Passive Roadside Restoration Reduces Management Costs and Fosters Native Habitat

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ABSTRACT

Roadside ecosystems are managed areas adjacent to roads that are undervalued for the ecological functions they provide. Reductions in roadside mowing is a passive restoration approach that can create habitat, lower management costs, and reduce fragmentation, but managers fear reducing mowing will allow invasive plants to proliferate. Our goal was to quantify changes in invasive plant cover due to decreased mowing. We compared plant diversity and percent cover at roadside sites under three types of vegetation management in Rhode Island—Reference (no-mow forested roadsides, n = 5), Restored (reduced mowing plan, n = 5), Mowed (traditional mowing plan, n = 5)—at four spatial scales using Modified-Whittaker vegetation surveys. Reference sites had the highest native species richness at two spatial scales, the lowest introduced species richness at three spatial scales, and the lowest introduced species percent cover. Invasive species diversity and abundance was not affected by mowing treatment. Because we did not observe an increase of invasive or introduced plant species at sites which are transitioning from Mowed to Restored, we recommend roadside managers implement passive roadside restoration wherever possible. Additionally, because Reference sites had significantly higher native plant diversity and lower introduced plant diversity and cover, managers may consider allowing roadsides to continue through the stages of succession and transition to young forests. Alternatively, managers could restore roadsides to varying stages of succession to increase habitat heterogeneity. These kinds of roadside management plans facilitate biodiversity, maintain habitat important for rare and endangered wildlife, can decrease atmospheric CO_2 emissions, and are a cost-effective form of restoration.

Keywords: early successional habitat, fragmentation, invasive species, mowing, road ecology

Restoration Recap

- There is a widespread trend to decrease roadside mowing in roadside ecosystems to both conserve funds and passively restore degraded and underutilized grassland and early successional habitat.
- Roadsides that were historically clear-cut but are now managed as no-mow roadsides (young forests, reference sites) provide significantly more native habitat than frequently mowed roadsides and those undergoing passive restoration.
- We found that passively restored roadsides did not have significantly higher invasive species richness or density when compared to roadside forests or frequently mowed roadsides.
- Because invasive species did not proliferate in passively restored roadsides, managers can confidently reduce or eliminate roadside mowing in any areas which do not compromise driver safety.
- Roadsides where mowing is eliminated should continue to be monitored to track and prevent the establishment and spread of invasive species.
- Implementation of reduced or eliminated roadside mowing could dramatically improve air quality by reducing CO_2 emissions by 35 kilograms per shoulder-kilometer.

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In the United States alone, there are over 100,000 square km of public road surfaces and associated roadside ecosystems (Forman 2004). Roadside ecosystems, the managed areas adjacent to roads that buffer neighboring ecosystems, represent 45% of this total (Forman 2004). Roadside management prioritizes driver safety and considers mitigating

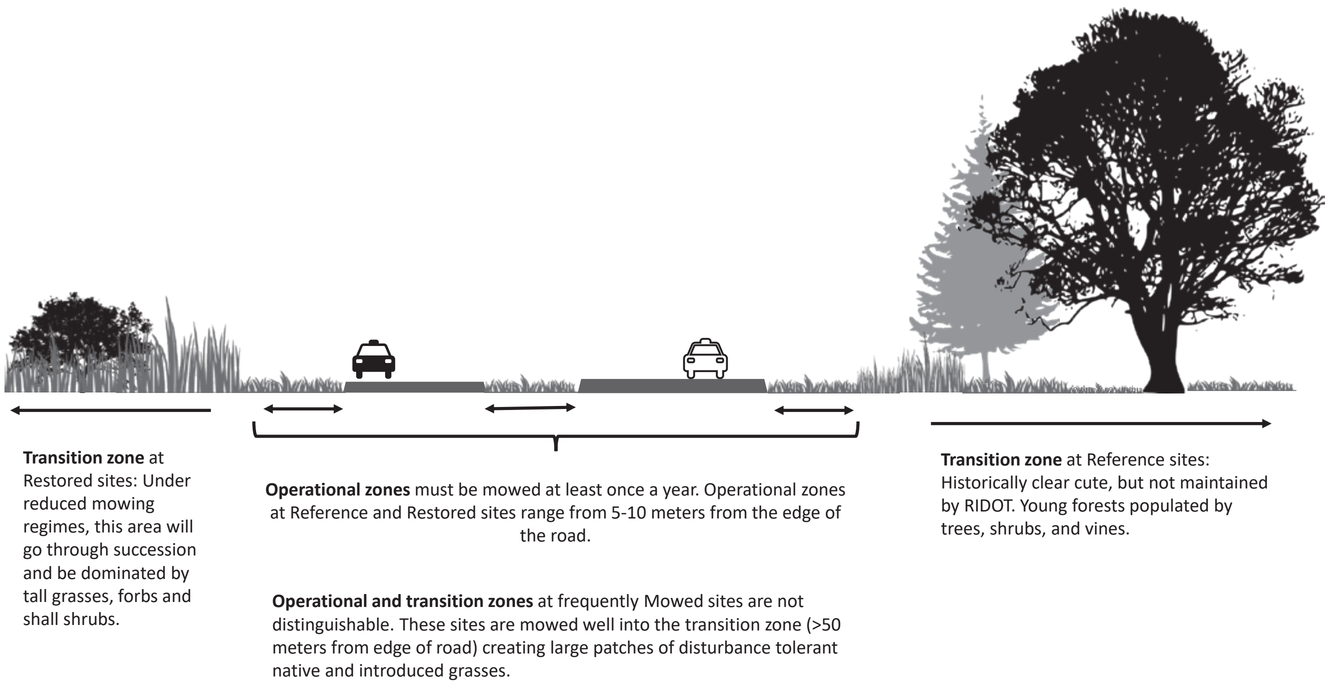

Figure 1. Highway zonal system and description of zones under different mowing treatments. (FHWA 2009, developed by the Washington State Department of Transportation).

the negative ecological effects of roads only after motorist safety is assured. High levels of resources are dedicated to roadside management, but these could be better leveraged to protect and enhance native species and habitats without sacrificing driver safety or increasing costs.

Because of their ubiquity, roadside ecosystems provide an important conservation and restoration opportunity, but, globally, many are undermanaged, underutilized, and undervalued for their ecological functions. Adding to our understanding of biodiversity and ecosystem function in highly managed ecosystems is also important to address a bias that currently exists in ecological monitoring (Martin et al. 2012). Roadside ecosystems provide habitat for native wildlife (McCleery et al. 2015), refugia for rare native plants (Forman et al. 2003, Forman and McDonald 2007, Brown and Sawyer 2012), and create buffer zones between developed areas and sensitive ecosystems like wetlands by filtering pollutants from storm water runoff (Rammohan 2006). However, roads and roadway activities are also a major cause of landscape fragmentation, habitat loss, and non-point source pollutants (US EPA 1990, Laurance et al. 2014). Because they are highly disturbed, roadsides are also vulnerable to plant invasions (Forman and McDonald 2007).

Vegetation establishment and control, including mowing, is the primary tool of roadside vegetation management. Frequent mowing can improve driver safety by increasing sight lines, reducing fire fuel loads, and decreasing costs associated with control of some invasive plant species (AASHTO 2011). However, mowing is also a frequent and intense disturbance, is expensive in terms of labor and fuel, can facilitate the spread of invasive plants, and emissions from mowers can result in up to 35 kg of CO_2 emissions per shoulder-kilometer (AASHTO 2011, Sonntag et al. 2011, Cal-IPC 2012).

To balance the pros and cons of mowing, many Departments of Transportation (DOTs) have altered vegetation control guidelines to reduce mowing in areas where driver safety is not affected (AASHTO 2011). This reduces CO_2 emissions, habitat fragmentation, management costs, and creates better habitat for some wildlife (AASHTO 2011) as it transitions from frequently mowed grassland to early successional habitat. McCleery et al. (2015) found that many avian species increase their use of roadside habitats when vegetation is taller and denser. At-risk species, such as the *Sylvilagus transitionalis* (New England cottontail) that suffer from decreased availability of early successional habitat in New England, may benefit from increased structural complexity afforded by reduced mowing (Fenderson et al. 2014). However, increased roadside habitat may increase the potential risk for road related mortality in vertebrates, which have been found to increase with vegetation cover (Clevenger et al. 2003).

Insects and native plant species may benefit from taller and denser vegetation without risking road related death (Brown and Sawyer 2012). Bees and other pollinating species utilize restored roadside habitat (Ries et al. 2001, Hopwood 2008). Meadow butterflies, such as *Aphantopus hyperantus* (ringlet), have been observed in several types of roadsides and occur at higher densities in unmowed areas or those mowed in the late summer compared to those that are mowed in the early summer (Valtonen and Saarinen

Table 1. **Roadside Vegetation Community Descriptions under three different vegetation management plans (W. Whelan, Rhode Island Department of Transportation, pers. comm.; Brown and Sawyer 2012).**

Management Approaches	Description
Mowed	Mowed completely 3–6 times a year. Medians are mowed pavement to pavement; shoulders are mowed in the operational and transition zone. Dominated by short grasses.
Restored	The operational zone is mowed 1–2 times annually, while the transition zone is not mowed at all. These areas have not been mowed for 5–8 years. Characterized by tall grass, shrubs, and small trees. Early successional.
Reference	Areas that were historically clear-cut for agriculture, but have since afforested. These communities have never been managed by RIDOT through mowing, except for a narrow operational zone. Characterized by self-sustaining communities dominated by trees. "Young" forest.

2005). Roadsides are also important habitat for *Asclepias syriaca* (common milkweed)—the single host for monarch butterflies (*Danaus plexippus*)—whose populations will benefit from a careful mowing plan (Pleasants 2016).

Reducing roadside mowing has many advantages, but a major concern of transitioning to this passive form of management is increasing the establishment and spread of weedy and invasive plant species (Dubner 2017). Many invasive plants—those non-native species which spread quickly and are likely to cause harm to environmental, economic, and human health—are fast-growing, shade intolerant, and disturbance tolerant—traits that allow them to thrive in roadsides (Harper-Lore and Wilson 2000, Forman and McDonald 2007). In addition to providing good habitat for invaders, roadsides provide a pathway for facilitated dispersal. Vehicles, wildlife, and wind move propagules along the roadside, increasing the range of non-native and invasive plants (Forman and McDonald 2007, Mortensen et al. 2009). Some invasive roadside plant species are capable of degrading road surfaces, impede drainage, and damage communication infrastructures if left unmanaged (Perron 2008). Once established, significant resources are often necessary for any level of control, and eradication may not be possible (Perron 2008), as is the case with *Celastrus orbiculatus* (Asian bittersweet), a common roadside invader that produces abundant seeds, has high rates of germination and establishment, and can reproduce clonally, making populations very difficult to control (Fryer 2011).

Following national trends, the Rhode Island Department of Transportation (RIDOT) implemented a low-mow maintenance regimen in many areas of the state over the last decade where taller vegetation does not impede horizontal sight distance. This shift has brought about two changes. First, mowing of the operational zone has been reduced from 4–6 mows to 1–3 mows per year. Operational zones are the vegetated areas directly adjacent to roadways that must be mowed at least once a year to prevent the regrowth of woody vegetation and to be available for safe vehicle recovery (Figure 1). Second, mowing was eliminated in the transition zone, the area between the operational zone and the surrounding landscape, (Figure 1) where high frequency mowing was the historic maintenance practice. The elimination of mowing has restored these areas to patches of open grassland and shrubland—a mixture of native and introduced grasses, forbs, and small shrubs (Brown and Sawyer 2012)

Brown and Sawyer (2012) found that native species naturally colonize roadsides in Rhode Island, and while half of the species in their roadside sites were non-native, they generally occurred in very low abundances or were naturalized species such as *Elymus repens* (quackgrass) and *Digitaria ischaemum* (smooth crabgrass). While reduced mowing has been observed to increase native diversity in roadside native forbs and grasses, such as *Solidago* spp. (goldenrod) and *Dichanthelium* spp. ([*Panicum* spp.] panicgrasses; Guyton et al. 2014), it may cause proliferation of woody invaders that are usually excluded from roadsides because of mowing (Brown and Sawyer 2012). This includes *C. orbiculatus*, *Rosa multifora* (multiforal rose), and *Elaeagnus umbellata* (autumn olive; Zouhar 2005).

Currently, RIDOT targets all weedy and invasive plant species growing along high-speed barriers (i.e., guard rails) by applying Razor Pro (Glyphosate, N (phosphonomethyl) glycine), a broad-spectrum herbicide (W. Whelan, Rhode Island Department of Transportation pers. comm). The only species RIDOT specifically targets for control or removal is the native nuisance, *Toxicodendron radicans* (poison ivy). *Toxicodendron radicans* is often found on forest edges, such as highway roadsides, and is effectively managed through a combination of mowing and herbicide treatment (Innes, Robin J. 2012). While it is native to New England, it can grow in dense mats, excluding other species (Innes, Robin J. 2012) and is the biggest hindrance to RIDOT operations (W. Whelan, Rhode Island Department of Transportation pers. comm). *Toxicodendron radicans* is a common early successional plant which may proliferate in roadsides undergoing passive restoration.

To address the issue of invasive and nuisance species control in restored roadsides, we quantified the effects of mowing frequency on native (all species native to RI), introduced (all species not native to RI), and invasive (all species listed as invasive by the state of RI) plant abundance in Rhode Island roadsides. We surveyed roadsides under three different vegetation management plans ("Mowed": traditional mowing plan, "Restored": low-mow plan, “Reference”: no-mow plan; Table 1) allowing us to compare the community composition in roadsides in different stages of succession for species richness (i.e., number of species) and percent cover. We predicted that: 1) Reference communities would have the highest native species richness and cover because they are less disturbed; 2) Mowed and Restored communities would have a greater percent cover of introduced and invasive plants relative to Reference communities because they experience more disturbance; and 3) Restored communities undergoing passive restoration would be at risk of having the highest invasive species diversity and percent cover because they are no longer receiving invasive species management via mowing.

Methods

Study Area

All sites were located within Rhode Island, a southern New England state with a total area of just over 3,000 km². The small state contains three topographic regions: (1) coastal plain with low elevations along the southern coastline; (2) rolling uplands in the eastern part of the state, near Narragansett Bay; (3) hilly uplands in the western portion of the state (RIDEM 2017). Rhode Island is humid and temperate, with an average annual temperature of 9°C and average annual precipitation of 105–115 cm. Winter weather often includes snow and ice. Annually, there are an average of four days with a maximum temperature over 32°C and four days with a low below 0°C (RIDEM 2017). The majority of Rhode Island’s soil parent materials are glacial till and glacial outwash; the most common soil orders found in RI include Histosols, Inceptisols, and Entisols (William and Sautter 1988).

Site Selection and Maintenance

Roads were mapped using ArcGIS Desktop 10.2 (Redlands, CA: Environmental Systems Research Institute) and Rhode Island Geographic Information System (RIGIS) mapping layers. Working closely with roadside managers at RIDOT, we visited 50 possible sites that fell into one of three vegetation management categories: Mowed, Restored, Reference (Table 1). We selected five sites under each of the three mowing treatments (Supplementary Figure S1 and Table S1). In order to choose these sites, we first analyzed sites for annual average daily traffic (AADT, 24-hour vehicle counts averaged over a year) using a RIDOT map layer (RIGIS 2003). All sites over 50,000 AADT were excluded for safety reasons. We then surveyed sites for characteristics shown to be significant to establishment of roadside vegetation, including soil type and hydrology, surrounding land use, hydrological conditions, general slope, and aspect (Kayhanian et al. 2002, Mortensen et al. 2009). These factors were kept as constant as possible across sites and site type.

Salt and herbicide application are two common RIDOT maintenance practices which impact vegetation composition and cover. RIDOT’s application of salt and sand is generally standard across the state, but areas further from the coast may receive more snow and freezing rain (Brown and Sawyer 2012). To control for the effects of deicing salts, we left a five-meter buffer between the road edge and survey plots. Sodium (Na) soil concentrations significantly decreases with the distance to the road surface and were markedly reduced within five meters of the road edge in Massachusetts roadsides (Bryson and Barker 2002). This buffer likely reduced selection based on salinity levels. Herbicide application is focused around high-speed barriers, such as guardrails (W. Whelan, Rhode Island Department of Transportation pers. comm.). Because none of our sites were located within sight of any high-speed barriers, it is unlikely that our sites were significantly affected by herbicide application.

Vegetation Surveys

At each site we used a nested plot design to assess plant communities at multiple scales. Specifically, we performed a modified Whittaker vegetation survey (Stohlgren 1995) to collect a comprehensive list of species during peak vegetation (phenological maximum). Each plot was 20 m wide and 50 m long (1000 m²), and contained 13 subplots of three different sizes: one 5-m × 20-m (100-m², subplot C) was in the middle of the plot, two 2-m × 5-m (10-m²) subplots (A and B) were at opposite corners of the plot, and 10 0.5-m × 2-m (1-m²) subplots were located around the perimeter of the main and center plots. Six of the 1-m² subplots were placed around the inside of the plot perimeter border, while the other four were placed around the outside perimeter of the center subplot (Figure 2).

Vegetation survey plots were placed with the long side of the plot running parallel with the road (Figure 2). A buffer of five meters between the plot and the pavement was maintained for safety and to reduce salinity effects on vegetation (Bryson and Barker 2002). Subplots B (10 m²) and two of the 1-m² plots were all within the operational zone. There is no standardized width of operational zones, but they are generally 5–10 m wide strips of low-growing herbaceous vegetation (W. Whelan, Rhode Island Department of Transportation pers. comm.). Subplots A (10 m²), C (100 m²), and eight of the 1-m² plots were in the transition zone. Transition zones are composed of short mowed grasslands in Mowed sites (indistinguishable from the operational zone), early successional grass and shrub land in Restored sites, and young forests in Reference sites (Figure 2).

All vegetation surveys were performed once from July 18–August 15, 2014. At each of the 15 sites, we recorded all species presence in subplots A, B, and C and then surveyed the 10 small subplots, recording species presence and percent cover. We then surveyed the rest of the 1000-m²

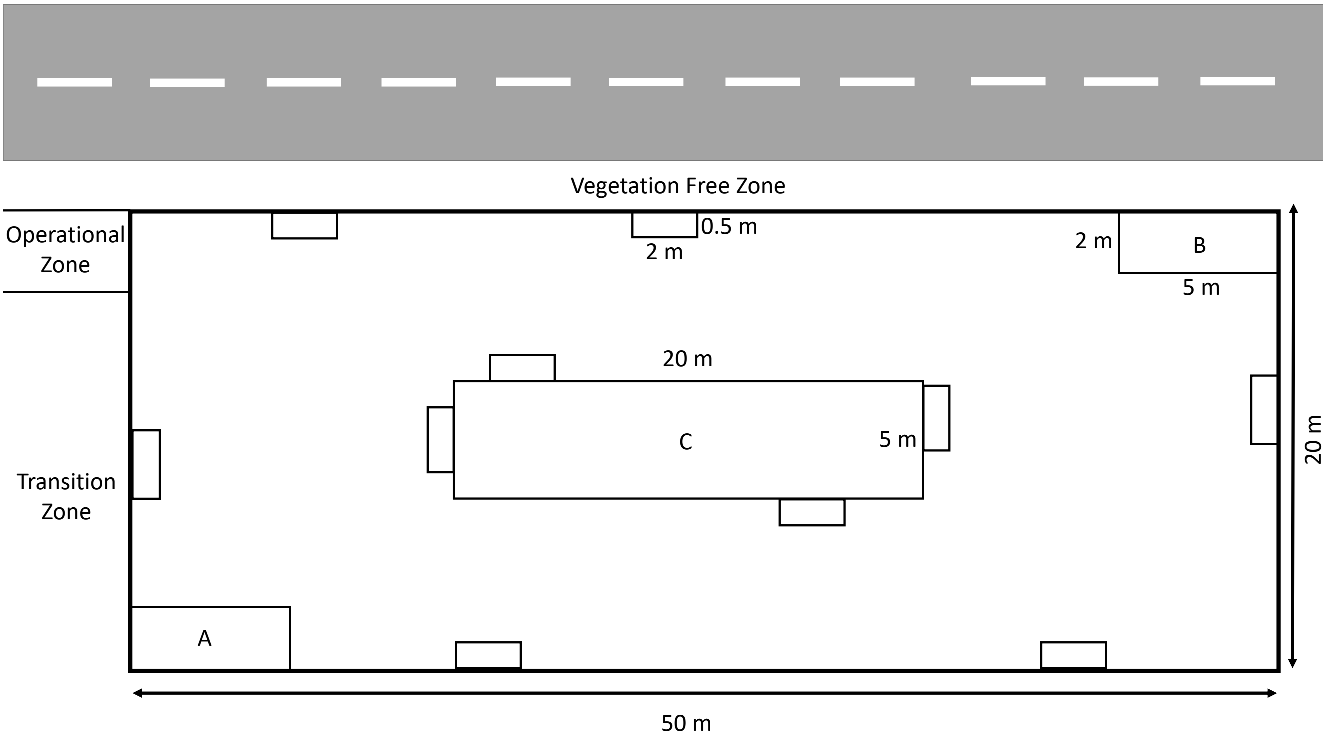

Figure 2. Modified Whittaker plot design and relative position to road and roadside zones. Subplots on the edge nearest to the road were always located within the operational zone during surveys.

plot and recorded any species that were not present in any of the subplots. Any broadleaf species not identified in the field were collected and later identified using "Flora of the Northeast" (Magee and Ahles 2007). Grass species were collected, planted in a greenhouse, allowed to flower and then identified under a compound microscope using the guide, "Some Grasses of the Northeast" (Phillips 1962). The 3% of plants that could not be identified to species were identified to genus and considered as individual species when calculating species richness, but were not included in native, introduced, or invasive species richness estimates or percent cover calculations.

Species were categorized as "native," "introduced," and/or "invasive" based on classifications determined using the New England Wild Flower Society's online dichotomous key, "GoBotany" (gobotany.newenglandwild.org). All species native to Rhode Island were categorized as "native," all non-native species were categorized as "introduced" and those introduced species that have a conservation concern of invasive in Rhode Island, or its border states (Connecticut and Massachusetts), were classified as "invasive."

Data Analysis

To assess differences in community composition among three management treatments (Table 1), we used one-way Analysis of Variance (ANOVA) to compare the following metrics: diversity indices (Simpson's and Shannon-Wiener), total species richness, native species richness, introduced species richness, and invasive species richness. For analysis of 10-m^2 and 1-m^2 subplots richness and percent cover of native, introduced, and invasive species (gathered at the 1-m^2 spatial scale), we used nested ANOVAs to address pseudoreplication. Percent cover data were log-transformed to achieve normality and homoscedasticity. To compare operational zone composition among mowing treatments we performed nested ANOVAs, only including those subplots that were within the operational zone (Figure 2). The same analysis comparing transition zone composition was performed, including only the subplots located within that zone (Figure 2). All data analysis was done in R Studio (R Studio v 1.0.153, R Foundation for Statistical Computing, Vienna, Austria) and $p < 0.05$ was used to determine significance for all tests.

Results

Species Composition

In our roadside surveys, we observed 15 species that have been given the conservation status of "invasive" in Rhode Island or its border states, Massachusetts and Connecticut (Supplementary Table S2). Most invasives were found in similarly low abundances between Mowed and Restored sites. However, *R. multiflora* was found in only one Mowed site, but in three Restored sites. *Toxicodendron radicans*, the main plant species of concern for RIDOT vegetation managers (W. Whelan, Rhode Island Department of

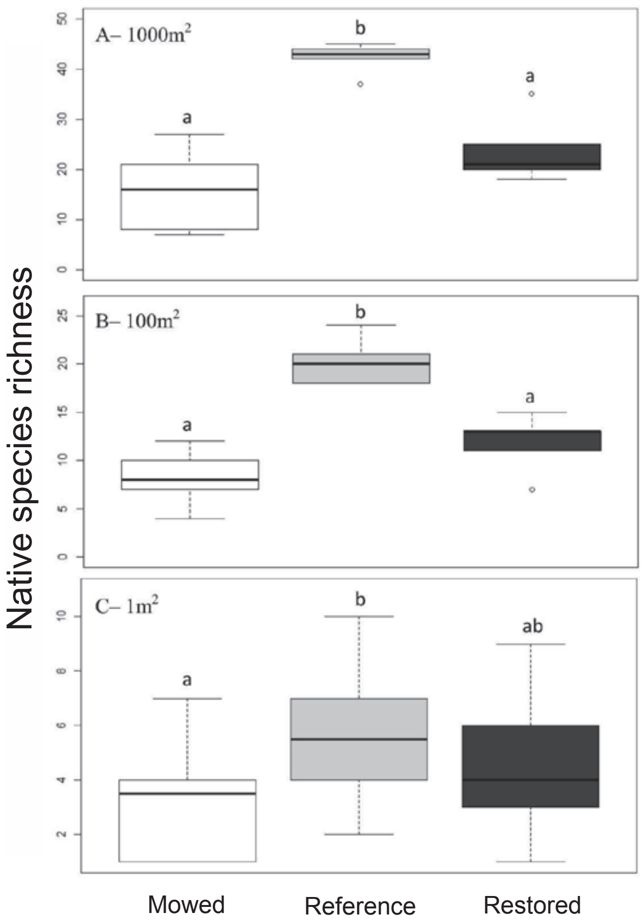

Figure 3. Differences in native species richness between three vegetation management plans (mowed, reference [roadside forests], and restored [infrequent/eliminated mowing]). A) Differences in native species richness in 1000-m² plots B) 100-m² subplots C) 1-m² subplots.

Transportation pers. comm.), was found in eight of the fifteen roadside sites (one Mowed, five Reference, and two Restored sites) and in 19 of the 1-m² subplots at an average 7.8% cover in the Reference sites.

The most common species we encountered was *Rumex acetosella* (common sheep sorrel), a prohibited invader in Connecticut. We encountered *R. acetosella* at 13 out of 15 sites and 26 of the total 150 1-m² subplots at an average of 1.4% cover (Supplementary Table S2). The average percent cover in subplots containing *R. acetosella* ranged from 0.5% in Restored sites to 2.3% in Reference sites. *Potentilla canadensis* (dwarf cinquefoil, native), *Andropogon virginicus* (broomsedge bluestem, native), *Juncus tenuis* (path rush, native), and *Digitaria sanguinalis* (hairy crabgrass, introduced) are also generally important roadside species, occurring in most roadside sites in similar abundances regardless of mowing treatment (Supplementary Table S2).

Plantago lanceolata (English plantain, introduced) and *Baptisia tinctoria* (yellow wild indigo, native) were common species at Mowed sites and Restored sites based on the prevalence of occurrence and average percent cover. *Eragrostis spectabilis* (purple lovegrass, native), *Hypochaeris radicata* (cat's ear), and *Trifolium pratense* (white clover, introduced) were additional dominant species in Mowed sites. Restored sites were also characterized by *A. virginicus* (broomsedge bluestem, native), *Dichanthelium acuminatum* (rosette-panicgrass [= *Panicum acuminatum*], native), and *Anthoxanthum odoratum* (sweet vernalgrass, introduced). At Reference sites the top species were *T. radicans* (native), *Agrostis perennans* (autumn bentgrass, native), *Vaccinium corymbosum* (highhush blueberry, native), *Smilax glauca* (glaucous-leaved greenbriar, native), and *Maianthemum canadense* (Canada mayflower, native [Supplementary Table S2]).

Measures of Richness

We found no significant differences in overall species richness between any of the mowing treatments. Additionally, we found no significant difference in the Simpson's or Shannon-Wiener diversity indices. However, we observed significant differences in native species richness depending on spatial scale (ANOVA; 1000-m²: $F_{2,12} = 21.46$, $p = 0.0001$; 100-m²: $F_{2,12} = 23.12$, $p < 0.0001$; 10-m²: $F_{2,12} = 3.69$, $p = 0.056$; 1-m²: $F_{2,12} = 4.69$, $p = 0.031$; Figure 3, Supplementary Table S3). Reference sites had higher native richness than did Mowed and Restored sites at the two largest spatial scales (1000-m²: Mowed-Reference, $p = 0.0001$, Restored-Reference, $p = 0.002$, Figure 3A; 100-m²: Mowed-Reference $p < 0.0001$, Restored-Reference $p = 0.002$, Figure 3B). Reference sites also had higher native species richness than Mowed sites at the 1-m² scale ($p = 0.025$, Figure 3C).

We also observed a significant difference in introduced species richness between vegetation management plans for the three smallest spatial scales (ANOVA; 100-m²: $F_{2,12} = 23.12$, $p = 0.003$; 10-m²: $F_{2,12} = 9.93$, $p = 0.003$; 1-m²: $F_{2,12} = 22.15$, $p < 0.0001$; Figure 4; Supplementary Table S3). Reference sites had lower introduced species richness than did Mowed or Restored sites at all three of these spatial scales (100-m²: Mowed-Reference $p = 0.003$, Restored-Reference $p = 0.038$, Figure 4A; 10-m²: Mowed-Reference $p = 0.005$, Restored-Reference $p = 0.008$, Figure 4B; 1-m²: Mowed-Reference $p = 0.0001$, Restored-Reference $p = 0.0005$, Figure 4C). We observed no significant difference in total, native, or introduced species richness between Mowed and Restored sites. Additionally, we observed no significant differences in roadside invasive species richness because of the vegetation management plan.

Species Cover

We found that the mean introduced species percent cover was significantly different between mowing treatments (ANOVA; $F_{2,12} = 23.16$, $p < 0.0001$; Figure 5, Supplementary Table S3). Reference sites had significantly lower introduced species cover than did Mowed sites ($p = 0.0002$) and Restored sites ($p = 0.0003$). We observed no significant differences in native ($p = 0.3$) or invasive ($p = 0.4$) species

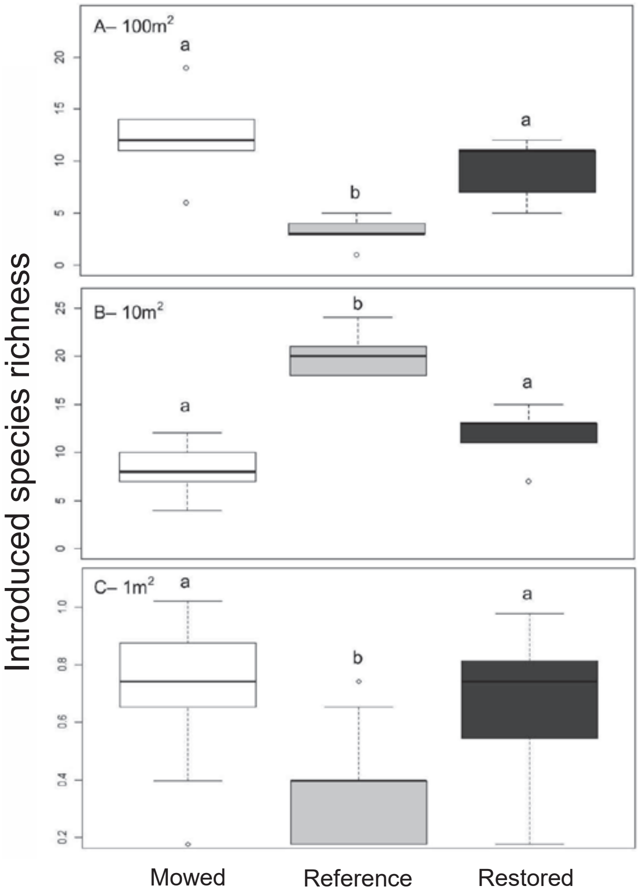

Figure 4. Differences in introduced species richness between three vegetation management plans (mowed, reference [roadside forests], and restored [infrequent/eliminated mowing]). A) Differences in native species richness in 100-m² subplots B) 10-m² subplots C) 1-m² subplots.

percent cover between any of the vegetation management plans.

Vegetation Zonal Effects

We found that native and introduced percent cover were significantly different in operational zones among mowing treatments, even though operational zones are mowed under all vegetation management plans (ANOVA; $F_{2,12} = 8.63$, $p = 0.005$; $F_{2,12} = 5.57$, $p = 0.018$; Supplementary Table S4). Operational zones adjacent to Reference sites had higher native percent cover than Mowed or Restored sites (Mowed-Reference $p = 0.027$, Restored-Reference $p = 0.005$) and lower introduced percent cover than Restored site operational zones ($p = 0.018$).

When we only included subplots located within the transition zone in our analysis, native species richness, introduced species richness, and introduced percent cover were all significantly different among site types (ANOVA; $F_{2,12} = 6.94$, $p = 0.01$; $F_{2,12} = 10.59$, $p = 0.002$; $F_{2,12} = 15.43$, $p = 0.0005$; Supplementary Table S4). Native species richness was higher in Reference transition zones than in Mowed transition zones ($p = 0.008$). Both introduced species richness and introduced species percent cover were lower in Reference site transition zones than in Mowed or Restored transition zones (Mowed-Reference: introduced richness $p = 0.003$, introduced cover $p = 0.0007$; Restored-Reference: introduced richness $p = 0.008$, introduced cover $p = 0.002$).

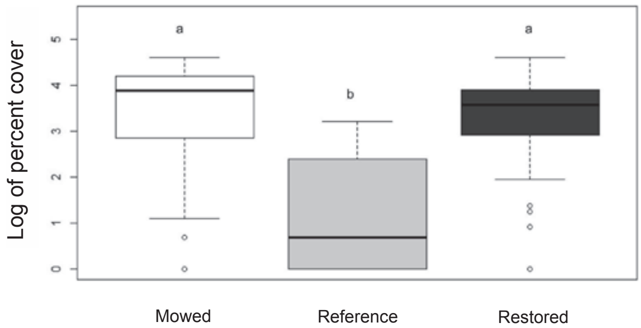

Figure 5. Differences in introduced species percent cover between three vegetation management plans (mowed, reference [roadside forests], and restored [infrequent/eliminated mowing]) in 1-m² subplots.

Discussion

Roadside ecosystems transitioning from a highly maintained to a passively restored management plan ("Restored" sites) did not significantly differ in native, introduced, or invasive plant species diversity from sites still managed through frequent mowing ("Mowed" sites). These two types of roadsides also had a similar composition, dominated by many of the same species (Supplementary Table S2). Reference sites (forested roadsides) were distinct from Mowed and Restored sites, with the highest native species diversity and lowest introduced species diversity. These patterns of biodiversity were generally consistent across both the transition and operational zones and for all spatial scales.

Rumex acetosella was the most widespread species encountered in our survey, occurring at all but one Reference and Restored site. It occurred in more subplots in Mowed and Restored sites than in forested Reference sites, but was always observed at generally low densities (Supplementary Table S2). While this species is listed as a potential invader in Connecticut, it is generally considered a naturalized species throughout the rest of New England (Brown and Sawyer 2012). Because it is not growing in dense patches, *R. acetosella* is likely not displacing native species and should not be a major concern to roadside managers.

Seedlings of the woody invaders *C. orbiculatus*, *E. umbellata*, and *R. multiflora* may be partially controlled through frequent mowing (Munger 2002, Munger 2003, and Perron 2008), so these are of concern during the shift from frequent mowing to passive restoration. We observed *C. orbiculatus* at six sites, one Mowed site, two Restored sites, and three forested Reference sites. Though it has only invaded two of the Restored sites, this species may need continued monitoring as it is somewhat widespread within the sites where it was located (Supplementary Table S2). This species was most widespread in the forested Reference sites, occurring at three of the five sites with an average cover of 9.1% (Supplementary Table S2), which indicates mowing may be important in controlling this species. *Rosa multiflora* appeared to be similarly affected by mowing, occurring in seven sites (one Mowed, three Restored, and three Reference sites) with highest densities in the forested Reference sites and low densities in the Restored sites. Alternatively, we found *E. umbellata* at four sites (one Mowed, one Reference, and two Restored; Supplementary Table S2), but at similar low densities for all mowing treatments. Restored roadsides where *C. orbiculatus* and *R. multiflora* were observed should be monitored and potentially controlled with the use of herbicide treatments.

We observed abundant *T. radicans* populations in every Reference site, illustrating its ability to thrive in forest edges (Innes 2012). Conversely, *T. radicans* was not widely distributed in Mowed or Restored sites. Because we did not observe proliferation of *T. radicans* in Restored sites undergoing succession, it should not create a management issue for RIDOT. Mowed and Restored sites contained many similar species, including *P. lanceolata*, a naturalized introduced species, and *B. tinctoria,* a native legume. Mowed sites were also characterized by introduced, perennial wildflowers such as *H. radicata* and *Trifolium repens* (white clover), and disturbance tolerant grasses including *E. spectabilis* and *Agrostis capillaris* (Rhode Island bentgrass). Restored sites were characterized by native and non-native grasses associated with early secondary succession such as *A. virginicus* (Bazzaz 1968) and *D. acuminatum* (Walsh 1995).

Because passively Restored roadsides are no longer being mowed, an oft-used management strategy for many invasive species (AASHTO 2011), we expected higher occurrences and density of invasive species at Restored sites than areas managed as forests (Reference sites) or as Mowed sites. Instead, we found no significant difference among sites. One explanation may be that invasive plants have not yet had a chance to colonize these areas, and continued monitoring over time may reveal a different pattern. One limitation to this study is that surveys were conducted only once. However, because these areas have been under a reduced mowing regimen for five to eight years, invasion should not be of high concern to managers.

While we found no differences in invasive species populations, introduced species occurred more frequently, and in higher densities, in Mowed and Restored sites than in Reference communities. Although most introduced species we found on roadsides are not considered invasive, monitoring remains critical because introduced plants can become invasive later, following a lag phase (Reaser et al. 2007). To address this concern, we recommend managers monitor invasive species every few years.

Our results suggest that roadside forested communities have greater native species richness and fewer non-native species, a trend that has been described in other roadside studies (Watkins et al. 2003). This is likely due to reduced disturbance, greater resource availability, and a reduced risk of exotic propagule spread through roadside maintenance practices. When roadside mowing is performed, reproductively viable plant parts of introduced species can be transported to new locations on the blades of improperly cleaned mowers, potentially introducing them elsewhere (Perron 2008). Because mowers only enter the operational zone of forested communities, there is a decreased opportunity for propagules to successfully establish within the transition zone. Additionally, the narrow operational zones adjacent to forested Reference sites had a significantly higher cover of native species and lower cover of introduced species compared to the operational zones of Restored and Mowed sites. It may be that mowed areas next to forested communities are under higher propagule pressure from native species, which are at higher densities in forests and under lower propagule pressure from introduced species, which are at lower densities in forests (Vilà and Ibáñez 2011).

Higher native species diversity may also confer resistance to invasion in Reference sites due to the tightly constructed niche partitions that arise when many species co-occur (Elton 1958, Case 1990). This pattern of biodiversity, known as the biotic resistance hypothesis, has been supported in small-scale field experiments that found negative relationships between community biodiversity and invasion (Case 1990, Tilman 1999). Conversely, studies conducted at larger spatial scales have found positive relationships between exotic and native species richness (i.e., The rich get richer; Stohlgren et al. 1999, Stohlgren et al. 2001). This opposing pattern at varying spatial scales is known as the "invasion paradox" (Fridley et al. 2007). Because of this paradox, it was important to capture plant dynamics at varying scales in this study.

In our roadside study, we found that there was an inverse relationship between native species richness and introduced species richness with the fewest introduced species established where native biodiversity is the highest (i.e., Reference sites), and more introduced species where native diversity was lower (i.e., Mowed and Restored sites; Figures 3 and 4). These findings support the biotic resistance hypothesis, suggesting native biodiversity is conferring biotic resistance in roadsides (Tilman 1999). Because the patterns we observed in roadside vegetation composition were consistent across multiple spatial scales (Supplementary Table S3), future monitoring efforts can likely be done at fewer spatial scales. However, we suggest retaining measurements at smaller scales so that percent species cover can still be collected.

Combining our findings that native species are proliferating in both zones of Reference sites with our findings that invasive and introduced species are not proliferating in areas that are undergoing natural succession supports a change in maintenance. Our results should give managers confidence to implement these sorts of passive restoration techniques in many roadside environments. Managers may choose to allow many areas to transition to young forests, a common habitat in the northeastern United States. Alternatively, managers may choose to mow areas every 5–10 years to keep them as early successional habitat, a currently rare ecosystem in the northeastern United States (Fenderson et al. 2014). Because this change in maintenance may risk increase road related mortality in some wildlife species, managers may need to carefully consider the locations of Restored roadsides. One potential solution is to ensure metal culverts and underpasses are present near passively restored areas to allow wildlife to cross under the roadway safely (Clevenger et al. 2003). Additionally, selecting restoration sites based on the surrounding lowland carrying capacity of wildlife species may help managers manage the risks associated with denser roadside vegetation (Guyton 2014).

A reduction in mowing has the advantage of being a low-cost passive habitat restoration technique, like passive restoration in abandoned old fields (Papnastasis 2007, Porensky et al. 2014), that can foster native habitat and potentially benefit water quality (Harrison 2014). Many roadside remediations, such as stormwater retention ponds, come at a high cost in terms of labor and funds. Reduced mowing, however, can increase ecological function of roadsides while saving money. Increasing development and ecosystem disturbance means humans are rapidly degrading many ecosystem services (Millennium Ecosystem Assessment 2005). Therefore, it is critical to ensure that semi-natural, managed areas such as roadside ecosystems provide and maximize as many ecosystem services as possible. Highly anthropogenically altered systems have received relatively little attention from ecologists and managers, which can dramatically bias our understanding of ecological processes. This study fills an important gap by adding to the understanding of the ecological function in a globally common, urban/suburban environment (Martin et al. 2012, Cadotte et al. 2017).

Moving away from traditional mowing practices and towards reduced, low, or no mow practices is a growing trend among roadside management agencies, and some states are already seeing benefits. Many other parts of the United States including Nebraska, Washington, Missouri, Minnesota, Wisconsin, Colorado, Iowa, New York, Utah, and Texas have incorporated a reduction in mowing as part of their mowing policies (AASHTO 2011). In 2014, the Florida DOT reported that a sustainable vegetation management plan, which includes a reduction in mowing, would cut the state's vegetation management bill by 30 percent (Harrison 2014). The same report found that utilizing a sustainable vegetation management plan doubled the ecosystem services economic value, gaining half a billion dollars. In Rhode Island, we can expect similar effects on ecosystem services from denser roadside vegetation, including increased stormwater filtration (Nagase and Dunnett 2012), erosion control, and soil carbon sequestration and nitrogen accumulation (García-Palacios et al. 2011). The potential benefits to sensitive species, including wildlife and rare plants, warrants further study.

Reducing mowing also has the potential to decrease carbon dioxide emissions. For example, RIDOT produces nearly 230,000 kg of CO_2 emissions each mowing season (Brown et al. 2011, Sonntag et al. 2011, Rhode Island Office of Management and Budget 2012, W. Whelan, Rhode Island Department of Transportation, pers. comm.). Reducing these emissions through a reduction in mowing could improve the air quality in southern New England. Assuming similar mowing practices between states across the country, CO_2 emissions could be cut by approximately 2 million kg every year if reduced mowing is implemented in just half of the roadsides associated with the National Highway System (FHWA 2011).

As natural landscapes decrease all over the world it is vital and urgent that we are creative and opportunistic in where and how we choose to focus management and restoration efforts to best serve the public as well as native plants and animals. One approach is to ensure that roadsides and other highly constructed areas provide as many ecosystem functions as possible while we mitigate the negative environment effects caused by our roadways. Reduced mowing is an example of sensible, realistic management shifts that can balance the requirement for human connectivity through linear construction with the need for habitat restoration that provides opportunities for cost-savings and reductions in CO_2 emissions.

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Restored roadside with native grass mix. *Photo credit: S.N. Handel.*