

The impact of a utility corridor on terrestrial gastropod biodiversity

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Abstract Utility corridors are often thought to be disruptive to biodiversity because they cause habitat fragmentation that may lead to increases in predation, parasitism, disease transmittance and vagrant species while decreasing migration rates, gene flow and genetic diversity for interior species. Species with poor dispersal abilities, sedentary lifestyles, and specialized habitats have been thought to be potentially the most vulnerable to these effects. Terrestrial gastropods thus serve as a valuable system in which to investigate these impacts because they are among the poorest active dispersers in the animal kingdom. To document the impact of corridor formation on land snail biodiversity, a 75-year old powerline right-of-way in the eastern Upper Peninsula of Michigan was chosen for analysis. While terrestrial gastropod richness and abundance was significantly reduced for corridor as compared to adjacent control subsamples, with a 2/3 turnover in species composition, the corridor fauna is similar to nearby native grassland sites in terms of species composition, abundance distribution, and numbers and abundance of species of conservation concern. The fauna of control subsamples immediately adjacent to the corridor remained similar to other undisturbed sites in the region, with multiple species of conservation concern persisting at distances of only 30 m from the corridor. Thus, the net impact of corridor generation has been arguably positive: while the surrounding forest fauna has not been degraded, within the corridor the reduction of forest species has been compensated for by establishment of even rarer grassland species.

Keywords Land snail · Right-of-way · Landscape · Community ecology · Community structure · Soil architecture

Introduction

Utility corridors have often been thought to be disruptive to biodiversity (Forman 1986; Andrews 1990) because they fragment habitats, leading to increased predation, parasitism and disease transmittance rates (Simberloff and Cox 1987; Yahner et al. 1989; Bennett

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1991), decreased migration abilities and lowering of gene flow and within-population genetic diversity (Fahig and Mirriam 1985; Goosem and Marsh 1997; Gerlach and Mustov 2000), and expansion of vagrant species at the expense of interior species (Arnold et al. 1987). Species with poor dispersal abilities, sedentary habits, and specialized habitat preferences have been thought to be the most vulnerable to these effects (Shaffer and Samson 1985; Andrews 1990).

Terrestrial gastropods would therefore appear particularly sensitive to utility corridor formation. The North American fauna, particularly at mid-to-high latitudes, is dominated by species with shells <5 mm in maximum dimension that represent approximately 50–80% of regional species richness and 80–95% of individuals (Nekola 2005). Such species have very poor active dispersal abilities: individuals move perhaps only 1–10 m over a lifetime (Schilthuizen and Lombaerts 1994; Hausdorf and Hennig 2003). Even active movement of larger species (maximum shell dimension >20 mm) has been effectively inhibited by barriers of no more than 3–8 m (Baur 1988; Baur and Baur 1990; Schilthuizen and Lombaerts 1994). Also, terrestrial gastropods exhibit a high degree of habitat specialization, with order-of-magnitude changes in richness and abundance over as little as 1 m (Nekola and Smith 1999).

Even though utility corridors may have serious negative impacts on terrestrial gastropod biodiversity and community structure, no prior research has specifically addressed this issue. This study therefore investigates changes in community structure and composition between paired corridor and matrix habitats along a 75-year old utility corridor passing through the Hiawatha National Forest in the eastern Upper Peninsula of Michigan. Comparisons were also made with other undisturbed habitats in the surrounding landscape.

Materials and methods

Study system

ESE-6904/6905 is a 42 km powerline operated by the American Transmission Company in Chippewa and Mackinac counties in the eastern Upper Peninsula of Michigan. The line connects St. Ignace in the south to the Pine River Substation near Rudyard in the north. The corridor was initially constructed in the 1930s and is 30–60 m in width. The line currently runs at 69,000 volts with approximately 395 double-circuit wood pole structures. In Mackinac County a considerable proportion of the corridor passes through the St. Ignace Ranger District of the Hiawatha National Forest, where it has been maintained by mowing and mechanical woody plant removal.

In total, 58 land snail species have been previously identified from the eastern Upper Peninsula (Hubricht 1985; Nekola 2004). Of these, 13 are listed as of conservation concern by the Michigan Natural Features Inventory (2011): *Catinella exile*—Threatened; *Euconulus alderi*—Threatened; *Planogyra asteriscus*—Special Concern; *Pupilla muscorum*—Special Concern; *Vallonia gracilicosta*—Endangered; *Vertigo bollesiana*—Threatened; *Vertigo cristata*—Special Concern; *Vertigo elatior*—Special Concern; *Vertigo hubrichti*—Endangered; *Vertigo morsei*—Endangered; *Vertigo nylanderi*—Endangered; *Vertigo paradoxa*—Special Concern and *Vertigo pygmaea*—Special Concern. Six species (*Cochlicopa lubrica*, *Oxychilus draparnaudi*, *Pupilla muscorum*, *Vallonia costata*, *Vallonia pulchella*, *Vertigo pygmaea*) appear to be Eurasian exotics based on their preference for anthropogenic habitats, known North American history and/or population genetics (Pilsbry 1948; Nekola and Coles 2010).

Sampling design

Eighteen sample sites were identified along the ESE-6904/6905 route as it passes through the Hiawatha National Forest in eastern Mackinac County, Michigan. Sample sites were spread across the entire corridor route, were separated by at least 0.5 km, and represented all natural habitats crossed by the corridor. These included marl ponds, fens, sedge meadows, upland and lowland Northern White Cedar stands, sandy pine forest, mixed deciduous forest, and rocky slopes. Sample sites were located in conjunction with pole numbers 505, 520, 567, 600, 605, 623, 652, 680, 696, 705, 717, 726, 728, 755, 772, 790, 811 and 813 (Fig. 1). At most sites three subsamples were collected: one within the existing corridor, and two controls located within intact vegetation 30 m to both the west and east of the corridor. No private lands were surveyed. For this reason only the corridor and west margin subsamples were collected at Pole 811 and only the corridor subsample was collected at Pole 600. Also, because of abundance of Poison Ivy and lack of leaf litter accumulation within the corridor, only the western margin at Pole 813 was sampled.

Comparisons were also made with 32 additional sites in the surrounding landscape, including 11 wooded bedrock outcrops, 5 upland forests, 7 lowland forests, 8 lowland grasslands and a single upland grassland. These capture the full compositional range of regional land snail assemblages (Nekola 2003, 2004, 2005; Fig. 1).

Field methods

The land snail assemblage of each 100 m² subsample was documented from September 25–30, 2009 through hand collection of larger shells and litter sampling for smaller taxa following protocols of Cameron and Pokryszko (2005) and Oggier et al. (1998).

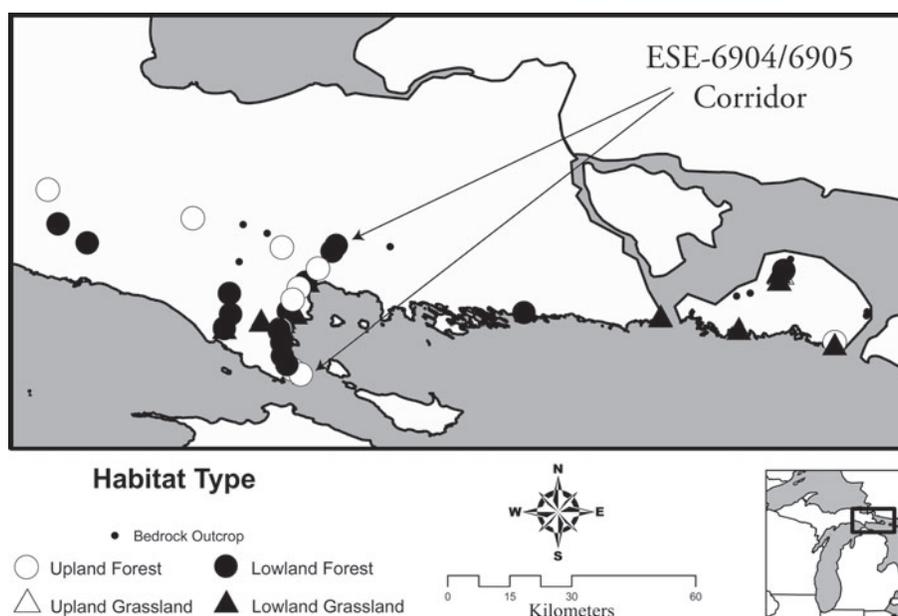


Fig. 1 Map of the eastern Upper Peninsula of Michigan showing location of the 18 sample sites analyzed along the ESE-6904/6905 corridor along with locations of the 32 additional comparison sites

Approximately 30 min were spent collecting each subsample. Soil litter collections followed protocols of Nekola and Coles (2010), and emphasized microsites known to support high micro-snail densities (e.g., Emberton et al. 1996). Approximately 200 ml of litter were collected per subsample. This generally captured ten times as many individuals as species, which is advocated by Cameron and Pokryszko (2005) for accurate land snail community documentation. The latitude-longitude position of each pole location was determined using a Garmin 12XL hand-held GPS unit.

Sampling of comparison sites elsewhere in the eastern Upper Peninsula was conducted from July 1997–October 2009 in a similar fashion (see Nekola 2003, 2004, 2005) although at an order of magnitude larger spatial sampling grain. Any systematic bias would thus result in underestimating the relative richness of ESE-6904/6905 subsamples through random undersampling of the rarest species. However, this will not obscure community composition gradients (Jobe 2007).

Laboratory procedures

As outlined by Nekola and Coles (2010), dried litter samples were passed through a standard sieve series and handpicked against a neutral-brown background. All shells and shell fragments were removed. All shells were assigned to species (or subspecies) using the author's reference collection, with the total numbers of shells per species per site being recorded. The number of unassignable immature individuals and fragmentary shells was recorded. Nomenclature is based principally on Hubricht (1985) with updates by Turgeon et al. (1998), Nekola (2004) and Nekola and Coles (2010).

Data summary and statistical analysis

Species richness and abundance

For each species, the total number of subsamples in which it was recorded and the total number of encountered individuals was calculated. Using the non-parametric Kruskal–Wallis Rank Sum Test, these values were compared among the west of corridor, corridor, and east of corridor subsamples, and were graphically illustrated using boxplots. To better visualize the upper and lower bounds, boxplots were constructed using a natural-log scale. However, raw values were used for statistical testing. Variation in community structure among the three subsample positions was illustrated by dominance–diversity curves generated from median proportional abundance values calculated within each of the three subsample locations. Median values were used because they are more robust descriptors of central tendency, being less influenced by outliers as compared to mean values. Variation in richness and abundance of three soil architecture preference classes (duff specialist, generalist, turf specialist) among the three subsample positions was also statistically tested using the Kruskal–Wallis Rank Sum Test and illustrated with boxplots. As before, abundance distributions were visualized using natural-log scaled box-plots, but tested using raw data. The soil architecture nomenclature and preferences of Nekola (2003) were used, with 'duff specialists' being species that favor soils with loose organic horizons and 'turf specialists' being those that favor organic horizons that are tightly bound with living plant roots. The only exception was *Striatura exigua*, which is here considered a 'generalist' rather than a 'turf' species (Nekola 2003) based on additional eastern North American data (Nekola 2010). Differences in richness and abundance for species of conservation concern

and alien species among the three subsample positions was also quantified using the Kruskal–Wallis Rank Sum Test.

Community composition

The impact of the corridor on community composition was analyzed through global non-metric multidimensional scaling (NMDS) using DECODA (Minchin 1990). NMDS makes no assumptions regarding the underlying nature of species distributions along compositional gradients, and is thus the most robust form of ordination for detection of ecological patterns (Minchin 1987). All 49 ESE-6904/6905 subsamples in addition to the 32 additional regional comparison sites were included in this analysis. To ordinate sites a matrix of dissimilarity coefficients was calculated based on species abundance data using the Czekanowski index (Faith et al. 1987). Data were untransformed to avoid mathematical artifacts (Nekola et al. 2008). NMDS in one through four dimensions was then performed with 200 iterations, a stress ratio stopping value of 0.9999, and a small stress stopping value of 0.01. Output was scaled in half-change units, so that points in the resulting diagram separated by a distance of 1.0 will correspond, on average, to a 50% turnover in species composition.

Because a given NMDS run may locate a local, rather than the global, stress minimum, solution stability was assessed via 50 NMDS runs using different random initial starting points (Minchin 1987). Solutions in each of the four dimensions were compared using a Procrustes transformation to identify those that were statistically similar. The number of unique solutions and number of individual runs that fell into each was then calculated. The global optimum solution was identified as the smallest stress solution that was achieved in a plurality of starts.

To assess the impact of corridor construction on community composition, a vector was generated using a given control subsample as the origin and the adjacent corridor subsample as the endpoint. Each of these vectors was plotted on the ordination diagram and its length and angle from vertical calculated. This allowed a median vector of compositional change to be determined across the entire dataset. The significance of these changes in ordination space was estimated using the non-parametric paired Wilcoxon Rank Sum Test.

Fisher Exact contingency table tests were used to identify those species that were statistically more abundant within the corridor or control subsamples as compared to a null hypothesis of uniform distribution. Analysis was limited to paired subsamples (i.e. 600C and 813W were eliminated). Species with fewer than ten total occurrences were not analyzed due to the likelihood of Type-II errors. Because this test was repeated for each species, a Bonferroni correction was used to modify the significance threshold. The results of this analysis were then compared to the results of the duff vs. turf soil preference tests of Nekola (2003) by use of a 3×3 contingency table. This table was compared to uniform expectations using a Fishers exact test.

Results

In total, 44 species were observed from the 49 subsamples collected along the ESE-6904/6905 corridor (Table 1). Of these, five (*Gastrocopta pentodon*, *Oxychylus draparnaudi*, *Vertigo bollesiana*, *Vertigo ovata* and *Vertigo pygmaea*) are reported here for the first time from Mackinac county (Hubricht 1985; Nekola 2004), raising the total county fauna to 54 species. Nine of the thirteen species of conservation concern known from the region

Table 1 Number of occupied subsamples and individuals for all encountered terrestrial gastropod species

Species name	Soil architecture preference	Number of subsamples/individuals		
		West of corridor	Powerline corridor	East of corridor
<i>Anguispira alternata</i>	D	2/3	1/1	1/2
<i>Carychium exiguum</i>	T	9/293	12/543	7/292
<i>Carychium exile</i>	D	6/99	3/19	7/88
* <i>Cochlicopa lubrica</i>	D	4/93	3/18	1/1
<i>Columella simplex</i>	D	14/127	10/49	16/167
<i>Deroceras</i> spp.	G	4/5	7/12	6/9
<i>Discus catskillensis</i>	D	9/167	4/5	12/109
<i>Euchemotrema fraternum</i>	D	0/0	1/2	1/1
<i>Euconulus alderi</i>	T	6/26	8/57	5/19
<i>Euconulus fulvus</i>	D	8/31	2/10	9/75
<i>Euconulus polygyratus</i>	D	3/16	2/9	2/4
<i>Gastrocopta pentodon</i>	D	1/1	1/33	0/0
<i>Gastrocopta tappaniana</i>	T	2/25	7/101	3/24
<i>Glyphyalinia indentata</i>	D	1/1	1/1	1/1
<i>Helicodiscus parallelus</i>	G	0/0	1/2	0/0
<i>Helicodiscus shimaki</i>	D	3/11	1/2	9/54
<i>Nesovitrea bimneyana</i>	D	8/102	0/0	9/144
<i>Nesovitrea electrina</i>	T	4/28	10/158	4/43
* <i>Oxychylus draparnaudi</i>	G	0/0	1/3	0/0
<i>Oxyloma retusa</i>	T	1/1	4/6	0/0
<i>Paravitrea multidentata</i>	D	1/8	0/0	0/0
<i>Planogyra asteriscus</i>	G	8/814	2/7	8/603
<i>Punctum minutissimum</i>	D	16/1,653	7/141	16/1,371
<i>Punctum</i> n.sp.	T	6/84	8/410	6/70
* <i>Pupilla muscorum</i>	G	1/9	1/8	0/0
<i>Striatura exigua</i>	G	13/248	9/195	15/351
<i>Striatura ferrea</i>	G	9/176	3/52	12/102
<i>Striatura milium</i>	G	12/332	6/65	14/334
<i>Strobilops labyrinthica</i>	D	15/1,279	14/275	16/993
<i>Succinea ovalis</i>	D	0/0	3/4	0/0
* <i>Vallonia costata</i>	G	2/55	1/5	0/0
* <i>Vallonia pulchella</i>	T	0/0	2/4	0/0
<i>Vertigo bollesiana</i>	D	6/15	0/0	6/14
<i>Vertigo cristata</i>	D	7/33	2/20	5/19
<i>Vertigo elatior</i>	T	5/42	11/118	7/17
<i>Vertigo gouldii</i>	D	2/3	0/0	2/7
<i>Vertigo morsei</i>	T	1/9	4/48	0/0
<i>Vertigo nylanderi</i>	T	2/24	0/0	2/8
<i>Vertigo ovata</i>	T	0/0	3/3	1/1
* <i>Vertigo pygmaea</i>	G	1/4	2/2	0/0
<i>Vitrina limpida</i>	G	2/8	2/7	0/0
<i>Zonitoides arboreus</i>	D	6/14	3/5	5/9

Table 1 continued

Species name	Soil architecture preference	Number of subsamples/individuals		
		West of corridor	Powerline corridor	East of corridor
<i>Zonitoides nitidus</i>	T	1/4	0/0	0/0
<i>Zoogenetes harpa</i>	D	2/4	1/4	1/2
Total terrestrial gastropods		16/5,847	17/2,404	16/4,934

Species underlined are species of conservation concern in Michigan (Michigan Natural Features Inventory 2011). Species preceded by an asterisk are Eurasian aliens. Soil architecture preference is based on Nekola (2003) with minor revisions as per text; *D* Duff specialist, *T* turf specialist, *G* generalist

(*Euconulus alderi*, *Planogyra asteriscus*, *Pupilla muscorum*, *Vertigo bollesiana*, *Vertigo cristata*, *Vertigo elatior*, *Vertigo morsei*, *Vertigo nylander*, and *Vertigo pygmaea*) were observed. In total, 14, 242 individuals were collected, of which 13,185 were identifiable to species. Thirty-one of the subsamples included at least 200 individuals. The 32 eastern Upper Peninsula comparison sites ranged in richness from 3 to 25 species and in abundance from 19 to 1,480, with a total of 12,831 individuals being identified to species.

Impact on species richness and abundance

Based on paired observations, both species richness and abundance were lower within the corridor than in adjacent control subsamples (Fig. 2): median richness fell by approximately 1/4 (from 14 to 10; $P = 0.015$) and abundance by approximately 3/4 (from 400 to 100; $P < 0.00003$). However, dominance-diversity curves demonstrated that median proportional abundance was very similar for up to approximately the 7th most abundant species (Fig. 3), after which median abundance fell off more rapidly for the corridor subsamples.

Comparison of richness and abundance across species with differing soil architecture preferences (Fig. 4) demonstrates that control subsamples were dominated by duff

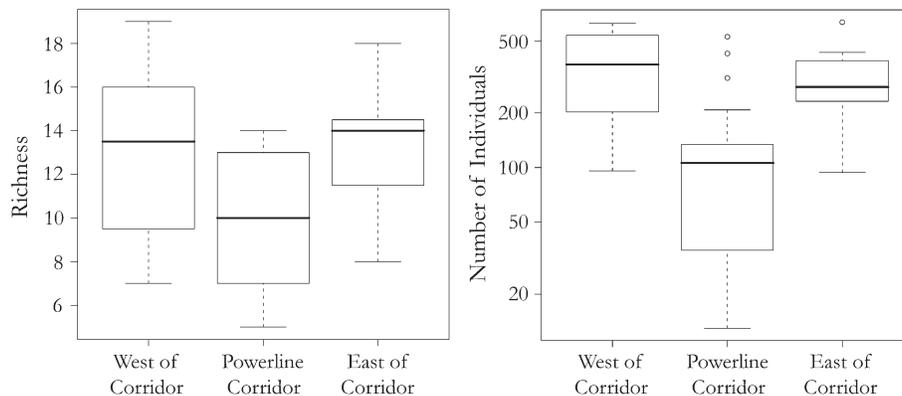


Fig. 2 Boxplots showing variation in terrestrial gastropod richness and abundance among the three subsample positions along the ESE-6904/6905 corridor. Abundance data are presented along a log-scaled axis. The central line represents the median of the sample, the margins of each box represent the interquartile distances, and the fences represent 1.5 times the interquartile distances. Outliers falling outside of the fences are shown with circles

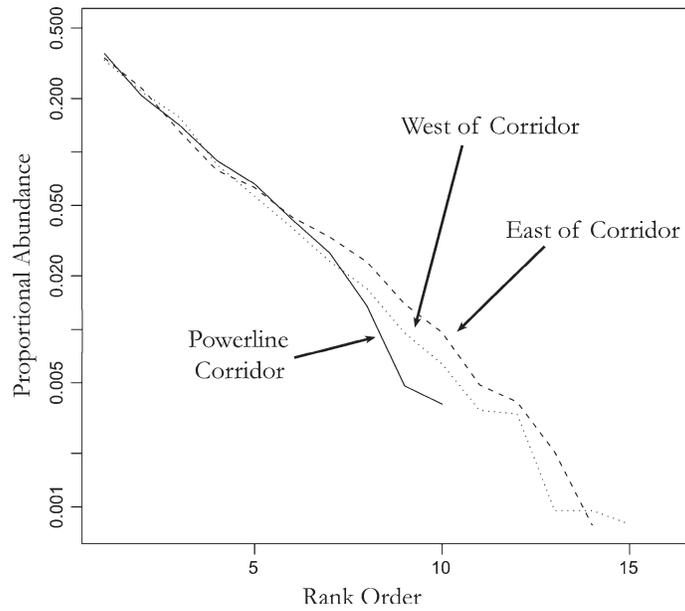


Fig. 3 Dominance-diversity curves demonstrating proportional abundance versus rank order of terrestrial gastropod species for the three sub-sample positions along the ESE-6904/6905 corridor

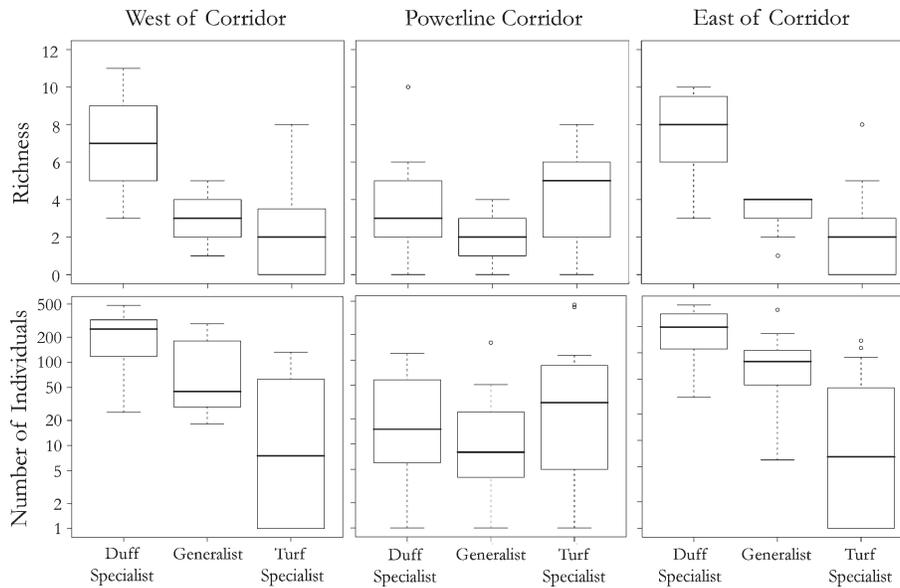


Fig. 4 Boxplots showing variation in duff specialist, generalist, and turf specialist terrestrial gastropod species richness and abundance among the three subsample categories along the ESE-6904/6905 corridor. Abundance data are presented along a log-scaled axis. The *central line* represents the median of the sample, the margins of each *box* represent the interquartile distances, and the *fences* represent 1.5 times the interquartile distances. Outliers falling outside of the *fences* are shown with *circles*

specialists (~57% of taxa and ~80% of individuals), followed by generalists (~27% and ~18%) and turf specialists (~16% and ~2%; Fig. 4). However, corridor subsamples were dominated by turf specialists (~50% and ~63%) followed by duff specialists (~30% and ~23%), and generalists (~20% and ~14%). While these differences were statistically significant for duff and turf specialists ($P = 0.016$ and $P = 0.0020$, respectively, for richness, and $P = 0.0095$ and $P = 0.0037$ for individuals), generalist species did not differ significantly ($P = 0.1054$ for richness and $P = 0.0948$ for individuals).

No significant differences were noted in richness ($P = 0.7842$) or abundance ($P = 0.7350$) of species of conservation concern or in exotic species richness ($P = 0.2095$) or abundance ($P = 0.2124$) among corridor and adjacent control subsamples.

Impact on community composition

NMDS along two dimensions was chosen as the most robust solution, given that all five minimum stress configurations fell into a single group. The 1-, 3-, and 4-dimensional solutions were not considered as they either possessed larger stress values or had no single modal solution. The chosen ordination documents a dramatic alteration of terrestrial gastropod community composition within the corridor (Fig. 5). While control subsample assemblages remain similar to other regional lowland conifer forest, upland forest, and lowland grassland assemblages, corridor faunas tend to be displaced down and/or left in the diagram, being similar to the faunas of native lowland grassland sites (e.g., sedge meadows, fens). Displacement vectors from a given control subsample to its paired corridor subsample ranged from 0.18 to 3.4, or 9% to 170% change in composition. Across all pairs, the median distance was 1.27 (indicating roughly a 2/3 turnover in composition) at -110° from the top of the diagram. This displacement was highly significant ($P < 0.00002$) along both axes.

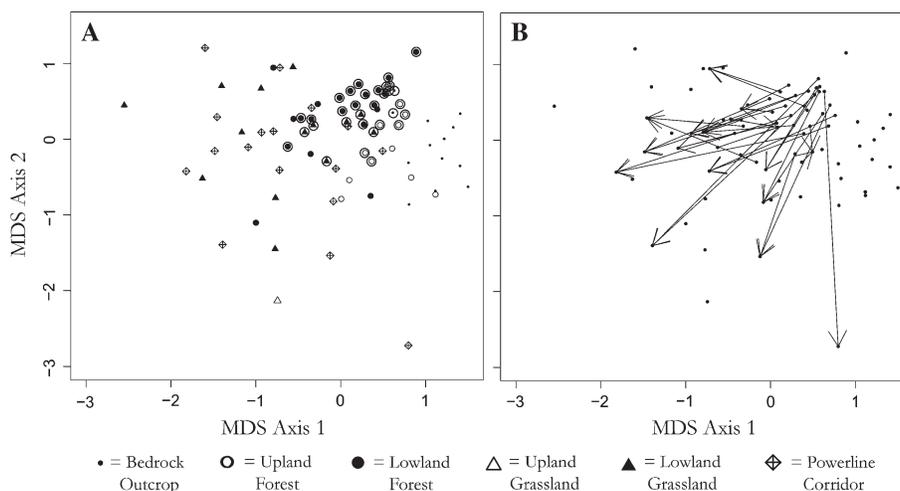


Fig. 5 NMDS ordination of terrestrial gastropod faunas from the 49 ESE-6904/6905 subamples and 32 comparison sites. Axes are scaled in half-change units. **a** Optimum two-dimensional NMDS solution. Powerline corridor subamples are represented by *hatched diamonds*; control subamples are indicated by a *circle* surrounding the appropriate *habitat icon*; *uncircled habitat icons* represent comparison sites. **b** Vectors demonstrating the change in composition between control (origin) and adjacent corridor (endpoint) samples

Following removal of unpaired subsamples, fifteen species were eliminated from further analysis because they were represented by ten or fewer individuals. Fisher exact tests of the remaining 29 species (Table 2) demonstrated that eight either significantly favored (Bonferroni corrected P -threshold = 0.0017) or tended to favor ($0.05 > P > 0.0017$) corridor subsamples, 14 significantly favored the adjacent control subsamples, while the remaining six were generalists ($0.05 < P$). While three species of conservation concern favored control subsamples (*Planogyra asteriscus*, *Vertigo bollesiana*, *Vertigo nylanderi*) an additional three favored corridor subsamples (*Euconulus alderi*, *Vertigo elatior*, *Vertigo morsei*) with two more being generalists (*Pupilla muscorum*, *Vertigo cristata*). Although *Vertigo pygmaea* was not statistically analyzed because not enough individuals were encountered, 2/3 of its occurrences were within the corridor.

Comparison of these responses to known soil architecture preferences (Nekola 2003) indicates that the two factors are significantly linked ($P = 0.0154$; Table 3): species that favored corridor subsamples tended to favor turf soils, while species favoring control subsamples tended to favor duff soils.

Discussion

The sampling protocols used in this study were found to be more than adequate to accurately characterize the land snail fauna and its response to powerline corridor formation. First, roughly 80% of the known county and 75% of the eastern Upper Peninsula fauna was encountered despite the fact that the corridor does not intersect the carbonate cliff sites that serve as one of the most important regional reservoirs for land snail biodiversity (Nekola 1999). This sampling design also resulted in documenting well the regional species of conservation concern. Only four such species were not encountered: *Vallonia gracilicosta*, *Vertigo hubrichti* and *Vertigo paradoxa* were not observed because their stable carbonate cliff habitat was not intersected by the ESE-6904/6905 corridor; and *Catinella exile* was also not recorded even though it has been observed in low numbers on the marl fen at Summerby Swamp to the northwest of the corridor. While seemingly appropriate habitat for this species exists within the ESE-6904/6905 corridor and adjacent habitats, its absence was not surprising as it is also absent from the immediately adjacent Martineau Creek fen (Nekola 1998). Additionally, both the entire dataset as well as 3/4 of the individual subsamples meet the criteria of Cameron and Pokryszko (2005) for accurate portrayal of land snail community patterns.

These data show that creation of a treeless powerline corridor has led to profound changes in the terrestrial gastropod community. Both the richness and abundance of land snails within the corridor have fallen in comparison to adjacent habitats, with composition turning over by roughly 2/3 as turf (i.e., grassland) specialists replace duff (i.e., forest) specialists.

This change, however, has not led to a reduction in total land snail biodiversity. First, faunas of control subsamples remain compositionally similar to those of other undisturbed sites in the region, with multiple species of conservation concern persisting only 30 m from the corridor edge. Second, species abundance distributions were generally unaffected, with proportional abundance being similar for corridor and control subsamples up to the seventh-most abundant species. Although abundance levels trailed off more rapidly for corridor subsamples from the eighth-most-abundant species on, this general pattern is characteristic for native grassland faunas throughout the region (Nekola 2002, 2010). As a result, the more rapid fall off of abundance is probably not due to the corridor, per se, but

Table 2 Impact of powerline corridor on species abundance

Name	Corridor samples		Control samples		P value
	Obs.	Exp.	Obs.	Exp.	
A. Species with too few observations (10 or less) to characterize preference					
<i>Anguispira alternata</i> ; <i>Euchemotrema fraternum</i> ; <i>Glyphyalinia indentata</i> ; <i>Helicodiscus parallelus</i> ; <i>Oxychilus draparnaudi</i> ; <i>Oxyloma retusa</i> ; <i>Paravitrea multidentata</i> ; <i>Succinea ovalis</i> ; <i>Vallonia costata</i> ; <i>Vallonia pulchella</i> ; <i>Vertigo gouldii</i> ; <i>Vertigo ovata</i> ; <u><i>Vertigo pygmaea</i></u> ; <i>Vitrina limpida</i> ; <i>Zoogenetes harpa</i>					
B. Generalist species					
Name	Corridor	Subsamples	Control	Subsamples	P value
	Obs.	Exp.	Obs.	Exp.	
<i>Deroceras</i> sp.	12	9	14	17	0.572488900
<i>Euconulus polygyratus</i>	9	10	20	19	1.000000000
<i>Punctum</i> n.sp.	85	81	154	158	0.773239300
<u><i>Pupilla muscorum</i></u>	8	6	9	11	0.728282100
<u><i>Vertigo cristata</i></u>	20	25	52	47	0.472278900
<i>Zonitoides arboreus</i>	5	10	23	18	0.226957500
C. Species that favor ($P < 0.0017$) or tend to favor ($0.05 > P > 0.0017$) corridor subsamples					
<i>Carychium exiguum</i>	465	357	585	693	0.000001676
<i>Cochlicopa lubrica</i>	18	8	6	16	0.008414732
<u><i>Euconulus alderi</i></u>	48	32	45	61	0.026030660
<i>Gastrocopta pentodon</i>	33	12	1	22	0.000000047
<i>Gastrocopta tappaniana</i>	95	49	49	95	0.000000090
<i>Nesovitrea electrina</i>	151	76	71	146	0.000000000
<u><i>Vertigo elatior</i></u>	118	60	59	117	0.000000001
<u><i>Vertigo morsei</i></u>	48	19	9	38	0.000000047
D. Species that favor ($P < 0.0017$) or tend to favor ($0.05 > P > 0.0017$) control subsamples					
<i>Carychium exile</i>	19	70	187	136	0.000000001
<i>Columella simplex</i>	49	116	293	226	0.000000002
<i>Discus catskillensis</i>	5	96	276	185	0.000000000
<i>Euconulus fulvus</i>	10	39	106	77	0.000004013
<i>Helicodiscus shimeki</i>	2	23	65	44	0.000002788
<i>Nesovitrea binneyana</i>	0	84	246	162	0.000000000
<u><i>Planogyra asteriscus</i></u>	7	485	1,417	939	0.000000000
<i>Punctum minutissimum</i>	141	1,028	2,879	1,992	0.000000000
<i>Striatura exigua</i>	195	270	599	524	0.000043710
<i>Striatura ferrea</i>	52	112	278	218	0.000000083
<i>Striatura milium</i>	65	249	666	482	0.000000000
<i>Strobilops labyrinthica</i>	275	867	2,271	1,679	0.000000000
<u><i>Vertigo bollesiana</i></u>	0	10	29	19	0.000767735
<u><i>Vertigo nylanderi</i></u>	0	11	32	21	0.000347028

Species considered of conservation concern by the Michigan Natural Features Inventory are underlined

rather indirectly to the conversion to grassland habitats/faunas. Third, ordination demonstrates that within 75 years the corridor fauna has evolved into assemblages very similar to other native lowland grassland sites in the region, in particular sedge meadows and fens.

Table 3 Species response to subsamples placement versus duff/turf soil architecture preference, with numbers in each cell representing number of species

	Soil architecture preference		
	Duff species	Generalist species	Turf species
Corridor preference			
Control subsamples	9	4	1
Generalist	3	1	1
Corridor subsamples	2	0	6

Fisher's exact test: $P = 0.0154$

The ultimate impact of corridor formation has been for the expansion of lowland grassland land snail faunas into the previously largely forested matrix. Fourteen species (~30% of total) were found to favor control subsamples, while eight (~20%) favored the corridor itself. These changes are similar to those previously noted with forest clearing (Nekola 2003). Because species of conservation concern in this region are roughly equally partitioned between forests and open habitats, the decrease in population occurrence/size of forest-favoring rare species (*Planogyra asteriscus*, *Vertigo bollesiana*, *Vertigo nylanderi*) in the corridor has been compensated by the increase of grassland-favoring rare species (*Euconulus alderi*, *Vertigo elatior*, *Vertigo morsei*), with *Vertigo morsei* representing one of the rarest land snail species in the Great Lakes region (Nekola 2004). As a result, no significant change in either the total richness or abundance of species of conservation concern was noted between corridor and adjacent forest habitats. However, the increase in coverage and population sizes of grassland species that would otherwise be rare or absent from the corridor has enriched total biodiversity. This result holds even when the two alien species listed by the Michigan Natural Features Inventory (*Pupilla muscorum*, *Vertigo pygmaea*) are removed from analysis.

Even though terrestrial gastropods appear to be ideal candidates for documenting detrimental biodiversity impacts from corridor formation, these data demonstrate that system-wide diversity has not been lowered by corridor formation. Rather, the net impact appears positive, as the corridor has allowed for an expansion of grassland/turf specialists, including one of the rarest species in the landscape, while at the same time not seriously impacting the faunas of adjacent habitats.

How have small grassland snails with poor active dispersal abilities been able to occupy the new grassland habitats created by corridor formation within the relatively short ecological time frame that the ESE-6904/6905 corridor has been in existence? The explanation is probably that small land snails, such as those that dominate the Upper Peninsula fauna, possess great passive dispersal capabilities. For example, DNA sequence data demonstrate that members of the genus *Balea* have been repeatedly carried across 9,000 km of open eastern Atlantic Ocean by migrating birds (Gittenberger et al. 2006). Similarly, in North America many members of the *Vertigo gouldii* group have ranges exceeding 5,000 km in extent even though they inhabit areas covered by continental ice as recently as 10 ka (Nekola et al. 2009). Passive dispersal of some small land snail species is also facilitated by their ability to reproduce uniparentally (Pokryszko 1987), allowing only single individuals to found populations. As a result, small land snails tend to possess much larger ranges and to more completely saturate their available habitats than larger taxa (McClain and Nekola 2008; Nekola 2009).

The most likely vectors for passive land snail dispersal in the ESE-6904/6905 corridor are birds and small mammals. For both of these groups, utility corridors represent travel paths for grassland species through forested landscapes (Kroodsma 1982; Gates 1991). This will allow for movement of grassland/turf specialist land snails through corridors as well. Additionally, narrow corridors such as that for ESE-6904/6905 have been found to not restrict movements of small mammals in eastern North American forests (Schreiber and Graves 1977; Gates 1991), and gliding mammals (Asari et al. 2010), small mammals, reptiles, and amphibians (Carthew et al. 2009) in Australia. Consequently, the ESE-6904/6905 corridor probably does not serve as a barrier to passive movements of minute forest snails. It should thus not be surprising that the richness, abundance, and community structure of land snail assemblages on either side of the corridor were found to be very similar.

These results mirror numerous studies that have shown that utility corridors serve as refuges for grassland species within forested landscapes. This effect has been repeatedly shown for birds (Kroodsma 1982; King et al. 2009; Meehan and Haas 1997) and mammals (Gates 1991) in eastern North America and for a variety of small vertebrates in Australia (Goosem and Marsh 1997; Clarke et al. 2006; Clarke and White 2008a, b). As was found in the current study, these grassland species may be quite uncommon elsewhere within the landscape (Clarke and White 2008b). Similar patterns exist for vascular plants in the southeastern USA, where powerline corridors serve as refuges in an otherwise forested matrix for a number of critically endangered grassland/savanna species (Sorrie and Weakley 2001).

Thus, as long as a given utility corridor (1) does not substantially impact the overall population of a given forest-specialist species, (2) exists within a forest-dominated landscape that also includes native grassland habitats and (3) is maintained through manual vegetation cutting, it may actually benefit terrestrial gastropod biodiversity by maintaining refuges for both common and rare grassland species while not leading to the extirpation of sensitive forest species. For the current alignment of ESE-6904/6905 this equates to roughly 3–6 ha of grassland habitat per kilometer of corridor. However, it should not be assumed that these positive benefits will also accrue in landscapes lacking native grassland habitats, or for corridors maintained through herbicide application (Nowak et al. 1993). Although quantitative sampling for land snails was not conducted in areas subjected to this type of management, it appeared that terrestrial gastropod richness and abundance was much lower in herbicide-managed sections of the corridor just outside of the National Forest boundary.

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