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ORIGINAL PAPER

Road size and carrion beetle assemblages in a New York forest

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Abstract In many parts of the world, roads are the most common causes of forest fragmentation. We know roads can affect wildlife, but understand little the extent to which these effects depend on road type and use. We compared the effects of several road types upon a diverse, carrion frequenting beetle assemblage in rural New York State. We found no consistent effects of distance from road on the diversity, abundance or species density of beetles across road types. However, forests near highways and two-lane paved roads were significantly less diverse than were forests near dirt roads. The reduced diversity of beetles near roads was at least in part due to lower species turnover in space near dirt roads than near either type of paved roads. Our data suggest that all roads are not created equal and that comparably sized minimum-use paved roads have a substantially greater affect on fauna than dirt roads. Highways and two-lane paved roads appear to depress biodiversity even among relatively vagile animals like beetles.

Keywords Roads · Carrion · Burying beetles · Fragmentation · Diversity · Turnover

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Forest fragmentation has arguably been one of the most-studied phenomena in conservation. However, most studies of forest fragmentation still focus on a relatively narrow range of topics, such as the effects of fragment size (Cook et al. 2001; Estrada and Coates-Estrada 2002; Rosenzweig 2003; Driscoll and Weir 2005), distance between fragments (Cabeza and Moilanen 2001; Wahlberg et al. 2002), and fractal size and spatial distribution of fragments (Laurence et al. 1997; Elkie and Rempel 2001; Hill et al. 2001; Rosenzweig 2003). Historically, the area around forest fragments has been characterized as a uniformly unusable matrix, the composition of which has been assumed to be less important than the characteristics of the fragment. Only recently has more focus begun to be placed on the conservation value of the matrix surrounding forest fragments, mostly in the context of evaluating corridor efficacy in connecting fragments (e.g., Norris and Stutchbury 2001; see Driscoll 2005 for a direct evaluation of matrix quality). Nonetheless, basic questions regarding the impacts of different types of matrix remain unanswered. Roads provide an ideal context in which to test the effects of matrix on forest habitat because different road types (the matrix) can be considered while holding fragment size and other variables relatively constant. The opportunity that roads provide for the study of matrix effects has been poorly realized. For example, although new roads fragment thousands acres of forest every year in the United States alone (Forman et al. 2003), we do not know to what degree different types of roads detrimentally impact assemblages. If a new road is proposed through a forest, does it matter to animal and plant assemblages if it is paved or not? Does it matter to those same assemblages how wide the road is?

Roads can affect species in at least three ways, by reducing available habitat, by affecting patterns of movement, and by extending edge conditions into forests (e.g.

Andrews 1990; Spellerberg 1998; Trombulak and Frissell 2000; Forman et al. 2003; Lassau and Hochuli 2003). Road construction clears and often paves over forest, thereby directly removing habitat from surrounding forests (Laurence 1990; Forman et al. 2003). Roads also fragment forests in the most literal sense, by preventing or at least reducing the movement of species from one forest patch to another. Movement can be prevented because of changes in species interactions near roads, because animals avoid roads, due to negative changes in habitat quality via edge effects and automotive exhaust or because of heavy mortality associated with road traffic. (e.g. Andrews 1990; Laurence 1990; Cadenasso and Pickett 2001; Keller et al. 2004). Finally, roads, like all kinds of clearances create edges which alter microclimatic conditions in such a way as to further reduce available habitat.

Intuitively, it seems obvious that roads of different sizes could have different effects on species. Larger roads with greater width, paving, less permeable surfaces, and higher traffic volume can be expected to have greater edge effects that penetrate deeper into the fragment than do smaller roads (Laurence 1990; Forman et al. 2003). Larger roads might also pose more complete barriers to movement than smaller roads, leading to greater isolation of populations within the surrounding forest fragments. Anecdotal evidence suggests that wider roads pose a greater direct barrier to larger animals than do smaller and minimally used roads, in that road kills are more common on larger than smaller roads (Spellerberg 1998). However, whether larger roads also have more general effects on biotic assemblages remains unknown. We know of no studies on the relative magnitude of edge effects along differently sized roads.

Carrion beetles include those that feed on the carrion directly, and others that prey upon the organisms found at carrion. Collectively these beetles can be referred to as carrion beetles, shorthand for the diverse assemblage that depends on carrion (note that this polyphyletic group includes many more families than just the family Silphidae, which are commonly referred to as carrion beetles). The beetles that feed on and at carrion form a well-studied and ecologically unique guild prone to forest fragmentation, with more fragmented areas having fewer species of carrion beetles (Klein 1989; Roslin and Koivumen 2000; Trumbo and Bloch 2000; Gibbs and Stanton 2001; Haffter and Arellano 2002; Andressen 2003). One species of North American carrion-feeding beetles, *Nicrophorus americanus* is endangered at least in part as a consequence of habitat fragmentation (Lomolino and Creighton 1996). One possible explanation for the lower species richness of beetles in more fragmented areas is that more fragmented areas tend to have more and larger roads with greater automobile traffic.

Using the carrion-feeding beetle assemblage as a model system, we sought to address the degree to which roads of different sizes affect species composition at forest edges. Are road-related edge effects consistent across road types? Do larger roads have edge effects that penetrate deeper into the forest? Finally, we also address whether the effect of roads is progressively greater at larger spatial scales (from pitfalls to landscapes). *A priori*, there is no obvious null expectation for the shapes of diversity gradients from roads into forests with respect to road type. We tested for a simple positive and linear relationship between species richness and abundance with distance from road, but also sought other non-linear patterns. We examined the effects of roads and road type both on local diversity of carrion-feeding beetles, on turnover in species composition across space and finally on landscape scale diversity.

Materials and methods

Study organisms

We chose carrion beetle assemblages for study for a variety of reasons. Carrion beetle assemblages are relatively diverse, easily attracted to baits and perform the important ecological function of carrion decomposition. We consider beetles to be part of the carrion beetle assemblage if they are attracted to carrion-baited traps. The carrion beetle assemblage as we define it here thus includes all those species that are attracted to carrion, whether to feed on it directly or to feed on those species that more directly feed on carrion. Carrion beetle assemblages are known to be sensitive to forest edges and forest fragmentation (Klein 1989; Roslin and Koivumen 2000; Gibbs and Stanton 2001; Haffter and Arellano 2002; Andressen 2003), and hence might be expected to be sensitive indicators of the effects of increasing road size.

Sampling

We conducted our study in the second-growth forests in and around the Black Rock Forest, in Orange County, New York. This area of the Hudson Highlands, located less than two miles from the Hudson River, contains many relatively large sections of forests (10s to 100s of acres) that are currently unfragmented except for that fragmentation due to roads.

Study sites were selected to be similar based on degree and time since fragmentation, so that differences among transects were due primarily to road type. There was no correlation between road type and time since fragmentation in that all sites were second-growth forests between 30 and 50 years of age. All of the study forests had been originally

cleared by 1900 for agricultural purposes and subsequently abandoned to allow for natural succession without human intervention. All had a mixed oak-hickory deciduous canopy with beeches, maples, and hemlocks among the less dominant trees. Canopies were between 10 and 15 m height with sparse understory vegetation dominated by mountain laurel, low-bush blueberry, and other co-occurring annuals. No attempt was made to study primary, uncut forests as such forests are exceedingly rare in the Hudson Highlands and now represent only a tiny part of New England forests overall due to the extensive historic human habitation and forestry across the area (e.g. Foster 1992).

Transects were established perpendicular to the roadside along five distinct roads in each of three road types: one-lane unpaved and little-used dirt road, two-lane paved but minimal use rural road, and four-lane divided highway (Fig. 1). All transects were separated from each other by at least 500 m and as such were treated as true replicates. Each of the transects consisted of pitfall traps located at 0, 6, 12, 24, 48, 84, and 120 m. from the road verge. The traps were concentrated near the edge in case edge effects were restricted to a short distance from the road and were spaced to approximate a doubling of distance from the road between each trap. No traps were placed in the road verge itself. Trap placement and collection was randomized across transects to control for phenological effects. Traps were placed and collected from the 10–18th of July, 2000.

The seven pitfall traps located along each transect were constructed of 2 L soda bottles, the tops of which were cut off and inverted to form funnels within the base of the bottle such that the bottom of the funnel was a minimum of 5 cm from the trap bottom. Traps were buried to the rim and allowed to settle for 48 h prior to use. Traps were baited with 25 g chicken liver that had been left to putrify one day prior to placement and the top of the funnel was covered with a piece of 1 cm^2 wire mesh. The mesh was weighted with rocks on the corners to keep out vertebrate scavengers, however the holes were large enough to let through our largest carrion feeding beetle species (*Nicrophorus orbicollis*). Traps were covered with a rain hood and left for four days, after which they were harvested. All insects were collected and preserved directly into 70% ethanol with the exception of four large and easily field identified silphid species (*Nicrophorus orbicollis, N. tomentosus, Necrophila americana* and *Necrodes surinamensis*). Smaller specimens were later identified to at least family and morphospecies.

Analyses

We compared several measures of diversity among treatments, trap level species density (species per trap), meta-sample species richness (rarefacted), landscape level richness (estimated based on all traps) and among pitfall and among meta-sample turnover.

Species density—We consider species density, as discussed herein, to be the number of species per some unit area or number of samples. At the trap scale, species

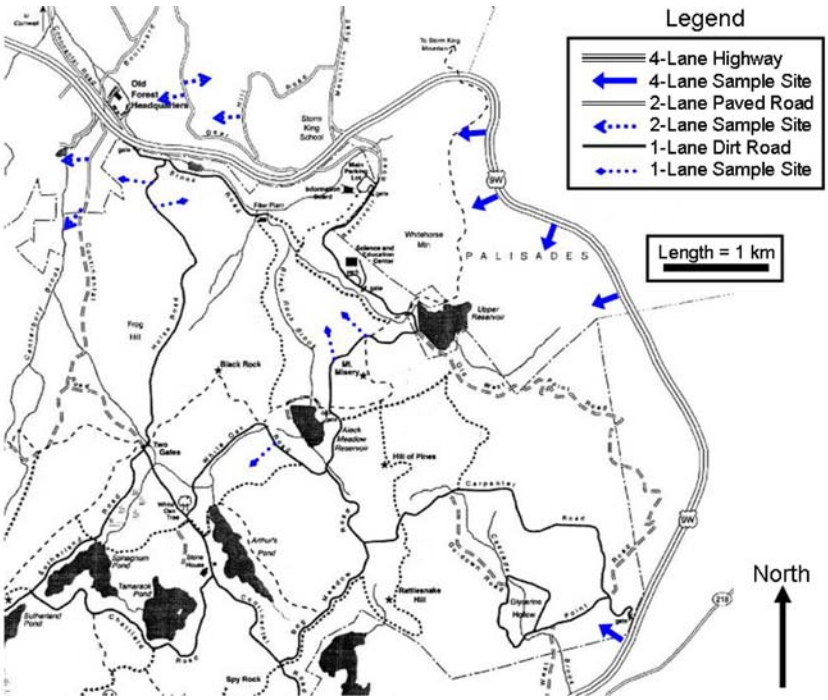

Fig. 1 Map illustrating the sample locations within and around the Black Rock Forest in Orange County, New York. Map is modified from an earlier map by F. Schuster and T. Murray

density was the only measure of species diversity that could be used. Because some traps had few or even no beetles, we could not rarefact (see below) at the trap scale. In addition to the comparisons of species density at the trap level, we also compared abundance among traps.

Rarefaction—Because species density is potentially biased both by differences in abundance among treatments and differences in abundance distributions (Gotelli and Colwell 2001), we employed species richness as a measure of diversity at larger scales (meta-samples and landscapes). Species richness is the expected number of species for a given number of randomly sampled individuals (*sensu* Gotelli and Colwell 2001). Species richness was calculated for each road type by edge distance class by drawing a predetermined number of individuals randomly from the relevant samples. Each set of five replicate traps for a given distance by road type combination was considered a meta-sample (e.g. the five traps for which distance from road = 6 m and road type = dirt were combined for 1 sample). The meta-sample with the fewest individuals had 28 individuals, so we randomly subsampled 28 individuals from each sample one thousand times and calculated the mean of those one draws (Gotelli and Entsminger 2005). We then used that mean as our estimate of richness for each meta-sample in further analyses of species richness.

Landscape-scale richness—In addition to the meta-sample comparisons of the effects of both distance from edge and road type on richness, we also estimated richness at a larger landscape scale to make comparisons of the total number of species potentially found at each distance from the road and near each road type. For these analyses, we estimated the Chao1 overall richness using the program EstimateS (Colwell 2001).

Species density and abundance per trap were compared among treatments using an ANOVA with distance from road, road type and the interaction term as factors. Similarly, the species richness per meta-sample was compared among road types and distances using a multi-factorial regression with distance from road, road type and the interaction term as factors. Landscape-scale richness was considered graphically.

In addition to comparing richness, diversity and abundance among samples, transects and meta-samples, we also compared the similarity of meta-samples and transects. We compared similarity among transects by road type to test whether the similarity among transects differed by road type. Within each road type, we also compared the similarity between transects at each distance from the road, to test whether similarity between transects varied consistently with distance from road.

At different scales, measures of similarity capture different aspects of species turnover across space (broadly defined). At large scales, measures of similarity capture turnover of species across biogeographic, altitudinal or other gradients. At smaller scales such as in this study, measures of similarity capture a mix of heterogeneity among samples and actual turnover in space. Throughout the rest of paper we refer to similarity as a measure of ''turnover'' though we acknowledge that we are unable to distinguish turnover per se from patchiness.

A variety of indices of similarity have been used to measure the similarity or dissimilarity of pairs of sites. Although these indices vary somewhat in their origin, they appear to be very similar in terms of both their biases and successes (e.g. Lennon et al. 2001). We used four indices of similarity, Jaccard, Sorenson Incidence, Sorenson Abundance, and Morisita-Horn, but because qualitative conclusions were identical for the four measures, we present only Sorenson Abundance, which is abundance rather than incidence based, here (Magurran 2004).

Although the similarity of pairs of sites within different treatments is often compared, it is seldom compared statistically, in part because all measures of similarity among pairs of sites are inherently non-independent. For example, a comparison of the species composition between sites A and B involves many of the same species as a comparison of the species composition between sites A and C. It is possible, however, to compare similarity values (for comparisons within a treatment type) among treatments using randomization-based analyses, which do not assume data are independent (e.g. Manly 1997). Using the program Ecosim (Gotelli and Entsminger 2005), for each comparison of similarity values, we randomized similarity values 1000 times with respect to treatment (e.g. highway vs. dirt road) and then compared the mean and variance of observed similarity indices for each treatment to the distribution of the mean and variance of simulated values to determine statistically dissimilar samples.

The relative rarity of many of the species collected precluded analysis of the effects of the treatments on particular species. However, we could compare the responses of different major taxa to the treatments. We focus on the effects of road size on the species density and abundance of the beetle families collected.

Results

In total, we collected 1,569 beetles of 72 species. Most of the beetles collected were from taxa known to be carrion-feeders (Silphidae, Trogidae) or predators on fly eggs or maggots (e.g. Staphylinidae). Like other studies of carrion (e.g. Sikes 1994) the assemblages also included beetles from families such as Curculionidae whose role in the carrion beetle assemblage is unclear. Nonetheless, because species of these taxa are consistently attracted to carrion we

think it important to include them in analyses despite our lack of knowledge of their biology.

At the trap level, patterns in species density (the number of species per trap) and abundance varied with road type (Abundance $P < 0.001$; Species density $P = 0.002$), but not with distance from road or the interaction term (Overall ANOVA models-Species density $R^2 = 0.22$, df = 78, $P = 0.001$; Abundance $R^2 = 0.191$, df = 78, $P < 0.001$). In pairwise comparisons, traps in transects near highways had a lower species density than those near two-lane paved roads ($P = 0.004$) and near dirt roads ($P < 0.001$), but the two paved road types did not differ from one another ($P = 0.32$). Traps in transects near two-lane paved roads had higher abundance than did transects near dirt roads ($P < 0.001$) or highways ($P < 0.001$). Pairwise comparisons of abundance between dirt roads and highways were not significant ($P = 0.1$). Species density and abundance were not correlated with distance from road (Abundance $P = 0.63$, Species density $P = 0.66$), nor with the interaction between distance from road and road type (Abundance $P = 0.75$, Species density $P = 0.27$). Species density and abundance were highly correlated with each other ($R^2 = 0.756$, $P < 0.001$).

Similar to abundance and species density, species richness (the number of species collected, once the number of individuals sampled was standardized) of meta-samples varied with road type but not with distance from road or the interaction term (Overall model $R^2 = 0.51$, df = 18, $P < 0.001$; Figs. 2, 3). In Bonferroni pairwise comparisons, highway transects had greater species richness than dirt road transects (p = 0.01), but transects near one-lane paved roads and dirt roads did not differ, nor did one-lane paved roads and highways ($P > 0.1$, Overall road type $P = 0.002$; Fig. 2a). Species richness was not correlated with distance from road ($P = 0.62$), nor with the interaction between distance from road and road type ($P = 0.27$, Fig. 3). When all traps for each road type were considered together, both the estimated species richness (Fig. 2b) and species accumulation curves (Fig. 3) indicated that total richness on transects near dirt roads was nearly five times as high as near four-lane highways, with one-lane paved roads being half that of the one-lane dirt roads.

Similarity in species composition among transects differed between road types. Species composition varied more (in that the average similarity values were lower) between transects in the dirt road sites than in the two-lane paved and highway sites (Table 1) Similarity between transects did not vary consistently with distance from road for two-lane paved roads or highways (p for highway and two-lane paved road >0.06 for both road types). However, between transects near dirt roads, sites near the road were more different from one another than sites further away from the road ($P = 0.034$, $R = 0.23$).

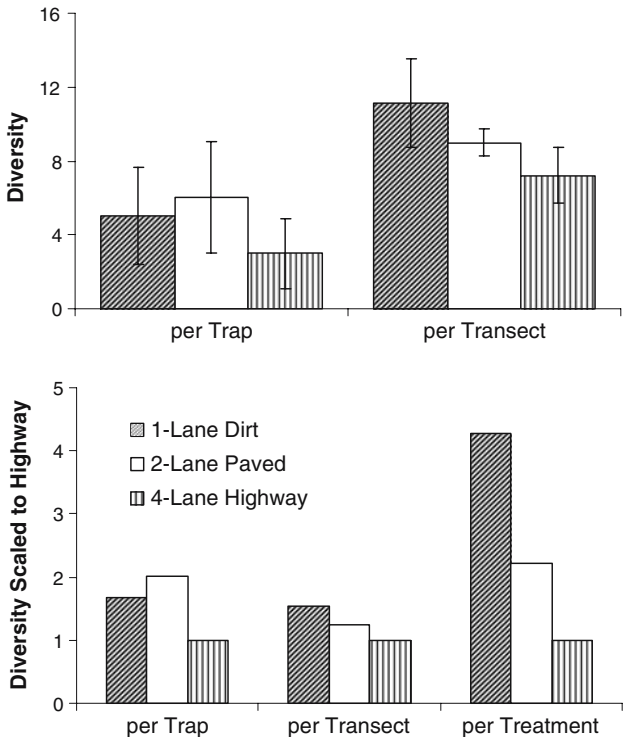

Fig. 2 Diversity by road type at different spatial grains, where diversity is measured in absolute terms (**a**) and relative to diversity found near highways (**b**). For per trap analyses, diversity is measured as species density, the number of species per trap. For transect level analyses, twenty-eight individuals were randomly chosen from each road type by distance from road grouping (e.g. dirt road, 6 m) 1000 times to estimate the species richness were 28 individuals collected. For treatment level analyses, diversity is the Chao1 estimated number of species per treatment type and includes all transects. Legend in (**b**) applies to both (**a**) and (**b**). In (**b**), diversity scaled to highway is the diversity at each scale relative to the diversity found in the highway, such that, if diversity is twice as high along the one-lane dirt road as along the highway, the scaled diversity of the one-lane dirt road is 2. Error bars show standard error in (**a**)

Because the strongest signal of the effects of roads on carrion beetle assemblages appeared to be due to the effects of road size (see first paragraph), we chose to focus in more detail on the effects of road size on carrion beetles, by examining the response of familial composition and of particular beetle families to road size. The relative diversity (measured as species density) and abundance of different beetle taxa differed with road size. The relative species density of most beetle taxa decreased with increasing road size and activity (dirt > 2-lane paved > 4-lane highway). The Staphylinidae was the only family better represented (in terms of proportion of total diversity) near highways than elsewhere. Four families, the Silphidae, Trogidae, Carabidae and Tenebrionidae were entirely absent from transects near highways, despite being present along the other two road types.

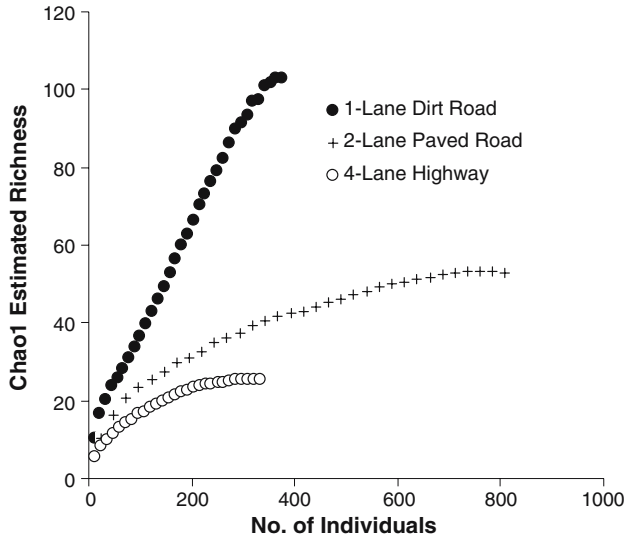

Fig. 3 Chao1 estimates of carrion-feeding beetle species richness near each road type. X-axis is the number of cumulative individuals sampled. Each curve represents 500 randomizations, using the program EstimateS (Colwell 2001)

Table 1. Similarity among transects by road type. *P* overall <0.001. Averages are for all possible comparisons within road type. A higher value indicates greater similarity between sites. N for each road type and index = 10 comparisons

Road type	Sorenson index (±SE)
1-Lane Dirt	0.68 (0.004)
2-Lane Paved	0.80 (0.002)
4-Lane Highway	0.78 (0.002)

Discussion

The effects of different road types on fauna have not been well investigated. We found that carrion beetle species richness was lower near highways and two-lane paved roads relative to that near dirt roads. Differences in diversity between beetle assemblages near roads of different types were relatively greater at larger spatial grains. Overall, estimated richness of carrion beetles near highways was one-fifth that near dirt roads, such that 80% of those species that could be found near dirt roads are lost near highways (Figs. 3, 4). Because species accumulation curves leveled off near the highways but not the smaller roads, we believe that additional sampling would have accentuated the pattern observed. We know of no studies that have compared animal assemblages, or the assemblages of any organism for that matter near roads of different types. However, a number of studies have now compared the effects of different matrix types around forest fragments. Gascon et al. (1999), for example, found that the condition of the matrix had strong effects on the organisms surviving within forest fragments. When the matrix habitat was highly disturbed, many fewer species were able to survive within forest fragments. Our results extend the results of Gascon et al. (1999) and other similar work on matrices around forest fragments to the matrix of roads; a type of matrix that, while infrequently considered, is perhaps one of the most abundant globally.

The higher species richness of beetles along dirt roads relative to larger paved roads was not due to higher abundance and species density at individual baited traps, but rather at least in part to great turnover between traps and transects. Individual traps were relatively similar in the number of species captured across road types. However, when entire transects were compared, the reduction of species abundance and density near highways relative to that near dirt roads was dramatic. In other words, the beta but not alpha diversity of beetles was greatest near dirt roads relative to that near paved roads. As a result, the effect of larger roads is progressively greater as the spatial grain increases and greatest at the scale of the entire landscape (based on species richness estimators).

Several mechanisms may have led to the lower diversity near paved roads relative to dirt roads. Compacted soils in more urban areas prevent carrion beetles from burying carrion (Gibbs and Stanton 2001; Haffter and Arellano 2002; Andressen 2003). Soils might also be more compacted near heavier used roads relative to low use roads. Carrion availability and competition with vertebrates for carrion may also vary systematically with road type. Large roads may have more roadkill, but perhaps also more competition for that roadkill with scavenging vertebrates such as raccoons, crows, and vultures (e.g. Trumbo and Bloch 2000). Alternatively, carrion feeding beetles may respond directly to the altered environmental conditions near large roads by behaviorally avoiding them. Carrion beetles tend to frequent more moist microhabitats with significant litter and vegetational cover (Gibbs and Stanton

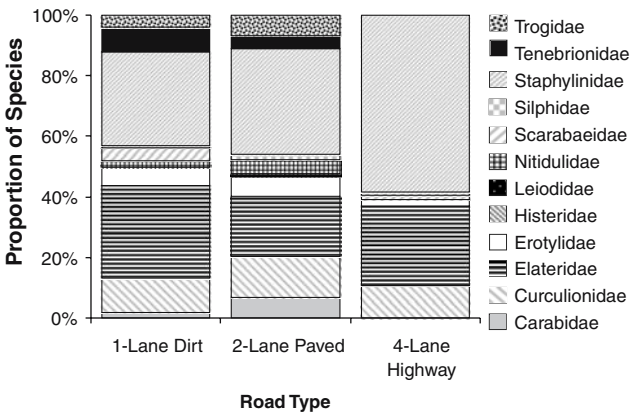

Fig. 4 Proportion of species along different roads from each of eight beetle families collected

2001; Haffter and Arellano 2002) and abiotic shifts due to these edge effects could be expected to concomitantly depress carrion beetle biodiversity near larger roads.

Not only was species diversity reduced near highways, but so was the number of families present. Four families, Carabidae, Scarabaeidae, Tenebrionidae and Trogidae were entirely absent near highways yet present near the other road types. Notably, these are families, with the exception of the Trogidae, in which species are large-bodied. At least for the Carabidae and Scarabaeidae these families also have diets biased towards predation on carrion feeding organisms rather than carrion-feeding per se. In contrast to the trends shown for these families, one family, the Staphylinidae, increased in both abundance and relative diversity near highways. The staphylinid species collected are, like carabids recognized as being primarily predators. Anecdotally, we thus see evidence of not only an overall reduction in diversity in carrion beetles near highways, but also a shift in those predators present, with staphylinids taking the place of a phylogenetically more diverse assemblage of predators found in less disturbed sites. Similar to the results of studies of forest fragments (Trumbo and Bloch 2000; Gibbs and Stanton 2001; Wolf and Gibbs 2005) we also see a reduction in the numbers of species and individuals of species of the genus *Nicrophorus* along highways. Because species of *Nicrophorus* bury carrion, loss of these species may have particularly strong effects on the carrion assemblage more broadly.

A number of authors have suggested that reduced species diversity near road edges could lead to changes in ecological processes (e.g. Haskell 2000; Wolf and Gibbs 2005). It could be argued that the loss of diversity in carrion feeding beetles near highways could alter carrion decomposition rates. The effects of diversity loss on ecological processes are contingent, however, on the scales at which species diversity is reduced. In our study system, the difference among road types is almost entirely due to differential turnover between transects near different road types. Species density and abundance at individual baited traps are actually similar between road types. Consequently, to the extent that the decomposition rate and fate of carcasses in forests are tied to the number of species or abundance of individuals on those carcasses (e.g. Wolf and Gibbs 2005), decomposition rate might not vary dramatically with road type. Decomposition rate, could, however, still decrease as a function of changes in species identity at carcasses between different road types.

Richness, species density and abundance did not consistently increase with distance from the road, in contrast to the results of Haskell (2000), who studied the effects of roads in southern Appalachia on soil fauna. Several authors (e.g. Murcia 1995) have pointed out that diversity and abundance can vary in a complex fashion with respect to distance from edge. A linear relationship between distance from edge and diversity is perhaps too simple an expectation. Samways et al. (1997) have even shown that some taxa have increased diversity near roads. Unfortunately, when considering relationships more complex than a simple decline in diversity and abundance with distance from edge, it is easy for explanations of the pattern to become *ad hoc*. In Fig. 5 for example, richness apparently peaks at 24 m from the road's edge along both one-lane dirt roads and four-lane highways. Such a peak could be due to the overlap of forest interior and disturbance specialist species (e.g. Murcia 1995), but other explanations are also possible.

Our preferred explanation for the lack of a linear relationship between distance from edge and abundance, species density and richness is that we did not sample deep enough into the forest to get much beyond the edge effects. Sites deeper in the forest than those we sampled might have higher (or lower) species richness than we measured at 120 m. In fact, the low richness along the entire length of our transects near four-lane highways seems to suggest that edge effects can permeate 120 m in New York forests. Given that in many suburban areas roadless forest patches are often no wider than a few dozen meters such deeply penetrating edge effects are a troubling, but real, possibility.

Overall, our results suggest that high use paved roads can have serious effects on the richness of carrion frequenting beetle assemblages, and that these effects are greater than those seen for smaller paved roads. The absolute numbers of species of carrion beetles we observed to be missing near highways is surely an underestimate of broader losses, both because not all species of beetles were sampled and because many other taxa depend on carrion beetles (e.g. Gibbs and Stanton 2001) and may thus have gone locally extinct with

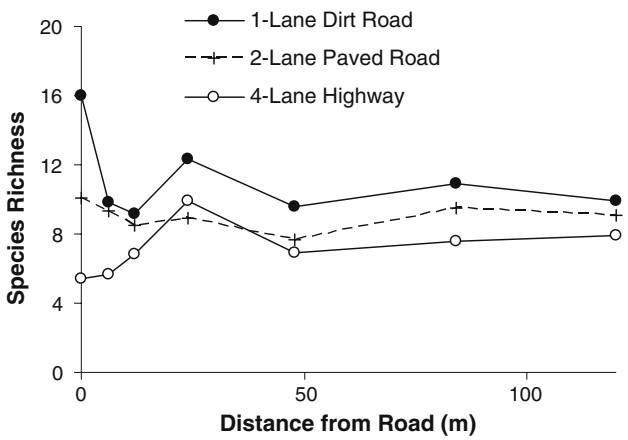

Fig. 5 Species richness for meta-samples for each distance from the road by road type. Twenty-eight individuals were randomly chosen from each distance for each road type meta-sample (e.g. dirt road, 6 m from road) 1000 times to estimate rarefacted species richness for that sample

the loss of the beetles (e.g. Koh et al. 2004; Dunn 2005). Key to understanding how to mitigate the effects of highways on invertebrate assemblages will be a clearer understanding of the mechanism underlying the effects of paved roads on carrion beetle assemblages. Meanwhile, our results suggest that high use roads may not be reconcilable with conservation of species either directly alongside such roads or even in the neighboring areas, which may be greater than 100 m on either side.

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References

Andrews A (1990) Fragmentation of habitat by roads and utility corridors: a review. Aust Zool 26:130–141

Andressen E (2003) Effect of forest fragmentation on dung beetle assemblages and functional consequences for plant regeneration. Ecography 26:87–97

Cabeza M, Moilanen A (2001) Design of reserve networks and the persistence of biodiversity. Trend Ecol Conserv 16:242–248

Cadenasso ML, Pickett STA (2001) Effect of forest structure on the flux of species into forest interiors. Conserv Biol 15:91–97

Colwell RK (2001) *EstimateS: statistical estimation of species richness and shared species from samples* (Software and User's Guide), Version 7. http://viceroy.eeb.uconn.edu/estimates

Cook WM, Holt RD, Yao J (2001) Spatial variability in oviposition damage by periodical cicadas in a fragmented landscape. Oecologia 127:51–61

Driscoll DA (2005) Is the matrix a sea? Habitat specificity in a naturally fragmented landscape. Ecol Entomol 30:8–16

Driscoll DA, Weir T (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. Conserv Biol 19:182–194

Dunn RR (2005) Insect extinctions, the neglected majority. Conserv Biol 19:1030–1036

Elkie PC, Rempel RS (2001) Detecting scales of pattern in boreal forest landscapes. Forest Ecol Manage 147:253–261

Estrada A, Coates-Estrada R (2002) Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodivers and Conserv 11:1903–1918

Foster DR (1992) Land-use history (1730–1990) and vegetation dynamics in central New England, U.S.A. J Ecol 80:753–772

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) Road ecology: science and solutions. Island Press, USA

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurence WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Conserv 91:223–229

Gibbs J, Stanton E (2001) Habitat fragmentation and arthropod assemblage change: carrion beetles, phoretic mites and flies. Ecol Appl 11:79–85

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gotelli NJ, Entsminger GL (2005) Ecosim: null models software for ecology, Version 6.0. Acquired Intelligence Inc, & Kesey-Bear. http://homepages.together.net/gentsmin/ecosim.htm

Haffter G, Arellano L (2002) Response of dung beetle diversity to human-induced changes in a tropical landscape. Biotropica 34:144–154

Haskell DG (2000) Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian mountains. Conserv Biol 14:57–63

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss DB, Huntley B (2001) Impacts of landscape structure on butterfly range expansion. Ecol Lett 4:313–321

Keller I, Nentwig W, Largiader CR (2004) Recent habitat fragmentation due to roads can lead to significant genetic differentiation in an abundant flightless ground beetle. Mol Ecol 13:2983–2994

Klein B (1989) Effects of forest fragmentation on dung and carrion beetle assemblages in central Amazonia. Ecology 70:1715–1725

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species co-extinctions and the biodiversity crisis. Science 305:1632–1634

Lassau S, Hochuli DF (2003) Effects of Roads on Ant Assemblages in the Sydney Region: Are patterns scale-dependent? Rec South Austr Mus 7:283–290

Laurence WF (1990) Comparative responses of five arboreal marsupials to tropical forest fragmentation. J Mammal 71:641–653

Laurence WF, Laurence SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE (1997) Biomass Collapse in Amazonian Forest Fragments. Science 278:1117–1118

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70:966–979

Lomolino MV, Creighton JC (1996) Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. Biol Conserv 77:235–241

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford, UK

Manly BFJ (1997) Randomization, Bootstrap, and Monte Carlo methods in Biology. Chapman and Hall, London, UK

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trend Ecol Evol 10:58–62

Norris DR, Stutchbury BJM (2001) Extraterritorial movements of a forest songbird in a fragmented landscape. Conserv Biol 15:729–736

Rosenzweig ML (2003) Reconciliation ecology and the future of species diversity. Oryx 37:194–205

Roslin T, Koivumen A (2000) Distribution and abundance of dung beetles in fragmented landscapes. Oecologia 127:69–77

Samways MJ, Osborn R, Carliel F (1997) Effect of a highway on ant (Hymenoptera: Formicidae) species composition and abundance, with a recommendation for roadside verge width. Biodivers Conserv 6:903–913

Sikes DS (1994) Influences of ungulate carcasses on coleopteran communities in Yellowstone National Park, USA. MS Thesis, Montana State University

Spellerberg IF (1998) Ecological effect of roads and traffic: a literature review. Global Ecol Biogeogr Lett 7:317–333

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic assemblages. Conserv Biol 14:18–30

Trumbo ST, Bloch PL (2000) Habitat Fragmentation and Burying Beetle Abundance and Success. J Insect Conserv 4:242–252

Wahlberg N, Klemetti T, Selonen V, Hanski I (2002) Metapopulation structure and movements in five species of checkerspot butterflies. Oecologia 130:33–43

Wolf JM, Gibbs JP (2005) Silphids in urban forests: diversity and function. Urban Ecosyst 7:371–384

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