

Modeling the Invasion of Holly (*Ilex aquifolium*): Spatial Relationships and Spread Trajectories

Santiago López & David L. Stokes

To cite this article: Santiago López & David L. Stokes (2015): Modeling the Invasion of Holly (*Ilex aquifolium*): Spatial Relationships and Spread Trajectories, *The Professional Geographer*, DOI: [10.1080/00330124.2015.1102029](https://doi.org/10.1080/00330124.2015.1102029)

To link to this article: <http://dx.doi.org/10.1080/00330124.2015.1102029>



Published online: 20 Nov 2015.



Submit your article to this journal [↗](#)



Article views: 24



View related articles [↗](#)



View Crossmark data [↗](#)

Modeling the Invasion of Holly (*Ilex aquifolium*): Spatial Relationships and Spread Trajectories

Santiago López and David L. Stokes

University of Washington Bothell

In this study, we investigated the environmental factors associated with the establishment of invasive English holly (*Ilex aquifolium*) and the spatiotemporal trajectories of its potential spread. We collected georeferenced presence and absence and demographic data of holly between 2011 and 2014 in Saint Edward State Park, Washington. We analyzed them through a spatially explicit framework that combines multiple logistic regression, cellular automata, and bivariate quadratic modeling. Results showed that the presence of holly is influenced by the proximity to evergreen coniferous vegetation and forest edge, distance to streams, forest structure, and slope direction. Our study confirmed that local environmental conditions, species characteristics, and vegetative and dispersal mechanisms play a significant role in determining the rate and success of holly establishment across the different phases of invasion. Invasive species management plans should consider both species characteristics and their habitat and the interactions among them when planning long-term strategies for control and eradication. **Key Words:** cellular automata, *Ilex aquifolium*, invasive species, multiple logistic regression, Pacific Northwest.

我们于本研究中, 探讨与入侵的英国冬青树 (*Ilex aquifolium*) 定殖有关的环境因素, 及其潜在扩散的时空轨迹。我们蒐集华盛顿州的圣爱德华州立公园自 2011 年至 2014 年间, 以地理坐标为参考的冬青树存在及缺席与统计数据。我们透过结合多元逻辑回归、细胞自动机与二元二次式模式化的明确空间架构, 分析上述数据。研究结果显示, 冬青树的存在, 是受到与常青针叶林及森林边缘的邻近性、与溪流距离、森林结构和坡向带的影响。我们的研究确认了地方环境与条件、物种特征和栽植及分布机制, 在决定冬青树在不同入侵阶段的定殖比率及成功中, 扮演了显著的角色。入侵物种管理方案, 在规划控制与根除入侵物种的长期策略时, 应同时考量物种特征及其栖地, 以及两者之间的互动。 **关键词:** 细胞自动机, 冬青树, 入侵物种, 多元逻辑回归, 太平洋东北岸。

En este estudio investigamos los factores ambientales asociados con el establecimiento de la planta invasora acebo inglés (*Ilex aquifolium*) y las trayectorias espaciotemporales de su dispersión potencial. Recogimos datos demográficos de la presencia y ausencia georreferenciadas del acebo entre 2011 y 2014 en el Parque Estatal Saint Edward, en Washington. Analizamos esos datos por medio de un marco espacialmente explícito que combina modelaje de regresión logística múltiple, autómatas celulares y cuadrática bivariable. Los resultados mostraron que la presencia del acebo es influida por la proximidad a vegetación de coníferas de hoja perenne y el borde del bosque, distancia a las corrientes de agua, estructura del bosque y dirección de la pendiente. Nuestro estudio confirmó que las condiciones ambientales locales, las características de la especie y los mecanismos vegetativos y de dispersión juegan un papel significativo en determinar la tasa y éxito de la fijación del acebo a través de las diferentes fases de la invasión. Los planes de manejo de las especies invasoras deben considerar tanto las características de la especie como sus hábitats, y las interacciones entre éstos, cuando se planean estrategias de control y erradicación a largo plazo. **Palabras clave:** autómatas celulares, *Ilex aquifolium*, especies invasoras, regresión logística múltiple, Pacífico del Noroeste.

The invasion of nonnative species is a multidimensional problem that threatens natural and human systems in a wide variety of ways (Pyšek and Richardson 2010). Nonnative species have been associated with the loss of native biodiversity (Wilcove et al. 1998); alteration of nutrient cycles and modification of food webs (Pétillon et al. 2005); and losses in agriculture, forestry, and other fronts of the economy (Pimentel, Zuniga, and Morrison 2005). Effective management of invasives requires improved understanding of the pattern and process of spread to prevent negative impacts (Parker and Reichard 1998; Lockwood, Hoopes, and Marchetti 2007). This study presents methodological approaches for analyzing,

visualizing, and predicting the site-scale spatial spread of an invasive tree species—English holly *Ilex aquifolium*—in Washington State.

Research on the dispersion of nonnative species has been motivated by the need to mitigate negative impacts (Higgins, Richardson, and Cowling 1996) and because invasions offer insights into the roles that the environment and species characteristics play in shaping land cover structure (Liao, Tao, and Jiang 2014). For this purpose, researchers have developed mathematical and statistical models that evaluate the spread of alien organisms in new environments (e.g., Skellam 1951; Shigesada, Kawasaki, and Takeda 1995; Higgins, Richardson, and Cowling 1996; Strickland,

Dangelmayr, and Shipman 2014). Less common are spatially explicit models that consider both species–habitat relationships and population dynamics in space and time. Some examples include neutral landscape models (Gardner et al. 1987; With 2002) and spatially explicit logistic regression procedures (Ibáñez et al. 2009; Liao, Tao, and Jiang 2014). Spatially explicit models are useful from a management standpoint because they are often accompanied by geovisualizations that allow managers to explore the effects of different control strategies (Turner et al. 1995). In this study, we follow this approach to characterize an early invasion process and develop spatial scenarios that might help inform field interventions.

Mapping and monitoring an invasion process is critical for weed control and management (Lu et al. 2013). Most efforts to map canopy-dominant invasive species rely on remote sensing with imagery acquired at different spatial and spectral resolutions (Wang et al. 2013). Many alien plant species are often hidden in the background of prominent natural land cover, however, and are thus difficult to detect using remotely sensed data (C. Huang and Asner 2009). Recent advances in remote sensing have been able to solve some of these challenges. These studies rely on high spatial and spectral resolution digital imagery (e.g., Quickbird, IKONOS, AISA) to characterize the spatial distribution of alien species and model invasion processes over time. Some examples include invasion studies of leafy spurge (*Euphorbia esula*; Lawrence, Wood, and Sheley 2006) and saltcedar (*Tamarisk* spp.; Wang et al. 2013). Despite the valuable contributions of these studies, they are often constrained by the lack of information about age, location, and other attributes of individual plants that allow tracing site-level trajectories that could be useful for managing invasions locally. Furthermore, the analysis of the spatiotemporal dynamics of plant invasions requires a basic understanding of the invader’s demographic attributes and types of environments that allow a successful establishment (Higgins, Richardson, and Cowling 1996). These two requirements can be rarely met through remote sensing alone; however, the combination of field surveys that link data from sampled individuals with spatial attributes derived from remotely sensed data might provide an effective way to model invasion trajectories locally.

In this study, we focus on English holly, which is a relatively new invader of the Pacific Northwest (PNW) natural areas (Olmsted 2006; Zika 2010). Holly is a dioecious medium-size tree native to Eurasia and northern Africa (Peterken and Lloyd 1967) introduced to the PNW in the 1860s mainly for ornamental purposes (Olmsted 2006). Holly is typically an understory species but has the potential to form monospecific woodlands (Arrieta and Suárez 2005). Holly has been catalogued as a “weed of concern” in King County, Washington (King County 2014). Clear evidence exists that it represents a long-term management problem (Zika 2010) and that holly populations

are rapidly increasing in less disturbed forests (Stokes et al. 2014). Little information exists, though, about the environmental conditions that influence holly establishment and even less about the processes and patterns of spread. By examining the spread of holly, we could improve our understanding of its trajectory and how landscapes either facilitate or prevent invasion (With 2002).

This study tries to fill these information gaps and addresses two general questions: (1) what are the environmental factors associated with the presence of holly at the site scale? Holly presence is defined as a temporary condition of a site when it is occupied by holly or covered by its canopy. We hypothesize that the presence of holly is influenced by measurable environmental conditions such as interactions within a plant community, edge effects, vegetation canopy height, and topography. (2) What are the past and possible future spatiotemporal trajectories of holly spread? The identification of environmental filters together with information about age characteristics of individual trees and dispersal mechanisms might provide insights into the patterns and processes of holly dispersion.

Study Area and Methods

Our study site is located in Saint Edward State Park (47.73° N and 122.25° W) near the city of Seattle (Figure 1). The park includes 125 contiguous hectares of maturing successional forest characterized by mainly native vegetation and dominated by tree species of large size (Green, Ramsey, and Ramsey 2013; Stokes et al. 2014). Forests in the park are typical of Washington’s west-side low elevation forest (western hemlock zone, *sensu*; Franklin and Dyrness 1988) in both composition and successional stages (Smith 2006).

Our surveyed area consists of approximately 9.1 contiguous hectares and is primarily mixed evergreen and deciduous forest, characterized as an *Alnus rubra*/*Polystichum munitum* community (Chappell 2006), a common forest type in western Washington (Franklin and Dyrness 1988). Invasion by nonnatives is one of the chief threats to the ecological condition of the park (Stokes et al. 2014), and English holly is the most widespread invasive plant species present (Smith 2006); however, no systematic attempt has been made to control holly in the park, and prior to our study, no holly removal had occurred in the study area.

We employed a stepwise multivariate logistic regression (MLR) procedure to estimate location-specific holly occupancy probabilities based on a series of environmental predictors. We defined our model as

$$P = \frac{\exp(\alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)}{1 + \exp(\alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)} \quad (1)$$

where P is the probability of the presence of holly, α is the intercept, and β_n are the slope parameters



Figure 1 Study area in Saint Edward State Park, Washington State. (Color figure available online.)

estimated via maximum likelihood. The slope parameters represent how variations of the predictor affect the likelihood of finding holly at a particular location. X_1, X_2, \dots, X_n are the independent variables.

We obtained data on the presence and absence of holly using systematic field searches in the winter and early spring of 2011 (6.1 ha), 2012 (2.3 ha), and 2013 (0.8 ha; Figure 2A). Subsequent searches indicated that we found more than 99.5 percent of all holly plants and 100 percent of holly ≥ 0.5 m tall (mean age of plants 0.5 m tall = 4.04 years, $SD = 2.65$; Stokes et al. 2014). We included in our sample holly plants with a basal diameter ≥ 1 cm or > 1 m from the nearest sample plant employing one of two methods: (1) Global Positioning System (GPS) mapping with a Trimble Juno SB with estimated errors of 2 to 5 m after differential correction using two local continuously operating reference stations (CORS) or (2) if a plant was within a distance of 25 m of a previously located plant, we determined its location based on distance and bearing measurements using a meter tape and handheld compass (estimated error < 1 m).

We determined the age of all sampled plants, and for holly sampled in 2012 and 2013, we also determined whether they originated from seed or vegetative spread. To determine the age of holly trees, we collected ground-level cross sections of their stems. After drying and sanding the cross sections, we examined them under a dissecting scope and counted annual growth rings (Schweingruber, Börner, and Schultz 2013). Our analysis excluded all trees younger than

ten years of age. Very young plants have unknown mortality rates; however, once holly at our study site reach an age of ten years they appear to have negligible mortality (Stokes et al. 2014). Thus, our record of tree ages and locations allows a continuous record of the population ten years old and older ($n = 160$) in the study area since the start of the invasion.

We processed the data within a geographic information system (GIS) framework (ArcGIS version 10; ESRI 2011). We used a grid of 2 m cells ($N = 23,052$ cells) to plot tree locations. The cells that contained at least one holly tree were coded as one and the others as zero. To reduce the problem of spatial autocorrelation and obtain more efficient coefficients through the MLR procedure, we selected a random sample of cells that were at least 10 m apart from each other. We used a stratified procedure to obtain a representative number of observations associated with the extent of the main plant communities and the presence or absence of holly. From our total number of cells ($N = 207$), approximately 34 percent ($n = 70$) were coded as one (holly) and the remaining ($n = 137$) as zero (nonholly).

For each cell in the sample, we obtained information about the different environmental covariates. Based on a priori observations during field surveys, holly seemed to occur more frequently in sites closer to evergreen coniferous vegetation. We obtained vegetation information from the classification of a digital infrared image collected by the National Agriculture Imagery Program (NAIP; U.S. Geological Survey 2010). We classified this image using an iterative

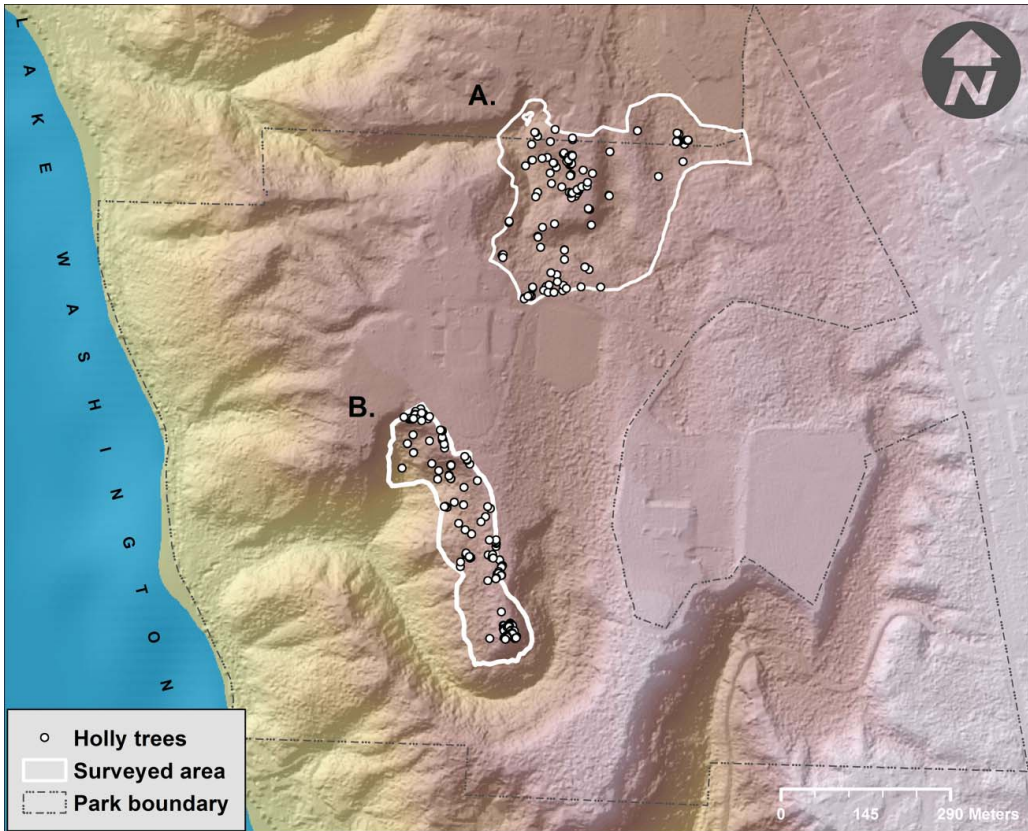


Figure 2 Areas surveyed for English holly in St. Edward Park. (A) Sample used to calibrate the multivariate logistic regression model (data collected between 2011 and 2013). (B) Sample used to test the predictive capability of the spatially explicit probability model (data collected in 2014). (Color figure available online.)

self-organizing clustering (ISO-Cluster) unsupervised procedure (Ball and Hall 1965) and calculated the distance from each cell in the sample to the closest pixel of the evergreen vegetation class. We also observed that holly seemed to cluster around forest edges. We mapped the edge of forested areas by visual interpretation of a high-resolution orthoimage collected by the City of Kenmore in 2012 and all the trails in the park with the aid of the Trimble GPS unit. We calculated the shortest distance to forest edges and trails using standard raster functions in a GIS. We also observed that most holly trees established in areas away from water sources. We calculated the distance from each holly location to the closest stream as a measurement of interaction between holly and water channels. Because holly spread patterns seemed to associate with topographic conditions, we derived elevation, slope, aspect, and curvature information from LiDAR Bare-Earth data (Puget-Sound-Lowlands-LiDAR-Project 2000–2005). We also analyzed landscape contextual influences through a characterization of forest height. We applied a focal operation on the LiDAR top-surface data set with a 5×5 pixel window to obtain an average value.

Before undertaking the multivariable analysis, we ran a series of Pearson correlation tests to measure the

strength of the association between pairs of explanatory variables. We also calculated the variance inflation factor (VIF) of all pairwise combinations to determine whether extreme multicollinearity existed among them. Then, we applied an MLR procedure to evaluate the combinatory effect of the explanatory variables on the presence of holly. We assessed the significance of the variables by examining the Wald statistic and the robustness of the model by inspecting an error matrix. Although informative, measures such as the percentage of cases correctly classified have been criticized for inflating the correct classification rate (Hosmer and Lemeshow 2004). Therefore, in addition, we used a receiving operating characteristic (ROC) curve to illustrate the performance of a binary classification system as its discrimination level varies. We also obtained an independent sample of observations ($N = 111$) in 2014 to empirically validate the spatial probability model (Figure 2B). Vegetation in this new area was similar to that of the original surveyed area (Smith 2006), and we used the same field methods to collect holly data and location information.

We used the coefficients obtained through the MLR procedure to generate a raster (employing Equation 1) that depicts the likelihood of holly presence. From this raster, we derived a series of binary

grids depicting suitable and unsuitable areas for holly occupation using different threshold values ($P_t \geq 0.1$ – $P_t \geq 0.9$). Although all rasters used for variable operationalization had a high spatial resolution ($1 \text{ m} \leq \text{cell size} \leq 2 \text{ m}$), we increased the spatial resolution of the probability model to ensure that the cell size was compatible with the invasion process being analyzed (Higgins, Richardson, and Cowling 1996). Stokes et al. (2014) showed that canopy grows at an average rate of approximately 0.1 m year^{-1} based on the modeled relationship between age and canopy area. We used this estimate to resample all suitability maps.

Vegetative Spread

We combined the MLR results with cellular automata (CA) to simulate vegetative spread. CA is a spatially explicit technique that is applied to model a dynamic spatial process. A CA system consists of a regular grid of cells, each in one of a finite number of states (e.g.,

occupied and unoccupied). Time advances in discrete steps and cells interact locally, with the next state of a cell being a function of the current state of itself and its neighbors (Sui and Zeng 2001). The integration of MLR and CA has been successfully applied to study urbanization processes (Wu 2002), landscape dynamics (Soares-Filho, Cerqueira, and Pennachin 2002), land use allocation (Zhu et al. 2009; Verburg, Neumann, and Nol 2011; López 2014), and plant invasion processes (Lu et al. 2013).

The CA mechanism accounts for the four possible spatial transitions over time based on each cell’s spatiotemporal neighborhood: (1) holly to holly, (2) holly to nonholly, (3) nonholly to holly, and (4) nonholly to nonholly. Although the model formally includes these transitions, as holly in the age range of our sample (>10 years and <50 years) have a negligible mortality rate (Stokes et al. 2014), the second transition is non-existent, and because holly at this site is well below the typical maximum age for the species (Peterken and

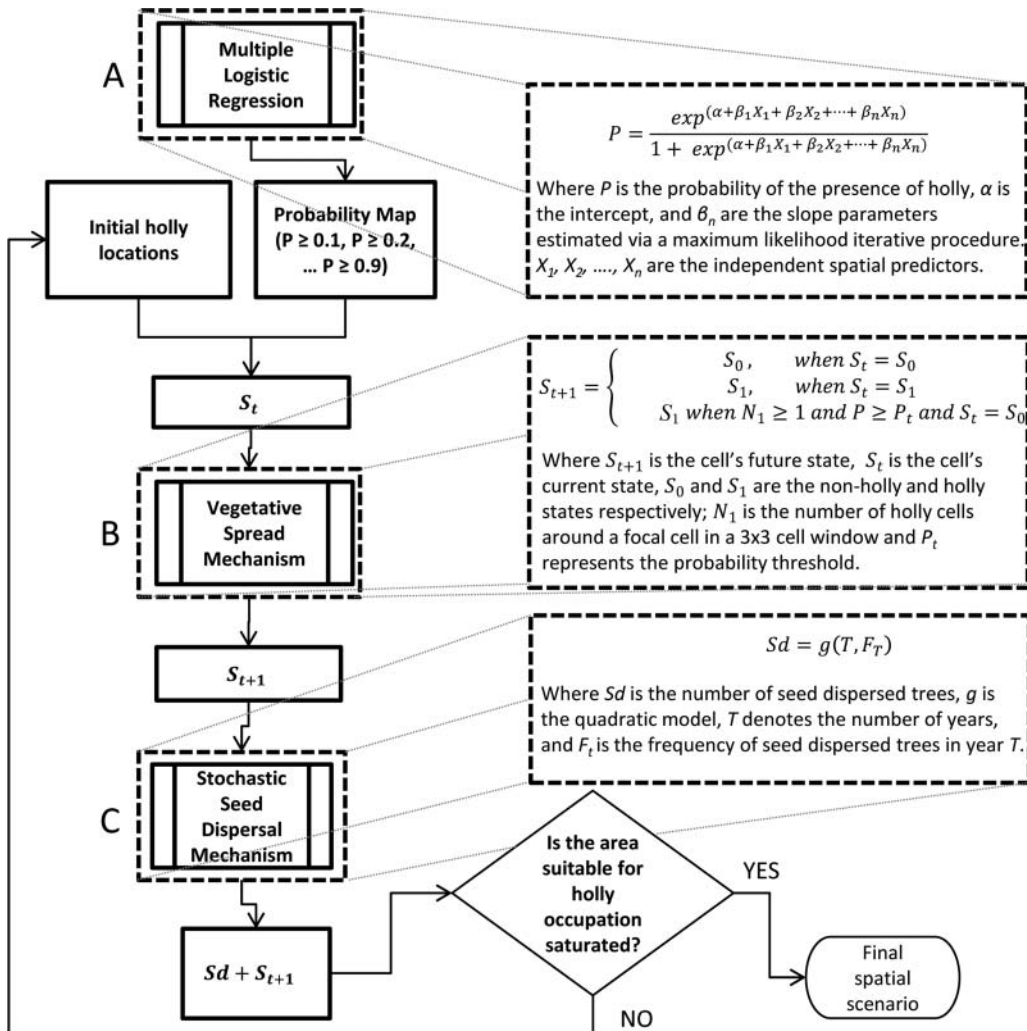


Figure 3 The conceptual modeling framework used in this study: (A) multivariate logistic regression, (B) two-dimensional cellular automata, and (C) bivariate quadratic modeling.

Table 1 Results of the bivariate analysis showing weak Pearson correlations and low variance inflation factors of pairwise evaluations of explanatory variables

		Distance to streams	Distance to forest edge	Distance to evergreen conifer vegetation	Distance to trails	Elevation	Slope	Curvature	Aspect	Canopy height
Distance to streams	Pearson correlation	1	0.018	-0.292**	-0.211**	0.511**	-0.091	0.106	0.316**	0.321**
	Sig. (two-tailed)	—	0.801	0.000	0.002	0.000	0.194	0.129	0.000	0.000
	VIF	—	1.922	1.909	1.936	1.429	1.948	1.947	1.776	1.609
Distance to forest edge	Pearson correlation	0.018	1	0.024	-0.242**	0.102	0.120	-0.138*	0.074	0.081
	Sig. (two-tailed)	0.801	—	0.733	0.000	0.144	0.086	0.048	0.287	0.245
	VIF	1.125	—	1.133	1.092	1.116	1.121	1.122	1.130	1.120
Distance to evergreen conifer vegetation	Pearson correlation	-0.292**	0.024	1	0.104	-0.127	-0.014	0.063	-0.136	-0.230**
	Sig. (two-tailed)	0.000	0.733	—	0.135	0.068	0.837	0.365	0.050	0.001
	VIF	1.119	1.135	—	1.137	1.140	1.142	1.134	1.138	1.114
Distance to trails	Pearson correlation	-0.211**	-0.242**	0.104	1	-0.342**	0.026	0.083	-0.066	0.079
	Sig. (two-tailed)	0.002	0.000	0.135	—	0.000	0.706	0.233	0.341	0.256
	VIF	1.234	1.189	1.237	—	1.172	1.239	1.217	1.242	1.224
Elevation	Pearson correlation	0.511**	0.102	-0.127	-0.342**	1	-0.271**	0.225**	0.093	-0.120
	Sig. (two-tailed)	0.000	0.144	0.068	0.000	—	0.000	0.001	0.181	0.085
	VIF	1.359	1.812	1.850	1.749	—	1.752	1.769	1.828	1.708
Slope	Pearson correlation	-0.091	0.120	-0.014	0.026	-0.271**	1	-0.090	-0.061	0.166*
	Sig. (two-tailed)	0.194	0.086	0.837	0.706	0.000	—	0.195	0.383	0.017
	VIF	1.131	1.111	1.131	1.129	1.070	—	1.132	1.127	1.119
Curvature	Pearson correlation	0.106	-0.138*	0.063	0.083	0.225**	-0.090	1	0.004	-0.088
	Sig. (two-tailed)	0.129	0.048	0.365	0.233	0.001	0.195	—	0.954	0.209
	VIF	1.117	1.100	1.110	1.096	1.067	1.118	—	1.118	1.116
Aspect	Pearson correlation	0.316**	0.074	-0.136	-0.066	0.093	-0.061	0.004	1	0.084
	Sig. (two-tailed)	0.000	0.287	0.050	0.341	0.181	0.383	0.954	—	0.227
	VIF	1.039	1.129	1.136	1.140	1.125	1.135	1.140	—	1.136
Canopy height	Pearson correlation	0.321**	0.081	-0.230**	0.079	-0.120	0.166*	-0.088	0.084	1
	Sig. (two-tailed)	0.000	0.245	0.001	0.256	0.085	0.017	0.209	0.227	—
	VIF	1.125	1.338	1.330	1.343	1.257	1.348	1.361	1.358	—

Note: N = 207. VIF = variance inflation factor.

*Correlation is significant at the 0.05 level.

**Correlation is significant at the 0.01 level.

Lloyd 1967), it is expected to remain very low for many decades. The CA model follows the formulation of H. M. Huang et al. 2008:

$$S_{t+1} = f(S_t, N), \tag{2}$$

where S is the cell state, t denotes a time interval, f is the transitional rule, and N is the cell's neighbors. We

defined the transition rules based on observed expansion trajectories and expressed them as the likelihood of a cell state transforming from one state to the other or remaining in the same state. Time advances in steps of one year, which is the temporal resolution of the data collected in the field. Although holly appears to cluster in certain areas more than others, this does not imply that it is impossible to find holly in areas below a probability threshold. Thus, setting just one cutoff

Table 2 Results of the multivariate logistic regression evaluation showing a significant relationship (p < 0.01) between the presence of holly and a series of environmental factors

Variables	B	SE	Wald	df	Sig.	Exp(B)
Aspect (N/S)	-0.927	0.419	4.884	1	0.027	0.396*
Distance to evergreen vegetation (DstEV)	-0.511	0.144	12.592	1	0.000	0.600**
Canopy height (CanHE)	0.029	0.011	6.748	1	0.009	1.029**
Distance to edge (DstED)	-0.016	0.006	8.778	1	0.003	0.984**
Distance to streams (DstST)	0.009	0.003	7.536	1	0.006	1.009**
Constant	-1.756	0.959	3.352	1	0.067	0.173

Note: N = 207. Multivariate logistic regression model is significant at the 0.01 level.

*Correlation is significant at the 0.05 level.

**Correlation is significant at the 0.01 level.

Table 3 Evaluation of the multivariate logistic regression model's predictive ability based on an error matrix with $P_t \geq 0.5$

	Selected cases (N = 207) used in the calibration of the model			Unselected Cases (N = 61) used for validation only		
	Absence ^a	Presence ^a	% Correct	Absence ^a	Presence ^a	% Correct
Absence ^b	144	15	90.6	43	6	87.8
Presence ^b	28	20	41.7	10	2	16.7
Overall accuracy			79.2			73.77

Note: The cut value is 0.500. Results show both selected (observations used in the model's calibration) and unselected cases (observations not used for calibration).

^aPredicted.

^bObserved.

value to investigate the dispersion process can leave aside feasible scenarios. Instead, we used different probability thresholds by referring to the corresponding spatial model. Based on the spatiotemporal characteristics of holly trees in the study area, we defined the general structure of the CA algorithm as follows:

$$S_{t+1} = \begin{cases} S_0, & \text{when } S_t = S_0 \\ S_1, & \text{when } S_t = S_1 \\ S_1, & \text{when } N_1 \geq 1 \text{ and } P \geq P_t \text{ and } S_t = S_0, \end{cases}$$

where S_{t+1} is the cell's future state; S_t is the cell's current state; S_0 and S_1 are the nonholly and holly states, respectively; N_1 is the number of holly cells around a focal cell in a 3×3 cell window; and P_t represents the probability threshold.

Stochastic Seed Spread

CA is an effective tool to simulate dispersion when the spread occurs in the immediate vicinity of a plant; however, it is not adequate when the immediate spatial neighborhood does not play an important role in

Table 4 Results of the receiver operating characteristic curve evaluation showing the sensitivity of the model to correctly predict holly locations at different probability thresholds

Positive if greater than	Sensitivity	1 - Specificity
0.00	1.00	1.00
0.05	0	
98	0.64	
0.10	0.96	0.45
0.15	0.94	0.36
0.20	0.85	0.28
0.25	0.81	0.22
0.30	0.71	0.20
0.35	0.67	0.15
0.40	0.56	0.13
0.50	0.44	0.09
0.55	0.38	0.06
0.60	0.29	0.04
0.65	0.25	0.03
0.70	0.19	0.03
0.75	0.15	0.02
0.80	0.08	0.01
0.85	0.06	0.00
0.91	0.02	0.00
1.00	0.00	0.00

determining where the species will spread. Holly disperses not only by vegetative spread but also by the movement of drupes carried by birds far from the drupe-producing trees (Zika 2010). In this case, the incorporation of a statistical procedure to model seed dispersal caused by stochastic processes can account for factors that are not fully understood (Skel-lam 1951; Levin et al. 2003). The number of trees at a particular time step can be estimated from the past spatiotemporal trajectory of seed-dispersed trees. Our analysis of tree age based on ring counts and identification of seed-dispersed trees allowed us to determine this trajectory. We fitted a quadratic model to past seed-dispersed tree establishments ten or more years old to predict future numbers. The seed dispersion model can be expressed as

$$Sd = g(T, F_t), \tag{3}$$

where Sd is the number of seed-dispersed trees, g is the quadratic model, T denotes the number of years, and F_t is the frequency of seed-dispersed trees in year T . We used a random point generator within the GIS to place the predicted number of new tree locations (as determined by a particular probability threshold) not previously occupied by holly.

An Integrated Spatiotemporal Model

We combined the MLR/CA and stochastic spread algorithms to emulate the spatial and temporal

Table 5 Results of the empirical validation of the spatially explicit probability model using an independent sample of holly observations

Probability threshold	Predicted holly locations	Predicted nonholly locations	% correct
$P \geq 0.1$	110	1	99
$P \geq 0.2$	108	3	97
$P \geq 0.3$	105	6	95
$P \geq 0.4$	99	12	89
$P \geq 0.5$	93	18	84
$P \geq 0.6$	81	30	73
$P \geq 0.7$	56	55	50
$P \geq 0.8$	43	68	39
$P \geq 0.9$	15	96	14

Note: $N = 111$.

Downloaded by [University of Washington Libraries] at 09:05 22 December 2015

population dynamics of holly (Figure 3). We generated nine invasion scenarios (one for each probability threshold) showing the presence and absence of holly. Each scenario shows the evolution of the invasion process in a T year period constrained by the probability for successful establishment. When models are based on the characteristics of the focal neighborhood, such as CA, parametric statistical comparisons on a cell-by-cell basis are not meaningful (Maeda et al. 2011). Thus, we derived a diverse set of standard landscape metrics with aid of the software FRAGSTATS (McGarigal et al. 2002) to compare the simulated patterns with the geographic landscape and to quantify errors. Examples of studies that have used a similar approach include Dale et al. (1994), Frohn et al. (1996), Haines-Young and Chopping (1996), and Carlson et al. (2012).

We obtained the following metrics: (1) total extent of holly occupation (CA), (2) percentage of the landscape occupied by holly (PLAND), (3) patch density (PD), (4) mean and median patch area (AREA_MN and AREA_MD), (5) mean and median fractal dimension (FRAC_MN and FRAC_MD), (6) mean and median nearest Euclidean distance between holly patches (ENN_MN and ENN_MD), (7) aggregation of holly patches (AI), and (8) clumpiness. We used the Kruskal–Wallis one-way analysis of variance (ANOVA) nonparametric test (Kruskal and Wallis 1952) to assess whether the predicted metrics were significantly different from the observed ones. For this purpose, we randomly placed fifty quadrats (100 m \times 100 m) over the study area and obtained an average

estimate for each metric for both the modeled and observed landscapes. We performed seventy-two pairwise comparisons between the modeled and observed patterns of holly (i.e., eight metrics for each of the nine scenarios). In addition, we derived a series of error estimates from the ratios between each metric of the simulated landscapes and the observed one. We used these errors to evaluate the model's ability to predict landscape structure.

Spatiotemporal Spread Trajectories

We let the model run for I iterations, until the suitable area in each scenario was completely saturated by holly. Because the spatial outcomes generated by the spatially explicit model followed an S-curve trajectory, we fitted a four-parameter logistic curve (Richards 1959) to determine the inflection points where exponential growth and saturation occur (Gottschalk and Dunn 2005). We defined the logistic model as

$$Lp = h(T, A, B, C, D), \quad (4)$$

where Lp is the estimated percentage of the landscape occupied by holly; h is the four-parameter logistic model; T denotes the number of years; A is the minimum asymptote or the time estimate when spread begins; B is the slope factor that refers to the steepness of the curve and can be thought of as the expansion rate when growth becomes exponential; C is the inflection point where the curvature changes direction or

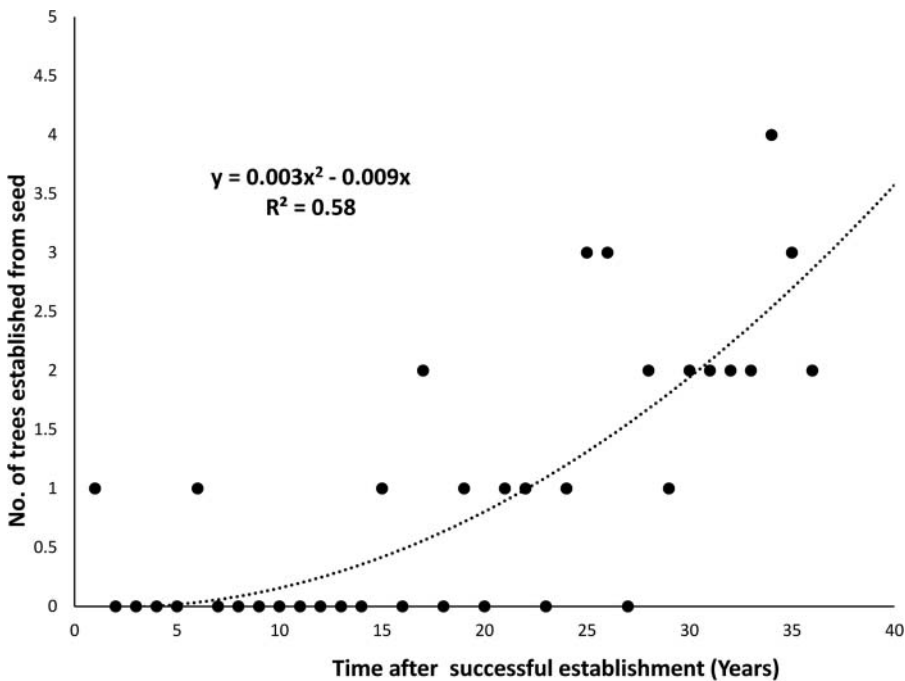


Figure 4 Positive quadratic relationship between year of establishment and number of trees (age ≥ 10 years) established from seed in the area surveyed between 2011 and 2013.

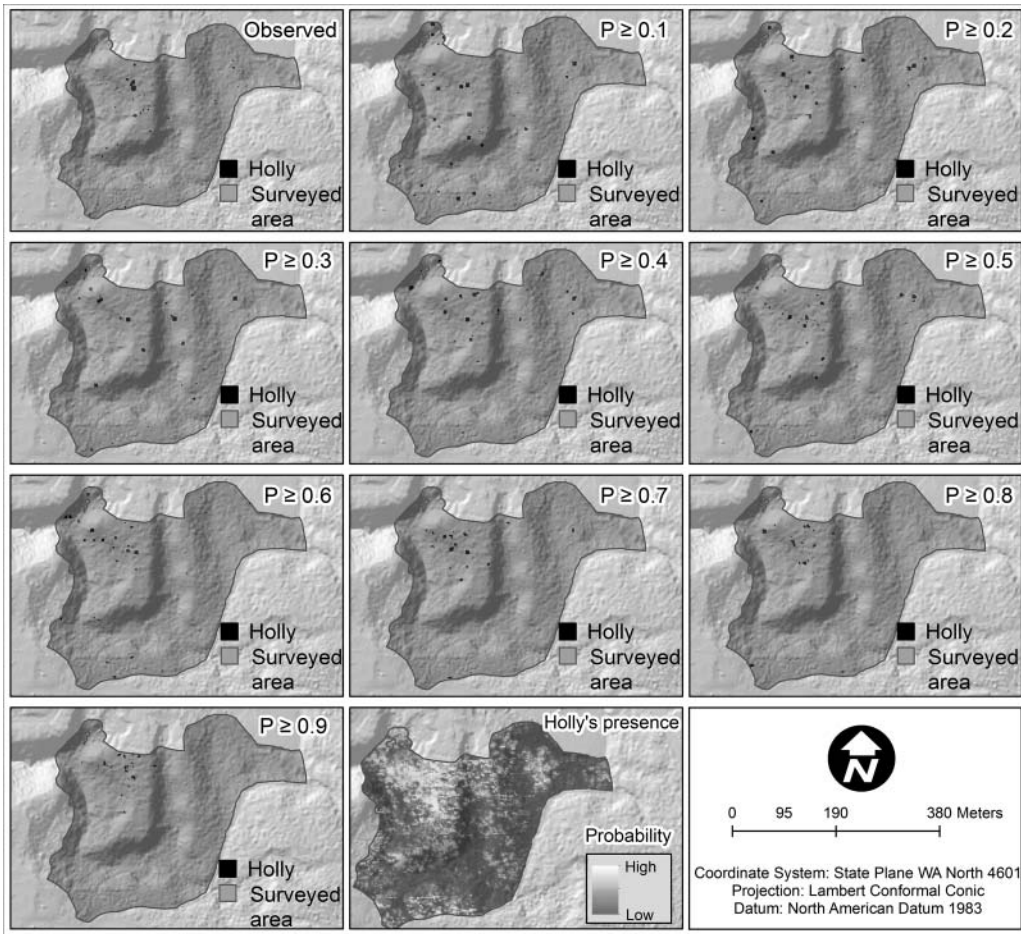


Figure 5 Observed and predicted patterns of holly dispersion using nine probability thresholds: $P_t \geq 0.1$, $P_t \geq 0.2$, $P_t \geq 0.3$, ..., $P_t \geq 0.9$.

sign and can be thought of as the point in time where saturation starts; and D is the maximum asymptote or time estimate when saturation approximates the environment's carrying capacity at a particular threshold.

Results

Our first research question focused on the relationship between the presence of holly and a series of

environmental covariates. Results of the bivariate analyses showed either weak or nonsignificant correlations among environmental predictors and low levels of collinearity (Table 1). We applied an MLR procedure to analyze the combinatory effect of these spatial factors on the presence of holly. In general, the MLR model had a medium explanatory power and was statistically significant (Nagelkerke $R^2 = 0.41$; $p < 0.01$). A significant strong negative correlation existed between holly

Table 6 Results of the Kruskal–Wallis tests showing only significant differences between the observed and predicted holly dispersion patterns using different probability thresholds: Only 11 percent of 72 differences between observed and predicted means were statistically significant

Cutoff value	Landscape metric	Kruskal–Wallis statistic	SE	Standard test statistic	Sig.	Adj. Sig
$P \geq 0.1$	AREA_MN	142.298	25.537	5.572	0.000	0.000
$P \geq 0.1$	ENN_MD	85.263	23.324	3.656	0.000	0.012
$P \geq 0.3$	AREA_MN	113.468	25.537	4.443	0.000	0.000
$P \geq 0.3$	ENN_MD	77.819	23.434	3.321	0.001	0.040
$P \geq 0.6$	FRAC_MD	-180.390	25.472	-7.082	0.000	0.000
$P \geq 0.8$	AREA_MD	-109.429	28.469	-3.844	0.000	0.005
$P \geq 0.8$	FRAC_MD	-188.583	27.760	-3.713	0.000	0.009
$P \geq 0.9$	ENN_MN	-112.292	28.575	-3.930	0.000	0.004

occupancy and distance to evergreen vegetation (DstEV) and edge (DstED; $p < 0.005$), whereas relatively weaker ($0.005 < p < 0.05$) significant positive relationships existed between holly occupation and distance to streams (DstST), vegetation height (CanHE), and south-facing slopes (N/S; Table 2).

The results of the error matrix evaluation showed an overall accuracy of 79 percent ($P_t \geq 0.5$; Table 3). The ROC curve analysis showed a lower accuracy with $P_t \geq 0.5$ (Table 4). The evaluation of the MLR model based on the independent sample of observations indicated that the model performs well. At $P_t \geq 0.5$, the model correctly predicted holly locations 84 percent of the time (Table 5), showing a much higher prediction accuracy than what the error matrix and ROC curve evaluations indicated.

Our second research question investigated the past and possible future spatiotemporal trajectories of holly spread. To answer this question, we concurrently considered both the environmental conditions and dispersal mechanisms to identify potential trajectories of holly spread. The seed spread model showed a relatively strong correlation ($R^2 = 0.58$) between number of years after detection and number of seed-dispersed trees ten years old or older (Figure 4). Results of the Kruskal–Wallis evaluation showed that most pairwise differences between the modeled and observed patterns of holly occupancy (Figure 5) were not significantly different. Only a few pairs (11 percent of all seventy-two comparisons) differed at a 0.05 significance level, nearly all at the very low ($P_t \geq 0.3$) or high ($P_t \geq 0.8$) thresholds (Table 6). The integrated spatially explicit model accurately forecasted the extent of holly cover (CA and PLAND) at probability

thresholds of 0.5 and 0.6 (5.0 and 0.4 percent errors, respectively). Percentage error estimates varied depending on the landscape metric, but most metrics had small errors on average (< 5 percent; Table 7).

To objectively forecast time horizons for the different phases of holly spread, we applied a series of logistic curves to the outcomes of the spatially explicit model because their trajectory followed an almost perfect S curve (Figure 6A). Results showed that as the percentage of the landscape suitable for occupation increased (lower probability threshold), the year at which exponential growth and saturation occur (the inflection points) also increased (Figure 6B and Table 8, Parameters B and C). The relationship between the percentage of the landscape that is suitable for occupation and the number of years that it takes to occupy it follows relatively strong nonlinear trajectories ($R^2 = 0.68$ for exponential growth, $R^2 = 0.99$ for saturation; Figure 7).

Discussion

First, this article addressed the relationship between the presence of holly and a series of environmental factors locally. The results of the MLR model corroborated our a priori expectations and confirmed that the likelihood of holly occurrence increases with proximity to evergreens, forest edge, canopy height and southern exposures, and decreases with proximity to streams. Although some studies have shown a negative relationship between complex forest structure (e.g., richer diversity, more mature) and invasibility at a local level (Symstad 2000; Kennedy et al. 2002; Mandryk and Wein 2006), we found that it is more likely

Table 7 Landscape metrics and error estimates in relation to the observed spatial pattern of holly dispersion

Probability threshold	CA (m ²)	PLAND (%)	PD (number of patches per 100 ha)	AREA_MIN (m ²)	AREA_MD (m ²)	ENN_MIN (m)	ENN_MD (m)	FRAC_MIN (no units) ^a	FRAC_MD (no units) ^a	AI (no units) ^b	CLUMPY (no units) ^c
$P \geq 0.1$	0.07	0.81	585.81	0.00	0.00	19.05	15.72	1.02	1.00	98.11	0.98
Error (%)	59.28	59.21	-32.50	133.33	200.00	91.44	154.08	2.35	-11.31	1.47	1.48
$P \geq 0.2$	0.07	0.73	574.97	0.00	0.00	16.27	12.56	1.34	1.00	98.06	0.98
Error (%)	43.92	43.82	-33.75	116.67	100.00	63.44	103.05	34.19	-11.31	1.42	1.43
$P \geq 0.3$	0.06	0.61	553.27	0.00	0.00	16.59	15.18	0.90	1.00	97.85	0.98
Error (%)	20.04	19.96	-36.25	83.33	100.00	66.66	145.39	-9.49	-11.31	1.20	1.21
$P \geq 0.4$	0.06	0.60	553.27	0.00	0.00	18.16	15.87	1.34	1.00	97.82	0.98
Error (%)	17.48	17.49	-36.25	83.33	50.00	82.42	156.54	34.34	-11.31	1.17	1.18
$P \geq 0.5$	0.05	0.53	574.97	0.00	0.00	12.95	8.37	1.05	1.00	97.49	0.97
Error (%)	5.12	5.01	-33.75	50.00	100.00	30.12	35.28	5.16	-11.11	0.83	0.84
$P \geq 0.6$	0.05	0.51	574.97	0.00	0.00	12.13	8.30	1.01	1.00	97.45	0.97
Error (%)	-0.43	-0.43	-33.75	50.00	100.00	21.83	34.18	1.61	-11.31	0.78	0.79
$P \geq 0.7$	0.04	0.43	499.03	0.00	0.00	12.88	7.27	1.09	1.02	97.52	0.98
Error (%)	-14.71	-14.74	-42.50	50.00	50.00	29.39	17.51	9.00	-9.53	0.85	0.87
$P \geq 0.8$	0.03	0.35	531.61	0.00	0.00	12.29	6.94	1.05	1.00	97.19	0.97
Error (%)	-31.77	-31.87	-38.75	16.67	0.00	23.47	12.24	5.26	-11.17	0.52	0.53
$P \geq 0.9$	0.03	0.29	477.33	0.00	0.00	10.34	3.99	1.00	1.00	96.78	0.97
Error (%)	-42.43	-42.46	-45.00	0.00	50.00	3.89	-35.47	0.37	-11.06	0.09	0.10
Observed value	0.05	0.51	867.93	0.00	0.00	9.95	6.19	1.00	1.13	96.69	0.97

^aFRAC values greater than 1 for a two-dimensional patch indicate an increase in shape complexity.

^bAI values range from 0 (no clustering) to 100 (completely clustered).

^cCLUMPY values range from 0 (no aggregation) to 1 (completely aggregated).

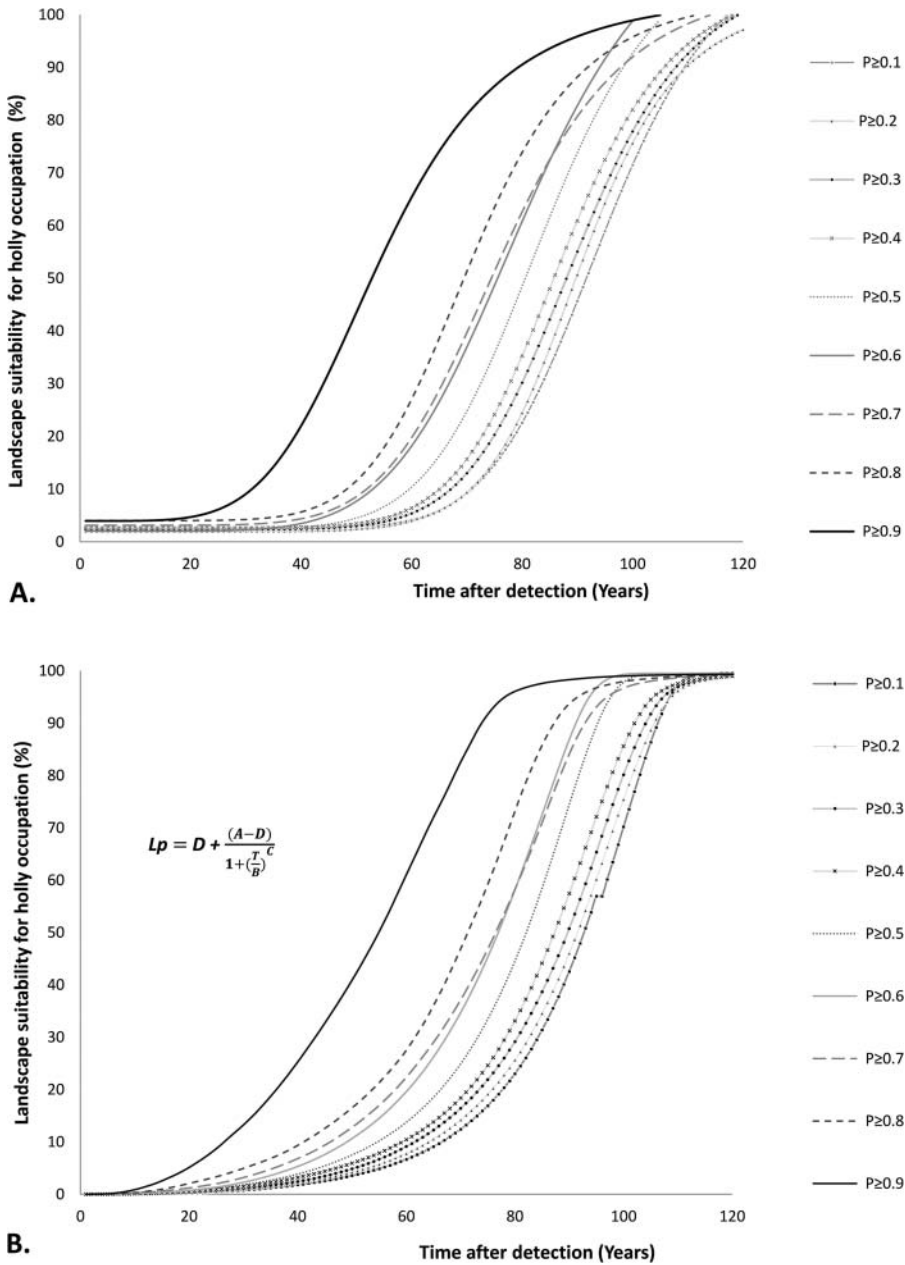


Figure 6 Spatiotemporal trajectories of holly dispersion in the area surveyed between 2011 and 2013. (A) Results from the integrated spatial model. (B) Results from the fitting of a four-parameter logistic model (L_p) to the outcomes of the integrated spatial model.

to find holly in the proximity of native evergreen conifer vegetation and where canopies are taller, suggesting that holly may be able to invade undisturbed PNW forests, possibly even old growth. Interestingly, Huebner and Tobin (2006) found a similar pattern in exotic plants invading forests in West Virginia, suggesting that some invasives might be successful at establishing where resources (e.g., soil nutrients, moisture, or light conditions) are adequate. This finding

highlights the evident vulnerability of less stressed areas to invasion, such as those found in protected areas in the United States. The positive correlation between holly occupancy and proximity to forest edge shows that holly is more successful at establishing in transitional environments. Several studies have shown that forest edges are the starting point for invasions, acting as facilitators of the percolation of alien species into less disturbed environments, especially of weedy

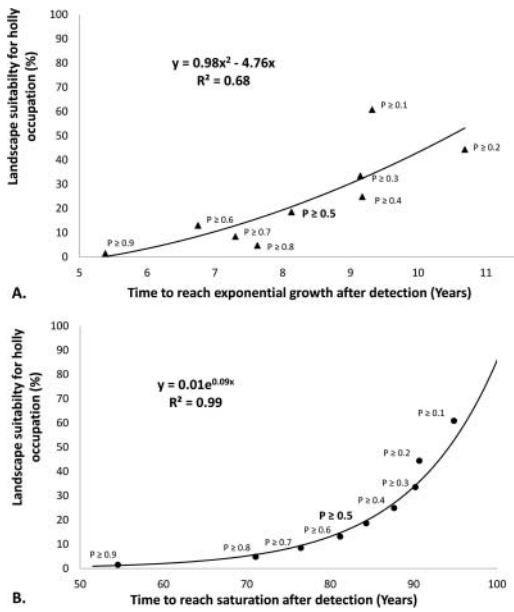


Figure 7 Positive quadratic and exponential relationships between suitable area for holly occupation and the expected number of years after detection. (A) Before exponential growth. (B) Before saturation. A $P_t \geq 0.5$ is highlighted as reference only.

plants (Cadenasso and Pickett 2001; Honnay, Verheyen, and Hermy 2002; González-Moreno et al. 2013). It also appears that holly is more successful at establishing in areas far away from watercourses. This finding suggests that holly is not water limited in PNW forests or that streams are not necessarily a main conduit of its spread, at least not as important as other dispersal channels. A careful analysis of dispersal agent behavior, for instance, could help improve our understanding of key conduits of spread. Finally, topographic characteristics, more specifically south-facing slopes, significantly correlate with the probability of holly occupancy, although the association is weak (Wald = 4.884; $0.01 < p < 0.05$). This outcome coincides with other studies that showed that terrain

conditions influence the distribution of invasive plant species (Bradley and Mustard 2006; Blumenthal et al. 2012). The effect of slope direction could have been enhanced, however, by the limited variation of aspects in the sample area, and additional observations are needed to make this finding conclusive.

Second, our study evaluated past and possible future spatiotemporal trajectories of holly spread. For this purpose, we used the MLR coefficients to generate a probability surface that depicts a site's transition potential from one state to another. Because most explanatory variables are static or are changing slowly relative to the speed of holly invasion, it is reasonable to assume that the factors that control holly establishment today will also affect its future distribution over the next several decades. Nevertheless, the spatial probabilities surface is just one of the two inputs necessary to project holly's spatial trajectories into the future. The other input is a detailed spatiotemporal characterization of individual trees that can help us understand past trends. With this information and a combination of a series of techniques (i.e., MLR, CA, and logistic analysis) we were able to model the spatial and temporal population dynamics of holly and generate nine suitability scenarios. We compared these scenarios with the observed landscape to evaluate the integrated model's performance.

The results of the evaluation of the eight landscape parameters showed that the model did very well in predicting landscape spatial structure in terms of extent and overall patch arrangement. Stokes et al. (2014) and Arrieta and Suárez (2005), for instance, demonstrated that holly trees and seeds tend to cluster in forestlands and around forest edges. Our results are consistent with these studies as shown by the aggregation and clustering index values (i.e., $AI \approx 100$; $CLUMPY \approx 1$; Table 6). Further, current observed spatial patterns of holly occupation could be explained by the interaction of controlling environmental factors and the effect of stochastic seed dispersal and vegetative spread across the area (e.g., dispersers perching on particular trees and depositing seeds or environmental variability making certain areas more favorable for establishment).

Table 8 Results of a four-parameter logistic model fit to the outcomes of the integrated spatial model

Cutoff point	Percentage of landscape suitable for holly occupation	A ^a	B ^a	C ^a	D ^a	R ²	RMSE
$P \geq 0.1$	60.82	1.96	8.82	94.83	115.05	0.9955	2.63
$P \geq 0.2$	44.36	2.72	10.19	90.70	102.63	0.9960	2.76
$P \geq 0.3$	33.48	2.37	8.65	90.21	108.81	0.9972	2.55
$P \geq 0.4$	24.84	2.68	8.68	87.66	107.23	0.9966	2.53
$P \geq 0.5$	18.58	2.41	7.63	84.31	117.21	0.9943	2.81
$P \geq 0.6$	13.07	2.02	6.25	81.19	125.10	0.9962	2.53
$P \geq 0.7$	8.46	3.14	6.80	76.48	106.30	0.9966	2.84
$P \geq 0.8$	4.78	4.02	7.13	71.05	103.80	0.9951	2.94
$P \geq 0.9$	1.47	3.96	4.88	54.53	103.85	0.9964	2.19

Note: Parameters B and C show the inflection points (number of years) at which exponential growth and saturation occur, respectively. RMSE = root mean square error.

^aLogistic curve parameter.

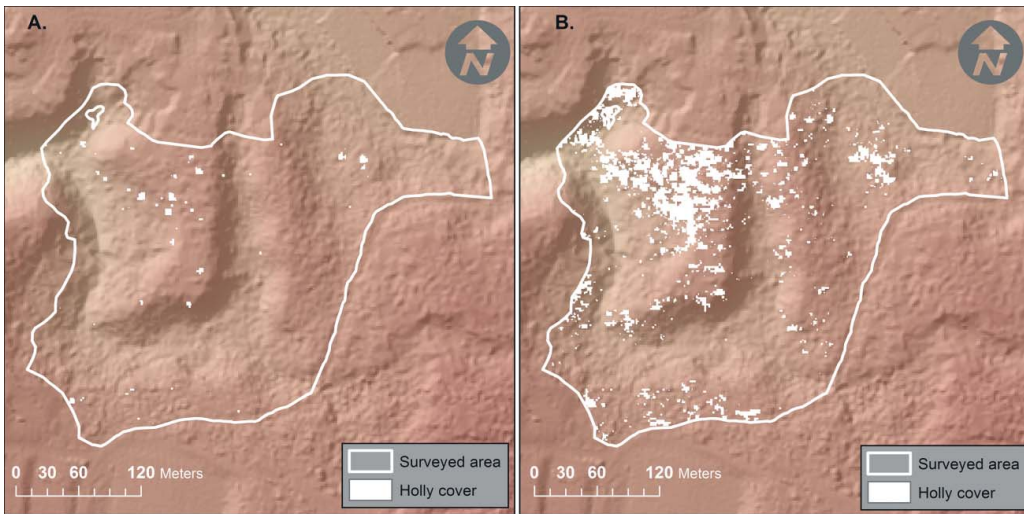


Figure 8 A spatial scenario showing two critical stages of the invasion process with $P_t \geq 0.5$. (A) Holly spreads exponentially at a maximum rate of $45 \text{ m}^2 \text{ year}^{-1}$ (≈ 38 years after detection). (B) Holly spread approaches saturation at a rate of $530 \text{ m}^2 \text{ year}^{-1}$ and comes near to the carrying capacity of the environment (≈ 85 years after detection). (Color figure available online.)

Results of the logistic analyses showed a clear pattern: As the percentage of landscape that is suitable for occupation increases, the year at which exponential growth and saturation occur also increases. This is logical because it just takes longer for an invasion to reach these phases as the suitable area increases. Nevertheless, these outcomes could be used for extrapolation purposes as these relationships apparently hold true across scales, as shown by the validation procedure with data collected outside the original surveyed area (Figure 2). For instance, if we know that 20 percent of the area is suitable for holly occupation and a similar proportion exists at the park level, we could expect that it will take about eight years for holly to start spreading exponentially and approximately eighty-five years for the invasion to reach saturation after detection in the whole park (Table 8, $P_t \geq 0.5$). Additional landscape structural characteristics (e.g., patch density or extent) could be inferred from these relationships at coarser scales that could be helpful for managers. For example, we could expect a mean holly density of $7 \text{ patches ha}^{-1}$ ($\pm 2.1 \text{ patch ha}^{-1}$) covering approximately $77 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 4 \text{ m}^2 \text{ ha}^{-1}$) on average when holly reaches its maximum spread rate (Figure 8A). When the saturation phase begins, the values could increase up to $94 \text{ patches ha}^{-1}$ ($\pm 28 \text{ patch ha}^{-1}$) and $964 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 49 \text{ m}^2 \text{ ha}^{-1}$), respectively (Figure 8B). By building scenarios like this it is possible to assist managers in designing environmental interventions (e.g., spread control or eradication strategies) across the different phases of the invasion process.

Conclusions

In this study, we combined components of population dynamics and environmental suitability to help

understand an invasion process locally. We examined several key components (i.e., environmental conditions and dispersion mechanisms) because of their strong influence in predicting spread patterns. This study shows that local environmental conditions, species characteristics, and specific dispersal mechanisms play a significant role in predicting the rate and success of holly establishment across the different phases of invasion. Thus, invasive species management plans should consider both species characteristics and their habitat and the interactions among them when planning long-term strategies for control and eradication.

The capability to simulate an invasion process spatially and forecast time horizons of critical invasion phases is useful from a species management perspective. The estimation of time horizons is ultimately important not only for theory development (e.g., carrying capacity or spatial pattern forecasting) but because managers must plan in advance to optimally allocate resources from limited budgets (Hyder, Leung, and Miao 2008). Because managers typically operate at fine spatial scales and short time horizons, studies like this one offer new possibilities to spatially analyze the consequences of not taking control measures in a timely manner. Improved decision-making plans based on spatiotemporal explicit information is beneficial for all stakeholders involved in invasive species management. Users can easily relate to and engage with this type of information as it identifies where the problems are and when to expect them. ■

Acknowledgments

This research was conducted under Washington State Parks Research Permit # 110101. We thank Washington State Parks and the staff of St. Edward State Park for their assistance with the project. We also thank

Joanna Mead, Amy Vondette, and Katrina Fisk for help with GIS data processing and collection; and Elliot Church, David Cronkright, Caitlin Campbell, Rachel Phillips, Jenna Beverly, Justin Bales, Dexter Chan, Michael Crepps, Shannon Kehoe, Evan Krelow-Carnes, Chuong Pham, and James Watson for help with the field work. We also thank the Editor, Barney Warf, and two anonymous reviewers for their helpful comments on the article.

Funding

Fieldwork was made possible in part through a grant to support undergraduate participation in research from the University of Washington.

Literature Cited

- Arrieta, S., and F. Suárez. 2005. Spatial dynamics of *Ilex aquifolium* populations seed dispersal and seed bank: Understanding the first steps of regeneration. *Plant Ecology* 177 (2): 237–48.
- Ball, G. H., and D. J. Hall. 1965. *ISODATA, a novel method of data analysis and pattern classification*. Menlo Park, CA: Stanford Research Institute.
- Blumenthal, D. M., A. P. Norton, S. E. Cox, E. M. Hardy, G. E. Liston, L. Kennaway, D. T. Booth, and J. D. Derner. 2012. *Linaria dalmatica* invades south-facing slopes and less grazed areas in grazing-tolerant mixed-grass prairie. *Biological Invasions* 14 (2): 395–404.
- Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications* 16 (3): 1132–47.
- Cadenasso, M. L., and S. T. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15 (1): 91–97.
- Carlson, K. C., B. S. Soares-Filho, G. P. Asner, S. N. Trigg, D. A. Gaveau, D. Lawrence, and H. Rodrigues. 2012. Committed carbon emissions, deforestation, and community land conversion from oil palm plantation expansion in West Kalimantan, Indonesia. *Proceedings of the National Academy of Sciences of the United States of America* 109 (19): 7559–64.
- Chappell, C. B. 2006. Upland plant associations of the Puget Trough ecoregion, Washington. Natural Heritage Report 2006–01, Washington Department of Natural Resources, Natural Heritage Program, Olympia, WA.
- Dale, V. H., R. V. O'Neill, F. Southworth, and M. Pedlowski. 1994. Modeling effects of land management in the Brazilian Amazonian settlement of Rondônia. *Conservation Biology* 8 (1): 196–206.
- Environmental Systems Research Institute. 2011. *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Corvallis: Oregon State University Press.
- Frohn, R. C., K. C. Mcgwire, V. H. Dale, and J. E. Estes. 1996. Using satellite remote sensing analysis to evaluate a socio-economic and ecological model of deforestation in Rondônia, Brazil. *International Journal of Remote Sensing* 17 (16): 3233–55.
- Gardner, R. H., B. T. Milne, R. V. O'Neill, and M. G. Turner. 1987. Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology* 1 (1): 19–28.
- González-Moreno, P., J. Pino, N. Gassó, and M. Vilà. 2013. Landscape context modulates alien plant invasion in Mediterranean forest edges. *Biological Invasions* 15 (3): 547–57.
- Gottschalk, P. G., and J. R. Dunn. 2005. The five-parameter logistic: A characterization and comparison with the four-parameter logistic. *Analytical Biochemistry* 343 (1): 54–65.
- Green, A. F., S. Ramsey, and J. Ramsey. 2013. Polyploidy and invasion of English ivy (*Hedera* spp., Araliaceae) in North American forests. *Biological Invasions* 15 (10): 2219–41.
- Haines-Young, R., and M. Chopping. 1996. Quantifying landscape structure: A review of landscape indices and their application to forested landscapes. *Progress in Physical Geography* 20 (4): 418–45.
- Higgins, S. I., D. M. Richardson, and R. M. Cowling. 1996. Modeling invasive plant spread: The role of plant–environment interactions and model structure. *Ecology* 77 (7): 2043–54.
- Honnay, O., K. Verheyen, and M. Hermy. 2002. Permeability of ancient forest edges for weedy plant species invasions. *Forest Ecology and Management* 161 (1–3): 109–22.
- Hosmer, D. W., Jr., and S. Lemeshow. 2004. *Applied logistic regression* (2nd ed.). Hoboken, NJ: Wiley.
- Huang, C., and G. P. Asner. 2009. Applications of remote sensing to alien invasive plant studies. *Sensors* 9 (6): 4869–89.
- Huang, H. M., L. Q. Zhang, Y. J. Guan, and D. H. Wang. 2008. A cellular automata model for population expansion of *Spartina alterniflora* at Jiuduansha Shoals, Shanghai, China. *Estuarine, Coastal and Shelf Science* 77 (1): 47–55.
- Huebner, C. D., and P. C. Tobin. 2006. Invasibility of mature and 15-year old deciduous forests by exotic plants. *Plant Ecology* 186 (1): 57–68.
- Hyder, A., B. Leung, and Z. Miao. 2008. Integrating data, biology, and decision models for management: Application for leafy spurge (*Euphorbia esula*). *Ecology and Society* 13 (2): 12.
- Ibáñez, I., J. A. Silander, Jr., J. M. Allen, S. A. Treanor, and A. Wilson. 2009. Identifying hotspots for plant invasions and forecasting focal points of further spread. *Journal of Applied Ecology* 46 (6): 1219–28.
- Kennedy, T. A., S. Naem, K. M. Howe, S. J. Knop, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–38.
- King County. 2014. Noxious weeds. <http://www.kingcounty.gov/environment/animalsAndPlants/noxious-weeds/weed-identification/english-holly.aspx> (last accessed 13 November 2014).
- Kruskal, W. H., and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association* 47 (260): 583–621.
- Lawrence, R. L., S. D. Wood, and R. L. Sheley. 2006. Mapping invasive plants using hyperspectral imagery and Breiman Cutler classifications (RandomForest). *Remote Sensing of Environment* 100 (3): 356–62.
- Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics* 34:575–604.
- Liao, J., M. Tao, and M. Jiang. 2014. Spatial arrangements affect suppression of invasive *Alternanthera*. *Acta Oecologica* 59:46–51.
- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2007. *Invasion ecology*. Oxford, UK: Blackwell.

- López, S. 2014. Modeling agricultural change through logistic regression and cellular automata: A case study on shifting cultivation. *Journal of Geographic Information System* 6:220–35.
- Lu, M. L., J. Y. Huang, Y. L. Chung, and C. Y. Huang. 2013. Modelling the invasion of a Central American Mimosoid tree species (*Leucaena leucocephala*) in a tropical coastal region of Taiwan. *Remote Sensing Letters* 4 (5): 485–93.
- Maeda, E. E., C. M. De Almeida, A. De Carvalho Ximenes, A. R. Formaggio, Y. E. Shimabukuro, and P. Pellikka. 2011. Dynamic modeling of forest conversion: Simulation of past and future scenarios of rural activities expansion. *International Journal of Applied Earth Observation* 13 (3): 435–46.
- Mandryk, A. M., and R. W. Wein. 2006. Exotic vascular plant invasiveness and forest invasibility in urban boreal forest types. *Biological Invasions* 8 (8): 1651–62.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS v3: Spatial pattern analysis program for categorical maps. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (last accessed 15 July 2014).
- Olmsted, D. 2006. English holly, *Ilex aquifolium*. In *Invasive species in the Northwest*, ed. P. D. Boersma, S. H. Reichard, and A. M. Van Buren, 42–43. Seattle: University of Washington Press.
- Parker, I. M., and S. H. Reichard. 1998. Critical issues in invasion biology for conservation science. In *Conservation biology for the coming decade*, ed. P. L. Fiedler, and P. M. Kareiva, 283–305. New York: Springer.
- Peterken, G. F., and P. S. Lloyd. 1967. Biological flora of the British Isles: *Ilex aquifolium* L. *Journal of Ecology* 55 (3): 841–58.
- Pétillon, J., F. Ysnel, A. Canard, and J. C. Lefevre. 2005. Impact of an invasive plant (*Elumus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: Responses of spider populations. *Biological Conservation* 126 (1): 103–17.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52 (3): 273–88.
- Puget-Sound-Lowlands-LiDAR-Project. 2000–2005. *LiDAR Bare Earth—6 foot Super Mosaic. Seattle, WA*. <http://puget.soundlidar.ess.washington.edu/index.htm> (last accessed 9 February 2013).
- Pyšek, P., and D. Richardson. 2010. Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35 (1): 25–55.
- Richards, F. J. 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10 (2): 290–300.
- Schweingruber, F. H., A. Börner, and E. Schultz. 2013. *Atlas of stem anatomy in herbs, shrubs, and trees*. Vol. 2. Berlin: Springer-Verlag.
- Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. *American Naturalist* 146 (2): 229–51.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38 (1): 196–218.
- Smith, H. 2006. *Rare plant and vegetation survey of Saint Edward State Park*. Winthrop, WA: Pacific Biodiversity Institute.
- Soares-Filho, B. S., G. C. Cerqueira, and C. L. Pennachin. 2002. DINAMICA—A stochastic cellular automata model designed to simulate the landscape dynamics in an Amazonian colonization frontier. *Ecological Modeling* 154 (3): 217–35.
- Stokes, D. L., E. D. Church, D. M. Cronkright, and S. Lopez. 2014. Pictures of an invasion: English holly (*Ilex aquifolium*) in a semi-natural Pacific Northwest forest. *Northwest Science* 88 (2): 75–93.
- Strickland, C., G. Dangelmayr, and P. Shipman. 2014. Modeling the presence probability of invasive plant species with nonlocal dispersal. *Journal of Mathematical Biology* 69 (2): 267–94.
- Sui, D. Z., and H. Zeng. 2001. Modeling the dynamics of landscape structure in Asia's emerging Desakota regions: A case study in Shenzhen. *Landscape and Urban Planning* 53 (1–4): 37–52.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81 (1): 99–109.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5 (1): 12–16.
- U.S. Geological Survey. 2010. The National Map Viewer. <http://viewer.nationalmap.gov> (last accessed 25 May 2013).
- Verburg, P., K. Neumann, and L. Nol. 2011. Challenges in using land use and land cover data for global change studies. *Global Change Biology* 17 (3): 974–89.
- Wang, L., J. L. Silván-Cárdenas, J. Yang, and A. E. Frazier. 2013. Invasive saltcedar (*Tamarisk* spp.) distribution mapping using multiresolution remote sensing imagery. *The Professional Geographer* 65 (1): 1–15.
- Wilcove, C. S., D. Tothstein, J. Dubow, and A. Phillip. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48 (8): 607–15.
- With, K. A. 2002. The landscape ecology of invasive species. *Conservation Biology* 16 (5): 1192–1203.
- Wu, F. 2002. Calibration of stochastic cellular automata: The application to rural–urban land conversions. *International Journal of Geographical Information Science* 16 (8): 795–818.
- Zhu, Z., L. Liu, Z. Chen, J. Zhang, and P. H. Verburg. 2009. Landuse change simulation and assessment of driving factors in the Loess Hilly Region—A case study as Pengyang County. *Environmental Monitoring and Assessment* 164 (1–4): 133–42.
- Zika, P. F. 2010. Invasive hollies (*Ilex, Aquifoliaceae*) and their dispersers in the Pacific Northwest. *Madrõno* 57 (1): 1–10.

SANTIAGO LOPEZ is an Assistant Professor in the School of Interdisciplinary Arts and Sciences at the University of Washington Bothell, Bothell, WA 98011. E-mail: cslopez@uw.edu. His research interests include geographic information science, land use and land cover changes in the Americas, and issues related to the human dimensions of global environmental change.

DAVID L. STOKES is an Associate Professor in the School of Interdisciplinary Arts and Sciences at the University of Washington Bothell, Bothell, WA 98011. E-mail: dstokes@uw.edu. He is an ecologist and conservation biologist whose current research focuses on animal movement and migration, conservation and restoration of endangered populations, and invasive species spread.