

Developing Dynamic Mechanistic Species Distribution Models: Predicting Bird-Mediated Spread of Invasive Plants across Northeastern North America

Cory Merow,* Nancy LaFleur, John A. Silander Jr., Adam M. Wilson, and Margaret Rubega

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269

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ABSTRACT: Species distribution models are a fundamental tool in ecology, conservation biology, and biogeography and typically identify potential species distributions using static phenomenological models. We demonstrate the importance of complementing these popular models with spatially explicit, dynamic mechanistic models that link potential and realized distributions. We develop general grid-based, pattern-oriented spread models incorporating three mechanisms—plant population growth, local dispersal, and long-distance dispersal—to predict broadscale spread patterns in heterogeneous landscapes. We use the model to examine the spread of the invasive *Celastrus orbiculatus* (Oriental bittersweet) by *Sturnus vulgaris* (European starling) across northeastern North America. We find excellent quantitative agreement with historical spread records over the last century that are critically linked to the geometry of heterogeneous landscapes and each of the explanatory mechanisms considered. Spread of bittersweet before 1960 was primarily driven by high growth rates in developed and agricultural landscapes, while subsequent spread was mediated by expansion into deciduous and coniferous forests. Large, continuous patches of coniferous forests may substantially impede invasion. The success of *C. orbiculatus* and its potential mutualism with *S. vulgaris* suggest troubling predictions for the spread of other invasive, fleshy-fruited plant species across northeastern North America.

Keywords: *Celastrus orbiculatus*, cellular automaton, grid-based model, spatially explicit model, species distribution model, *Sturnus vulgaris*.

Introduction

Species distribution models are a fundamental tool in biogeography, ecology, and conservation biology; they are useful for addressing questions about biodiversity, morphological/genetic diversity, and habitat suitability under past, present, and future climatic conditions. Species distribution models (also known as ecological niche models) typ-

ically identify potential species distributions by associating species occurrence with environmental characteristics and are static in time. The literature on species distribution models has grown substantially in the past decade, with a variety of new modeling methods, for example, Bayesian generalized linear models (Ibáñez et al. 2009a, 2009b), boosted regression trees, ecological niche factor analysis, Maxent, and multivariate adaptive regression splines (see summaries in Franklin 2009). Ecologists now rely on these models for conservation planning and understanding occurrence patterns. While informative, these models are generally phenomenological: they ignore dynamic factors affecting species distributions, such as dispersal and spread patterns, that link potential and realized distributions (Franklin 2010; Gallien et al. 2010). The omission of dispersal mechanisms from species distribution models may lead to model output that overestimates the presence of species in unreachable locations or underestimates it in low-suitability areas with high propagule rain. Dynamic models allow inference about temporal change in species' distributions. Temporal variation in distributions can be particularly important when species ranges are in flux, such as during invasions, periods of land use change or climate change, or after disturbance (Franklin 2010).

Mechanistic models of species' distributions are critical because they go beyond identifying spatial patterns; they make it possible to identify the factors, and the relationships among factors, that cause the spatial patterns. For example, phenomenological statistical models can identify latent spatial patterns in species distributions using spatial random effects. However, these random effects cannot explain species' distributions (e.g., Ibáñez et al. 2009a, 2009b). Dynamic models can also estimate the timescales associated with species spread. We argue that the types of dynamic mechanistic models we develop here provide the critical link between phenomenological static models that

* Corresponding author: e-mail: cory.merow@uconn.edu.

identify distribution patterns and a more complete understanding of those distributions (cf. Franklin 2010).

We focus here on the problem of invasions by bird-dispersed plant species to demonstrate the importance of dynamic mechanistic models. Because the models are quite general, they can be applied to the spread of any plant species across a landscape. Our capacity to successfully manage invasive alien species is commonly limited by our understanding and ability to predict the rates and patterns of spread (With 2002). Fleshy-fruited invasive plants are among the most aggressive invasive species and are primarily spread by birds (Richardson et al. 2000). Bird-dispersed seeds may be moved farther (e.g., Willson 1993) and to more favorable habitats (e.g., Wenny 2001) than those moved by other natural means, and this interaction can be a determining factor in the invasion process. This is particularly true in northeastern North America, where bird-dispersed, invasive woody species are pervasive; they are found in approximately 61% of 11,000+ field records in the Invasive Plant Atlas of New England (IPANE; Mehrhoff et al. 2003).

While there is a long history of study and a wealth of information on the biology and ecology of both plant invasions and fruit-frugivore interactions, little progress has been made in developing predictive mechanistic models for the spread of plants with animal-dispersed seeds (but see, e.g., Nathan and Muller-Landau 2000 and Higgins et al. 2001 for mechanistic models for wind-dispersed species). Existing animal-mediated seed dispersal models, with a few exceptions (e.g., Higgins et al. 2001; Levey et al. 2005; Will and Tackenberg 2008), are phenomenological and lack a detailed mechanistic understanding of the interplay between plants and their dispersers in response to variation in environmental factors. Dispersers may forage more frequently in some habitats than others (e.g., Guitian et al. 1992) or deposit seeds in a nonrandom pattern with respect to habitat type (Wenny 2001; Russo et al. 2006). The environmental conditions preferred by dispersers may not be optimal for seed germination or establishment.

We used grid-based (GB) simulation models to capture spread dynamics in a framework that is discrete in space, time, and state. These types of models are alternatively called cellular automata or spatially explicit models, depending on the context (Jongejans et al. 2008b), and are often found in individual-based modeling schemes (Grimm and Railsback 2005; Berger et al. 2008). We use a pattern-oriented approach (Grimm and Railsback 2005) to develop GB models that can reproduce observed patterns of spread in both space and time. GB models are appealing because they can incorporate more biological and geographic realism through complex interacting factors than comparable analytic techniques (Jongejans et al. 2008b). GB models have been used extensively in plant

ecology (for recent reviews, see Higgins and Richardson 1996; Jeltsch and Moloney 2002; Grimm and Railsback 2005; Winkler 2006; Berger et al. 2008; Jongejans et al. 2008b; Franklin 2010; Hui et al. 2010; Tsoar et al. 2010). GB models have the advantage of decoupling a complex space-time problem into two simpler problems: a temporal model within a cell and a spatial model that connects adjacent cells. In landscape models for population dynamics, this decomposition typically corresponds to local population growth within a cell and dispersal among cells. GB modeling has previously been applied to invasions with much success (see reviews listed above). It is particularly instructive for modeling invasions across large spatial scales because GB models readily incorporate landscape heterogeneity based on GIS data plus stochastic, rare long-distance dispersal (LDD) events that can greatly affect spread dynamics (Kot et al. 1996; Jeltsch et al. 1997; Higgins and Richardson 1999; Clark et al. 2001). However, most mechanistic models for dispersal consider only homogeneous landscapes (Jongejans et al. 2008b). Our models are unique in the combination of factors they incorporate in a GB framework, although elements of our approach can be found in earlier spatial spread models that include mechanistic seed dispersal (e.g., Nathan and Muller-Landau 2000; Higgins et al. 2001; Russo et al. 2006; Tsoar et al. 2010), LDD (e.g., Higgins et al. 2001; Levey et al. 2005, 2008; Cannas et al. 2006), heterogeneous landscapes (e.g., With 2002; Schurr et al. 2008), and large (landscape to regional) spatial scales (e.g., Ostendorf et al. 2001; Perry and Enright 2002). Our analysis also provides one of the most detailed and comprehensive explorations of model parameterization and validation (see appendixes, available in a zip file) that we have found, following the recommendations of Grimm and Railsback (2005) and Schmolke et al. (2010).

As a case study, we consider the spread of an invasive woody liana (Oriental bittersweet *Celastrus orbiculatus*) facilitated by invasive European starlings (*Sturnus vulgaris*) over the past century across northeastern North America (New England; see fig. 1). European starlings (*Sturnus vulgaris*), which are particularly abundant frugivores in New England, are important seed dispersal agents for bittersweet. Large flocks of starlings forage heavily on the plentiful bittersweet fruits during the late autumn and winter months when other resources are scarce (LaFleur 2006) and increase germination of the seeds they ingest (LaFleur et al. 2009). The first records of starlings in New England (New Haven, CT, 1906) predate those of bittersweet (Derby, CT, 1916), and their range expansion preceded that of bittersweet throughout New England (fig. 1). The sheer numerical dominance of starlings (on average 77 times more abundant than other potential dispersers) in Christmas Bird Count surveys across New England sug-

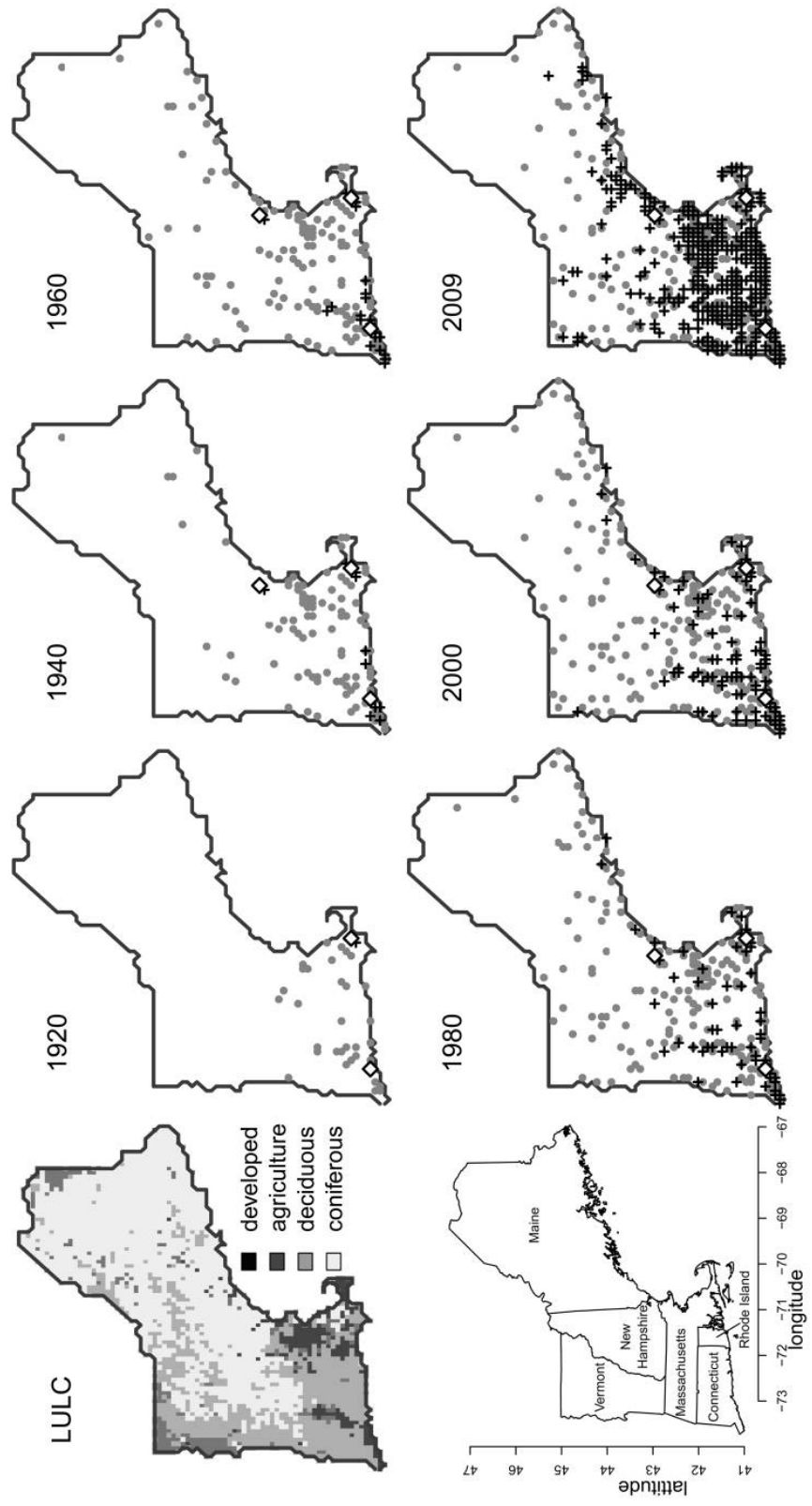


Figure 1: Presence records of Oriental bittersweet and European starlings in New England. Both field and herbarium data are shown for bittersweet records for 2009. We assume that land use/land cover (LULC) has not changed appreciably at this resolution during this time period (cf. Mosher et al. 2009). Note the spatial similarity in presence patterns; the starting expansion front leads the bittersweet expansion front by approximately 40–60 years.

gests that they are the dominant dispersal vector (fig. S17 [figs. S1–S21 are available in the zip file]; see “Discussion” for a justification to focus on starlings as the primary dispersal vector). Both starlings and bittersweet flourish in developed and agricultural landscapes and particularly along forest edges and hedgerows (Ibáñez et al. 2009a, 2009b; Latimer et al. 2009; Mosher et al. 2009); expanding starling populations may have been largely responsible for delivering seeds to suitable habitats.

We present a comprehensive GB approach that scales from local behavior to landscape patterns, simulating the spread of a bird-dispersed invasive plant. We focus on answering the following questions: (1) What mechanisms drive the spread of bittersweet in New England? (2) How can dynamic mechanistic models be used to complement static phenomenological models to better understand the nonequilibrium species distributions? (3) How can the model be generalized to other systems?

Empirically calibrated GB models for our study system investigate how starling movement, starling habitat use, and bittersweet habitat preferences affect invasion dynamics in a heterogeneous landscape, allowing us to test the hypothesis that dispersal by starlings is sufficient to explain the spread of bittersweet in New England over the past century. We evaluate the predicted patterns of bittersweet spread by comparison with the historical pattern of occurrence since 1916. We demonstrate how mechanistic and phenomenological modeling approaches complement each other by comparing our dynamic models to static, correlative species distribution models (Ibáñez et al. 2009a, 2009b) to better understand distribution dynamics. The appendixes provide extensive discussion of modeling considerations, evaluation, and R code (R Development Core Team 2009) to help users develop their own models.

Methods

Model

A brief conceptual overview of the model will simplify its presentation. The objective of the model was to determine the extent to which robust predictions of spread are possible using a simple set of mechanisms. There are four empirically derived components to our model. First, each cell is classified by land use type. Plant spread is modeled on this landscape using three mechanisms: (1) local population growth within cells, (2) local seed dispersal among nearby cells, and (3) random LDD. It is important to distinguish the simplicity of the model from the methods used to estimate values for each of these parameters (see table 1 for a summary of parameters). We first describe the model in detail and then discuss a way of estimating these parameters from available data for our study system.

Landscape. We begin the model by specifying a landscape on which to model species spread. This consists of overlaying the landscape with a two-dimensional square grid of appropriate size and classifying the land use/land cover (LULC) in each grid cell. LULC designations in each cell can be determined by majority rule of smaller, resampled composite cells to accommodate different landscape spatial resolution (e.g., Borrough and McDonnell 1998). Next, we specify the duration of the time step associated with each iteration of the model.

Local Population Growth. The model has one parameter for plant population growth for each habitat type. Local population growth occurs geometrically in each cell, with abundance defined on the interval between 0 and a carrying capacity:

$$N_{t+1} = \lambda N_t \quad \text{if } N_t < \text{carrying capacity,}$$

$$N_{t+1} = N_t \quad \text{if } N_t = \text{carrying capacity,}$$

where N is the number of individuals, λ is the asymptotic population growth rate reflecting the balance between growth and mortality, and t is time; λ could be >1 , corresponding to population growth, or <1 , corresponding to decline. For simplicity, we round noninteger abundance up at the end of each time step.

Local Dispersal. Changes in population in a single cell were achieved by either geometric growth within a cell or immigration from other cells. Immigration by a single seed increased the population of the cell by 1. Each cell was connected to adjacent cells by stochastic local dispersal. In our case study, birds constitute the local dispersal mechanism; however, in principle, any dispersal mechanism can be used. We refer here to cells that produce emigrants as source cells and the set of neighbors as target cells. The number of emigrants produced by each cell was determined on the basis of the population growth rate and local dispersal kernel; $N_i(\lambda_i - 1)$ represented the number of offspring produced in cell i at time t , which were then distributed according to the local dispersal kernel. Many of these land in the source cell, while some (approximately 17% in the best-supported model; fig. S19) land in nearby cells. We used 7×7 -cell local dispersal neighborhoods (our dispersal kernel had negligible weight outside this neighborhood; fig. S19), with the strength of the connection among cells modeled by an exponential function of distance. We chose an exponential kernel because it has only one parameter and thereby represents the simplest dispersal distribution among those widely used for dispersal kernels (Jongejans et al. 2008b). However, any suitable distribution can be used. The exponential distribution

Table 1: Summary of model parameters

Parameter	Best value	Data	Parameter estimation
Mean local bird dispersal distance	.286 cells \cong 2.14 km	Radio tracking, banding recapture	Use tracking data to estimate velocity and combine with seed retention times to obtain movement distances; fit these distances to an exponential distribution
Population growth rate		Transplant experiments: seedling survival, adult survival, growth (biomass)	Use pattern-oriented parameterization consistent with the ranking of population growth rates according to adult survival and biomass accumulation
Developed	2.1		
Agricultural	1.5		
Deciduous	1.4		
Coniferous	.5		
Starling landscape use		Proportion of (1) each landscape where radio tracking conducted and (2) time spent in each landscape type during radio tracking	Divide the proportion of time spent in each landscape by the proportion of each landscape type to obtain relative values, then normalize to estimate proportion of time spent in each landscape type
Developed	.39		
Agricultural	.44		
Deciduous	.06		
Coniferous	.11		
Random LDD	1 event/year	Banding recaptures	Use pattern-oriented parameterization and minimum annual contribution of LDD consistent with relative frequency of long-distance movements from banding recapture data

Note: LDD, long-distance dispersal.

is combined with a disperser habitat use index to incorporate variation in LULC:

$$P(\text{target}_i | \text{source}_j) \propto$$

$$\text{disperser habitat use}_i \times \exp(-k|x_i - x_j|),$$

where $1/k$ is the mean of the dispersal kernel and x_i refers to the position (center) of cell i . Hence, the probability of dispersing to a cell is an exponential function of the distance between cell source and target cell centers, up-weighted or downweighted by a discrete index of the disperser habitat use of the target cell.

Long-Distance Dispersal. We separately modeled LDD, which can be interpreted to correspond to anthropogenic agents or emigration by birds. We model LDD using a single parameter, the number of events per year. A single dispersal event increases the population of the target cell by one individual. The LDD emigrant disperses from a randomly chosen occupied site to a random unoccupied site in the LDD neighborhood. The LDD neighborhood of a given source cell is defined as all cells within some maximum distance of the source (e.g., the entire landscape in our case study) but excluding the local dispersal neigh-

borhood (e.g., 7×7 cells, or roughly $65 \text{ km} \times 65 \text{ km}$, in our case study). The choice of source and target cells is independent of LULC classification.

Parameter Estimation for Starling-Bittersweet System

We estimated parameter values with available data when possible and used pattern-oriented modeling methods when little or no data were available (also known as inverse modeling; Grimm and Railsback 2005). Pattern-oriented parameterization seeks combinations of parameters that reproduce multiple observed patterns (in our case the spatial and temporal patterns of spread) while searching over a large range of parameter values. We performed sensitivity analyses to examine the implications of variation in these estimates. While we provide the “best” parameter estimates for simplicity (table 1), it is important to recognize that this parameterization strategy describes a range of parameter values over which observed patterns are reproduced (for details, see table S1 [tables S1–S4 are available in the zip file]). Testing a range of parameter values against observed patterns allowed us to fully explore the model, particularly when more precise empirical estimates are not available. We consider a time step of 1 year; hence, all

parameters can be interpreted as annual rates. However, the model could be readily scaled to accommodate other temporal resolutions.

Landscape. We modeled population dynamics in 5×5 -ft cells, which required 3,057 cells to cover New England. We used LULC classifications for the region (National Oceanic and Atmospheric Administration 1995–), in conjunction with data on starling movement patterns and bittersweet seed survival, to reclassify the original 30 classes into four appropriate LULC classes: developed, agricultural/grassland, deciduous forest, coniferous, and mixed deciduous-coniferous forest (henceforth coniferous; table S4). This spatial resolution and LULC classification has been used effectively to explain bittersweet distributions in earlier static models (Ibáñez et al. 2009a, 2009b) and allows a direct comparison to our dynamic mechanistic model. We assume that LULC has not changed appreciably at this resolution in the past 90 years. This seems reasonable, given that the largest change in the region over the past 2 centuries—the return of agricultural lands to forest—occurred primarily from 1850 to about 1900 (cf. Foster 1992; Mosher et al. 2009).

Local Population Growth. To initialize the model, we used the first three observed naturalized occurrences of bittersweet in the New England landscape (from herbarium records; Mehrhoff et al. 2003). These occurred in Derby, Connecticut (1916); Falmouth, Massachusetts (1919); and New Durham, New Hampshire (1938). We started the model in 1919 with the first two sites, later introduced a population in New Durham in 1938, and iterated a total of 90 years. In the model, we seeded the introduction sites with a population size equal to half that of the carrying capacity in order to avoid stochastic extinctions resulting from small populations (history confirms that the real source populations overcame this complication). This assumption is equivalent to permitting an extremely high population growth rate for the first 2 years after introduction, a phenomenon that has been empirically observed for aggressive invasive species in a number of systems (e.g., Jongejans et al. 2008a; Schutzenhofer et al. 2009).

Asymptotic population growth rates for each landscape were based on survival rates in different landscapes measured in transplant experiments using seedling and adult survival (Leicht 2005; Leicht-Young 2007; table S3). These are, in some sense, free parameters that can be adjusted using a pattern-oriented approach (Grimm and Railsback 2005) to overcome imprecise or unavailable data at the chosen spatial scale (as will usually be the case for coarse spatial scales). The transplant experiments indicated that bittersweet had the highest survival (>95%) and greatest

mean biomass accumulation at harvest in developed and agricultural landscapes. Plants in deciduous landscape also showed high survival (90%–95%) but grew substantially (60%–70%) less, while coniferous landscapes were relatively unfavorable for survival (60%–80%; Leicht 2005; Leicht-Young 2007). We adopted this hierarchy for landscape preference (the data component; table 1) and adjusted λ values to obtain the minimum amount of spread necessary to predict the majority of presences (the pattern-oriented component). We then used sensitivity analysis to ensure that our results were robust to deviations in the chosen λ values. While most perennial plant population growth rates remain close to 1 (Silvertown et al. 1993) over short time periods, growth rates may be much higher (e.g., Schutzenhofer et al. 2009). We considered λ values on the interval [0, 2.1], since these reflect the range of sustainable growth during invasion (cf. Jongejans et al. 2008a).

In order to make the model run faster, we take advantage of the observation that varying the per-cell carrying capacity between 50 and 50,000 had no significant effect on predicted presence or absence (see app. S1). For the local dispersal neighborhood size and population growth rates we considered, we find that allowing larger carrying capacities does not affect early spread and affects the number of dispersing seeds only after 8–20 years have passed. After 8–20 years, most cells in the local dispersal neighborhood of an inhabited cell have already been colonized during this interval, and hence patterns of presence are not affected. Given these considerations, we chose a carrying capacity of 200 as a modeling convenience to allow the model to run quickly.

Local Dispersal. Starlings were introduced to New York City in 1890–1891 (Cabe 1993), and the Christmas Bird Counts, beginning in 1900, record their yearly spread across the New England landscape (fig. 1; National Audubon Society 2002). The historical presence of bittersweet appears to lag starling presence by approximately 40–60 years (fig. 1). We therefore assumed in the model that starlings are effectively present throughout the landscape wherever bittersweet is present, and we did not model starling dynamics.

Seed dispersal was partitioned between local dispersal by birds and random LDD that captured infrequent bird movement or human-assisted dispersal. Landscape structure has been shown to influence feeding behavior (e.g., Evans et al. 2009) as well as fruit abundance (e.g., Sallabanks 1993), so we interpret local seed dispersal to derive from feeding behavior and movements among roosts. To obtain a distribution of local movements by starlings, we used empirical data collected by LaFleur (2006) as part of a study examining their effectiveness as seed dispersers of

invasive plants. During this study, radiotelemetry was used to measure the distances that free-living starlings moved per unit time (methods in LaFleur 2006). Distance was measured as the net displacement between observation points and thus represents an underestimate of the total distance moved. Radio tracking documented movements of up to ~7 km (maximum distance = 7,301 m [over 184 min], mean \pm SD = 771 \pm 972 m). Such local movements have been used to estimate bird movements at larger scales (Levey et al. 2005). We obtained estimates of starling velocities by assuming straight-line movement between observation points; since observation points only rarely represented consecutive stops on a bird's route, these represent conservative underestimates. Gut passage rate data were collected from captive starlings that were fed bitter-sweet fruits (LaFleur 2006; LaFleur et al. 2009). The mean passage rate of bittersweet seeds was 43 \pm 20 min (SD), so we considered retention times ranging from 20 to 90 min (fig. S19). By multiplying the distribution of starling velocities by the passage rates, we estimated the seed dispersal kernel (see similar approaches in Holbrook and Smith 2000; Vellend et al. 2003), which we fit with an exponential distribution (fig. S19). Since these data focus on local movement, the seed dispersal kernels provide potential lower bounds on starling dispersal.

Similarly, we obtained an upper bound for the local bird dispersal distribution from larger-scale bird movements described by banding recaptures. While radio tracking of starlings suggests that they typically move seeds on the scale of hundreds to a few thousand meters during foraging (LaFleur 2006), movements on the order of many kilometers occur. For example, starlings roost in large groups every night as far as 12 km from feeding sites (Morrison and Caccamise 1990). Such distances can easily be traversed within typical seed retention times (LaFleur 2009), indicating that less frequent, longer-distance movements may also be important for plant spread. We estimated the upper bound on seed dispersal from banding recaptures that describe these and even longer movements. To estimate maximum starling velocities, we focused only on recaptures where birds moved more than 10 km in less than 2 days because these provide an upper bound for starling velocities. Using 46 records (U.S. Geological Survey Bird Banding Laboratory, unpublished data) that met these criteria, estimating that starlings could fly up to 8 h per day, and dividing the distance between recaptures by flight time, we obtained an average velocity. This provides a conservative velocity estimate, since it ignores indirect paths. We combined these velocities with gut passage times in the same manner as above and obtained exponential seed dispersal kernels. We used a distribution of movement distances with a mean (0.29 cells) that constitutes a balance between long- and short-distance movement (fig. S19).

We used sensitivity analysis to check that our results were robust to deviations from this mean.

Birds use some landscapes more than others, and this mediates their delivery of seeds. We estimated starling landscape use on the basis of our data documenting starling landscape visitation rates during tracking in the winters of 2003–2004 and 2004–2005. We matched the coordinates obtained from the first location of each track with LULC data (CLEAR 2006) at 30 \times 30-m resolution to determine the proportion of observations in each landscape type and used this as a proxy for the time spent in each landscape type. We estimated a landscape selectivity index by weighting the time spent in each landscape by the proportion of the landscape in Connecticut (Manly et al. 2002; table 1), where the starling movement data were collected.

Long-Distance Dispersal. We incorporated rare random LDD events separately from local bird-mediated dispersal, in part to reflect the difficulty of getting estimates of rare LDD events (Clark et al. 2001). As with population growth parameters, we used a pattern-oriented approach to parameter estimation. We used one event per year to allow the minimum contribution of this mechanism without making more detailed assumptions about the nature of LDD, but we found that using five or fewer events per year produced equivalent results (table S1). We avoid linking LDD to more complex factors such as landscape structure or specific sources because there is little generality in conclusions regarding LDD (other than the difficulty of accurately predicting it; Clark et al. 2001) and a more complex parameterization is apparently unnecessary to capture dynamics in the cases we study (fig. 2). Data from the U.S. Geological Survey Bird Banding Laboratory indicate the capability of starlings to traverse long distances quickly and contribute to LDD. They have recorded at least three cases of starlings recaptured more than 68 km away from the original banding site just 2 days after capture out of 25,000 total records; one individual traveled as far as 178 km (U.S. Geological Survey Bird Banding Laboratory, unpublished data; cf. fig. S19, *inset*). Given that between approximately 100,000 and 600,000 starlings have been observed during Christmas Bird Count surveys each year since 1960 (fig. S19), a single LDD event per year is likely a conservative estimate.

In our model, the LDD emigrant disperses from a randomly chosen occupied site to a random unoccupied site outside the local bird dispersal neighborhood. This was justified because rare LDD events are typically uncorrelated with standard means of dispersal (Higgins et al. 2003), which might otherwise tend to deposit seeds in occupied sites during starlings' foraging movements. Equivalent results were achieved by removing the restric-

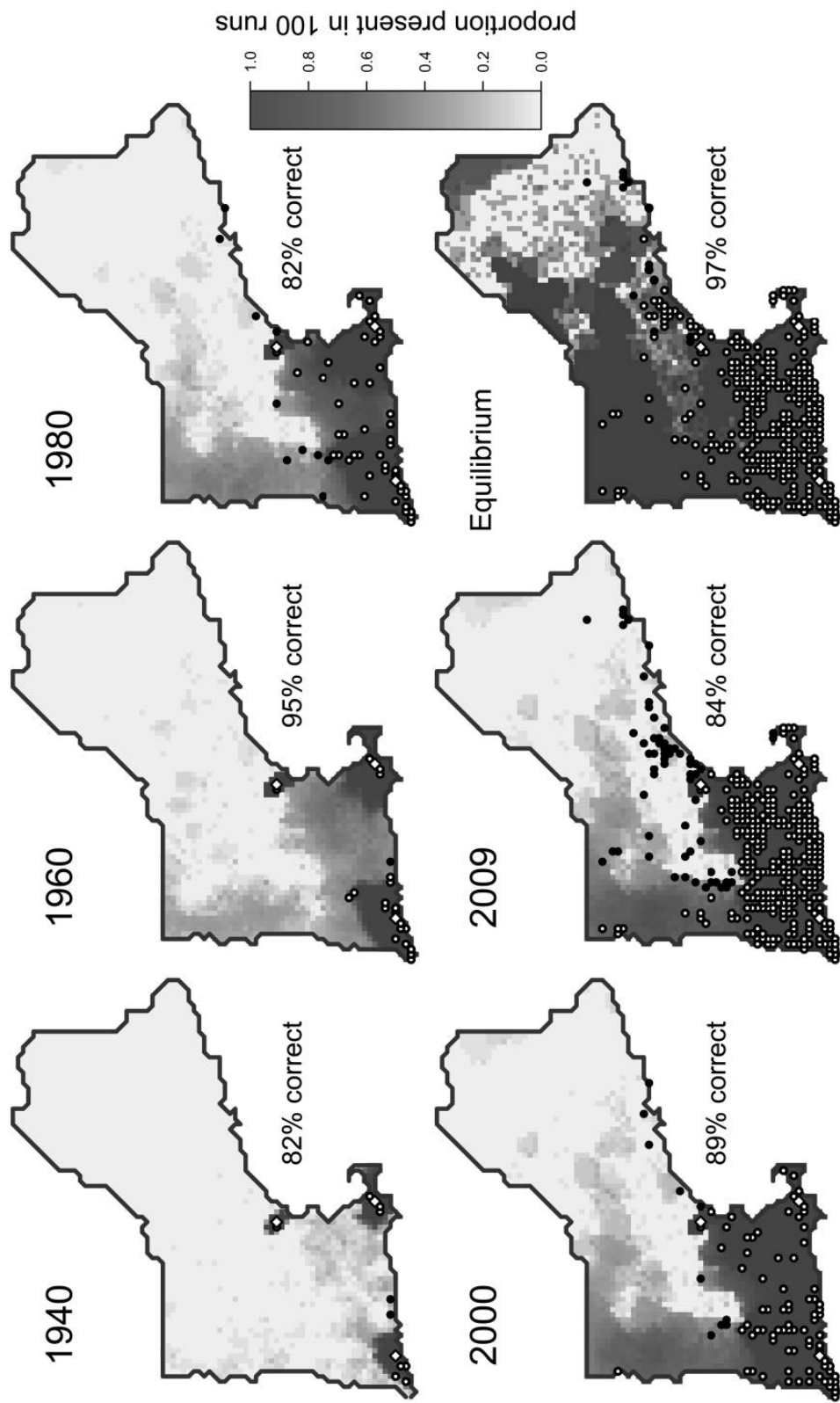


Figure 2: Invasion probability of *Celastrus orbiculatus* for best parameter estimates (table 1). Herbarium records (1916–2009) and field records (2002–2009) provide validation data. Open circles represent observed presences correctly predicted by at least 50% of model runs, and filled circles mark incorrect predictions of known presences. Diamonds indicate introduction points. The bottom right of each inset shows the proportion of observed presences correctly predicted at each time step. “Equilibrium” represents predictions after 800 time steps.

tion on occupied sites while increasing the number of LDD events. LDD immigrants could occur in any cell. However, we also tested restricted LDD neighborhoods (51×51 or 25×25 cells) centered on the source cell (figs. S14, S15). Starlings have also been noted to fly at 60–80 km/h (Feare 1984); thus, traveling such distances within feasible seed retention times is quite possible. Furthermore, we expect LDD to occur through a variety of other mechanisms (not just starlings), so modeling the entire landscape as the LDD neighborhood seemed appropriate.

Model Evaluation

We evaluated the predicted range expansion by comparison to two presence-only data sets from the IPANE project (Mehrhoff et al. 2003): (1) a time series derived from 179 herbarium specimens collected from 1916 to 2009 (fig. 1) and (2) 991 field records collected from 2002 to 2009. The field data set provided greater sampling intensity than the herbarium data but essentially captured only a single snapshot of the population in time. We compared model predictions, averaged over 100 runs, to the observed presences at five points during the historical time series (1940, 1960, 1980, 2000, and 2009). Finally, we evaluated the model using sensitivity analysis on all parameters.

Model evaluation is challenging when comparing models with different parameter values because allowing greater spread will necessarily increase model sensitivity (i.e., correctly predicted presences). For example, we use a growth rate of 2.1 in developed landscape cells; using a growth rate of 25 would improve the sensitivity but would be completely unrealistic. Because alternative methods do not exist (Boyce et al. 2002), we report the sensitivity (percent correct) and chose parameter values that produce the minimum spread necessary to fit the approximate observed invasion front without overestimating spread. In evaluating model prediction success, we required that 50% of model runs predicted presence accurately (following Ibáñez et al. 2009a, 2009b).

To assess the robustness of our model and to assess whether simpler models adequately captured historical spread patterns or whether a more complex model might be indicated (Jongejans et al. 2008b), we examined the consequences of different assumptions. We tested whether the three plant population expansion mechanisms—local population growth, local dispersal by birds, and random LDD—were all necessary. We also modified assumptions about the landscape by considering three alternative landscapes: homogeneous (all favorable landscape), binary (where developed, agricultural and deciduous landscapes were grouped as favorable, and coniferous landscape and water were unfavorable), and randomly sorted heterogeneous landscapes. We considered alternate introduction

scenarios by changing the location of the first three naturalized populations. We also initiated the model in 1939 and 1959, using the records obtained before the respective date as the initial populations. We used sensitivity analyses to explore the parameter space of the model, measuring sensitivity as the change in the proportion of presences correctly predicted (table S1). Details of the methods and results of the sensitivity analyses are provided in appendix S3.

Results

Our model correctly predicted the spread of bittersweet throughout southern New England by 2009 and its continued spread to northern New England. When compared to the observed time series, the full model successfully predicted between 82% and 95% of the observed presences (fig. 2). The model successfully predicted the temporal spread patterns, with initial spread along the southern coast of New England, extending into the Connecticut River Valley and Greater Boston, then spreading through much of southern New England and isolated patches in the north. Our model predicted that virtually all of southern New England and Vermont is occupied, while much of New Hampshire and Maine were invaded in fewer than 10% of runs. Many of our false negatives occurred in New Hampshire and coastal Maine. The main results of the sensitivity analysis were as follows: (1) plant population growth, local bird dispersal, and random LDD were all essential to produce accurate predictions; and (2) the model was most sensitive to developed and agricultural land use parameters (i.e., bittersweet growth rate, starling landscape use, and landscape geometry) before 1960 and deciduous and coniferous forest parameters after 1960 (tables S1, S2).

Changing plant population growth rates (λ) had a large impact on predictions (table S1). In general, increasing growth rates across all landscapes improved predictions slightly. However, increasing λ above 1 in coniferous forests led to vast overprediction. Reducing growth rates reduced spread substantially. High growth rates in developed landscapes were essential to match the rapid range expansion through 1980. Growth in deciduous forests was also important because this landscape is widespread across New England and separates developed and agricultural landscapes that are more favorable to population growth. Population growth rates in deciduous forest below 1.4 limited early spread into forests, while higher values overpredicted spread.

Incorporating the geometry of a heterogeneous landscape was also critical to accurately predicting patterns of spread. Spread patterns depended strongly on the introduction points (figs. S7–S11; table S2). For example, if the

initial introductions had been in the north, spread would have been contained by coniferous forest barriers (fig. S8). If initial introductions had occurred in the west, much of Vermont would have been occupied by 1980, while early spread along the Connecticut coast would have been much slower than what was observed empirically (fig. S10). Differential plant population growth rates among landscapes allow for more accurate models. The lower bounds on the population growth rates necessary to reproduce spread patterns in both deciduous landscapes (1.4) and developed landscapes (2.1) were particularly critical early in the invasion, when propagule pressure may have been exceptionally high in proximity to developed landscapes (table S1).

Discussion

We have developed a dynamic mechanistic, spatially explicit GB model that accurately predicts landscape invasion patterns of Oriental bittersweet across New England. Agreement between predicted and observed presence provides evidence that we have incorporated the necessary system complexity and that the mechanisms included are reasonable representations of the real processes affecting spread (Jongejans et al. 2008*b*). However, GB models are very flexible and permit a wide variety of pattern formation with highly customizable rules. It is essential that parameter values and assumptions have empirical justification because of the need to ensure that model accuracy is not a spurious result of optimized parameters. Our analysis represents the exhaustive exploration of assumptions and parameter space necessary for robust inference on real systems (cf. Grimm and Railsback 2005; Schmolke et al. 2010).

We draw several conclusions that pertain to the broad spectrum of invasion models. Most significantly, we find that landscape heterogeneity and geometry can determine range expansion rate, the pattern of spread from different introduction points, and sensitivity to landscape barriers (figs. 3, S7–S11). We also demonstrate the necessity of incorporating plant population growth, local dispersal, and LDD into models if the aim is to accurately reproduce broad, regional-scale spatial and temporal dynamics. High plant population growth parameters in some landscapes provided sufficient propagule pressure to fuel the spread of bittersweet across less favorable landscapes. In spite of dispersal by wide-ranging starlings (local bird dispersal mean ~ 2.1 km), random LDD was still critical to produce realistic patterns of spread. LDD is responsible for establishment in remote areas and seeding nascent foci (Moody and Mack 1988; Jeltsch et al. 1997) sooner than would local bird dispersal, which mainly controls the rate of backfilling.

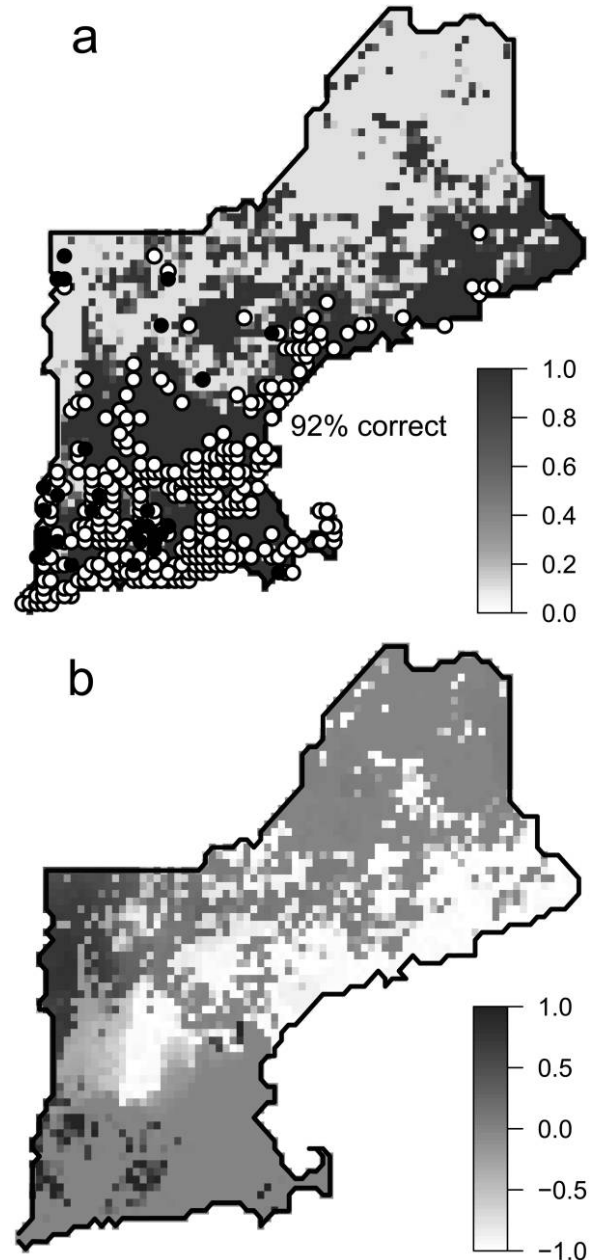


Figure 3: Comparison to static phenomenological hierarchical Bayesian (HB) model. Symbols follow figure 2. *a*, Predicted probability of presence (between 0 and 1; see scale bar) from HB model. *b*, Difference in predicted probability of presence between our grid-based (GB) model from 2009 and the HB model. The scale bar indicates the probability of presence in the GB model minus the probability of presence from the HB model. Dark gray indicates that predicted probabilities are higher in the GB model, and light gray indicates that predicted probabilities are higher in the HB model.

Mechanisms driving Bittersweet Spread

Our model provides insight into factors driving bittersweet's spread. The response of bittersweet to different landscape types was particularly important. In the model, the early invasion (through 1960) was primarily driven by parameters in agricultural and developed landscapes (table S1; see also Mosher et al. 2009), since these represent the main corridors through which the invasion began. The model proved largely insensitive to variation in all coniferous land use parameters through 1960 because there is relatively little of this landscape type in southern New England. In contrast, the later stages of invasion were apparently dictated by these same parameters for deciduous and coniferous forests because these constitute the areas that were reached only after 1980 (table S1). Population growth rates must have been exceptionally high in developed areas (>1.9 before 1980; table S1; Leicht-Young 2007). Such rapid growth suggests that density dependence was absent (at least initially) or that anthropogenic cultivation and reintroduction was an important contributor to spread. Sensitivity analysis revealed the importance of landscape geometry; prediction accuracy increased when populations were initiated in the south (where human population density is highest and where the species was first observed to be naturalized), suggesting that anthropogenic influences may have been important in this area (fig. S8). Deciduous landscapes provided the main potential corridor between the favored developed and agricultural landscapes. Our sensitivity analysis indicated that when deciduous forest is a sufficiently favorable habitat, there is little to inhibit spread throughout much of southern New England (table S1); population growth rates >1.4 in deciduous landscapes were necessary to accurately reproduce spread patterns (table S1). Small patches of favorable landscape embedded in deciduous forest may actually be sufficient to sustain such high growth ($\lambda > 1$) because the interface between forest and developed or agricultural areas is a prime place for establishment and growth of bittersweet (cf. Mosher et al. 2009). Thus, our model may underestimate spread in the north because it may underestimate the amount of suitable habitat there.

While the seed dispersal kernel generated by starling movement was essential to predicting patterns of spread, variation in starling landscape use had a smaller role. The model showed high sensitivity to starlings' use of deciduous landscape and developed landscape only during the early phase of introduction (pre-1960; table S1). Essentially, landscape use parameters in deciduous and developed landscape trade off with one another: when the value of one is too high, there is insufficient spread in the other landscape to match observations. Low sensitivity to starling landscape use from 1980 to 2009 (table S1) occurred

because the high-density source populations in and around developed areas produced a relatively dense propagule rain throughout the bird dispersal neighborhoods. This then obscures variation in landscape use. Use by starlings of coniferous landscapes was insensitive to variation because the bittersweet growth rate there was below 1, while agricultural landscape use was insensitive because only a small portion of the landscape is classified as agricultural. Starling landscape use affected only temporal, not spatial, dynamics of bittersweet; the long-term predictions are constant and driven by landscape-specific plant population growth rates and LDD. The minor impact of landscape use by birds on predictions is not entirely surprising. We know of no evidence suggesting that starlings avoid traveling through particular landscapes, and thus they may deposit seeds anywhere along their route.

Projecting spread over hundreds of years allowed informative patterns to emerge that reflect the importance of landscape heterogeneity and its geometric configuration (fig. 2; Latimer et al. 2009; Mosher et al. 2009). Much of Maine is apparently resistant to invasion, as evidenced by the poor population growth of bittersweet in the large expanse of coniferous landscapes. Coniferous forests may provide a safety buffer around favorable landscape that requires independent introductions (LDD) for bittersweet to establish. Isolated regions of northern Maine could potentially harbor bittersweet, but the time span required to reach these areas from elsewhere in New England may be large (400–800 years; fig. S13). In contrast, there are few substantial barriers to long-term spread in southern New England. The time necessary for bittersweet to infest northern Maine is inherently difficult to predict because it depends on the stochasticity associated with LDD.

Our model supports the idea that the immense success of bittersweet in New England has been facilitated by starlings, suggesting an important mutualism between these species. Movements on the order of kilometers drive spread (fig. S19; as much as 17% of seeds; figs. S14, S15; table 1). We suspect that these movements correspond to actual starlings traveling to roosts because these distances are larger than typical foraging movements (LaFleur 2006). Joint use of developed and agricultural landscapes—and associated edges—by starlings and bittersweet make such a mutualism more likely because starlings could deposit large numbers of seeds at favorable sites. Increasing LDD cannot account for these movements because it would lead to a much more random pattern of historical spread (fig. S18), as opposed to the relatively smooth invasion front that we observe (figs. 1, 3).

While other dispersers cannot be ruled out in the real range expansion of bittersweet, we have shown that starlings alone are sufficient to explain historical spread patterns. The numerical dominance of starlings, based on

Christmas Bird Counts (National Audubon Society 2002; fig. S20), compared with other species that are known (or suspected) to feed on bittersweet (LaFleur 2006; LaFleur et al. 2007) implicates them as a particularly important disperser. From 1960 to 1997, starlings were observed to be between 6 and 451 times more abundant than all other potential avian dispersers combined (mean 77). More recently (1998–2009), a dip in starling abundance has been coupled with an increase in native birds. Nonetheless, starlings remained an average of 2.3 times more abundant than all other potential avian dispersers combined.

The timing with which starlings eat bittersweet fruit may also be important. Bittersweet tends to be eaten later in winter when few other fruits are available (N. LaFleur and J. A. Silander, personal observations). It may provide a critical limiting resource in the winter months when starvation is a threat, thereby supporting the growth of starling populations. There is high mortality in first-winter starlings (Kessel 1957), so widely distributed, abundant winter food resources have the potential to drive population growth. This aspect of their mutualism requires more study. The spread of bittersweet is of concern, given the variety of other bird-dispersed invasive plants beginning to spread across New England (e.g., *Euonymus alatus* [burning bush], *Elaeagnus umbellata* [autumn olive], invasive *Lonicera* species [honeysuckles]).

Dynamic Mechanistic Models Complement Static Phenomenological Models

Dynamic mechanistic models that link potential and realized distributions are a critical complement to more commonly used static phenomenological models. For example, comparing the equilibrium potential distribution typical of many statistical models to GB model predictions for a particular time period (e.g., present or future) identifies high-risk areas for future spread, as we demonstrate below.

Comparison of our GB model predictions in 2009 to a hierarchical Bayesian (HB) generalized linear regression model for bittersweet (Ibáñez et al. 2009a) illustrates the importance of multimodel inference. The HB model predicts the potential distribution (probability of presence at equilibrium; reproduced in fig. 3a) on the basis of the same heterogeneous landscape lattice as our model but without reference to any dispersal mechanisms. It also accounts for smaller-scale variation through site-level habitat characteristics, canopy closure, proportion of each LULC class within each cell, and a suite of climate variables. If we interpret the proportion of GB model runs as a probability of presence, the two models can be directly compared by plotting the difference between their predicted probabilities of presence (fig. 3b).

Our model shares many predictions with the HB model but also differs in some important ways. Both models predict that southern New England is almost completely colonized by bittersweet, even in low-suitability coniferous landscapes. The HB model predicted minimal occurrence in Vermont, while the GB model predicted ample spread there by 2000 (fig. 3). The clumps of suitable habitat in Vermont combined with potentially dense propagule rain originating from more favorable southern populations may be sufficient to offset the climatic limitations predicted by the HB model. In coastal Maine, the HB model predicts high suitability while the GB model predicts no spread into this region. This comparison suggests that there may be sufficient suitable habitat should bittersweet reach the region. Identifying differences such as these between models can guide management by locating high-risk areas and predicting the timescales over which spread will occur. These examples provide just a glimpse of the advantages of using complementary modeling strategies and represent an important area for future research.

Generalizing the Model

Our model is general and can easily be adapted to study other systems. Parameters may be estimated with different or fewer data than we have demonstrated here; pattern-oriented parameterization combined with sensitivity analysis can ensure that the uncertainty in parameter values does not lead to qualitatively different predictions. For example, one might lack explicit information regarding landscape use by birds, but more general kinds of observation can broadly identify the landscape types used by many birds, while sensitivity analysis can be used to test the importance of precise parameter values.

The grid can be modified to represent any spatial scale. Population units can be scaled for different spatial and temporal resolutions and different measures of population size. Large carrying capacities can be used to represent individual plants/larger cells, or smaller carrying capacities can indicate plant populations/smaller cells. If smaller cells are used, one might consider an individual-based model (Grimm and Railsback 2005). A demographic model for plants can be easily incorporated within each cell to determine plant population growth rates and the number of seeds available for dispersal (Grimm and Railsback 2005; Jongejans et al. 2008b). Population growth rates can be estimated from a variety of sources and need not be generated from small-scale transplant experiments, as we have done here. The dispersal rates can also be scaled, with larger mean distances indicating smaller cell size. Local dispersal kernels can be constructed for any dispersal agent (e.g., wind, passive, animal; e.g., Greene et al. 2004; Bullock

et al. 2006). A more detailed treatment of LDD is possible when particular dispersal agents are known or suspected.

The simplicity of the model allows for quick and efficient exploration of different parameter scenarios to explore broadscale patterns when precise empirical data are unavailable. Sensitivity analysis can easily reveal relatively more and less important parameters, which can be used to refine data collection plans. Further refinements are also possible; incorporation of climatic variables or modeling a temporally variable landscape may be the most informative. For example, if many populations are observed, growth rates could be regressed on environmental covariates, and regression predictions could be used to estimate growth rates in an arbitrary cell from GIS maps of covariates. Ultimately, however, part of our model's appeal is its simplicity. Given this attribute and the coarse spatial scale, it is encouraging that we can predict spread with some degree of confidence.

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