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CONSTRUCTION OF A SUBURBAN-RURAL RECREATIONAL TRAIL PRODUCES DEVELOPING EDGE EFFECTS

Eric S. McCloud[1] and **James H. Bandoli**: Biology Department, University of Southern Indiana, 8600 University Blvd., Evansville, IN 47712 USA

ABSTRACT. The development of edge effects due to increased light penetration attendant to the construction of a bicycle–pedestrian recreational trail through a forest in southwest Indiana was studied. Though the trail roughly followed the route of an existing path through the forest, light penetration was dramatically increased by the construction of the trail and transiently increased in the forested edge within 10 m of the trail. Decreased light penetration in the forested edge compared to the forest interior had also developed five years after trail construction, indicating the development of a side canopy. Over the study period of five years post-trail construction, there was no evidence of decreasing light penetration over the trail itself. The findings will be relevant for land managers and others involved in recreational trail construction through Indiana forests.

Keywords: Forest edges, forest understory, light penetration, magnitude of edge influence, side canopy, PAR, photosynthetically active radiation

INTRODUCTION

Urban recreational trails can confer diverse benefits to human communities. They allow individuals using the trails to experience greater connection with the natural world and opportunities for outdoor exercise and play; they may also provide for a nexus of community social connection. Locally greater biodiversity is observed at edges created along corridors between habitat types as these corridors support a mixture of introduced species, edge specialists, and core habitat species (Harris 1988; Hall & Kuss 1989; Parendes & Jones 2000; Roovers et al. 2004; Honu & Gibson 2006; Avon et al. 2010). Green spaces and forest fragments at the urban – rural interface provide habitat for wildlife. However, roads, trails, lawns, and maintained park landscapes also cause fragmentation of wild and semi-natural habitats. Such fragmentation reduces the effective habitat size for species of core habitats and can result in increased vulnerability to disease, predation, parasitism, and competition from invasive species as well as generating direct effects from reduced habitat area (Ries et al 2004). Habitat size is reduced further because the edges of natural habitat fragments adjacent to constructed environments are affected for some distance into the fragment. While such edge-effects have been long studied, efforts to develop comprehensive and mechanistic models have met with success only relatively recently (Ries et al. 2004). Reviews and careful descriptive work allow recognition of different classes of fragments and edges, and all of these efforts have pointed to the importance of light penetration at edges in driving edge effects at the interface between forests and other habitat types (Matlack 1993; Murcia 1995).

Edge effects in northern hemisphere temperate deciduous forests are characterized by gradual changes in both abiotic and biotic features as one moves from one habitat type to another or from an anthropogenic matrix into natural habitat fragments. Among the abiotic changes observed are changes in light penetration into the forest, temperature, soil moisture, relative humidity, and vapor pressure deficit (Matlack 1993). Where forests adjoin more open habitats, increased light penetration in the forest edge — a positive edge effect — is seen (Matlack 1993; Murcia 1995). Biotic changes often include changes in plant species richness, occurrence of introduced species, and increased understory foliage growth along edges as these edges age, but many changes in plant and animal communities have been inconsistent among different studies (Murcia 1995). Increased growth of understory foliage at an edge is observed as the increased light availability drives proliferation of lateral branches (Matlack 1993). As a newly created edge ages, the development of this "side canopy" then decreases light penetration into the edge. Thus, side canopy

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[1] *Corresponding author:* Eric S. McCloud, 812-465-1228 (phone), emccloud@usi.edu.

growth may produce a zone just inside the edge where light penetration is decreased relative to the habitat interior (Murcia 1995; Ries et al. 2004).

Because the forest canopy may close or nearly close over them, trails and roads present a type of edge that can be expected to differ from edges between forest fragments and agricultural or other anthropogenically influenced habitats. Paved and graded recreational trails with engineered improvements for drainage and slope retention can be expected to affect the forest habitat through which they pass as if they were narrow roads.

This study had two goals. The first was to document the increased light penetration over a recreational trail and at the edge of the trail due to its construction and the attendant opening of the canopy. This was accomplished by measuring PAR (photosynthetically active radiation) in 2010, one year before trail construction, and again in 2012, 2014, and 2016. The second was to examine the development of any complex edge with side canopy growth that may have occurred. This work, with higher spatial resolution, was conducted in 2016. A strong positive edge effect resulting from the construction of the trail, followed by a diminution of this effect as the side canopy developed, was predicted.

METHODS

Study site.—The USI–Burdette Park Trail, a locally developed trail that is part of the larger American Discovery Trail, extends from the campus of the University of Southern Indiana (USI) to Burdette Park, a municipally owned and operated park in southern Vanderburgh County in southwest Indiana. From the southern portion of the developed part of the USI campus, the trail continues south-southeast through an agricultural area and into a mesic, upland, mixed hardwood forest before it descends to a creek bottom and re-ascends into Burdette Park. Most of the forested portion of the trail south of the USI campus-proper follows a ridge above a tributary of Bayou Creek, which flows into the Ohio River. Along this section of the trail to the southwest, is a hillside that descends into a large forest tract owned by USI (Forest side) while the northeast side of the trail drops sharply by 27 to 29 m over a distance of about 300 m to the creek (Creek side) and an abandoned agricultural field on its opposing side. The route taken by the trail roughly follows the route of a former log skidding trail that had been infrequently used for recreational purposes as a footpath and ATV trail by local residents. Built to Indiana Department of Transportation standards with efforts taken to minimize overall width and cutting of large trees, the trail is asphalt with gravel and grass borders and occasional small retaining walls and concrete curbs where it either cuts into or runs over the edge of the ridge. Engineering drawings for the trail specified that the width of the cleared corridor would be 20 feet (6.1 m); the resulting trail was then to be 10 feet (3.05 m) wide. This asphalt trail was to be flanked with a gravel verge and a mowed border on each side that would add another 10 feet (3.05 m). The actual width of the cleared corridor was measured shortly after trail paving and found to average 10.5 m (± 1.6, SD) and vary between 7.5 and 12.9 m. Along the forested portion of the trail, the width of the asphalt portion is typically 3.8 m (± 0.4, SD) and the gravel and grass border on either side is normally 2.6 m (± 0.6, SD), varying between 1.6 m and 3.7 m at the transects where we worked. Presently, periodic mowing and herbicide applications are used to maintain the grassy edges next to the trail. The width of the mowed border and herbicide applications varies somewhat from year to year as does mowing frequency.

Along the ridge top and down the slopes on either side of the trail, the composition of the shrub layer in the understory typically included *Asimina triloba* (pawpaw), *Lindera benzoin* (spicebush), and *Sassafras albidum* (sassafras). The canopy layer included *Acer saccharum* (sugar maple), *Carya* species including *C. glabra* and *C. laciniosa,* and *Liriodendron tulipifera* (tulip poplar). The herb layer, especially near the trail, included *Impatiens capensis* (jewelweed), *Parthenocissus quinquefolia* (Virginia creeper), and *Podophyllum peltatum* (mayapple). Introduced invasive species, such as *Alliaria petiolata,* (garlic mustard) and *Lonicera japonica* (Japanese honeysuckle), were present but coverage was not extensive.

Four 150 m transects were installed roughly perpendicular to the footpath and ridgeline in 2010 prior to the construction of the trail. These transects extended across the ridge, 75 m to the north-northeast and south-southwest on either side of the ridge. Stations were marked along each transect with painted wooden grade stakes that were later replaced with metal fence posts at 10 m intervals. The transects were parallel to each other and spaced roughly 80 m apart along the trail such that the last transect crossed the trail 235 m from the first. Posts marking transect stations were numbered with number 1 at the southwest end and number 16 at the northeast end; the trail crossed transects between stations 8 and 9.

PAR measurements.—Available light was measured as the fraction of PAR (photosynthetically active radiation) in the forest relative to open sky PAR. To do this, light was measured along the transects with a PAR sensor (LiCOR 190R, LiCOR Biosciences, Lincoln, NE) mounted on a telescoping fiberglass pole for heights over 1 m or a horizontal aluminum rod affixed to a vertical aluminum pole for heights ≤ 1 m. The sensor was leveled with two orthogonal bubble levels for each measurement and read with a LiCOR 1400 datalogger. At points where PAR measurements were made, the time of measurement to the nearest minute was noted. Measurements were made at 0, 1, 2, and 4 m above the ground at each measurement location; on each transect, measurements were made at transect stations 1, 3, 5, 7, 9, 10, 12, 14, and 16. To allow for increased sampling in the region where transects crossed the trail, additional measurements were made halfway between transect stations 7 and 8, 8 and 9, and 9 and 10. Concurrent with measurements along transects, a separate set of time-marked PAR measurements were recorded simultaneously on a gravel road in a nearby (less than 1 km distant) agricultural field. The PAR sensor here (Apogee MQ200, Apogee Instruments, Logan UT) was mounted ~2 m above ground on a fiberglass pole. All PAR measurements were made in the early morning or late afternoon with the sun low in the sky such that little or no direct sunlight struck either sensor. On rare occasions when direct sunlight did strike either sensor, notes were made and any PAR readings at these times were excluded from analysis. Forest PAR measurements were divided by open sky PAR measurements taken at the same time.

Measurements from each sensor were found to be slightly different but highly correlated ($r^2 > 0.97$). Accordingly, measurements made with the open sky sensor were adjusted to match the sensor used in the forest using a calibration equation previously obtained by linear regression (Corrected field measurement $= 1.0103 \times$ field measurement $+4.6465\ \mu\text{mol m}^{-2}\text{s}^{-1}$). Measurements were made along each transect in 2010, 2012, 2014, and 2016. Trail construction began with preliminary surveys and flagging of the proposed route in 2010 after we completed our measurements. In spring 2011, brush and trees were cleared and the trail was completed before summer.

Magnitude of edge influence.—In 2016 a separate set of measurements were made that were designed to allow direct evaluation of edge development and the distance that any edge effect penetrated into the surrounding forest. For these, three measurements were made 0.5 m apart along 1 m bands perpendicular to the transects at heights of 0, 1, 2, and 4 m above the forest floor. Measurements were made along each transect at the center of the paved trail, at either edge on the border between the mowed grass and the forest, and at distances along transects of 1, 2, 5, 10, and 15 m in both directions into the forest. In this way, the distance of edge effect influence could be evaluated on both sides of the trail.

Data analysis.—Because the paved trail was wider than the previous footpath/ATV path, the strip of land under it and within the boundaries of the mowed grass edges were exposed to a greater fraction of open sky by trail construction. To reveal this and to test for an edge effect in the forest adjacent to the cleared edge, the measurement locations were divided into three groups along each transect. Measurements termed "Trail" measurements included those measurements that were taken over the paved trail or inside the edge of the mowed border. Measurements termed "Edge" measurements were measurements from locations at the border or within 10 m (shortest straight line distance) from the trail's mowed border, and measurements termed "Forest" were taken at locations greater than 10 m from the trail border. The shortest straight line distance to the mowed border of the trail edge was measured because, while the transects cut straight lines across the trail, the trail itself and the mowed border adjacent to it had varying widths and meandered markedly such that distances measured along transects often varied from the shortest straight line distance to the forest opening. With measurement locations grouped in this way, PAR fractions were evaluated with repeated measures analysis of variance using SPSSx v. 23 so that we could examine the change in light penetration over time, at different heights in the understory, and at different distances from the mowed edge – forest border. Measurement location groups (Trail, Edge, Forest) were the treatment levels and measurement years (2010, 2012, 2014, 2016) were the levels of the within-subjects factor. F statistics and degrees of freedom reported reflect the Huynh-Feldt correction for any violations of sphericity (Huynh & Feldt 1976).

Analysis of the distance of edge influence with the separate measurements made in 2016 followed the randomization method of Harper & MacDonald (2011). In this method, the magnitude of edge influence (MEI) is estimated as a difference between the average of edge measurements at a given distance from the border and a reference set of interior measurements. In our case, replicate reference measurements were made at a distance of 15 m deep into the forest on both sides of the trail. MEI is calculated as:

$$MEI = \frac{E - R}{E + R}$$

where E is the mean of edge measurements at a given distance and R is the mean of reference measurements. This quantity will vary between -1 and 1. Here, positive values indicate more light penetration than the reference while negative values indicate less. The significance of the difference between the estimated MEI and zero is then calculated with a randomization test (RTEI) at each distance from the edge where measurements are made such that the distance of edge influence can be assessed. Because reference measurements included all the measurements made at all the plots that were 15 m deep, MEI calculations account for natural variation in the extent of undisturbed canopy cover.

RESULTS

Construction of the trail strongly increased light penetration over the region within the edge as well as over the location of trail itself ($F = 22.60$, $p < 0.0009$ for years–within subjects effect; Fig. 1). However, the significant main effects of years and distance ($F = 41.48$, $p < 0.0009$ for distance–between subjects effect) showed a significant interaction ($F = 19.27$, $p < 0.0009$ for year by distance interaction) because the effect of distance arose after construction of the trail. At sites on the paved trail or within the cleared region that included the mowed edges as well as the asphalt, light levels were more than three fold higher one year after trail construction and remained similarly high for the length of the study (Figs. 1 & 2). Light levels for measurements within 10 m of the trail were approximately doubled in the year after trail construction, but had fallen by the third year after trail construction and were not significantly different from light levels deeper in the forest for the remainder of the study (Fig. 1). No significant changes in light levels were found for forest measurements. There was a strong effect of height; light level was greater as heights increased above the forest floor ($F = 48.00$, $p < 0.0009$ for height–within subjects effect; Fig. 2) and increased from 2.9 (± 0.2, SE) percent of open sky to 5.4 (± 0.4, SE) between the ground and 5 m. Despite the fact that measurements made on the paved trail contrasted markedly with measurements made under forest canopy, there was no significant height by distance interaction following adjustment of degrees of freedom with the Huynh-Feldt correction ($F = 1.521$, $p = 0.213$). However, the effect of height varied with measurement years (significant height by year interaction, $F = 2.077$, $p = 0.042$).

MEI estimates and depth of edge estimates were different on each side of the trail. On the northeast side of the trail, there was a significant positive edge influence at the border of the mowed edge and forest (0 m distance; Table 1) at all heights except 4 m. This positive effect extended 1 m into the forest at ground level and at 1 m above ground. At greater distances into the forest, there were no significant edge effects. On the southwest side both positive and negative edge effects were observed. The edge of the mowed border and forest was significantly brighter at all heights and, at 1 m into the forest, light levels were higher at the 1 m height (Table 2). Strong negative edge effects were present at 2 and 5 m distances past the mowed border at the 4 m height; there was also a negative edge effect on the ground at 5 m (Table 2).

DISCUSSION

While a strong edge effect for light penetration two years after the construction of the paved trail was observed, this was transient and light levels at measurement points between the edge of the mowed border and within 10 m of the edge were indistinguishable from forest light levels after three years had passed. Conceptual analyses predict that, following creation of an edge between forest and more open terrain, increased

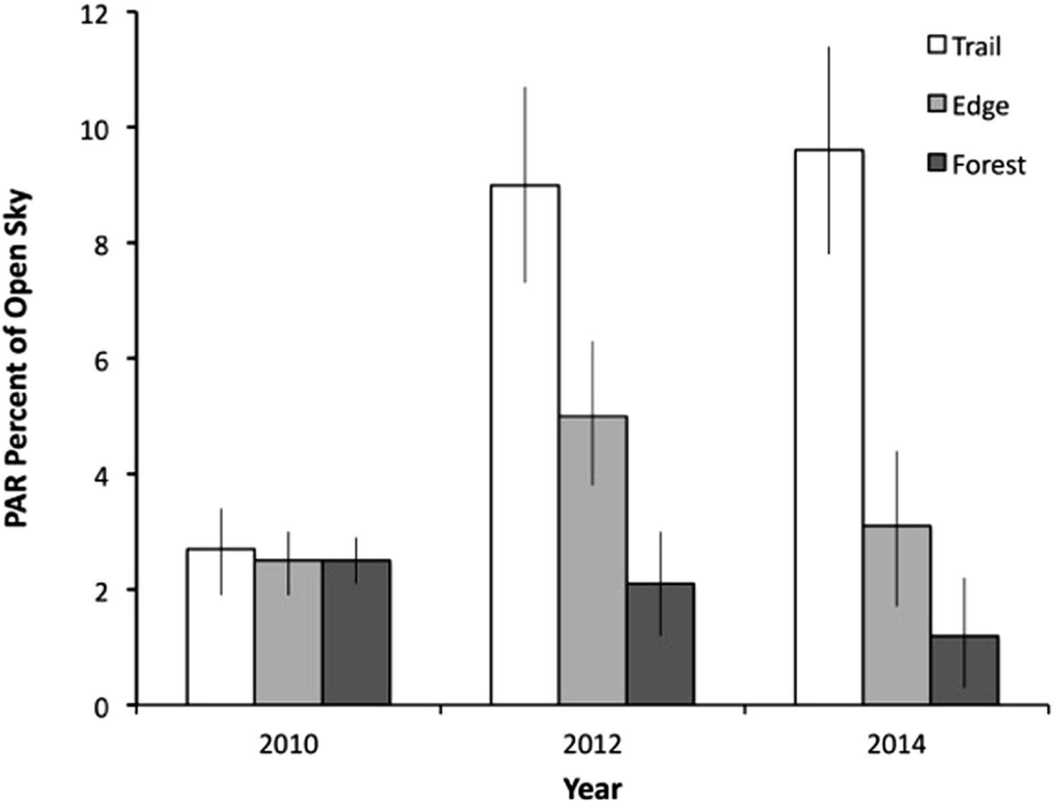

Figure 1.—Light penetration around the USI–Burdette Park bicycle and pedestrian trail. Clear bars (trail) show mean percent photosynthetically active radiation (PAR) above the paved trail and mowed borders, light grey bars (edge) show mean radiation above the forested zone within 10 m of the mowed edges, and dark grey bars (forest) show mean radiation above the forested zone greater than 10 m and up to 80 m beyond the mowed edges. Whiskers represent 95% confidence intervals.

light availability at the edge should stimulate shoot proliferation and foliage density should increase just beyond the edge. This has been termed "side canopy" and is thought to seal edges and create a shallow zone of decreased light availability just beyond the edge (Matlack 1993; Murcia 1995). While a clear decrease in light penetration in this region was observed, increased shadiness close to the trail edge was not noted in either the first or third year after trail construction with our transect measurements. It is possible that the side canopy may not have fully developed by the point of our 2016 measurements. Alternatively, the spatial resolution needed to observe this predicted dip in light availability may have been absent. Previous work has indicated that development of side canopy and closing of forest edges can take at least 5 years (Matlack 1993).

Over the paved and mowed trail itself, light penetration was greatly increased. Interestingly, this increase showed little sign of diminution over the study period although the ground level measurements may be an exception (Fig. 2a). This decrease may have been the result of proliferation of lateral shoots and development of side canopy near the ground, particularly on the southwest side of the trail.

The findings for individual transect by height combinations show little evidence of increased shadiness (Fig. 2b) but, by 2016, five years post construction, side canopy effects, if present, should have been detectable. MEI measurements on the edge of the mowed trail border and the forest had higher light levels than the reference plots as did measurements at lower heights 1 m deep into the forest. Mowing and herbicide treatments varied somewhat in the years following trail construction; higher light levels at lower heights just inside the mowed border likely reflected this practice. The sign of edge influence

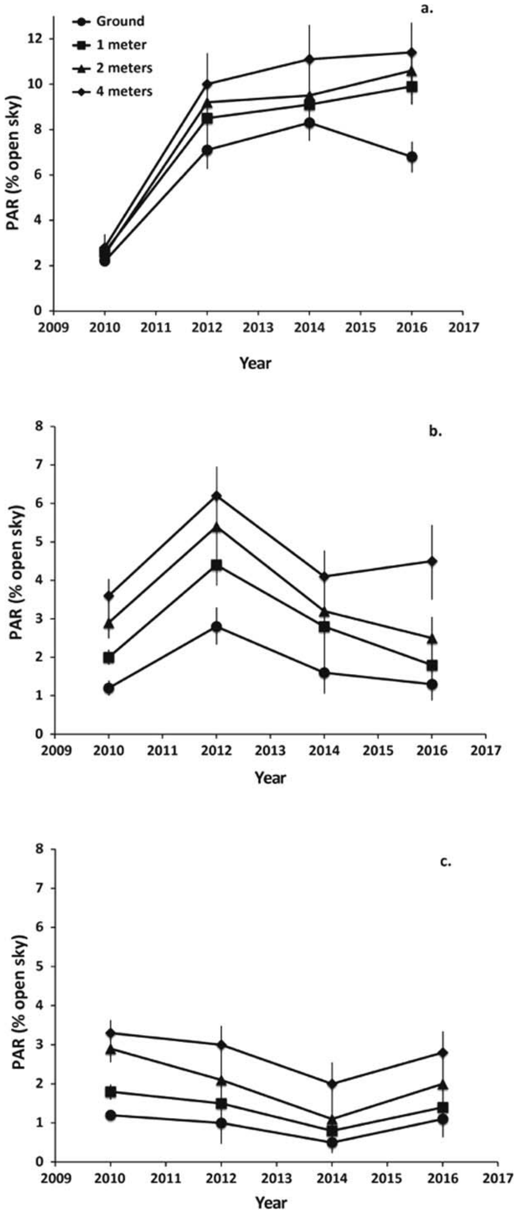

Figure 2.—Light penetration at different heights above ground around the USI–Burdette Park bicycle and pedestrian trail. Circles, squares, triangles, and diamonds represent different heights above ground (0, 1, 2, and 4 m, respectively). Lettered panels show bands around the trail: (a) paved trail and mowed border, (b) forested zone within 10 m of the mowed edges, and (c) forested zone greater than 10 m and up to 80 m beyond the mowed edges. Whiskers represent standard errors. Note that in some cases, symbols obscure error bars and ordinate for panel (a); trail data, in particular, have a different axis scale to improve clarity.

changed from positive to negative at 2 m deep into the forest. At a distance of 2 m or greater, five of 12 MEIs on the northeast side and eleven of 12 MEIs on the southwest side were negative (Tables 1 & 2). Distinct and significant decreases in light levels were observed at distances of 2 and 5 m into the forest on the southwest side of the trail, while negative edge effects on the northeast side were of marginal significance ($p = 0.055$ at 10 m deep into the forest; Table 1). These findings suggest that a side canopy had developed and that it resulted in lowered light levels in belts on either side of the trail, ending somewhere before 10 m deep into the forest and beginning somewhere past 1 m deep. Further, development of the side canopy was more distinct on the southwest side of the trail. Greater development of side canopy on the southwest side is expected given the position of the trail on a ridge where its southwest exposure should yield greater sun exposure (Matlack 1993; Ries et al. 2004).

In other work, edge effects of narrow roads and trails on light availability and other responses have been rather shallow compared to edge effects where two extensive habitat types adjoin. For example, changes in plant diversity and the influence of exotic species were found to extend 3 m past the edge of gravel walking trails (LaPaix et al. 2012) in Nova Scotia, while Avon et al. (2010) found typical road influences, including light levels, not to extend 5 m past the road embankment–forest edge in French managed oak forests. In contrast, edges between forests and adjacent open habitats tend to extend more deeply into the forest. In a study of edges in the Shawnee National Forest (Illinois, USA), Honu & Gibson (2006) found that canopy openness was significantly greater 40 and 50 m from the edge for crop–forest and hayfield–forest interfaces, while the influence for access road–forest interfaces was 30 m. Additionally, in their study of forest edges in Nova Scotia, LaPaix et al. (2012) found edge influences to extend 50 m into the forest along boundaries between forest and open habitat.

Thus, edge effects created by roads and trails are smaller than effects generated by boundaries with extensive open habitat and may scale with the size of the road or trail (Parendes & Jones 2000). Nevertheless, direct and indirect effects on animals may extend further into the forest than expected as roads and paved trails represent a type of qualitatively different "habitat", especially to mobile animals (Ries et al. 2004). For example, edge effects on salamander abundance and

Table 1.—Changes in light penetration on the northeast side of trail. Magnitude of edge influence (MEI – top number in each cell), average PAR (PAR percent of open sky – middle number in each cell), and *p* values (two – tailed tests; bottom number in each cell) at distances from the mowed edge-forest border into the forest. Reference values were taken at 15 m deep into forest. Significant *p* values are in bold print.

		Distance into forest from mowed edge (m)					
Height (m)		0	1	2	5	10	Reference
Ground	MEI	0.271	0.311	0.150	-0.006	-0.089	-
	PAR	1.75	1.91	1.36	0.99	0.84	1.00
	p	**0.008**	**0.023**	0.094	0.940	0.25	-
1 meter	MEI	0.534	0.440	0.417	-0.043	-0.133	-
	PAR	5.06	3.96	3.74	1.41	1.18	1.54
	p	**0.023**	**0.047**	0.125	0.656	0.055	-
2 meters	MEI	0.484	0.333	0.304	0.236	-0.096	-
	PAR	5.95	4.13	3.87	3.34	1.70	2.07
	p	**0.016**	0.328	0.391	0.484	0.055	-
4 meters	MEI	0.497	0.315	0.256	0.208	-0.092	-
	PAR	6.80	4.39	3.86	3.49	1.90	2.28
	p	0.102	0.469	0.469	0.469	0.133	-

diversity caused by narrow and lightly used logging roads in the Nantahala National Forest extended between 35 m and 60 m into the surrounding forest (Smelitsch et al. 2007). Abundance of interior bird species was affected up to 75–100 m from recreational trails running through forests and grasslands around the city of Boulder, Colorado and rates of nest predation were higher near trails (Miller et al. 1998). In contrast, Smith-Castro & Rodenwald (2010) found no effect of distance from recreational trails on nest survival in Northern Cardinals, which are highly tolerant of humans.

In their conceptual model of edge effects, Ries et al. (2004) argued that altered ecological flows of energy, materials, and individuals, as well as increased access to spatially separated resources, change edge habitat quality while the ecological responses of resource mapping and altered species interactions at edges combine to influence species abundance and distribution. Thus, while altered light environment (an energy flow) may be the primary driver of edge effects for neotropical forest birds, resulting indirect effects may play a role as well (Patten & Smith-Patten 2012). In this work, the authors noted that landscape charac-

Table 2.—Changes in light penetration on the southwest side of trail. Magnitude of edge influence (MEI – top number in each cell), average PAR (PAR percent of open sky – middle number in each cell), and *p* values (two – tailed tests; bottom number in each cell) at distances from the mowed edge-forest border into the forest. Reference values were taken at 15 m deep into forest. Significant *p* values are in bold print.

		Distance into forest from mowed edge (m)					
Height (m)		0	1	2	5	10	Reference
Ground	MEI	0.295	0.115	-0.043	-0.105	-0.084	-
	PAR	2.14	1.47	1.07	0.94	0.98	1.16
	p	**0.000**	0.383	0.328	**0.023**	0.063	-
1 meter	MEI	0.481	0.178	0.086	-0.018	-0.094	-
	PAR	5.06	3.96	3.74	1.41	1.18	1.36
	p	**0.023**	**0.047**	0.125	0.656	0.055	-
2 meters	MEI	0.353	0.090	-0.062	-0.124	-0.005	-
	PAR	4.90	2.81	2.07	1.83	2.32	2.34
	p	**0.000**	0.328	0.336	0.305	0.946	-
4 meters	MEI	0.253	0.063	-0.248	-0.293	-0.038	-
	PAR	6.45	4.36	2.31	2.10	3.56	3.84
	p	**0.000**	0.664	**0.047**	**0.008**	0.578	-

teristics can be expected to affect resource mapping and the degree of spatial separation of resources; when roads and trails run through more developed residential areas, edge influences on bird nest predation were greater than forested areas.

Our work focused on a forest fragment at the edge of an interdigitated rural–suburban landscape. A strong but transient positive edge effect was found for light penetration. Forest regrowth at and near the edges possibly accounts for the transience of this positive effect. Further regrowth and the likely development of a side canopy allowed the development of negative edge effects by the fifth year following trail construction. A side canopy is expected to develop further as these edges age. Nevertheless, variation in mowing and herbicide treatments inherent in the current haphazard management scheme will likely maintain a strong positive edge effect near ground level. Oddly, there was no evidence of decreased light penetration directly over the trail that would be driven by canopy overlap and merging of driplines on opposite sides of the trail. Additional time may be required for this to happen.

Although landscape characteristics may modulate edge effects and light penetration may be the primary driving factor for edge effects in some species, indirect effects related to species movements, resource mapping, and interactions are expected to add complexity to edge effects, even for narrow edges with overlapping canopy. Wildlife managers and planners can minimize edge effects due to light penetration by minimizing the width of recreational trails and keeping mowed edges at a constant width to allow side canopies to develop and seal the forest beyond. Our findings on light penetration into edges and over trails should help to provide guidance for recreational trail construction through forests in Indiana, especially those using INDOT trail specifications.

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LITERATURE CITED

Avon, C., L. Berges, Y. Dumas & J. Dupouey. 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management 259:1546–1555.

Hall, C. & F. Kuss. 1989. Vegetation alteration along trails in Shenandoah National Park, Virginia. Biological Conservation 48:211–227.

Harper, K.A. & S.E. Macdonald. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. Ecosphere 2:art94.

Harris, L.D. 1988. Edge effects and conservation of biotic diversity. Conservation Biology 2:330–332.

Honu, Y.A.K. & D.J. Gibson. 2006. Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. Journal of the Torrey Botanical Society 133:255–266.

Huynh, H. & L.S. Feldt. 1976. Estimation of the box correction for degrees of freedom from sample data in randomized block and split-plot designs. Journal of Educational Statistics 1:69–82.

LaPaix, R., K. Harper & B. Freedman. 2012. Patterns of exotic plants in relation to anthropogenic edges within urban forest remnants. Applied Vegetation Science 15:525–535.

Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185–194.

Miller, S.G., R.L. Knight & C.K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8:162–169.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58–62.

Parendes, L.A. & J.A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conservation Biology 14:64–75.

Patten, M.A. & B.D. Smith-Patten. 2012. Testing the microclimate hypothesis: light environment and population trends of neotropical birds. Biological Conservation 155:85–93.

Ries, L., R.J. Fletcher, Jr., J. Battin & T.D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics 35:491–522.

Roovers, P., S. Baeten & M. Hermy. 2004. Plant species variation across path ecotones in a variety of common vegetation types. Plant Ecology 170:107–119.

Smelitsch, R.D., T.J. Ryan, K. Hamed, M. Chatfield, B. Drehman, N. Pekarek, M. Spath & A.

Watland. 2007. Salamander abundance along road edges and within abandoned logging roads in Appalachian forests. Conservation Biology 21:159–167.

Smith-Castro, J.R. & A.D. Rodenwald. 2010. Behavioral responses of nesting birds to human disturbance along recreational trails. Journal of Field Ornithology 81:130–138.

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