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Differences in landscape drivers of garlic mustard invasion within and across ecoregions

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Abstract While landscape models of invasive plant distributions have potential for targeting management areas, we focus on two reasons such models may be limited in their application. First, models to date are biased towards explaining establishment in ruderal habitat but not spread of invasives into adjacent habitat, where they may most impact native plants. Second, models are usually developed across ecoregions or for a single ecoregion, and it is unclear how well models for different regions and spatial extents agree. Our aims were to (1) test how landscape variables explain garlic mustard (*Alliaria petiolata*) occurrence on forest edges and its incursion into forest understory habitat; (2) compare models constructed for two ecoregions, separately, and both ecoregions together. In 183 sites in two ecoregions in Massachusetts, we recorded whether garlic mustard occurred on the forest edge (edge occurrence) and in the understory (understory incursion). We used logistic regression to relate either edge occurrence or understory incursion to elevation and four variables describing land use surrounding each site: percent open land in 1830, percent developed and agricultural land in 2005, and forest-edge length in 2005. Elevation was negatively associated with edge occurrence within regions but positively associated across regions. Land use from 2005 explained edge occurrence and understory incursion in only one region. These results suggest that mechanisms driving garlic mustard distributions are scale- and region-dependent. Our findings also suggest that region-specific invasive distribution models are necessary, and we caution against implying probability of understory incursion from the probability of edge establishment.

Keywords Garlic mustard · Invasive, understory · *Alliaria petiolata* · Land use · Distribution

Introduction

Identifying the landscape drivers of invasive plant distributions can help target management areas, reduce landscape invasion potential, and predict future spread (With 2002; Vilà and Ibáñez 2011; Thomas and Moloney 2015). Models are commonly parameterized with land uses related to past and present human disturbance, especially agriculture, developed areas, and road networks, which are associated with the establishment of invasive species (reviewed in Vilà and Ibáñez 2011). Human disturbance can facilitate invasive establishment by reducing the cover of competitors in an area and increasing the availability of limiting resources, especially light (Pyle 1995;

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Davis et al. 2000). Human activity can also increase propagule availability and dispersal when plants and seeds are intentionally or unintentionally introduced into an area (Chytrý et al. 2008). Therefore, sites within or near areas of human disturbance are expected to have a relatively high probability of invasive establishment. It is unclear, however, whether the landscape variables that explain establishment in ruderal habitats can also explain spread into adjacent habitats that are less disturbed, such as forest understory. This is an important area of research because it is in these new habitats where invasive plants are most likely to negatively impact native species (Brewer 2011). Furthermore, given that most models of invasive species are developed across ecoregions or within single ecoregions, it is unclear whether and how the effects of landscape variables on invasion vary between regions. Our study addresses these two important gaps in the literature.

Invasive distribution models often implicitly assume that the probability of occurrence is equivalent to the probability of invasive impact (Bradley 2013). However, the impact of an invasive at any point in the landscape depends on the local habitat and the presence of native species vulnerable to invasion (Brewer 2011). For example, invasive plant populations in understory habitats, where native plants are abundant, are more likely to have negative impacts on native plant communities than are invasive populations confined to forest edges. With over 100 species known to invade forest understories (Martin et al. 2009), it is important to explicitly model probability of incursion into understory habitats in addition to probability of establishment in disturbed edge habitat. Landscape variables may influence incursion into forest understory via two main mechanisms. First, landscape variables associated with disturbance may alter habitat quality. For example, historical agricultural practices can have legacy effects on secondary forest composition and soil properties, which may facilitate invasive spread (Foster et al. 1998; Compton and Boone 2000; McDonald et al. 2008). Second, because understory invasive populations may be sinks dependent on source populations on forest edges (Warren et al. 2011; Stinson and Seidler 2014), landscape variables that influence establishment on forest edges, as discussed above, may in turn influence incursion into the understory.

The landscape variables that are important in explaining invasive edge occurrence and understory incursion may change from one region to the next due to regional differences in invasion stage (Theoharides and Dukes 2007), historical and present land use, the abiotic environment, and the biotic community (Randin et al. 2006), as well as local adaptation of populations (Oduor et al. 2016). For example, across climatically distinct regions, a species can shift its apparent habitat within the landscape to consistently meet its physiological requirements, such as a set of temperature and soil moisture conditions (Randin et al. 2006). Furthermore, because invasive species may be strongly locally adapted to regional conditions (Blossey et al. 2017), models based on separate populations may perform better than models that treat a species as a single entity (Angert et al. 2011; Hällfors et al. 2016). While it is well known that invasive species vary in their preferred habitats between the native and introduced ranges (Broennimann et al. 2007; Gallagher et al. 2010; González-Moreno et al. 2015), how such differences play out between regions within the introduced range is not well explored (Riitters et al. 2018). It is possible that models relevant in one region may not be relevant in another (Ervin and Holly 2011), creating a management trade-off between the simplicity of having a multi-regional model and the necessity of having region-specific models.

As a case study, we focused on garlic mustard (*Alliaria petiolata*, Brassicaceae), which is a biennial herb that was introduced into North America in the 1800s (Grieve 2013). While garlic mustard first becomes established on forest edges and other areas of disturbance, it can spread into the understory and reduce native plant diversity and abundance there (Stinson et al. 2007). Large populations of garlic mustard tend to occur along roadside edges throughout both regions. Importantly, previous studies have shown that garlic mustard invasion and impacts vary by region (Nuzzo 1999; Rodgers et al. 2008; Stinson and Seidler 2014; Davis et al. 2015), suggesting that region-specific factors may be driving garlic mustard establishment and understory incursion. We produced models for two sub-ecoregions in Massachusetts that are characterized by distinct geologies, soils, and vegetation. We parameterized our models with well-established landscape variables known to explain the distribution of other invasives. To extend previous work, our aims were to (1) test how elevation and land-

use variables related to past and present human disturbance explain not only garlic mustard occurrence on forest edges but also incursion into the forest understory and (2) compare models built using datasets from each region separately (single-region datasets) and both regions together (cross-regional dataset) to determine how spatial extent and focal region influenced the results.

Methods

Study area

We surveyed garlic mustard in two sub-ecoregions in Massachusetts: the Berkshire Valley (BV) and the Connecticut River Valley (CRV). BV has a mean elevation of 307 m ($\pm$ 64 m SD), and its surficial geology is dominated by glacial till and bedrock. CRV has a mean elevation of 76 m ($\pm$ 31 m), and its surficial geology is dominated by sand and gravel (Hall et al. 2002). The forests in BV are dominated by transition hardwoods (maple-beech-birch and oak-hickory) and northern hardwoods (maple-beech-birch), while the forests in CRV are a mix of transition hardwoods and central hardwoods (oak-hickory; Griffith et al. 2009).

Field survey

We randomly selected sites along the roadside edge of forested areas that were (1) at least 100 m wide and 25 m deep, (2) continuously forested since 1971 (MassGIS 2017a; Kittredge et al. 2003; McDonald et al. 2006), (3) no more than 10 m from the road edge, and (4) at least 1 km away from each other. Furthermore, we stratified site selection by land use in 1830 (forested or open). BV had only 25 sites that were forested in 1830 and met our other site criteria. Therefore, BV had a total of 75 sites (25 forested in 1830 and 50 open in 1830), and CRV had a total of 100 sites (50 forested in 1830 and 50 open in 1830). We supplemented these sites with eight sites known to have garlic mustard growing on the forest edge, giving a total of 183 sites.

At each site, we recorded whether garlic mustard was present on the forest edge, resulting in a binary measure of edge occurrence. We also searched for garlic mustard in a 25-m-deep × 100-m-long forest understory area adjacent to the forest edge. As a binary measure of understory incursion, we recorded whether garlic mustard was growing anywhere in this understory area. Garlic mustard only invaded the understory in sites where it occurred on the edge; sites where garlic mustard did not occur on the edge were not assigned an understory incursion value and were excluded from the understory incursion analysis below. We surveyed the 1830-forested sites in the summer of 2006 and the remaining sites in the summer of 2007.

Landscape variables

The elevation of each site was extracted using a 5-m horizontal resolution digital elevation model (Mass-GIS 2017b). Elevation is a good proxy for temperature and precipitation (Daly et al. 2002) and has been used in other models of invasive plant distributions (Higgins et al. 1999). All spatial analyses here and below were conducted in ArcGIS 10.5.1 and Python 2.7.13.

We acquired land-use data from 1830 (Foster and Motzkin 2009), 1971 (MassGIS 2017a), and 2005 (MassGIS, 2017c). These datasets correspond to the time of garlic mustard introduction (Rodgers et al. 2008), the approximate time when garlic mustard became invasive in western Massachusetts (according to estimated population age; Lankau et al. 2009), and our field survey dates, respectively. The 1830 dataset was based on digitized maps of 1830 land use and is composed of forested areas and "open" areas (i.e., cultivated or pasture land; Hall et al. 2002). We reclassified the 1971 and 2005 land-use data to group all developed land (residential, commercial, industrial, and recreational) into a developed class and all agricultural land (pasture and cropland) into an agricultural class. These two classes were used to represent human disturbances that could facilitate invasive spread. Because some areas in the 2005 data had a minimum mapping unit (MMU) of less than one acre, we merged polygons less than one acre with surrounding polygons to accomplish a standardized MMU of 1 acre in the 1971 and 2005 datasets.

We obtained 2007 road centerline data (U.S. Bureau of the Census 2008) because the land-use datasets do not explicitly include roads, which can aid in invasive dispersal (Christen and Matlack 2006). Because garlic mustard is known to establish at forest

edges (Stinson and Seidler 2014), we created a forest-edge layer by merging the perimeters of the 2005 forest polygons with road lines that cut through the forest polygons.

Within 50 m and 1000 m of each point, we calculated the following seven land-use variables: percent cover of open area in 1830, percent covers of agriculture and developed areas in 1971 and 2005, total road length in 2007, and total forest-edge length in 2005. We used radii of 50 m and 1000 m to represent land use adjacent to the site (50 m), which could influence local conditions and propagule pressure, and the landscape context (1000 m), which could also influence propagule pressure (Thomas and Moloney 2015; Riitters et al. 2018). To broadly compare ecoregions, we also calculated these variables for each ecoregion.

Statistical analysis

We initially constructed a logistic regression model to explain garlic mustard occurrence on forest edge for the cross-regional dataset (BV and CRV together) that included elevation and all seven land-use variables within 1000 m of the sites. We examined the model's variance inflation factors (VIF) and used a cut-off of 4 to remove variables that were causing multicollinearity (Table S1, Zuur et al. 2010). We removed road length, which was correlated with 2005 developed area, and the 1971 land-use variables, which were correlated with the 2005 land-use variables. We maintained variables from 2005 instead of 1971 to allow comparisons with other studies that use contemporary land use. The remaining landscape variables (elevation, percent cover of open area in 1830, percent covers of agriculture and developed areas in 2005, and total forest-edge length in 2005; Fig. 1) were used in our final analyses, below. Statistical analyses here and below were conducted in R version 3.3.1 (R Core Team 2016).

With the reduced set of landscape variables, we used logistic regression to explain garlic mustard occurrence on forest edge for both regions together (cross-regional dataset) and each region separately (single-region datasets). For each dataset, we constructed two separate logistic regression models using elevation and the four land-use variables within either 50-m or 1000-m of the survey points (hereafter, 50-m and 1000-m models, respectively), resulting in a total
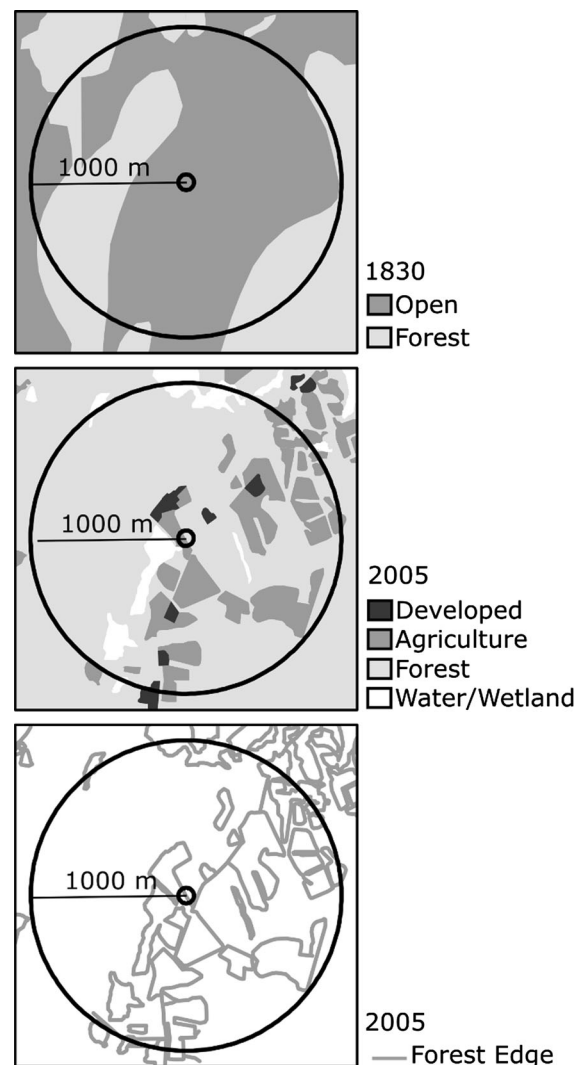

Fig. 1 Examples of land-use variables within 50 m and 1000 m of a site. Concentric black circles have radii of 50 m and 1000 m. We used the following four land-use variables in our final analyses: percent cover of open land in 1830, percent covers of developed land and agricultural land in 2005, and forest-edge length in 2005

of six models of garlic mustard edge occurrence. The significance of each landscape variable was assessed using a likelihood ratio test. We used the same variables and methods to construct models for garlic mustard incursion into the understory. However, we used penalized logistic regression (logistf function in the 'logistf' package; Heinze et al. 2016) because of a small sample bias and perfect separation.

Results

Overall, garlic mustard occurred on the forest edge in 58% of sites in BV and 21% of sites in CRV (Fig. 2). Of the sites where garlic mustard occurred on the forest edge, 77% of sites in BV and 59% of sites in CRV had incursion into the understory. Compared to BV, CRV had more developed area in 1971 and 2005 and higher road density (Table 1).

Occurrence on forest edges

For all datasets, elevation significantly explained occurrence on forest edges (Table 2). However, the models for the cross-regional dataset showed a positive association between elevation and the probability of edge occurrence (Fig. 3a), while the models for the single-region datasets showed a negative association (Figs. 3b, c). No land-use variables were significant in the 50-m or 1000-m models for the cross-regional dataset or BV. For CRV, 2005 forest-edge length was negatively associated with edge occurrence in both the 50-m and 1000-m models. Additionally, 2005 percent developed area was negatively associated with edge occurrence in the CRV 1000-m model (Table 2).

Table 1 Summarized land-use variables for Berkshire valley (BV) and Connecticut River Valley (CRV), Massachusetts

Land-use variable	BV	CRV
Open area 1830 (%)	69	71
Agricultural area 1971 (%)	13	19
Developed area 1971 (%)	10	27
Agricultural area 2005 (%)	14	13
Developed area 2005 (%)	17	33
Road density (km/sq km)	3.2	4.8
Forest edge density (km/sq km)	8.8	8.5

Incursion into forest understory

In the cross-regional dataset and BV, no variable significantly explained incursion into the understory in the 50-m and 1000-m models (Table 3). In CRV, understory incursion was negatively associated with elevation and positively associated with percent agricultural area in the 50-m model (Table 3). It should be noted that only three sites in CRV had agricultural land area within 50 m, and garlic mustard invaded the understory at all three sites.

Fig. 2 Garlic mustard occurrence and incursion into the understory in Berkshire Valley and Connecticut River Valley, Massachusetts. The inset shows elevation across Massachusetts
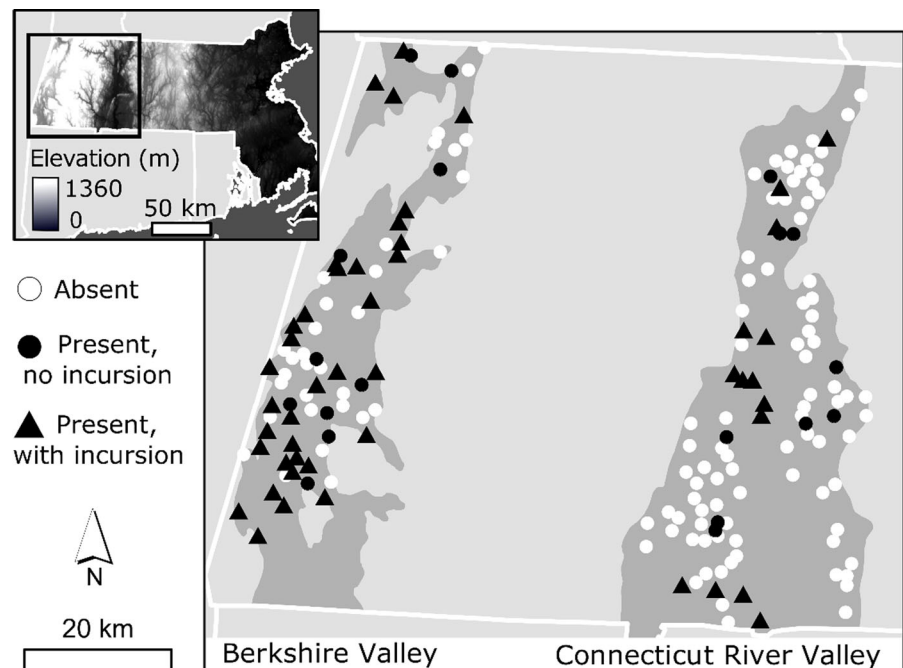
Table 2 Logistic regression results for GM occurrence at the forest edge

	Variable	Cross-regional		Berkshire valley		Connecticut River Valley	
		Log odds (SE)	p	Log odds (SE)	p	Log odds (SE)	p
50-m model	Elevation (m)	0.0045 (0.0014)	0.00087**	− 0.019 (0.0062)	0.00078**	− 0.027 (0.011)	0.0053*
	Open area 1830 (%)	0.0047 (0.0034)	0.16	0.007 (0.0061)	0.25	0.0043 (0.0056)	0.44
	Agricultural area 2005 (%)	0.0062 (0.014)	0.67	− 0.018 (0.026)	0.49	0.013 (0.02)	0.52
	Developed area 2005 (%)	0.0041 (0.0075)	0.59	− 0.001 (0.015)	0.95	− 0.0072 (0.012)	0.53
	Forest-edge length 2005 (km)	− 0.52 (2.8)	0.85	3.2 (4.7)	0.49	− 12.0 (5.9)	0.023*
1000-m model	Elevation (m)	0.0039 (0.0014)	0.0054**	− 0.018 (0.0058)	0.00038**	− 0.043 (0.015)	0.00082**
	Open area 1830 (%)	− 0.001 (0.0084)	0.91	− 0.0022 (0.017)	0.90	0.0051 (0.012)	0.68
	Agricultural area 2005 (%)	0.017 (0.018)	0.35	− 0.016 (0.033)	0.62	− 0.019 (0.031)	0.53
	Developed area 2005 (%)	− 0.0081 (0.011)	0.46	− 0.013 (0.023)	0.57	− 0.035 (0.018)	0.040*
	Forest-edge length 2005 (km)	− 0.014 (0.023)	0.55	− 0.0062 (0.039)	0.87	− 0.095 (0.043)	0.021*

Coefficients are expressed as log odds

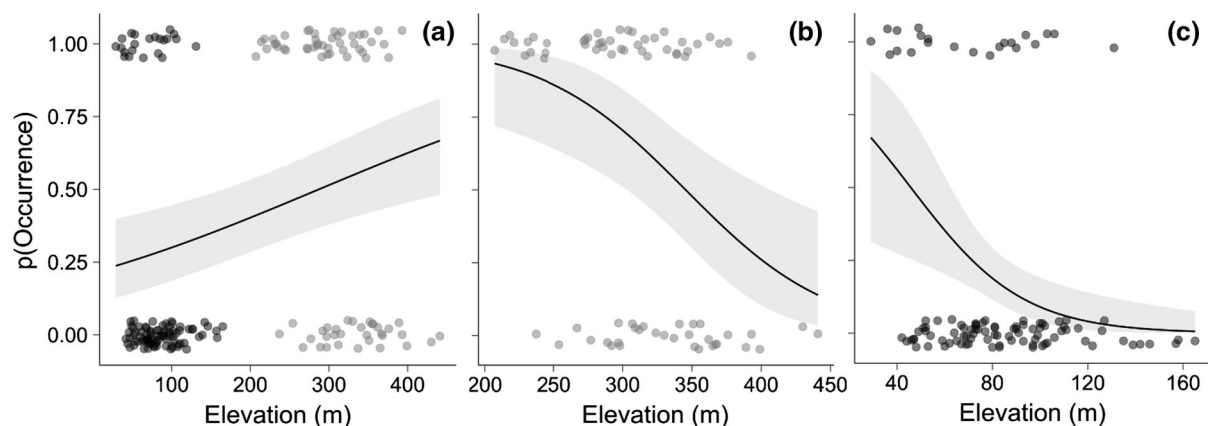Asterisks correspond to significance level: *$p < 0.05$, **$p < 0.01$

Fig. 3 The probability of garlic mustard occurrence as a function of elevation in **a** the cross-regional dataset, **b** Berkshire Valley, and **c** Connecticut River Valley. Light gray points correspond to Berkshire Valley sites, and dark gray points correspond to Connecticut River Valley sites. Points are jittered around 0 and 1 to better show data distribution. Note the change of scale on the x axes

Discussion

We studied the effects of elevation and historical and contemporary land use on garlic mustard occurrence on forest edges and incursion into the forest understory in two distinct ecoregions of western Massachusetts, the Berkshire Valley (BV), and the Connecticut River Valley (CRV). The effect of elevation on edge

Table 3 Logistic regression results for GM incursion into the understory

	Variable	Cross-region dataset		Berkshire valley		Connecticut River Valley	
		Log odds (SE)	p	Log odds (SE)	p	Log odds (SE)	p
50-m model	Elevation (m)	0.0031 (0.0025)	0.20	− 0.0088 (0.0083)	0.25	− 0.09 (0.047)	0.014*
	Open area 1830 (%)	0.0041 (0.0061)	0.49	0.0034 (0.0082)	0.77	− 0.025 (0.019)	0.22
	Agricultural area 2005 (%)	0.048 (0.037)	0.10	− 0.012 (0.042)	1.00	0.21 (0.11)	0.004**
	Developed area 2005 (%)	0.014 (0.015)	0.33	− 0.029 (0.022)	0.16	0.0063 (0.039)	1.00
	Forest-edge length 2005 (km)	− 5.2 (4.8)	0.28	− 7.5 (5.7)	0.17	3.2 (13)	1.00
1000-m model	Elevation (m)	0.0026 (0.0027)	0.32	− 0.0049 (0.0080)	0.57	− 0.027 (0.03)	0.34
	Open area 1830 (%)	− 0.0014 (0.015)	0.94	0.02 (0.023)	0.37	− 0.017 (0.026)	0.58
	Agricultural area 2005 (%)	0.052 (0.032)	0.070	− 0.02 (0.044)	1.00	0.051 (0.065)	0.52
	Developed area 2005 (%)	0.0018 (0.022)	0.81	− 0.053 (0.038)	0.13	0.013 (0.043)	1.00
	Forest-edge length 2005 (km)	0.031 (0.042)	0.43	0.062 (0.064)	0.34	− 0.024 (0.085)	1.00

Coefficients are expressed as log odds

Asterisks correspond to significance level: $*p < 0.05$, $**p < 0.01$

occurrence depended on spatial extent: elevation was positively associated with occurrence across regions but negatively associated within regions. Furthermore, different land-use variables explained edge occurrence and understory incursion in CRV, and no landscape variables explained incursion in BV, where garlic mustard was more prevalent and had a higher incursion rate. Regional differences in the response of garlic mustard to landscape variables found in this study are consistent with the considerable variation in garlic mustard distribution documented by previous regional observations (e.g., Nuzzo 1999; Rodgers et al. 2008; Stinson and Seidler 2014; Davis et al. 2015), and they suggest that region-specific models are needed to model the establishment and spread of this invasive plant.

Our findings highlight that models developed for different spatial extents may not agree, potentially because of various mechanisms operating at different scales. Across regions (cross-regional dataset), the positive association between edge occurrence and elevation was the result of the more mountainous BV having both a higher average elevation and a higher occurrence rate than the floodplain-dominated CRV (Fig. 3a). As would be expected at higher elevations, BV has cooler average temperatures and greater annual precipitation than CRV (Hall et al. 2002). BV is therefore more climatically suitable for garlic

mustard, which has higher population growth rates in cooler, wetter New England climates (Merow et al. 2017). Additionally, BV is dominated by relatively high pH, calcareous sedimentary soils (Hall et al. 2002) that favor garlic mustard growth over the acidic sedimentary soils in CRV (Cavers et al. 1979; Merow et al. 2017).

In contrast to the results for the cross-regional dataset, there was a *negative* association between elevation and garlic mustard edge occurrence when regions were analyzed separately. This result demonstrates the importance of finer-scaled processes driving garlic mustard distributions that were not captured when analyzing garlic mustard occurrence across regions. One possible mechanism may simply be that garlic mustard seeds, which can disperse by gravity and water (Susko and Lovett-Doust 1998), are likely to disperse downhill and colonize lower elevations at the local scale. Low-elevation deciduous forests may also provide better garlic mustard habitat than high-elevation coniferous forests. Compared to coniferous forests, deciduous forests have higher light availability during early spring, when garlic mustard flowers (Anderson et al. 1996), and more basic soils (Munger 2001).

Within CRV, garlic mustard occurrence on forest edges was negatively associated with forest-edge length and percent developed area within 1000 m of

a site. This result was surprising because fragmentation and disturbance in developed areas are often found to benefit invasive plants (Pavao-Zuckerman 2008; Vilà and Ibáñez 2011; Malavasi et al. 2014). While garlic mustard typically invades an area by becoming established along a forest edge, it also invades the understory, where it has similar survival and growth rates but lower seed production compared to high-light habitats (Merow et al. 2017). Merow et al. (2017) hypothesized that high seed production in open habitats allows garlic mustard to reach and fill in understory habitats, bridging the gap between edges. One possible explanation is that relatively small open areas within forests, such as recreational trails or tree falls, may facilitate garlic mustard spread, as has been shown for other invasives (Dickens et al. 2005). However, spatial data for these features were not comprehensive enough to include in our landscape models.

Unlike CRV, no land-use variable explained garlic mustard occurrence on forest edges in BV. One reason may be that there was less variation in percent developed area to explain garlic mustard occurrence in sites in BV (interquartile range [IQR] of 11%) than in CRV (IQR of 28%). Furthermore, a different land-use classification scheme may be needed in BV because our broad land-use classes did not capture heterogeneity in forest types and land-use intensity, which may influence habitat quality. Our region-specific results suggest that regional landscape models of invasive species are not transferable across space, even with a small state. These results are similar to the findings of previous studies that demonstrated the need for region-specific bioclimatic models of native plants (Randin et al. 2006; Heikkinen et al. 2012).

A unique aspect of this study is that we investigated incursion into the understory in addition to establishment on forest edges; other models do not distinguish between these two habitats. Garlic mustard has been found to reduce the diversity, abundance, and mycorrhizal associations of native understory species (Stinson et al. 2007; Rodgers et al. 2008; Brouwer et al. 2015). Therefore, incursion into the understory gives an indication of ecological impact that is often not accounted for in invasive species distribution models (Bradley 2013). Agricultural area within 50 m of a site was positively associated with understory incursion in CRV, potentially because agricultural areas and invasive species are both located in areas with high

soil nutrients. Furthermore, elevation was negatively associated with incursion in this region, potentially because of suitable habitat within low-elevation deciduous, as discussed above.

In contrast, none of the studied variables explained incursion in BV, which had a higher rate of incursion than CRV overall. This is a troubling result from a management perspective because it suggests that commonly used landscape variables may not predict understory incursion in regions where an invasive is most abundant and negatively impacting native plant communities. Rather, there is a need for more mechanistic studies that can help explain forest incursion. Other variables, such as nitrogen availability, increased light availability from canopy gaps (McDonald et al. 2008), and herbivore density (Knight et al. 2009), may have a stronger influence on understory incursion than landscape-scale variables. For example, although deer densities are similar across both ecoregions (Walters et al. 2016), white-tailed deer have been shown to facilitate garlic mustard success, potentially by altering the local abiotic environment or preferentially feeding on native plants (Knight et al. 2009; Kalisz et al. 2014). Variation in population age may also influence incursion. Over time, populations have more opportunities to take advantage of periodic disturbances and spread into understory areas, although older populations may also have weaker competitive abilities (Lankau et al. 2009).

Overall, our results for garlic mustard demonstrate that invasive distribution models based on commonly used landscape variables are not transferrable across space or habitat within the invasive range. Furthermore, given differences in the models explaining edge establishment and understory incursion, we suggest that these two processes be modeled separately, and the probability of incursion should not be inferred from the modeled probability of establishment. Field experiments are needed to resolve the mechanisms underlying the associations found in this study.

as an official Department of Defense position or decision unless so designated by other official documentation.

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