytic forest region, a transitional region characterized by mosaic patterns of dominant species. McNab (2011) recently defined this area as the Western Dry subregion of the Central Hardwood region. Oak-hickory forest dominates the upland areas, whereas pockets of mesophytic species can occur in ravine bottoms or on sheltered slopes (Braun 1950). Overall composition of the Shawnee National Forest, which contains >110,000 ha of forest across southern Illinois, is approximately 68% oak-hickory, 16% maple-beech, and 12% pine or oak-pine (Haugen 2003).

We chose stands across a gradient of oak-hickory dominance (Table 1). Average stand size was 4.7 ha (range: 3.6–6.9 ha) and stands were separated by at least 300 m. Stands comprised mature forest types varying due to elevation, slope, aspect, and disturbance history. No timber harvest has occurred in any of these stands for at least 20 years, with single-tree selection being the primary silvicultural method in Trail of

TABLE 1.—Tree and mast characteristics of 8 hardwood forest stands in southern Illinois, 2009–2010. Standard errors for mast production are given in parentheses.

Stand size (ha)	Hard-mast basal area (%)	Total basal area (m ² /ha)	Species diversity (H')	Species richness	2009 mast (g/m ²)			2010 mast (g/m ²)		
					Hard		Soft	Hard		Soft
					Acorn	Other		Acorn	Other	
6.9	2.9	51.41	1.14	19	0.03 (0.03)	0.12 (0.08)	5.63 (1.17)	0.21 (0.06)	0.48 (0.07)	14.47 (1.15)
4.1	8.7	34.88	1.44	20	0.09 (0.04)	1.66 (1.00)	5.63 (1.40)	1.08 (0.33)	3.16 (1.05)	10.71 (0.63)
5.2	21.29	34.27	1.57	22	0.71 (0.42)	4.44 (1.85)	7.25 (1.46)	1.66 (0.22)	2.59 (0.88)	11.25 (1.00)
4.2	46.95	37.43	1.34	15	29.02 (4.02)	0.00	6.47 (1.25)	36.35 (3.40)	0.00	5.88 (1.31)
5.0	53.34	40.32	1.69	10	0.72 (0.22)	36.86 (8.21)	1.47 (1.19)	1.47 (0.43)	22.80 (4.71)	6.62 (1.34)
4.2	84.77	26.12	1.99	20	19.34 (4.45)	7.07 (2.52)	0.03 (0.01)	6.89 (0.52)	7.74 (3.42)	0.34 (0.18)
4.5	90.39	33.97	1.47	14	13.20 (4.30)	10.22 (3.46)	0.04 (0.02)	5.44 (0.68)	13.41 (6.42)	0.30 (0.02)
3.6	94.75	36.94	0.50	11	4.87 (0.52)	0.00	0.04 (0.04)	35.91 (4.34)	0.06 (0.03)	0.54 (0.12)

Tears prior to 1989 (Ozier et al. 2006). Stands included bottomland oak-dominated forest with very little maple in the understory, oak-dominated upland sites with a minor understory component of beech and sugar maple, mixed oak–mesophytic forest, and mesophytic, nonoak forest. Bottomland oak stands were dominated by pin oak (*Quercus palustris*) and cherrybark oak (*Q. pagoda*); upland oak stands were dominated by white oak (*Q. alba*), black oak (*Q. velutina*), and hickory (*Carya* spp.); mixed-mesophytic stands were characterized by a combination of white oak, red oak, sweetgum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), and sugar maple; and nonoak stands were dominated by tulip poplar, sweetgum, and sugar maple.

Stand characteristics and mast production.—We measured habitat characteristics within 3 randomly placed 0.04-ha plots (radius = 11.3 m) in each forest stand in May 2009. We recorded tree species and diameter at breast height (DBH) of all >2-cm DBH trees, calculated basal area (BA) for trees using DBH measurements, and determined relative BA by dividing the BA for each species by the total BA. We also calculated percent of BA that was composed of hard-masting trees (i.e., *Quercus* spp., *Carya* spp., *Juglans nigra*). We calculated species richness, diversity (H'), and evenness of trees using the Shannon–Wiener index (Horn 1966). We measured stem density with two 2 × 10-m transects placed randomly through the center of each plot. All stems <2 cm DBH were counted and placed into height classes of 0–1, 1–2, and 2–3 m. Vines were counted as a part of stem density, but not placed in height classes. We recorded percent canopy cover using a densiometer at the center and 4 corners of the stem-density transects. We collected 4 readings at each of these 5 within-plot locations, and averaged them.

We collected mast on the ground from sixty 1-m² plots at each study stand during October–November 2009, and from 50 plots in October–November 2010. We randomly placed mast plots along transects placed within each study stand. We searched through the layer of leaf litter to bare ground, collecting any mast seeds found in this stratum. We sorted acorns and other mast seeds by species and grouped hickory nuts by genus. Acorns were identified by shape, size, and cap characteristics. We assumed that acorns without caps that were difficult to identify were the same species of oak as the

majority of loose caps collected at the plot. We recorded the initial mass using an electronic balance for seeds of each species, as well as the number of acorns and acorn caps collected for each plot. Caps still attached to acorns were broken off and discarded to avoid double counting of caps. We randomly selected mast from 20 plots from each site. We sorted seeds by species, placed them in paper bags, recorded the mass, and dried them at 60°C until they reached constant mass. We then calculated dry biomass estimates for each species in grams per square meter, grouping mast species into hard and soft mast.

Small-mammal density.—We livetrapped small mammals during June–August 2009–2011. We arranged Sherman live traps (7.5 × 9.0 × 23.0 cm; H. B. Sherman Traps, Tallahassee, Florida) in a trapping-web design (Parmenter et al. 2003) consisting of 12 transect lines 60 m in length radiating out from a center point every 30°. Traps were placed along each line at 5, 10, 15, 20, 30, 40, 50, and 60 m from the center point, producing 8 trap rings in the web. Additionally, 4 traps were placed at the center of each web, resulting in 100 traps per web. Traps were opened in late afternoon (approximately 1500–1700 h) and baited with rolled oats. We also set 24 Tomahawk traps (16.5 × 16.5 × 48.0 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) per site in 2009 and 12 Tomahawk traps per site in 2010, targeting tree squirrels. We baited these traps with walnuts and peanut butter. We conducted trapping at each site using a robust design (Pollock 1982) of 3 monthly sessions consisting of 1 night of prebaiting and 4 consecutive nights of trapping. We checked traps in the morning before 1000 h and closed them during the day. We identified rodents and shrews to species and examined them for mass, sex, hind-foot length, and reproductive condition before marking them with unique toe clips and releasing them at the appropriate trap stations. Capture and handling of animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were conducted under permits approved by the Southern Illinois University Carbondale Institutional Animal Care and Use Committee (permit 09–013). Trapping effort with Sherman traps was calculated using the method suggested by Beauvais and Buskirk (1999), wherein trapping effort is adjusted by multiplying all sprung traps, including both animal captures and accidentally sprung traps, by 0.5. This

method reduces the error associated with variation in trap-springing among sites (Beauvais and Buskirk 1999).

We used program Distance 6.0 (Thomas et al. 2010) to estimate population density for each site. We combined new captures of *Peromyscus leucopus* and *P. maniculatus* to obtain density estimates for the genus. These 2 species are ecologically very similar (Klein 1960) and were difficult to differentiate in the field by tail coloration. They composed the majority of total small-mammal captures each year. We analyzed 2009 data for each month with the uniform and half-normal key functions with cosine, polynomial, and hermite polynomial series expansions and varying orders of adjustment. Capture data were placed into distance categories (i.e., bins) specified to include the trap ring distance as the midpoint of each bin (see trapping-web description above). The most distant bin ranged from 55 to 65 m to include area outside the actual web that was likely to contribute to *Peromyscus* captures. We chose best models based on the lowest Akaike information criterion for small sample sizes (AIC_c) value; however, if ≥ 2 models were within 2 AIC_c points, we chose the most precise model (i.e., lowest coefficient of variation [CV]). We chose a specific model for each site and each month rather than use a common model for pooled data because individual models provided lower CVs and narrower confidence intervals for density estimates. Finally, we combined the 2 distance intervals nearest the center point (0–2.5 m and 2.5–7.5 m) to obtain a better “shoulder” near the center point in the detection probability curve, which helps satisfy the assumption that detection probability is 1.0 at the web center (Buckland et al. 2003). Monthly density estimates were averaged to obtain estimates of summer density for each site.

Carnivore occurrence.—We estimated mesocarnivore occurrence at our sites using photographs taken by Cuddeback Excite remotely triggered cameras sensitive to infrared motion (Non Typical, Inc., Green Bay, Wisconsin). We placed 1 camera per stand during February 2009–2010 and January 2011, positioning each camera 2–4 m away from a bait station consisting of a fatty acid scent disk (Department of Agriculture Pocatello Supply Depot, Pocatello, Idaho) and a can of sardines attached to a tree. We returned to each site once per week to change the bait and to collect photos taken during the previous week. This schedule resulted in three 1-week sampling periods for each site per month, allowing us to estimate detection probability (p) and occupancy (ψ) for each species (MacKenzie et al. 2002).

We used the multiseason model in program PRESENCE 3.0 (Hines 2010) to estimate detection probability and occupancy of gray fox, coyote, and bobcat at the 8 stands during February 2009–2010 and January 2011. We recognized the limitations in scale and sample size associated with our 8 intensively sampled plots relative to assessing occupancy of carnivores. Therefore, we added occupancy data collected from cameras located in 30 additional hardwood stands in the Ozark Hills (Jackson and Union counties) during January–April 2010 during a large-scale carnivore survey (Nielsen et al. 2011) to those collected in our 8 study stands. These additional stands were located in

2.6-km² sections containing $\geq 50\%$ forest cover. Stands were sampled at survey points using a 10 \times BA-factor prism to determine tree composition and BA. Although we did not have small-mammal data from these additional 30 stands, this analysis allowed us to assess relationships between forest stand composition and carnivore occurrence at a suitable spatial scale. We built models including month as a survey covariate to assess whether p differed between January–February and March–April. In the set of 38 stands, we tested null models and models varying ψ by percent hard-mast BA for gray fox, coyote, and bobcat. Model sets were ranked by AIC_c .

Trophic analyses.—We performed linear and logistic regression to assess relationships among forest composition measures, mast production, *Peromyscus* density, and carnivore occurrence. Independent variables included hard-mast BA (%), hard- and soft-mast biomass (g/m²), and *Peromyscus* average summer density (N/ha), as well as a suite of forest composition characteristics. Regressors included hard- and soft-mast biomass (g/m²), and *Peromyscus* average summer density (N/ha). The experimental unit in all cases was the forest stand. Log or square-root transformations were applied to 1 or both variables in some cases to obtain a better fit and to satisfy statistical assumptions. Linear regression code specified AIC_c values for each regression, by which we could later rank contribution of individual variables to variance explanation. To prevent comparison of highly correlated variables, we performed correlation analyses of regressors with Bonferroni corrections and excluded the lower-ranked variable in a pair of highly correlated regressors. For all analyses, significance was defined as $\alpha = 0.05$.

Logistic regressions regressed binary carnivore occurrence data (1 = detected, 0 = not detected) against independent variables including hard-mast BA (%), hard- and soft-mast biomass (g/m²), acorn biomass, and average summer *Peromyscus* density. Additionally, we included carnivore occurrence data collected from the 30 additional stands in the concomitant, large-scale carnivore survey with data collected at the 8 main sites and regressed these against hard-mast BA (%).

RESULTS

Mast production and mammal characteristics of forest stands.—Stand estimates ($n = 8$) of percent hard-mast BA ranged along a gradient from 3% to 95%, with an increasing gradient of hard-mast production and a decreasing gradient of soft-mast production across stands (Table 1; Fig. 2). We collected seeds of 14 species of hard mast, including the genus *Carya*, and 7 species of soft mast, including a group of assorted berries, for a total of 21 mast species in 2009. We collected 20 different species of mast seeds, including *Carya* spp. and assorted berries in 2010. Six species of acorns were collected, including 2 in the white oak group and 4 in the red oak group. Other species of hard mast were nuts of hickory, black walnut, and American beech. Acorns and hickory nuts composed the majority of hard mast collected (Table 1). Hickory nuts were most abundant at stands falling in the middle of the gradient of

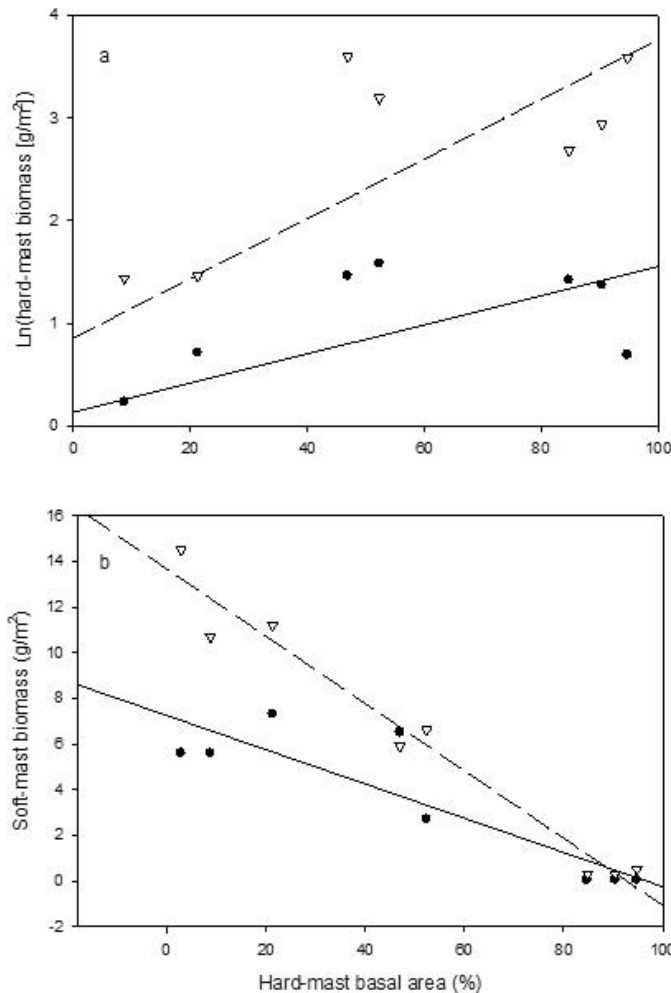


FIG. 2.—Regressions of mast biomass (averaged across 50–60 plots per stand) on hard-mast basal area (%) for a) hard mast and b) soft mast in 2009 (black circles; solid line) and 2010 (white triangles; dotted line) at 8 stands in southern Illinois. Hard-mast variables in both years were natural log-transformed to satisfy statistical assumptions.

percent hard-mast BA (Table 1). The soft-mast group included 11 species, such as sweetgum, tulip poplar, sugar maple, and ash (*Fraxinus* spp.).

Total effort with Sherman traps in 2009, 2010, and 2011 for small mammals was 8,050, 8,186, and 7,871 trap-nights, respectively, after adjusting for sprung traps at each site. Overall trapping success (total summer captures/adjusted summer trap-nights) ranged from 6.9% to 8.1% annually, with *P. leucopus* and *P. maniculatus* composing 87.3–96.5% of total small-mammal captures. Other species caught during the study in Sherman traps included southern short-tailed shrew (*Blarina carolinensis*), woodland vole (*Microtus pinetorum*), golden mouse (*Ochrotomys nuttalli*), marsh rice rat (*Oryzomys palustris*), eastern woodrat (*Neotoma floridana*), and eastern chipmunk (*Tamias striatus*); however, we did not capture adequate numbers of these species to estimate population density. We captured 0 gray squirrels (*Sciurus carolinensis*) in 2,304 trap-nights in 2009 and 4 gray squirrels in 1,152 trap-

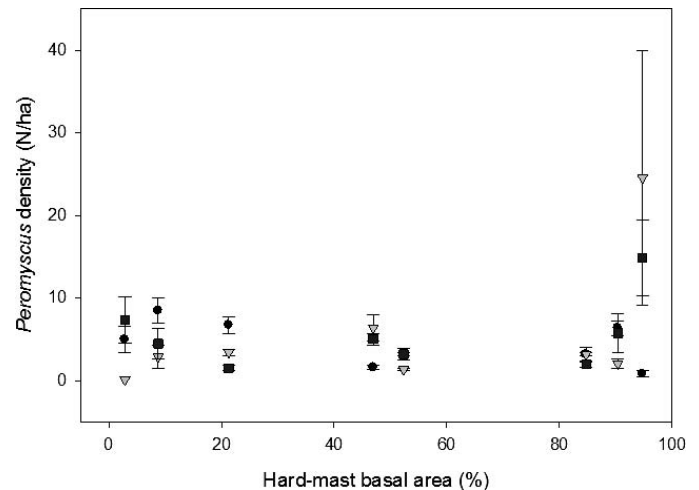


FIG. 3.—Relationship between *Peromyscus* spp. density ($\bar{X} \pm SE$) and hard-mast basal area (%) at 8 forest stands in southern Illinois during summer 2009 (black circles), 2010 (light gray triangles), and 2011 (dark gray squares). Relationships were nonsignificant in all years.

nights in 2010 using larger Tomahawk traps; we did not target squirrels in 2011. We estimated *Peromyscus* density for each month at all sites except for 2 site-month combinations in 2009 and 1 site in 2010 due to extremely low capture success. The range of average density estimates was 0.8–8.5 mice/ha in 2009, 0.1–24.5 mice/ha in 2010, and 1.5–14.9 mice/ha in 2011 (Fig. 3).

We detected each of the 4 targeted mesocarnivore species at least once during February 2009, all but the red fox during February 2010, and only coyotes and bobcats in January 2011. Gray fox occupancy was estimated to be 0.65 ($SE = 0.38$) with a detection probability of 0.25 ($SE = 0.13$) across all 8 sites. Limited data allowed parameter estimation only when occupancy and detection probability were held constant ($\psi(\cdot)p(\cdot)$). Parameters could not be estimated for coyotes or bobcats using only the original 8 stands; however, we obtained estimates after including data from 30 additional stands. For coyotes, the top-ranked model held p constant and allowed ψ to vary by percent hard-mast BA (Table 2). A model testing for differences in detectability by survey month showed no difference in p between January–February ($0.52 \pm 0.14 SE$) and March–April (0.49 ± 0.09). Conditional occupancy of coyotes (i.e., probability of occupancy given detection history) tended to decrease with increasing percent hard-mast BA, with average $\psi = 0.63$ ($SE = 0.10$). The top-ranked bobcat model held both ψ and p constant (Table 2). Detection probability was 0.15 ($SE = 0.09$) across sites, and average ψ was 0.82 ($SE = 0.47$).

Trophic relationships.—Not surprisingly, hard- and soft-mast production showed clear relationships with percent hard-mast BA (Fig. 2). Hard-mast biomass (g/m^2) showed a positive relationship with percent hard-mast BA in 2010 ($F_{1,6} = 9.67$, $P = 0.02$, $r^2 = 0.62$), and trended toward a positive relationship in 2009 ($F_{1,6} = 4.84$, $P = 0.07$, $r^2 = 0.45$; Fig. 2). Similarly, the

TABLE 2.—Model-selection results for occupancy (ψ) and detection probability (p) of coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) in 38 stands in the Ozark Hills, southern Illinois, during January–April 2010. Models were ranked by Akaike’s information criterion for small sample sizes (AIC_c). K is the number of parameters estimated.

Species	Model ^a	AIC_c	ΔAIC_c	AIC_c weight	K	Deviance
Coyote	$\psi(\text{HMBA})p(\cdot)$	134.13	0.00	0.86	3	127.42
Coyote	$\psi(\cdot)p(\cdot)$	138.33	4.20	0.11	2	133.99
Coyote	$\psi(\cdot)p(\text{Apr})$	140.66	6.53	0.03	3	133.95
Bobcat	$\psi(\cdot)p(\cdot)$	89.15	0.00	0.57	2	84.81
Bobcat	$\psi(\text{HMBA})p(\cdot)$	91.00	1.85	0.23	3	84.29
Bobcat	$\psi(\cdot)p(\text{Apr})$	91.29	2.14	0.20	3	84.58

^a HMBA = percent hard-mast basal area.

strong negative relationships between soft-mast biomass and percent hard-mast BA in both 2009 ($F_{1,6} = 21.98$, $P = 0.003$, $r^2 = 0.79$) and 2010 ($F_{1,6} = 170.11$, $P < 0.001$, $r^2 = 0.97$; Fig. 2) supported our choice of percent hard-mast BA as a predictor of both hard- and soft-mast production.

Relationships between population parameters of *Peromyscus* and measures of forest composition or mast were generally weak. We found no relationship of mouse density in any year with percent hard-mast BA (Fig. 3); nor did we see positive responses of mouse density in 2010 and 2011 to total hard-mast production from the previous year (2010: $F_{1,6} = 0.36$, $P = 0.60$, $r^2 = 0.06$; 2011: $F_{1,6} = 1.66$, $P = 0.24$, $r^2 = 0.22$; Fig. 4). Similarly, acorn-only production in the previous year was not related to summer mouse density in 2010 ($F_{1,6} = 0.01$, $P = 0.93$, $r^2 = 0.002$) and had a marginally positive relationship ($F_{1,6} = 3.73$, $P = 0.10$, $r^2 = 0.38$) in 2011. Likewise, soft-mast production in 2009 and 2010 did not influence mouse density in 2010 ($F_{1,6} = 0.59$, $P = 0.47$, $r^2 = 0.09$) or 2011 ($F_{1,6} = 0.46$, $P = 0.52$, $r^2 = 0.07$).

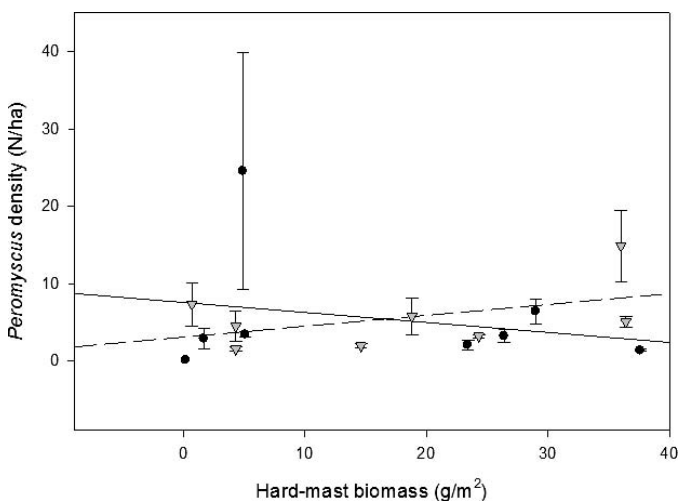


FIG. 4.—Relationship of *Peromyscus* spp. density ($\bar{X} \pm SE$) during summer 2010 (black circles, solid line) and 2011 (gray triangles, dashed line) with hard-mast production from the previous autumn in 8 forest stands in southern Illinois. Relationships were nonsignificant. 2010: density = $(-0.13 \times \text{hard mast}) + 7.56$; $F_{1,6} = 0.36$, $P = 0.60$, $r^2 = 0.06$. 2011: density = $(0.14 \times \text{hard mast}) + 3.07$; $F_{1,6} = 1.66$, $P = 0.24$, $r^2 = 0.22$.

We found no significant relationships between occurrence of any mesocarnivore in 2009–2011 and percent hard-mast BA in the 8 main study sites. Similarly, coyote occurrence and bobcat occurrence in 2010 and 2011 were not significantly related to the previous year’s *Peromyscus* density, nor to the previous year’s hard-mast or soft-mast production. No detections of red fox in 2010 or 2011, and no detections of gray fox in 2011 and only 1 in 2010 prevented statistical modeling of relationships. The analysis of data that included 30 additional sites in the Ozark Hills region in 2010 resulted in a negative relationship between coyote occurrence and percent hard-mast BA ($\chi^2_1 = 4.64$, $P = 0.03$). Bobcat occurrence was not related to percent hard-mast BA in the set of 38 sites ($\chi^2_1 = 0.05$, $P = 0.83$). There were no red fox detections and only 2 gray fox detections in 2010, which prevented statistical modeling of relationships.

DISCUSSION

We focused on the signal associated with a gradient of oak–hickory dominance to base our investigation of mesophication effects on higher trophic levels. Because our study area is in the midst of mesophication (Fralish and McArdle 2009; Ozier et al. 2006; Zaczek et al. 2002) and we did not have complete histories of each stand, we could not control for slope position and aspect along the full gradient from oak–hickory to mesophytic forest. We recognized that topographic and moisture differences among the stands may have contributed noise to the mast and mammalian metrics that we measured. Nevertheless, characteristics of overstory and understory habitat did not vary among stand types in our study area (Edmund 2011) with the exception of percent hard-mast BA (the basis of our gradient) and diversity of understory woody stems (higher in mesophytic stands).

In general, our hypotheses were not supported. We did not see expected variation in *Peromyscus* density and carnivore occurrence among forest types. We also expected to find positive relationships among hard-mast production, *Peromyscus* density, and carnivore occurrence; however, we found nonsignificant trends among trophic levels. Estimates of *Peromyscus* density on trapping webs at our sites were at the low end of density ranges reported in the literature using grid-based sampling, which typically underestimates effective area sampled and therefore overestimates density. Average densities

across all sites in our study were 4.1 mice/ha in 2009 and 5.5 mice/ha in 2010 and 2011. In comparison, longer-term (≥ 5 years) studies conducted in the eastern United States have recorded densities of *Peromyscus* ranging from 0 to >100 mice/ha (Clotfelter et al. 2007; Ostfeld et al. 1996; Wolff 1996). A study in the Missouri Ozarks estimated *Peromyscus* densities to range from about 5 mice/ha to about 23 mice/ha (Fantz and Renken 2005). The lack of relationship between *Peromyscus* density and percent hard-mast BA in our study points to unmeasured variation in the system.

The majority of the literature relating mast to small mammals has documented positive correlations between acorn mast and the following year's small-mammal populations (Clotfelter et al. 2007; McShea 2000; Ostfeld et al. 1996; Wolff 1996). Our estimates of hard-mast biomass compared reasonably well to estimates of acorn production in Virginia and North Carolina (Diamond et al. 2000; McShea 2000). Diamond et al. (2000) estimated total hard mast to be 28.0 g/m^2 ; 5 of our 8 stands produced $>23 \text{ g/m}^2$ in at least 1 year of this study. McShea (2000) collected acorns using stationary mast traps and defined a bumper acorn crop to be $>30 \text{ g/m}^2$ and a mast failure to be $<5 \text{ g/m}^2$. By these terms, hard-mast production in our study ranged from mast failure to bumper crops across the stands over the 2 years of sampling. However, despite hard-mast biomass estimates that spanned widely, we did not see the commonly observed relationship between total hard mast or acorn mast and mouse density.

We also found no relationship between *Peromyscus* density and soft-mast production in the previous year. This result contrasted with evidence from northern hardwood forests dominated by maple-beech communities, which indicated that soft mast can influence small-mammal abundance (Falls et al. 2007; Jensen et al. 2012; McCracken et al. 1999). Although the magnitude of population growth of *P. leucopus* from spring to summer was related to the spring crop of red maple mast, summer densities were only related to the previous year's acorn crop (McCracken et al. 1999). Martin et al. (1961) recorded some use of soft-mast by small mammals, but ranked oak mast above maple and tulip poplar mast in the diet of *P. leucopus*.

Peromyscus populations in southern Illinois may not exhibit the dramatic boom-and-bust cycles after mast years commonly seen in the northeastern United States. In a meta-analysis of population cycles in *P. leucopus* in North America, Wang et al. (2009) reanalyzed 6 long-term data sets ranging in length from 14 to 32 years. They noted a spatial cline in which cycles of *P. leucopus* were muted, exhibiting weaker direct and indirect density-dependence with decreasing winter severity and latitude. They proposed that a more diverse food base in southern sites may uncouple dynamics of *P. leucopus* from acorn production. Our data on considerable soft-mast production in stands with few oaks and hickories (Fig. 2), coupled with the lack of a mouse response to hard-mast variability, supports their conjecture. Alternatively, the timescale of our study may have been too short to detect a trend in *Peromyscus* density due to high variation between years. Long-term study (i.e., decades) could be more informative in determining the

relationship between *Peromyscus* density and hard mast in our study region.

The relationship between *Peromyscus* density and hard-mast production in southern Illinois forests could be muted by variability in insect assemblages based on forest type. Many species of small mammals, including *P. leucopus* and *P. maniculatus*, are omnivorous and consume insects (Ostfeld et al. 1996; Semel and Andersen 1988; Whitaker 1963). The literature documents variability in insect assemblages based on forest composition; however, much of this research supports positive links between oak forests and invertebrates, which would have additional positive effects on higher trophic levels (Butler and Strazanac 2000; Martel and Mauffette 1997; Summerville et al. 2008). Further research on how insect communities may differ along a gradient of oak-hickory cover and how invertebrate prey contribute to small-mammal diets should help clarify this relationship.

The landscape matrix of oak-hickory forest in which our study sites were located, in combination with the spatial scale of the stands, also may explain the lack of variation observed in *Peromyscus* density among forest types. Forest stands dominated by alternate species were relatively small and surrounded by the larger oak-hickory matrix; therefore, rodent communities living in nonoak or mixed mesophytic stands may be influenced by oak-hickory dominance. Although our stands were a magnitude larger than mice home-range sizes, mice will quickly occupy available space (Schmidt et al. 2001). Therefore, mice may move, for example, from upland oak forest into mesophytic, nonoak stands. Estimates of immigration and emigration rates for mice in individual stands were high (often >0.50 —Gillen 2011), implying that individuals living on the edges of stands may cross borders and homogenize mouse densities across forest types.

We did not observe a significant relationship between carnivore occurrence and *Peromyscus* density at our 8 sites. An important factor influencing carnivore occurrence is the distribution of prey (Chamberlain and Leopold 2000; Litvaitis and Shaw 1980). If carnivores move to areas with enough resources to support them (i.e., areas of high prey density), then carnivore occurrence should be related to prey density. However, in our study, the range of mouse densities may have been too narrow (Fig. 3), and the vagility of the mesocarnivores too great (Litvaitis and Shaw 1980; Major and Sherburne 1987; McDonald et al. 2008a) relative to the scale of our stands to detect the pattern. In addition, the availability of alternative prey (e.g., arthropods and birds) was unknown.

The negative relationship between coyote occurrence and percent hard-mast BA in the larger sample of sites ($n = 38$) was strong, but is not easily explained, especially with the lack of correlation between percent hard-mast BA and *Peromyscus* density seen at the 8 main study sites. Our sites comprised different stand types of mature forest with similar BA. Coyotes are generalists with regard to habitat selection, with large-scale estimates of abundance being positively correlated with forest cover, especially disturbed forest and natural edges, such as along wetland zones (Kays et al. 2008). Coyotes could be

exploiting resources that occur more frequently in mesic nonoak forest, such as alternative prey or den sites. Mesophytic stands in our study area were located in valleys drained by intermittent creeks that had potential to provide good cover for den sites (Hallett et al. 1985).

Mesophication has been widely assumed to be detrimental to a diversity of terrestrial vertebrates that depend on oaks for food (Aldrich et al. 2005; Fralish and McArdle 2009; Rodewald and Abrams 2002; Summerville et al. 2008); however, the magnitude of the potential effect has not been widely studied. Examination of our data, which contain a lack of significant relationships among hard-mast biomass or percent hard-mast BA, *Peromyscus* density, and mesocarnivore occurrence, suggests a less extreme view of the consequences of mesophication, at least in these forest stands in southern Illinois. As mentioned above, more diverse foods in southern hardwood forests may reduce the links between acorn production and *Peromyscus* dynamics (Wang et al. 2009). Furthermore, McShea et al. (2003) found that mesic forest patches in the southern Appalachians contained higher abundances of several species of small mammals than nearby xeric patches. Mice are generalist consumers that take advantage of abundant acorn crops when they occur, but can persist during years of mast failure (Clotfelter et al. 2007; McShea 2000; Wolff 1996). In the absence of oaks, the small-mammal boom-and-bust cycles associated with acorn mast years may disappear, but populations could potentially stabilize somewhat as small mammals take advantage of soft mast that provides more stable sources of food. Population increases due to bumper crops of soft mast, such as maple or ash (Jensen et al. 2012), may become more pronounced. Although generalist species, such as *P. leucopus* and *P. maniculatus*, will probably adapt to the loss of oak forest, some specialist species will no doubt be more negatively affected. It is also possible that effects may be felt more keenly by consumers in higher trophic levels.

If oak–hickory forests transition to maple–beech forests, beechnuts and maple mast could mitigate the loss of acorns to some extent, because their production can vary over time in a manner and magnitude similar to acorn production (Jensen et al. 2012; Overgaard et al. 2007). Indeed, long-term data from northern beech–maple forests showed strong links among beech and maple mast, small mammals, and 2 mustelid predators (Jensen et al. 2012) parallel to those modeled in oak forests (Fig. 1; Ostfeld et al. 1996). Based on average dry mass of a beechnut (0.1 g) and reports of nut abundances (Leak and Graber 1993; McNulty and Masters 2004; Rosemier and Storer 2010), we estimated peak beechnut production to be 2.3–19.8 g/m² in northern maple–beech forests. Jensen et al. (2012) reported peak beechnut production to be 4–16 g/m² based on seedfall traps. These estimates are within the bounds of total hard-mast biomass in oak–hickory stands from this study and from Diamond et al. (2000), and can be supplemented by equivalent or greater amounts of soft mast from *Acer* spp. (Jensen et al. 2012).

The process of mesophication has been occurring and will continue for several decades, likely altering mammalian and other wildlife assemblages (Rodewald 2003). Examination of our data showed no clear links between a gradient of oak–hickory dominance and *Peromyscus* density, suggesting that the consequences of mesophication may not be as severe for mice as for other species (Rodewald 2003) in the Central Hardwood region. Mammal assemblages in eastern forests have already dealt with the loss of a keystone resource through the demise of the American chestnut (*Castanea dentata*) in the early 20th century. Chestnut crops did not fluctuate as dramatically as acorn crops and therefore provided a more stable source of food (Diamond et al. 2000; Steele et al. 2005). We predict that *Peromyscus* populations would successfully adapt to changing forest conditions, allowing conservation efforts to be focused on other species or guilds likely to be detrimentally affected by mesophication. Accordingly, we recommend maintenance of forest stand diversity and heterogeneity (e.g., a mixture of oak–hickory and mesophytic forest patches) in the landscape to support a wider diversity of species (McShea et al. 2003; Sabo et al. 2005).

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