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Habitat fragmentation and burying beetle abundance and success

Stephen T. Trumbo[1,*] & Philip L. Bloch[2,**]
[1]*Department of Ecology and Evolutionary Biology, University of Connecticut, Waterbury, CT 06710, USA*
[2]*Department of Biology, Grinnell College, Grinnell, IA 50112, USA*
[*]*Author for correspondence: Department of Ecology and Evolutionary Biology, 32 Hillside Avenue, University of Connecticut, Waterbury, CT 06710 USA Tel: 203-236-9878; (Fax: 203-236-9805; e-mail: trumbo@uconn.edu)*
[**]*Current address: Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

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Abstract

Four species of burying beetle (*Nicrophorus marginatus* F., *N. tomentosus* Weber, *N. orbicollis* Say and *N. defodiens* Mannerheim) are attracted to small, fresh mouse carcasses in northern Michigan. The number of burying beetles and their success (burial of a carcass) were greater in woodlands than in edge or field habitats. Species diversity was least in open fields as assessed by two different indices of diversity. *Nicrophorus marginatus* was the only species captured in large fields (>25 ha). This species was never trapped in small fields (<5 ha) suggesting that a minimum habitat size might be necessary to maintain local populations. In contrast to previous studies which employed pitfall traps baited with a large quantity of carrion, *N. tomentosus* was caught exclusively in woodlands at single mouse carcasses. In Connecticut woodlands, burying beetle success, assayed as the proportion of carcasses buried and held for 7 days, was significantly greater in larger as compared to smaller woodlands. The limited success of burying beetles in smaller woodlands was due, in part, to a higher rate of scavenging by vertebrates.

Introduction

Human activity can impact biological communities in many ways including changing habitat characteristics and habitat patchiness. Habitat fragmentation reduces the area available to maintain minimum viable populations (Saunders *et al.* 1991), imposes barriers to dispersal (Klein 1989), and creates more edge habitat (Malcolm 1994) which may be poorer in quality (Yahner 1988). While an understanding of a species' known habitat requirements will aid in gauging responses to alteration of the landscape, this information alone is not sufficient to anticipate responses to habitat fragmentation. The response of a population to reduced numbers, barriers to dispersal, and creation of edge habitat must also be considered (Zabel & Tscharntke 1998; Golden & Crist 1999). In the tropics, fragmentation reduces the diversity of dung and carrion insects, resulting in decreased rates of decomposition of dung (Klein 1989). The impact of fragmentation on temperate burying beetles (*Nicrophorus* spp.), however, has not been assessed; it has been hypothesized that habitat fragmentation contributed to the decline of the endangered American burying beetle, *Nicrophorus americanus* Olivier (Lomolino *et al.* 1995). In this study we examine how habitat size affects burying beetle success, abundance and species diversity at two North American sites.

Burying beetles bury small vertebrate carcasses which they exploit as a food source for their young (Pukowski 1933). Extensive parental care is provided to young, including nest maintenance, regurgitations to larvae and defense of the brood (reviewed in Trumbo 1996; Eggert & Müller 1997; Scott 1998). Carrion is a valued resource and burying beetles must compete with vertebrate scavengers, carrion flies, ants and

Table 1. Summary of natural history of *Nicrophorus* of northeastern North America.

Species	Length[1]	Mass[2]	Breeding season[3]	Breeding habitat[4]	Breeding resource[5]
N. defodiens	12–18	0.13	Early June–early August	Forest	3–70 g
N. orbicollis	15–22	0.39	Mid June–early August	Forest	7–150 g
N. marginatus	15–22	0.47	Late June–early August	Field	7–120 g
N. tomentosus	12–18	0.22	Late July–September	Forest/field?	5–100 g
N. sayi	15–23	0.39	Mid May–mid June	Forest	7–100 g
N. pustulatus	15–20	0.32	??Early June–early August	Forest	Snake eggs
N. vespilloides	12–16	0.13	Late May–late August	Bog	3–50 g
N. americanus	25–35	0.80	Mid June–early August	Field/forest	30–500 g
N. investigator	13–18		Early July–early August	Field/shrub	15–80 g

[1]Distance from the tip of the mandibles to the edge of the elytra; value ranges from Anderson and Peck (1985).
[2]Mean mass of larvae at dispersal (Trumbo 1990a; Trumbo 1990b; Trumbo 1992, unpublished results).
[3]*N. americanus* (Kozol *et al.* 1988; Bedick *et al.* 1999); *N. investigator* (Smith and Heese, 1995); other species (Wilson *et al.* 1984; Trumbo 1990a,c; unpublished results).
[4]Data from Anderson (1982), Wilson (1984), Kozol (1988), Smith and Heese (1995), Beninger (1994), and Ratcliffe (1996).
[5]Range of acceptable carrion: *N. pustulatus* (Blouin-Demers and Weatherhead 2000); *N. investigator* (Smith & Heese 1995); *N. americanus* (Kozol *et al*. 1988); other species (Trumbo 1992, unpublished results).

other insects (Fuller 1934; Walker 1957). In general, *Nicrophorus* spp. win more carcasses in cooler, closed canopy habitats with loose soil than in warmer, open-canopy habitats with difficult-to-work soil (Scott *et al.* 1987; Trumbo 1990c; Lomolino & Creighton 1996). Individual species of *Nicrophorus*, however, exhibit marked differences in habitat, seasonal and diurnal activity as well as in body size (Table 1, Anderson 1982; Shubeck 1983; Wilson *et al.* 1984; Beninger 1994; Lingafelter 1995; Lomolino *et al.* 1995; Ohkawara *et al.* 1998). In these studies, a clear distinction between habitat use for feeding (assayed by trapping with a large quantity of well-rotted carrion) versus reproduction has not always been made. In the present study we measured burying beetle success, habitat use and species diversity by placing single, fresh mouse carcasses, suitable for reproduction in Michigan and Connecticut, USA. In northern Michigan, where the secondary forest established in the early 1900s continues to be opened, we examined the burying beetle community in and around small and large fields. In Connecticut, which is simultaneously undergoing reforestation and habitat fragmentation, burying beetle success was assessed in small and large woodlands.

Methods

Field fragments in northern Michigan

To determine the effect of the opening of small clearings within woodlands on the numbers and success of burying beetles, 4 small field sites (<5 ha) and 4 large field sites (>25 ha) were selected on or near the University of Michigan Biological Station (Pellston, Michigan, USA). The broader landscape in this area is primarily secondary woodlands with scattered fields and small towns. Two transects, one along the north–south axis and one on the east–west axis were established for each field. Transect points (where a fresh 30–33 g *Mus musculus* carcass would be placed) were stationed 90 m into the field, 50 m into the field, 10 m into the field, on the forest edge, 10 m into the woodland and 50 m into the woodland. On 8 days a fresh carcass was placed at each of 6 transect points in a small field and in a large field. Each carcass was tied with a 1 m section of dental floss to facilitate recovery. Carcasses at any one site were placed over 4 consecutive days between 17 and 25 July (mid-season) and over a second 4 day period between 28 July and 4 August (late season). The transect used (N–S vs. E–W) was chosen randomly at the beginning of the 4-day period. On the day following placement, each carcass was examined, and if buried, was carefully exhumed. The number and species of adult *Nicrophorus* were recorded.

The number of individuals discovering carcasses and the success of burying beetles (number of carcasses buried) were analyzed using General Linear Methods (Wilkinson 1989). The site of the trials did not affect the number of beetles coming to carcasses for either small fields ($F_{3,17} = 2.33$, $P > 0.10$) or large fields ($F_{3,17} = 0.54$, $P > 0.20$). Results from the four different sites were therefore used as replicates to examine the effects of habitat (3 levels: woods (10 and 50 m into the woods), edge (0 and 10 m into the field), field (50 and 90 m into field)), field size

(2 levels: small and large), and season (2 levels: mid and late). The measured (independent) variable was the number of beetles (or number of burials) totaled over the 4-day-period at the two points in each habitat. GLM was also used to examine variation in numbers of the two most common species (*N. orbicollis* Say and *N. defodiens* Mannerheim). *Nicrophorus tomentosus* Weber and *N. marginatus* F. were caught in lower numbers and their success (number of burials) relative to a single factor (season or field size) was analyzed using 2×2 contingency tables (Wilkinson 1989).

Species diversity in each of the three habitats was assessed in both small and large fields. Two different measures, $H^1 (= \sum p_i \log_e p_i)$ and $\Delta_3\ (= 1/\sum p_i^2)$, were used because diversity indices can produce inconsistent results (MacArthur & Wilson 1967; Hurlburt 1971).

Woodland fragments in Connecticut

To examine the effect of habitat size on the success of burying beetles, six study sites were selected. These were two small woodlands in Watertown, Connecticut: Nova Scotia Hills Park, 22 ha, 40% wooded; Fleischer Nature Preserve, 8 ha, 100% wooded; and one small woodland in Cheshire, Connecticut: Cheshire Park, 10 ha, 55% wooded. There also were two large woodlands in Watertown: Mattatuck State Forest and Black Rock State Park; and one large woodland in Cheshire: Naugatuck State Park. The broader landscape in this area is primarily suburban and semi-rural. The larger woodlands are part of the contiguous, although attenuated, secondary forest of the northeast, USA.

At the Cheshire sites (one small and one large woodland) 5 carcasses were tied with dental floss to a stake and placed along a N–S transect on each of 12 days beginning 6 June and ending on 26 August, 1999 (60 total carcasses at each site). After 7 days, each transect point was inspected and a determination made whether the carcass was buried by burying beetles (carcass rounded and taken beneath the leaf litter), scavenged by vertebrates (no sign of carcass), or won by other invertebrates (only skeletal and hair remains). After inspection, 5 fresh carcasses were placed along new transect points extended northward beyond the original transect.

At the Watertown site (two small and two large woodlands), 5 carcasses were placed along N–S transects on each of 6 days beginning 22 July and ending 26 August, 1999 (30 carcasses at each of 4 sites). After 7 days the carcasses were examined and fresh carcasses were placed at the sites, as described above. A total of 240 carcasses were placed in the 6 woodland study sites.

A low proportion of carcasses were buried by burying beetles in Connecticut. Burying beetle success (number of burials in small and large woodlands) was therefore assessed using contingency table analysis. Analyses of individual species were not carried out because only one species of *Nicrophorus* was active at the Cheshire site (*N. orbicollis*) and two woodland species (*N. orbicollis* and *N. defodiens*) at the Watertown site.

Results

Field fragments in northern Michigan

Four species of burying beetle (*N. marginatus*, *N. tomentosus*, *N. orbicollis* and *N. defodiens*) were trapped at fresh mouse carcasses from 17 July to 4 August in northern Michigan. The total number of *Nicrophorus* trapped was affected by habitat (wood, edge, field) ($F_{2,43} = 68.19$, $P < 0.001$) but not by season ($F_{1,43} = 1.27$, $P > 0.20$) nor size of the included field ($F_{1,43} = 0.83$, $P > 0.20$) (Figure 1, GLM Wilkinson, 1989). Similarly, the number of burials by burying beetles was significantly related to habitat ($F_{2,43} = 76.68$, $P < 0.001$) but not to season ($F_{1,43} = 0.62$, $P > 0.20$) nor to field size ($F_{1,43} = 2.83$, $P = 0.10$; Figure 2).

Habitat also affected the activity of each individual species. The number of *N. orbicollis* trapped was significantly related to both habitat ($F_{2,43} = 33.57$, $P < 0.001$) and season ($F_{1,43} = 7.25$, $P = 0.01$) but not to field size ($F_{1,43} = 1.00$, $P = 0.32$). The number of *N. defodiens* was significantly related to habitat ($F_{2,43} = 36.75$, $P < 0.001$) but not to season ($F_{1,43} = 0.16$, $P > 0.20$) nor field size ($F_{1,43} = 0.31$, $P > 0.20$). Only 19 carcasses (43 individuals) were discovered by *N. tomentosus* and only 9 carcasses (14 individuals) by *N. marginatus*. The number of burials by *N. tomentosus*, which was never recorded from open habitat, was greater late in the season than in mid season ($G = 7.59$, 1 df, $P = 0.006$; 2×2 Contingency test). The effect of field size was not adequately addressed using data from all *Nicrophorus* spp. because the large majority of discoveries were by woodland species. *Nicrophorus marginatus*, however, was clearly affected by field size. All burials occurred in the field,

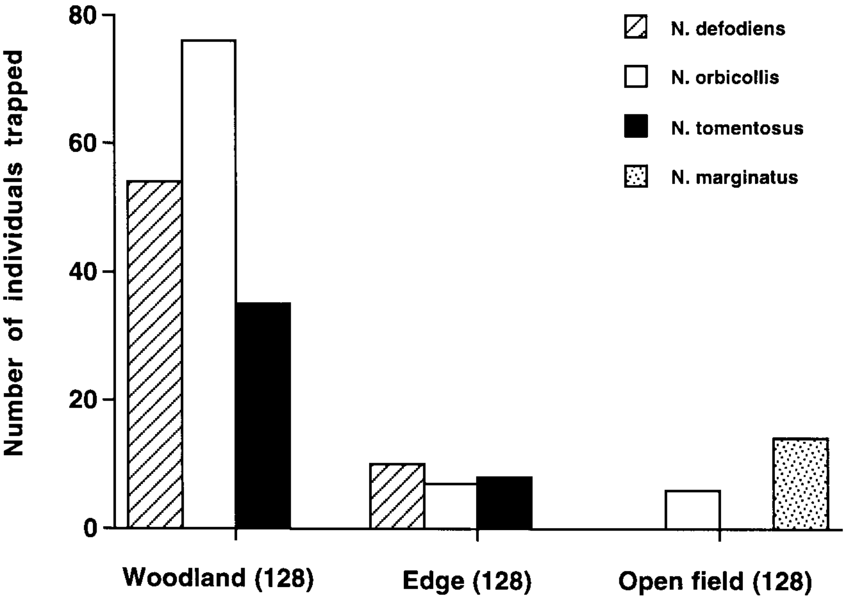

Figure 1. Number of *Nicrophorus* spp. caught at single mouse carcasses after 1 day in woodland, edge and open field habitats in northern Michigan. The number of carcasses placed is shown in parentheses.

Figure 2. Percentage of mouse carcasses buried by *Nicrophorus* after 1 day in woodland, edge and open field in northern Michigan. The number of carcasses placed is shown in parentheses.

Table 2. Two measures of species diversity of Nicrophorus communities in three habitats in northern Michigan.

Species diversity index	Woodland	Edge	Open field
Near small fields			
H^1	1.08	1.07	0
Δ_3	2.89	2.86	1.0
Near large fields			
H^1	0.99	1.09	0
Δ_3	2.44	2.97	1.0

and all of these were in large rather than small fields ($G = 9.68$, 1 df, $P = 0.002$).

While species richness was greater in woods compared to edge, species diversity was similar in these habitats as indicated by H^1 and Δ_3 (Table 2). Species diversity was not affected by the size of the field included in the landscape (Table 2).

Woodland fragments in Connecticut

There was minimal burying beetle activity at the Cheshire sites. Of 120 carcasses placed in woodlands, only 8 were discovered and buried by burying beetles. All 8 of these carcasses were from the large woodland ($G = 8.57$, 1 df, $P = 0.003$; Figure 3). In Watertown, the proportion of carcasses won by burying beetles did not differ between the two small woodland sites ($G = 0.00$, 1 df, $P > 0.20$) nor between the two large woodland sites ($G = 1.09$, 1 df, $P > 0.20$). The results for the two small woodland sites were therefore combined, as were the results for the two large woodland sites. The success of burying beetles in small woodlands in Watertown was significantly less than in large woodlands (Figure 4; $G = 24.32$, 1 df, $P < 0.001$). Of the carcasses not won by burying beetles, a higher proportion were scavenged by vertebrates in small woodlands than in large woodlands (88% vs. 50% of carcasses not occupied by burying beetles; $G = 14.70$, 1 df, $P < 0.001$).

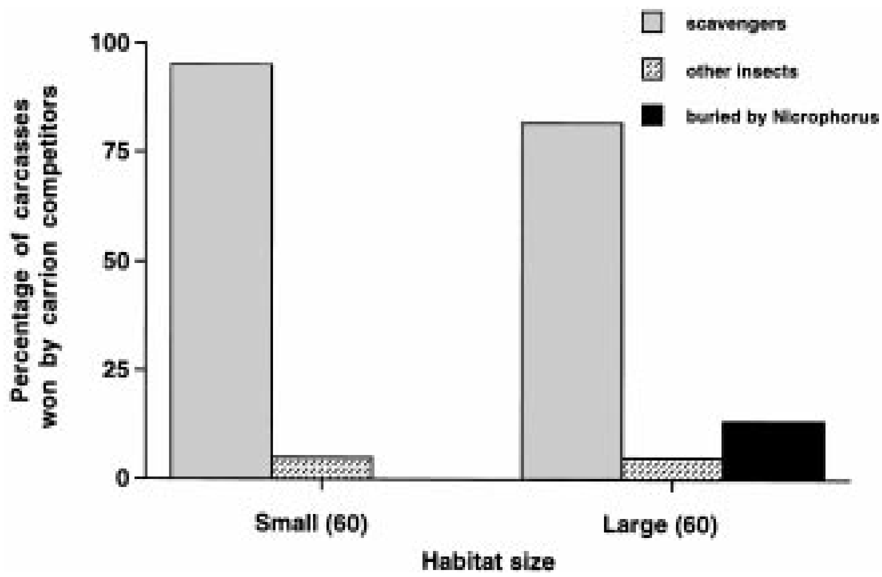

Figure 3. Percentage of single mouse carcasses exhumed after 7 days which were won by vertebrate scavengers, insects other than *Nicrophorus*, and by *Nicrophorus* in a small and large woodland in Cheshire, Connecticut. The number of carcasses placed is shown in parentheses.

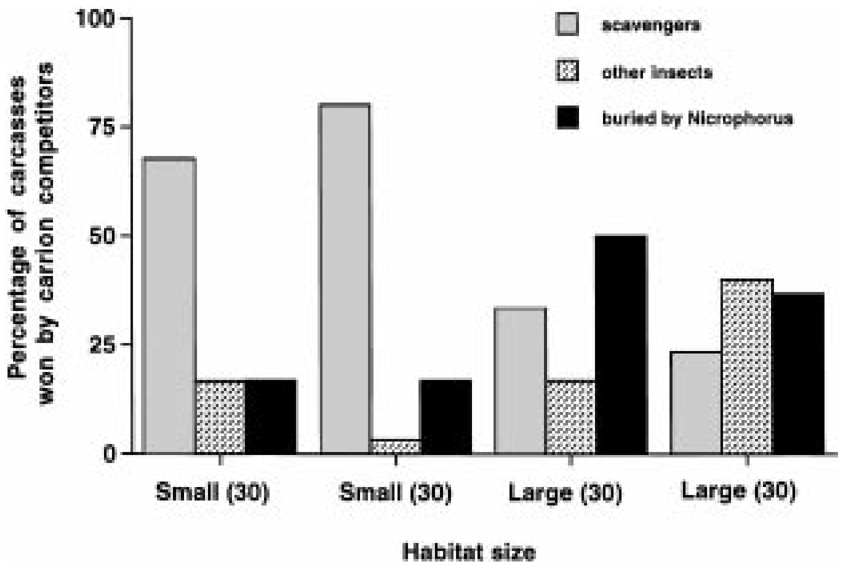

Figure 4. Percentage of single mouse carcasses exhumed after 7 days which were won by vertebrate scavengers, insects other than *Nicrophorus*, and by *Nicrophorus* in small and large woodlands at 4 sites in Watertown, Connecticut. The number of carcasses placed is shown in parentheses.

Discussion

In northern Michigan, the greatest abundance, diversity and success of burying beetles occurred in woodlands. In the broader landscape, the greatest diversity (but not abundance) will occur in areas incorporating large open fields. Habitat size had noticeable effects on burying beetle activity in Michigan fields and Connecticut woods and on community composition in Michigan. In northern Michigan, *N. marginatus* colonized fresh mouse carcasses exclusively in open habitats. Avoidance of closed-canopy habitats by *N. marginatus*, whether for feeding or reproduction, has been noted previously (Anderson 1982; Lingafelter 1995; Lomolino *et al.* 1995). *N. marginatus* was trapped only in large fields (>25 ha), and never in small fields (<5 ha). This species may have been missed during previous censuses at The University of Michigan Biological Station because the only open habitats sampled were 'small meadows' (Wilson *et al.* 1984). Even in large fields, *N. marginatus* did not come to carcasses placed 10 m from or at the edge of the woods. This finding was remarkable in that prior work with congeners has demonstrated that individuals easily travel >1 km in a single night through favorable habitat (Creighton & Schnell 1998; Bedick *et al.* 1999).

These findings suggest that *N. marginatus* may be a poor disperser across unfavorable woodland habitat. This characteristic may make it particularly vulnerable to local extinction in small habitat fragments (Klein 1989). We suggest that the absence of *N. marginatus* from small fields can be explained by the inability of these habitats to sustain minimum viable populations and the low rate of movement between isolated fields separated by woodlands. We believe these findings support the hypothesis that *N. marginatus* was native to the grasslands of the Midwest and has only invaded eastern North America during the historical period (Anderson 1982). Field specialist insects native to the eastern U.S. are generally well adapted to transitional habitats, and tend to be good colonizers of newly opened patches, while species native to the Midwest may have difficulty locating favorable habitat patches, even when corridors are present (Collenge 2000). Fragmentation of open habitat in the Midwest by development and fire suppression is likely to lead to a decline in *N. marginatus* numbers, greater than would be projected from loss of habitat alone. The loss of farms and the reforestation of eastern woodlands is likely to limit the eastward spread of this species.

Small populations are at higher risk of local extinction (Elton 1975). This may be especially true for species with narrow feeding requirements which must search widely for food (Christiansen & Pitter 1997; Zabel & Tscharntke 1998), and for invertebrates which often experience large population fluctuations (Andrewartha & Birch 1984). *Nicrophorus marginatus* is a moderately large-bodied species (Anderson & Peck, 1985) which may require larger habitat patches to sustain a minimum viable population. The largest burying beetles of North America (*N. americanus*) and of Europe (*N. germanicus* L.) are both endangered species which have experienced precipitous population declines over the past 70 years (Kozol *et al.* 1988). It recently has been suggested that reduced habitat size as well as changing habitat characteristics may be contributing to the decline of *N. americanus* (Lomolino & Creighton, 1996). The larger habitat area necessary to support larger-bodied species also may explain the greater success of *N. defodiens* compared to the larger *N. orbicollis* on small islands in Lake Superior (Trumbo & Thomas 1998). A decline in larger-bodied species of dung and carrion beetles has been documented in forest fragments in the tropics (Klein 1989).

In previous studies employing pitfall traps baited with large amounts of ripe carrion, *N. tomentosus* was found to be a habitat generalist (Anderson 1982; Wilson *et al.* 1984; Shubeck 1993) exhibiting the widest niche breadth of *Nicrophorus* spp. (Lomolino & Creighton 1996). In the present study using small, fresh carcasses, *N. tomentosus* was found exclusively in woodlands or edge habitat. This suggests that *N. tomentosus* may have narrower breeding than feeding habitat requirements, as has been suggested for *N. americanus* (Lomolino & Creighton 1996). This hypothesis is supported by the finding that *N. tomentosus* readily comes to pitfall traps in both forest and bogs in Ontario, but buries fresh carcasses almost exclusively in forest (Beninger 1994). *Nicrophorus orbicollis* and *N. defodiens*, on the other hand, appear to confine almost all of their activity to forested areas, whether for feeding or reproduction (Anderson 1982; Wilson *et al.* 1984; Shubeck 1993).

Habitat size also affected success of burying beetles in Connecticut woodlands. In both Cheshire and Watertown, success was higher in large than in small woodlands from the same township. The reasons for the higher success rate in Watertown (in both small and large woodlands) compared to Cheshire are not clear. Cheshire has but one woodland species active in midsummer (*N. orbicollis*) while Watertown, somewhat higher in elevation, has two (*N. orbicollis* and *N. defodiens*). A principal cause of the lower success of burying beetles in small woods was a higher rate of scavenging by vertebrates. Forest fragmentation in the eastern U.S. is often associated with development. In semi-rural areas this may be accompanied by increased numbers of raccoons, skunks and other vertebrate scavengers.

As a group, *Nicrophorus* spp. monopolize a higher proportion of small carrion in closed-canopy compared to open habitats (Lomolino & Creighton 1996, this study in northern Michigan). Forest fragmentation produces more edge habitat which may be lower in quality than forest interior (Yahner 1988). For burying beetles this could result from higher soil temperatures near edges as compared to forest interior (Brothers

& Spingarn 1992) which could make it more difficult for burying beetles to control carcass decomposition. Edge habitat also can provide pathways and access points for vertebrate scavengers. Although the eastern U.S. is currently undergoing reforestation, this reforestation is accompanied by smaller forest fragments with more edge. Human alteration of landscapes in the eastern U.S. is likely to negatively impact field specialists (effects of both reforestation and fragmentation of open areas); the effects on woodland species are less clear-cut. The increase in available woodland habitat may be countered by smaller habitat fragments. This fragmentation will be especially difficult for larger-bodied species which require larger areas to sustain viable populations.

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