Diversity and Distributions A Journal of Conservation Biogeography

Diversity and Distributions, (Diversity Distrib.) (2011) **17**, 552–565

BIODIVERSITY RESEARCH

Predicted range expansion of Chinese tallow tree (*Triadica sebifera*) in forestlands of the southern United States

Hsiao-Hsuan Wang[1]*, William E. Grant[1], Todd M. Swannack[1†], Jianbang Gan[2], William E. Rogers[2], Tomasz E. Koralewski[3], James H. Miller[4] and John W. Taylor Jr[5]

[1]*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA,* [2]*Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843, USA,* [3]*Department of Veterinary Integrative Sciences, Texas A&M University, College Station, TX 77843, USA,* [4]*US Forest Service, Southern Research Station, 521 DeVall Drive, Auburn, AL 36849, USA,* [5]*US Forest Service, Southern Region Forest Health Protection, 1720 Peachtree Road, NW, Atlanta, GA 30309, USA*

*Correspondence: Hsiao-Hsuan Wang, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA.
E-mail: hsuan006@tamu.edu

†Current address: US Army Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS 39180, USA.

ABSTRACT

Aim We present an integrated approach for predicting future range expansion of an invasive species (Chinese tallow tree) that incorporates statistical forecasting and analytical techniques within a spatially explicit, agent-based, simulation framework.

Location East Texas and Louisiana, USA.

Methods We drew upon extensive field data from the US Forest Service and the US Geological Survey to calculate spread rate from 2003 to 2008 and to parameterize logistic regression models estimating habitat quality for Chinese tallow within individual habitat cells. We applied the regression analyses to represent population spread rate as a function of habitat quality, integrated this function into a logistic model representing local spread, and coupled this model with a dispersal model based on a lognormal kernel within the simulation framework. We simulated invasions beginning in 2003 based on several different dispersal velocities and compared the resulting spatial patterns to those observed in 2008 using cross Mantel's tests. We then used the best dispersal velocity to predict range expansion to the year 2023.

Results Chinese tallow invasion is more likely in low and flat areas adjacent to water bodies and roads, and less likely in mature forest stands and in pine plantations where artificial regeneration by planting seedlings is used. Forecasted invasions resulted in a distribution that extended from the Gulf Coast of Texas and Louisiana northward and westward as much as 300 km, representing approximately 1.58 million ha.

Main conclusions Our new approach of calculating time series projections of annual range expansion should assist land managers and restoration practitioners plan proactive management strategies and treatments. Also, as field sampling continues on the national array of FIA plots, these new data can be incorporated easily into the present model, as well as being used to develop and/or improve models of other invasive plant species.

Keywords

Agent-based simulation model, biological invasions, dispersal model, habitat quality, invasive species, spatial–temporal dynamics.

INTRODUCTION

The forestlands of the southern United States are representative of ecosystems whose unique native flora and fauna are threatened by the introduction and range expansion of invasive plant species. Chinese tallow tree, Chinese tallow, tallow tree or popcorn tree [*Triadica sebifera* (L.) Small, Euphorbiaceae, synonyms include *Sapium sebiferum* (L.) Roxb and *Stillingia sebifera* Willd.], in particular, has been an aggressive invader throughout the south-eastern United States (Fig. 1) since the

DOI:10.1111/j.1472-4642.2011.00760.x
http://wileyonlinelibrary.com/journal/ddi

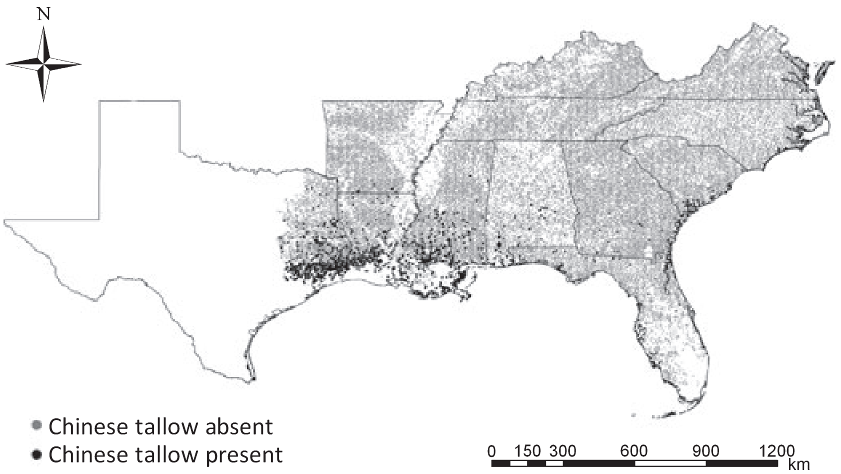

Figure 1 Current distribution of Chinese tallow in forestlands of the southern United States (USDA 2008a).

mid-1900s (Flack & Furlow, 1996; Bruce *et al.*, 1997; Grace, 1998), and has become naturalized from the Gulf Coast of Texas to the Atlantic Coast of North Carolina (Bruce *et al.*, 1997; Burns & Miller, 2004). In the Gulf Coast, coastal tallgrass prairies have been largely converted to Chinese tallow woodland thickets and it is aggressively invading wetlands, as well as a variety of southern forestlands (Bruce *et al.*, 1995). It has become the most abundant tree species (23% of all trees) in the eight-county area surrounding Houston, Texas (Nowak *et al.*, 2005), and the dominant woody sapling species in east Texas and Louisiana forests (Harcombe *et al.*, 1999; Rudis *et al.*, 2006). Moreover, feral hog disturbance (Siemann *et al.*, 2009) and recent hurricane damage in both Louisiana and Texas are hastening the conversion of the rich native forests to Chinese tallow-dominated ecosystems (Chapman *et al.*, 2008). This will likely have profound long-term ramifications for the ecological integrity of this biologically diverse region.

Management strategies to contain and reverse the Chinese tallow invasion would be aided by reliable predictions of spread rates, habitats at risk and potential distribution. This knowledge can lead to delineating zones of invasion that require specific actions to target outliers and the advancing fronts (Miller & Schelhas, 2008). Yet such predictions remain a challenge because of modelling and data limitations. We present an approach for predicting future range expansion of Chinese tallow in forestlands of east Texas and Louisiana that integrates statistical forecasting and analytical techniques within a spatially explicit, agent-based, simulation framework. Using this approach, we identify where new invasions are most likely to occur, and forecast the probable speed and geographical extent of future range expansion.

METHODS

Target ecosystem and invasive plant

Chinese tallow is an aggressive invasive species that has spread throughout the coastal forests and wet prairies of southern United States, especially in east Texas and Louisiana, where it occurred on 17% and 15.5 %, respectively, of forested plots recently sampled by the United States Forest Service (USDA, 2008a). The biology, ecology and impact of Chinese tallow in the forestlands of southern United States have been well studied (see Appendix S1 in Supporting Information).

Model structure and dynamics

To predict the future range expansion of Chinese tallow in forestlands of east Texas and Louisiana, we developed a spatially explicit, agent-based, simulation model, programmed in VB.NET© (Microsoft, Redmond, WA, USA). The model consisted of 11,553 geo-referenced cells (agents), each representing a 2428-ha plot of land. We assume that the size of one cell is 2428 ha based on the FIA sampling frame. FIA's network of permanent ground plots has a spatial sampling intensity of approximately one plot per 2428 ha (USDA, 2005). We merged the US Forest Service data sets using the FIA plot identification numbers and spatially joined them with land-use and land cover (LULC) data (USGS, 2009) via ArcMap™ 9.1 (ESRI, Redlands, CA, USA). Next we superimposed a grid of 4927 × 4927 m (2428-ha) cells, classifying cells containing > 50% of forest cover as forestlands. We then imported the data associated with each cell into VB.NET©, where each cell was represented as an agent with ascribed characteristics and rules governing its dynamics.

The rules governing each agent, which generated annual changes in the percentage of land occupied by Chinese tallow (i.e. the time step for solution of the model is 1 year; $\Delta t = 1$ year), represented spread within the cell plus invasion from other cells (Fig. 2):

$$N_{i,t+1} = N_{i,t} + r_i N_{i,t}\left[1 - N_{i,t}\kappa^{-1}\right] + \sum_{j=1, j\neq i}^{q} k_{ji} N_{j,t} \qquad (1)$$

where $N_{i,t}$ represents the percentage of land occupied by Chinese tallow in cell i at time t, r_i is the intrinsic spread rate, κ is the carrying capacity for each cell and k_{ji} is a lognormal dispersal kernel that varies with invasion velocity. We provide details regarding the manner in which we estimated k_{ji} and the

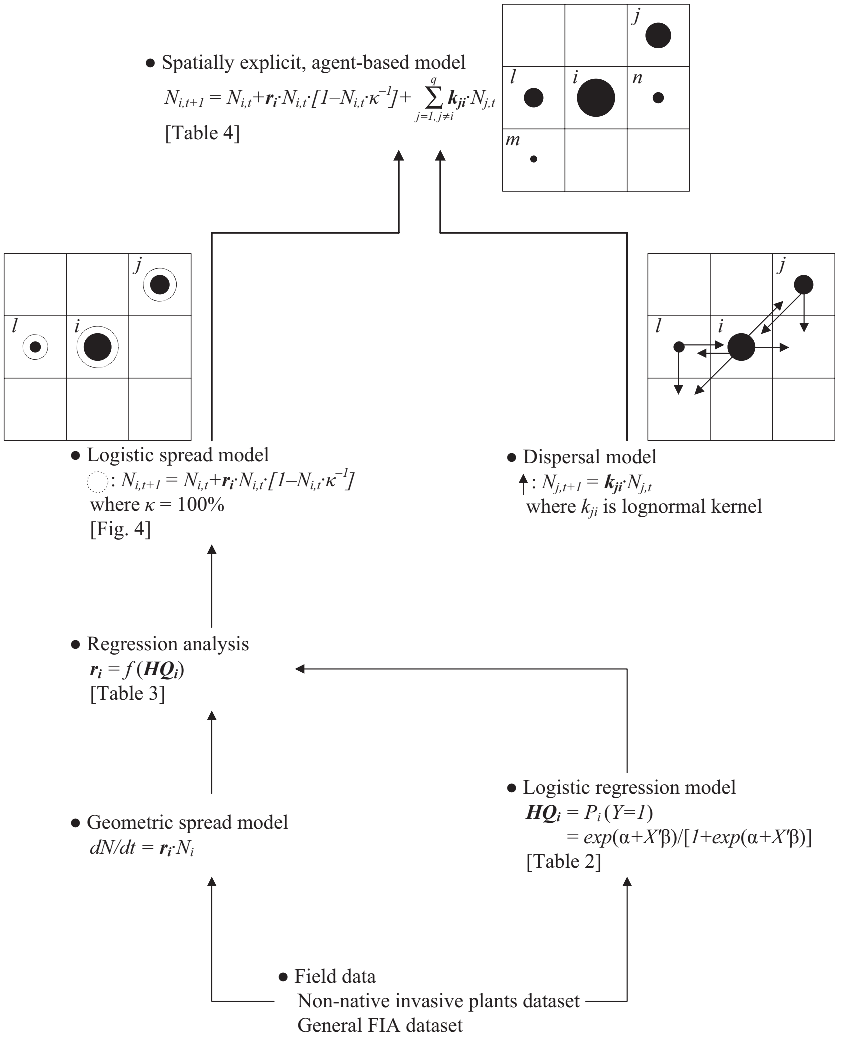

Figure 2 Diagrammatic representation of the linkages among field data, population spread model and dispersal model within a spatially explicit, agent-based, simulation framework. Bold letters represent parameters that were estimated (HQ$_i$, r_i) or calibrated (k_{ji}) based on field data.

other two model parameters, r_i and HQ$_i$ (the habitat quality of cell i, which determines r_i), as well as details regarding model structure in Appendix S2 in Supporting Information.

Model application

To project the invasions of Chinese tallow in forestlands of east Texas and Louisiana, we ran 240, 20-year, Monte Carlo simulations with the initial percentage land cover of Chinese tallow based on that reported during the first field sampling cycle (USDA, 2008b). These field data were collected from 2001 to 2005, thus projections extended over approximately the next two decades. We exported the geo-referenced simulated data to ArcMap™ to visualize the spatial–temporal patterns of invasions.

Also, to compare our model projections with estimates of northern range limits based on current climatic conditions (Pattison & Mack, 2008), we ran a set of long-term (240, 120-year, Monte Carlo) simulations, parameterized as described earlier except that we eliminated the relatively few Chinese tallow reported north of 31° N latitude (USDA, 2008b) to provide a more sharply defined initial northern range limit. To explore two additional considerations regarding potential range limits, the possible effects of climate change (Crowl *et al.*, 2008; Jarnevich & Stohlgren, 2009) and post-invasion adaptation (Thompson, 1998; Bossdorf *et al.*, 2005), we ran two additional sets of long-term simulations, once again initially eliminating the Chinese tallow north of 31° N latitude. In the first set, we increased mean extreme minimum temperatures by 2 °C. In the second set, we re-parameterized the habitat quality indexes (HQ$_i$, see Table S1 in Supporting Information) based on data from seven counties in South Carolina (USDA, 2008b), which we assumed represent Chinese tallow that have adapted to cooler climatic conditions (Pattison & Mack, 2009).

RESULTS

Model parameterization

Results of logistic regression, which showed no statistical evidence of zero inflation (P = 0.24), indicated that Chinese tallow is more likely to occur in low areas, flat areas, and areas adjacent to water bodies and roads, and less likely to occur in mature forest stands and stands in which there has been artificial regeneration (Table 2). It is also more likely to occur on private than public land (Table 2). HQ_i values, which ranged from < 0.01 to 0.78, generally decreased from south to north (Fig. 3), demonstrating the likelihood of occurrence of Chinese tallow was also related positively to mean extreme minimum temperature. These findings are similar to those of Gan *et al.* (2009). The best fit equation ($R^2 = 0.61$) relating spread rate to the index of habitat quality ($r_i = 0.3077 \times \exp(1.0182 \times HQ_i)$, Table 3) projected times from initial colonization in favourable habitat ($HQ = 0.7829$) to 99% occupancy in 18 years, with complete occupancy achieved in 29 years (Fig. 4). Bruce *et al.* (1995) reported that Chinese tallow could colonize and completely occupy a favourable habitat within 20–30 years.

Table 1 Landscape features, climatic conditions and forest conditions (NOAA, 2008; USDA, 2008a) identified as potential independent variables to estimate habitat quality (HQ = probability of invasion) for Chinese tallow on forested plots in east Texas and Louisiana.

Variable	Value or unit of measure	Expected sign of impact	Mean (min, max) or frequency
Landscape features			
Elevation	m	–	56.33 (−30.48, 1158.24)
Slope	Degree	–	4.65 (0, 77.5)
Adjacency to water bodies within 300 m	0: no	+	0: 4051
	1: yes		1: 957
Climatic conditions			
Mean extreme minimum temperature	°C	+	−7.89 (−12.22, 0)
Forest and site conditions			
Stand age	Years	–	37.55 (1, 145)
Site productivity (height-age curve categories)	1: 0–1.39	+/–	1: 12
	2: 1.40–3.49		2: 263
	3: 3.50–5.94		3: 1335
	4: 5.95–8.39		4: 1866
	5: 8.40–11.54		5: 1259
	6: 11.55–15.74		6: 242
	7: > 15.74 m^3 ha^{-1} per year		7: 31
Species diversity	Shannon's species diversity	+/–	1.37 (0, 2.81)
Forest management activities and disturbances			
Timber harvest*	0: no	+	0: 3641
	1: yes		1: 1367
Site preparation*	0: no	–	0: 4723
	1: yes		1: 285
Artificial regeneration	0: no	–	0: 3151
	1: yes		1: 1857
Natural regeneration	0: no	+/–	0: 4893
	1: yes		1: 115
Distance to the nearest road from the centre of plot	1: < 30	–	1: 336
	2: 30–91		2: 733
	3: 91–152		3: 593
	4: 152–305		4: 1022
	5: 305–805		5: 1429
	6: 805–1609		6: 593
	7: 1609–4828		7: 253
	8: 4828–8047		8: 24
	9: > 8047 m		9: 25
Fire damage*	0: no	+	0: 4834
	1: yes		1: 174
Animal damage*	0: no	+	0: 4981
	1: yes		1: 27
Wind damage* (including hurricanes and tornados)	0: no	+	0: 4826
	1: yes		1: 182
Others			
Forestland ownership	0: public	+/–	0: 502
	1: private		1: 4506

*Nominally within the past 5 years. With damage codes, at least 25% of the trees in a stand must be damaged to warrant a code of 1.

Table 2 Landscape features, climatic conditions and forest conditions (from Table 1) selected, based on the indicated results of logistic regression, to estimate habitat quality (HQ = probability of invasion) for Chinese tallow on forested plots in east Texas and Louisiana.

Variable	Estimated coefficient	Odds ratio	*P*-value
Elevation	−0.0030	0.9970	< 0.0001
Slope	−0.0851	0.9184	0.0061
Adjacency to water bodies within 300 m	0.6187	1.8565	< 0.0001
Distance to the nearest road	−0.1071	0.8984	< 0.0001
Mean extreme minimum temperature	1.7578	5.7997	< 0.0001
Stand age	−0.0112	0.9889	< 0.0001
Artificial regeneration	−0.1993	0.8193	0.0140
Forestland ownership	0.7213	2.0571	< 0.0001
Constant	−8.6334		< 0.0001
P-value of Hosmer–Lemeshow test	0.5422		
Akaike information criterion	3394.30		
Overall correct prediction	77.3%		
Number of observations	5008		

Of the various dispersal velocities that we evaluated, only a velocity 1231 m per year (1/4 the width of a grid cell) produced simulated invasion patterns that were not statistically significantly different ($P \le 0.05$) from the observed pattern (Table 4). This is somewhat faster than the dispersal velocity of approximately 1000 m per year estimated by Renne *et al.* (2000) based on field experiments involving Chinese tallow seed dispersal by birds in coastal South Carolina, and noticeably faster than the velocity of approximately 800 m per year estimated by Morales & Carlo (2006) using a spatially explicit simulation model for generic plant dispersal by frugivorous birds.

Prediction of range expansion

Predictions of range expansion in east Texas and Louisiana indicated that Chinese tallow has the potential to expand from < 1% (0.32%) of forestlands that it occupied in the year 2003 to approximately 7.54% of forestlands in 2023 (USDA 2008a,b; Fig. 5). This represents roughly 1.58 million ha. Geographically, the projected invasions extended from the Gulf Coast of Texas and Louisiana northward and westward as much as 300 km, with the most severe invasions occurring along rivers and other permanent inland water sources (Fig. 6).

Results of our long-term simulations assuming current conditions (no climate change and no post-invasion adaptations) suggested that Chinese tallow could expand northward to approximately 34° N latitude within 115 years (34° N latitude was the northern limit of the geo-referenced data used in this study), or roughly 334 km north of its current distribution, but with the rate of range expansion slowing markedly as the leading edge moved north (Fig. 7). Our long-term projections assuming either climate change (2 °C increase in mean extreme minimum temperatures) or post-invasion evolutionary adaptation to colder temperatures, as one might expect, suggested somewhat faster northward expansion, reaching 34° N latitude within 101 or 106 years, respectively (Fig. 7). The average annual rates of range expansion projected

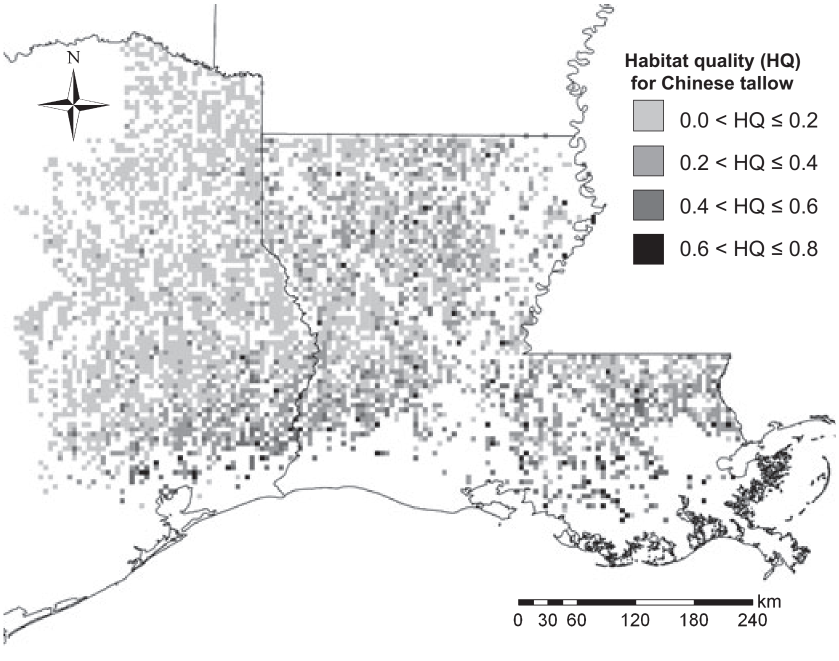

Figure 3 Estimated habitat quality (high HQ = high quality, estimated HQ values ranged from < 0.01 to 0.7829) for Chinese tallow in forestlands of east Texas and Louisiana.

Table 3 Comparison of several functional relationships between spread rate of Chinese tallow (r_i) and the index of habitat quality (HQ_i), including linear (1) $r_i = a + b\mathrm{HQ}_i$, logarithmic (2) $r_i = a + \ln\mathrm{HQ}_i$, power (3) $r_i = a + b\mathrm{HQ}_i^{-1}$ and (4) $r_i = a + b\mathrm{HQ}_i^2$, and exponential (5) $r_i = a{\cdot}\exp[b(\mathrm{HQ}_i)^{0.5}]$, (6) $r_i = a{\cdot}\exp(b\mathrm{HQ}_i)$ and (7) $r_i = a{\cdot}\exp\left[b\left(\mathrm{HQ}_i^2\right)\right]$. Adjusted R^2 values also are presented. P-values of all coefficients were < 0.01.

	Equation	R^2
(1)	$r_i = 0.3385 + 0.7088{\cdot}\mathrm{HQ}_i$	0.1634
(2)	$r_i = 1.0399 + 0.5670{\cdot}\ln(\mathrm{HQ}_i)$	0.2488
(3)	$r_i = 0.6839 - 0.0064{\cdot}\mathrm{HQ}_i^{-1}$	0.2820
(4)	$r_i = 0.3385 + 0.7088{\cdot}\mathrm{HQ}_i^2$	0.0803
(5)	$r_i = 0.3146{\cdot}\exp(0.7557{\cdot}\sqrt{\mathrm{HQ}_i})$	0.4887
(6)	$r_i = 0.3077{\cdot}\exp(1.0182{\cdot}\mathrm{HQ}_i)$	0.6142
(7)	$r_i = 0.2776{\cdot}\exp\left(1.5601{\cdot}\mathrm{HQ}_i^2\right)$	0.5035

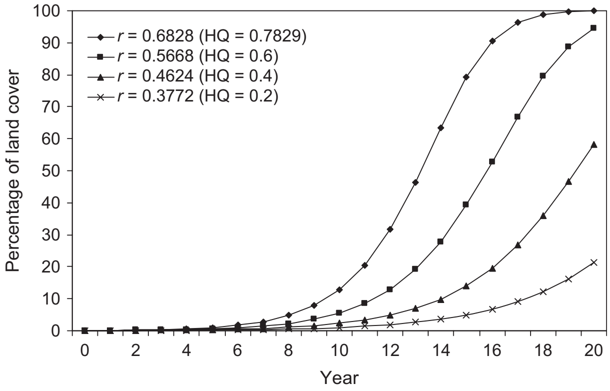

Figure 4 Spread rates (r) of Chinese tallow in habitats of different quality (HQ), as projected by equation (6) in Table 3 ($r_i = 0.3077{\cdot}\exp(1.0182{\cdot}HQ_i)$). Empirically estimated HQ values ranged from < 0.01 to 0.7829.

Table 4 Comparisons, via likelihood comparison and spatial correlation (cross Mantel's test), of the observed invasion pattern for Chinese tallow (USDA, 2008b) to those simulated assuming each of several invasion velocities (m per year). L is the scale parameter, which represents dispersal velocity in grid-width units.

Velocity	L	Likelihood	Mantel's r	P-value
4927.00	1	−163.5015	0.0056	0.933
2463.50	1/2	−93.4777	0.0114	0.915
1642.33	1/3	−91.6520	0.0731	0.308
1231.75	1/4	−87.4683	0.1497	0.028
985.40	1/5	−90.2572	−0.1033	0.237
821.17	1/6	−94.0599	−0.1003	0.229
703.86	1/7	−95.7848	−0.0726	0.468

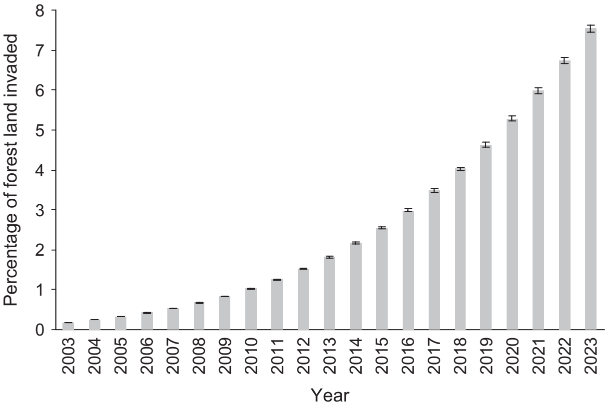

Figure 5 Mean (based on 240 Monte Carlo simulations) percentage (± SE) of forest land in east Texas and Louisiana invaded by Chinese tallow, as projected by Equation 1 assuming an invasion velocity of 1232 m per year.

for the current conditions, climate change, and post-invasion adaptation scenarios were 2.96, 3.34 and 3.19 km per year, respectively. We emphasize that these long-term projections are intended to provide only general points of comparison with ideas currently being discussed in the literature and to demonstrate the flexibility of our approach.

DISCUSSION

We have presented an approach for predicting future range expansion of an invasive species at temporal and spatial scales consistent with management needs and available data. Our approach integrates statistical forecasting with analytical techniques within a spatially explicit, agent-based, simulation framework. In the following sections, we consider the theoretical and empirical basis for our approach, interpret our findings in the light of Chinese tallow ecology and management, and provide some caveats.

Theoretical and empirical basis for modelling terrestrial plant invasions

The spatial spread of invasive species has been a subject of both theoretical and empirical study for decades and recently has been the topic of two excellent review papers (Hastings *et al.*, 2005; Jongejans *et al.*, 2008). The theoretical basis for much of this work can be traced back to the pioneering work by Fisher (1937) and Skellam (1951) on linear diffusion models, followed by seminal contributions recognizing the importance of age-specific differences in rates of movement and reproduction (Bosch *et al.*, 1992) and differences in the probability distribution of dispersal distances (Kot *et al.*, 1996). Building on these contributions, increased emphasis has been placed on representing both local demography and dispersal behaviour of invasive species. Representations have ranged from simple to complex depending on modelling objectives, ecological complexity of the system, data availability and the principle of parsimony (Jongejans *et al.*, 2008). Local demography can be represented by simple models of exponential or logistic spread (Begon *et al.*, 1996), more complex age-structured matrix

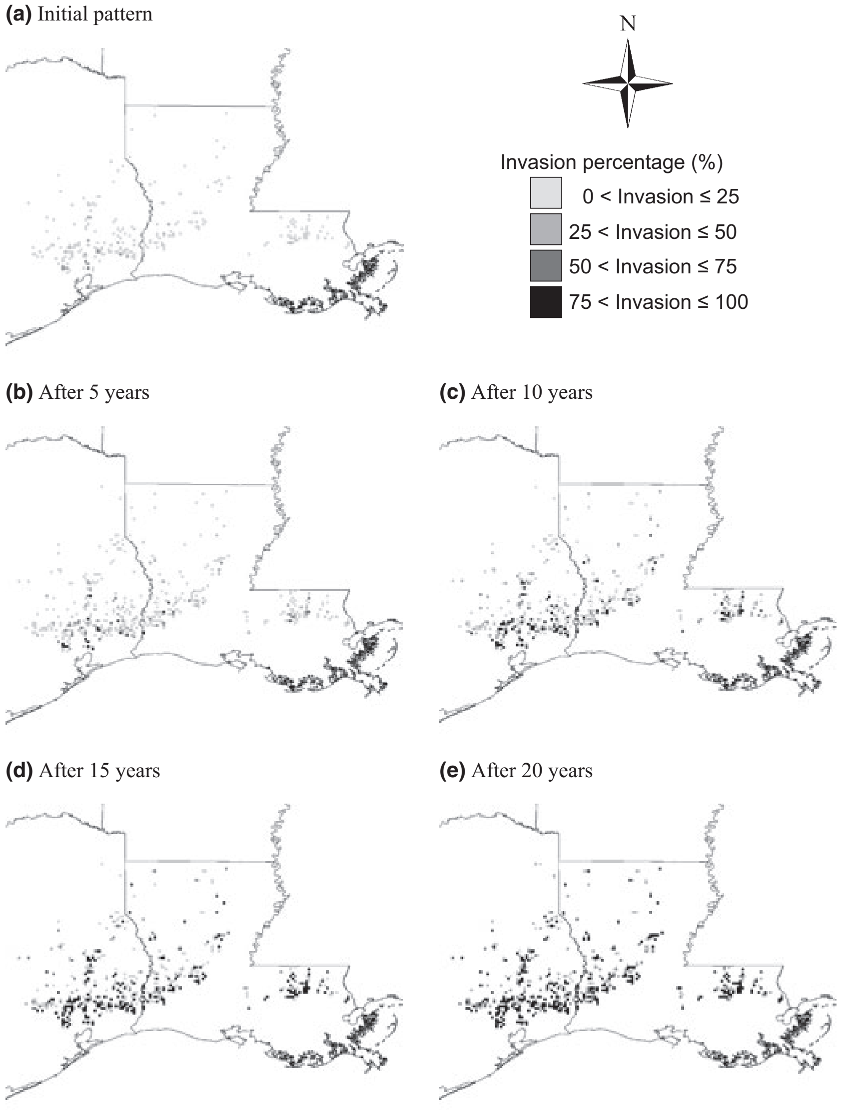

Figure 6 Typical simulated invasion pattern of Chinese tallow. (a) Pattern observed in the year 2003 (USDA, 2008b), with which all simulations were initialized. (b–e) Time series of patterns based on one typical stochastic simulation.

models (Caswell, 2000), or complex individual/agent-based models (DeAngelis & Gross, 1992; Grimm & Railsback, 2006). Dispersal can be represented by empirical/phenomenological models with simple, exponential or Gaussian probability distributions of dispersal distances. More complex representations are 'fat tail' distributions of dispersal distances or mechanistic models that represent the behavioural complexity of animal dispersers (see Table 2 in Jongejans *et al.*, 2008). Increased emphasis also has been placed on overcoming long-standing difficulties associated with representing the effect of habitat heterogeneity (Hastings, 1996; With, 2002; Sebert-Cuvillier *et al.*, 2008; Thuiller *et al.*, 2008; Smolik *et al.*, 2010). Habitat data limitations are becoming less severe with the availability of geo-referenced field data, while statistical tools such as logistic regression and principal component analysis are more commonly used to quantify static distribution models (Stephenson *et al.*, 2006; Yantis, 2006; Quesada-Moraga *et al.*, 2007), to place confidence intervals on forecasted rates of spread and to quantify landscape heterogeneity (Hastings *et al.*, 2005). Recently, Sebert-Cuvillier *et al.* (2008) applied principal component analysis to estimate probabilistic, spatially explicit, dispersal indices to simulate range expansion of an invasive tree species in France, and Smolik *et al.* (2010) used logistic regression to estimate spatially explicit, habitat suitability functions to simulate range expansion for an invasive forb species in Austria.

In the spatially explicit, agent-based, simulation framework developed for this study, we represented local (within cell) demography based on a simple model of logistic spread (Begon *et al.*, 1996). Local habitat quality significantly affects the spread rate of Chinese tallow (Bruce *et al.*, 1995; Renne *et al.*, 2001; Siemann & Rogers, 2007) because of intraspecific, density-dependent competition for availability light and nitrogen (Siemann & Rogers, 2003; Lin *et al.*, 2004). We estimated local spread rate as a function of local habitat quality via logistic regression, drawing upon geo-referenced field data from the US Forest Service's extensive national forest resource survey (Rudis *et al.*, 2006). Habitat quality, and hence spread

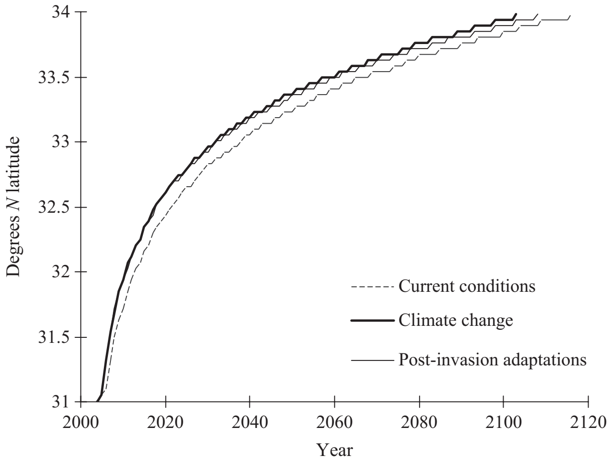

Figure 7 Preliminary projections of Chinese tallow range expansions assuming current conditions (no climate change and no post-invasion adaptations), climate change (2 °C increase in mean extreme minimum temperatures) and post-invasion evolutionary adaptation to colder temperatures (habitat quality indexes (HQ_i) re-parameterized based on data in South Carolina). See text for details.

rate, varied from cell to cell, to yield an explicit expression of habitat heterogeneity. We represented dispersal based on an empirical model, assuming a lognormal probability distribution of dispersal distances, which has been used successfully to approximate the observed dispersal patterns for a number of species with wind- and animal-dispersed seeds similar to Chinese tallow (Stoyan & Wagner, 2001; Greene & Calogeropoulos, 2002; Greene *et al.*, 2004; Russo *et al.*, 2006). We estimated the lognormal kernel by comparing simulated invasion patterns resulting from various hypothesized invasion velocities to observed invasion patterns based upon geo-referenced Forest Service data (Rudis *et al.*, 2006), likelihood comparisons and cross Mantel's tests (Dutilleul *et al.*, 2000). To complete our integrated model, we added an element of age structure, based on Chinese tallow life-history information, by not allowing invasions to originate from a cell until 3 years after its initial colonization, and an element of uncertainty by allowing cells to be invaded probabilistically.

Our simulated invasions exhibit spatial patterns and velocities similar to those reported in the literature; however, our simulations provide a dynamic, rather than static, projection of spread at a finer spatial resolution (4927 m vs. 55,659 m) than has been reported, to the best of our knowledge, previously. Our model projected the spread of Chinese tallow from the region close to the Gulf of Mexico northward and westward into the forests of Arkansas (Fig. 6), at a velocity of approximately 1231 m per year. Pattison & Mack (2008), using their CLIMEX model, which projects species distributions based on key climatic parameters, also projected the northward and westward spread of Chinese tallow through the forests of Arkansas. Renne *et al.* (2000), based on experiments involving Chinese tallow seed dispersal by birds in coastal South Carolina, estimated a dispersal velocity of around 1000 m per year. Our results also were similar to those reported by Morales & Carlo (2006), who used a spatially explicit simulation model to estimate a dispersal velocity of approximately 800 m per year for plants dispersed by frugivores. Clark *et al.* (2003) used a stochastic model based on information from a variety of sources to estimate a range of annual velocities of seed dispersal by birds: 90% of the seeds were dispersed from the parent tree 0–100 m, 8% were dispersed 100–500 m, 1.7% were dispersed 500–5000 m and 0.3% were > 5000 m.

Chinese tallow ecology

Our projections of spread and range expansion for Chinese tallow at local and regional scales are consistent with our current ecological knowledge of the species. Chinese tallow obviously is an aggressive invasive species that thrives in warm, moist climates (Pattison & Mack, 2008). Our simulated spread rates from initial colonization to complete local (within cell) occupancy in favourable habitats (HQ = 0.7829) indicated that 99% occupancy would be reached in 18 years and 100% occupancy in 29 years, overlapping broadly with local spread rates reported by Bruce *et al.* (1995) for favourable habitats (20–30 years). Some of the most extensive stands of Chinese tallow along the Texas and Louisiana coasts occur in lands adjacent to rivers and standing water (Bruce *et al.*, 1997; Burns & Miller, 2004), and as our simulations suggest, these rivers provide excellent dispersal corridors into major watersheds (Bruce *et al.*, 1995; Pattison & Mack, 2008). Our estimated dispersal velocity (approximately 1.2 km per year) is somewhat faster than the dispersal velocity (approximately 1.0 km per year) estimated by Renne *et al.* (2000) in coastal South Carolina, most probably reflecting differences in regional disturbance regimes, minimum temperatures and landscape structure (Collingham & Huntley, 2000; Davis *et al.*, 2000; With, 2002).

Several recent studies have raised questions regarding the northern limits to range expansion by Chinese tallow in North America. Although it has been considered frost intolerant (J.A. Duke, unpublished data), there are persistent populations of Chinese tallow in relatively cold climates in Asia (Lee, 1956), and recent experimental studies provide evidence that Chinese tallow can tolerate colder climatic conditions than it encounters at the current northern limit of its distribution in North American (Pattison & Mack, 2009). A projection based on matching climate parameters in Asia to those in North America, using the model CLIMEX (Sutherst & Maywald, 1985), suggests that Chinese tallow is capable of expanding 500 km northward from its current distribution in the south-eastern United States (Pattison & Mack, 2008). Our preliminary long-term projections suggest that Chinese tallow could expand northward to approximately 34° N latitude, or roughly 334 km north of its current distribution (Fig. 7).

Two additional considerations regarding potential range limits of Chinese tallow, and indeed of invasive species in general, are that they may be affected by (1) even modest temperature increases because of global climate change (Crowl *et al.*, 2008; Jarnevich & Stohlgren, 2009) and (2) relatively rapid post-invasion evolutionary adaptations because of strong selective pressures in new environments (Thompson, 1998; Bossdorf *et al.*, 2005). In fact, changes in physiological and morphological traits related to herbivore pressures have been demonstrated in invasive populations of Chinese tallow (Siemann & Rogers, 2001; Rogers & Siemann, 2005; Zou *et al.*, 2007). Our two long-term projections assuming representing (1) a modest increase in global temperature or (2) adaptation to cooler climatic conditions, as one might expect, suggest somewhat faster northward expansion of Chinese tallow, with average annual rates of range expansion projected approximately 3.34 and 3.19 km per year, respectively, faster than those projected under current conditions (Fig. 7). Once again, we emphasize that these long-term projections are intended to provide only general points of comparison with ideas currently being discussed in the literature and to demonstrate the flexibility of our approach.

Chinese tallow management

The control of biological invasions has become a topic discussed at the highest scientific, policy and management levels (Lodge *et al.*, 2006). While long-term invasive plant management strategies are recognized as essential to reduce the ecological damage and economic costs associated with invasions, the development and implementation of such plans lags considerably behind. Most invasive plant management, including that of Chinese tallow, has emphasized controlling highly infested areas, despite the knowledge that invasions are best mitigated during the early stages of recruitment and establishment (Moody & Mack, 1988; Sheley *et al.*, 2006) or control of outlier populations (Miller & Schelhas, 2008). Like many other invasive plant species, recruitment limitation and demographic time lags tend to slow the range expansion of Chinese tallow (Primack & Miao, 1992; Tilman, 1997; Crooks, 2005). However, after a threshold of adult, seed producing trees is surpassed, and dispersal probabilities increase greatly (Bower *et al.*, 2009), emphasizing the need for a spatially explicit, temporally dynamic model to predict where and when initial invasions might be expected, and where effective monitoring plots might be placed.

At present, we are aware of only two spatially explicit models for Chinese tallow, both of which are static (Pattison & Mack, 2008; Gan *et al.*, 2009). We are unaware of other models for Chinese tallow that are capable of incorporating geo-referenced field data and projecting invasions on temporal and spatial scales consistent with management needs. The models of Pattison & Mack (2008) and Gan *et al.* (2009) correlate data on presence or absence of Chinese tallow with land characteristics and climatic conditions to estimate invasion vulnerabilities. However, this binary representation of input data seems inappropriate for many invasion cases (Murphy & Lovett-Doust, 2004), and the resulting static vulnerabilities do not provide an understanding of invasion dynamics that can inform control strategies (Wilson *et al.*, 2007).

Our approach offers land managers and restoration practitioners the ability to project time series of annual range expansions at an appropriately fine spatial scale, providing an invasion chronology upon which to base proactive management plans. The integration of logistic regression into the spread model allows the spatial prediction of continuous gradients in suitability. Along such continuous gradients, trade-offs between local habitat quality and local population size, and time lags between initial invasion and subsequent dispersal from a given locality in promoting the invasion process can be captured more appropriately (Smolik *et al.*, 2010). Our approach also provides the flexibility to explore the potential influences of invasive species on a variety of processes that occur at markedly different spatial and temporal scales. Processes ranging from global climatic change, to regional changes in land use and land ownership, to local changes in habitat characteristics can be incorporated directly into the calculation of local habitat quality indexes, which affect local spread and, subsequently, invasion velocity.

As field sampling continues on the national array of FIA plots, these new data can be incorporated easily into the present model, as well as being used to develop and/or improve models of other invasive plant species. To date, we have developed similar models for Chinese privet (*Ligustrum sinense* Lour.), European privet (*Ligustrum vulgare* L.) and Japanese honeysuckle (*Lonicera japonica* Thunb) (Wang, 2009). The United States Forest Service currently is investigating a variety of methods, including use of remote sensing data, to interpolate field data and cover non-sampled areas (USDA, 2005). These data also could be incorporated into our model to provide a better understanding of the roles of different land-use types in facilitating or hindering the invasion process.

Caveats

Providing reliable predictions of the spread rates of invasive species, the habitats most at risk and potential distribution limits remain a challenge. Factors affecting invasion processes operate at different spatial and temporal scales, resulting in data limitations and modelling challenges. Habitat quality affects shorter-term population growth and local spread, while landscape characteristics interact with innate dispersal abilities of invaders to affect longer-term regional spread (Pyšek *et al.*, 2002; Bradley & Mustard, 2006; Wilson *et al.*, 2007). We have integrated statistical forecasting and analytical techniques within a spatially explicit, agent-based, simulation framework to predict future range expansion of Chinese tallow in forestlands of the southern United States. To paraphrase the oft-quoted statement regarding models, we are quite sure our model is wrong, but we believe it is useful. Below we provide some caveats with regard to our representations of habitat quality and local spread, dispersal and regional spread, and the effects of particular landscape features as dispersal corridors.

We estimated habitat quality and local spread by applying logistic regression to data on landscape features, climatic conditions and forest conditions collected over a 5-year period by the United States Forest Service. Three valid criticisms of such an approach are that (1) the calculations of habitat quality may be biased because of the zero-inflation problem (the absence of the focal species from relatively many sample plots; Lee *et al.*, 2001), (2) the inclusion of different independent variables might have markedly changed the likelihood estimates (Agresti, 2007) and (3) the relative importance of the independent variables may vary with the stage of invasion (Wilson *et al.*, 2007). In the present study, our logistic regression model showed no statistical evidence of zero inflation. The second two criticisms are generic problems related to structural uncertainty in the mathematical representation of natural systems (Walters, 1986). The possibility always remains that we failed to include some important explanatory variables and that the relative importance of those variables that we have included depends on the current state of the system. We identified our set of potential independent variables following Gan *et al.* (2009), who also recently studied the invasion of Chinese tallow in forestlands of the southern United States. Provided the data, others could be included easily in the calculation of habitat quality. Also, provided time series data on the independent variables, or the functional relationships between the variables and the stage of invasion, it would be easy to recalculate the habitat quality indexes for each cell each time step during a simulation. This is an interesting idea that could be pursued in future work.

We estimated dispersal and regional spread using a lognormal dispersal kernel. Estimation of seed and seedling empirical/phenomenological dispersal within forests has been an area of intensive study (Greene *et al.*, 2004), and many functional forms of dispersal curves have been used, including exponential power (Burczyk & Koralewski, 2005; Klein *et al.*, 2006), Gamma (Clark *et al.*, 1999; Klein *et al.*, 2006), generalized logistic (Klein *et al.*, 2006), geometric (Klein *et al.*, 2006), half-Cauchy (Skarpaas *et al.*, 2005), Laplace (Bullock *et al.*, 2006), lognormal (Skarpaas *et al.*, 2005; Bullock *et al.*, 2006), Weibull (Tufto *et al.*, 1997; Klein *et al.*, 2006) and 2Dt (Bullock *et al.*, 2006; Klein *et al.*, 2006). For example, Clark *et al.* (1999) argued that for predicting tropical seed dispersal, the 2Dt kernel is better than the Weibull kernel, which Ribbens *et al.* (1994) preferred for estimating hardwood seedling recruitment, while Stoyan & Wagner (2001) argued that the lognormal is better than the 2Dt for estimating wind-driven fruit dispersion in forests. Obviously, choice of the appropriate functional form depends on the biological complexity of the predominant dispersal mechanisms involved, as well as the management objective and the available data (Jongejans *et al.*, 2008). Empirical delineation of seed dispersal kernels has been particularly difficult because the individual dispersal curves of trees usually overlap (Greene *et al.*, 2004). Chinese tallow is a wind- and animal-dispersed species (Hukui & Ueda, 1999; Renne *et al.*, 2000, 2002), and the lognormal dispersal kernel has approximated observed dispersal patterns well for a number of trees with wind- and animal-dispersed seeds, because of its peaked, fat-tailed form (Stoyan & Wagner, 2001; Greene & Calogeropoulos, 2002; Greene *et al.*, 2004; Russo *et al.*, 2006). We assumed the shape parameter $S = 1$. This is the default value for wind- and animal-dispersed tree species in closed forests (Greene *et al.*, 2004), as decreasing S makes fat tails too thin to permit population persistence (Nathan & Muller-Landau, 2000). However, exploration of different combinations of the shape parameters S and L using maximum likelihood methods for species with different dispersal mechanisms remains a fruitful area of investigation.

Our representation of the effects of particular landscape features as dispersal corridors was implicit in our habitat quality indexes. Pattison & Mack (2008) indicated that rivers and other sources of perennial water could act as dispersal corridors for Chinese tallow, and the potential importance of the hydrological system in long-distance seed dispersal is well documented (Muneepeerakul *et al.*, 2008; Merritt *et al.*, 2010). Some of our highest habitat quality estimates occurred in low areas, flat areas and areas adjacent to water bodies, and our projections indicated that the most severe invasions spread along rivers and other permanent inland water sources. However, we did not explicitly represent the facilitation of longer-distance dispersal because of the hydrological connectivity of the landscape. Likewise, although some of our highest habitat quality estimates occurred along roads, we did not explicitly represent the facilitation of invasion by human transportation networks and human population growth (Davis *et al.*, 2000; Crowl *et al.*, 2008; Flory & Clay, 2009). The extent to which particular landscape features might accelerate invasion could be explored with the present model by hypothesizing movement rates along specific corridors and 'seeding' new trees in habitat cells along these routes at appropriate intervals during simulations. This would be an interesting exercise, but is beyond the scope of the present study.

The value of modelling in fields like ecology and natural resource management is not to make precise predictions, but rather to provide clear caricatures of nature against which to test and expand experience (Walters, 1986). The caricature of nature represented by the present model is based upon data from roughly 5008, 2428-ha plots of land that currently are forested (USDA, 2008a). Chinese tallow also can invade other land-use types for which comparable data are not available (Siemann & Rogers, 2003; Zedler Joy & Kercher, 2004; Siemann & Rogers, 2007). Other land-use types may serve either as dispersal corridors for invasion or as barriers to invasion (Bradley & Mustard, 2006; Flory & Clay, 2009; Bradley, 2010), and of course, changes in land-use patterns may significantly alter the dispersal of invasive species (Bradley & Mustard, 2005; Crowl *et al.*, 2008; Jarnevich & Stohlgren, 2009). As the new field data from the United States Forest Service become available, they can be incorporated within the modelling approach we described to test and improve the usefulness of our caricatures of nature.

ACKNOWLEDGEMENTS

We thank the USDA Forest Service Forest Health Protection of the Southern Region and Texas AgriLife Research for funding this study. We also thank three anonymous reviewers for their time and effort, and the manuscript is greatly improved as a result of their comments.

REFERENCES

Agresti, A. (2007) *An introduction to categorical data analysis*. John Wiley and Sons, Inc., Hoboken, NJ.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: individuals, populations and communities*. Blackwell Science, Oxford.

Bosch, F.v.d., Hengeveld, R. & Metz, J.A.J. (1992) Analysing the velocity of animal range expansion. *Journal of Biogeography*, **19**, 135–150.

Bossdorf, O., Auge, H., LaFuma, L., Rogers, W.E., Siemann, E. & Prati, D. (2005) Phenotypic and genetic differentiation in native versus introduced plant populations. *Oecologia*, **144**, 1–11.

Bower, M.J., Aslan, C.E. & Rejmánek, M. (2009) Invasion potential of Chinese tallowtree (*Triadica sebifera*) in California's central valley. *Invasive Plant Science and Management*, **2**, 386–395.

Bradley, B.A. (2010) Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. *Ecography*, **33**, 198–208.

Bradley, B.A. & Mustard, J.F. (2005) Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. *Remote Sensing of Environment*, **94**, 204–213.

Bradley, B.A. & Mustard, J.F. (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, **16**, 1132–1147.

Bruce, K.A., Cameron, G.N. & Harcombe, P.A. (1995) Initiation of a new woodland type on the Texas coastal prairie by the Chinese tallow tree (*Sapium sebiferum* (L.) *Roxb.*). *Bulletin of the Torrey Botanical Club*, **122**, 215–225.

Bruce, K.A., Cameron, G.N., Harcombe, P.A. & Jubinsky, G. (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese Tallow Tree, *Sapium sebiferum* (L.) *Roxb*. *Natural Areas Journal*, **17**, 255–260.

Bullock, J., Shea, K. & Skarpaas, O. (2006) Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, **186**, 217–234.

Burczyk, J. & Koralewski, T.E. (2005) Parentage versus two-generation analyses for estimating pollen-mediated gene flow in plant populations. *Molecular Ecology*, **14**, 2525–2537.

Burns, J.H. & Miller, T.E. (2004) Invasion of Chinese tallow (*Sapium sebiferum*) in the Lake Jackson area, northern Florida. *American Midland Naturalist*, **152**, 410–417.

Caswell, H. (2000) *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Inc., Sunderland, MA.

Chapman, E.L., Chambers, J.Q., Ribbeck, K.F., Baker, D.B., Tobler, M.A., Zeng, H. & White, D.A. (2008) Hurricane Katrina impacts on forest trees of Louisiana's Pearl River basin. *Forest Ecology and Management*, **256**, 883–889.

Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.

Clark, J.S., Lewis, M., McLachlan, J.S. & HilleRisLambers, J. (2003) Estimating population spread: what can we forecast and how well? *Ecology*, **84**, 1979–1988.

Collingham, Y.C. & Huntley, B. (2000) Impacts of habitat fragmentation and patch size on migration rates. *Ecological Applications*, **10**, 131–144.

Crooks, J.A. (2005) Lag times and exotic species: the ecology and management of biological invasions in slow motion. *Ecoscience*, **12**, 316–329.

Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G. & Lugo, A.E. (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment*, **6**, 238–246.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

DeAngelis, D.L. & Gross, L.J. (1992) *Individual-based models and approaches in ecology: populations, communities and ecosystems*. Chapman & Hall, New York.

Dutilleul, P., Jason, D.S., Frigon, D. & Legendre, P. (2000) The Mantel test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. *Journal of Agricultural, Biological, and Environmental Statistics*, **5**, 131–150.

Fisher, R.A. (1937) The wave of advance of advantageous genes. *Annals of Eugenics*, **7**, 355–369.

Flack, S. & Furlow, E. (1996) America's least wanted purple plague, green cancer and 10 other ruthless environmental thugs. *Nature Conservancy*, **46**, 17–23.

Flory, S.L. & Clay, K. (2009) Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation*, **142**, 2531–2537.

Gan, J., Miller, J.H., Wang, H.-H. & Taylor, J.W.J. (2009) Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. *Canadian Journal of Forest Research*, **39**, 1346–1356.

Grace, J.B. (1998) Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? *Endangered Species Update*, **15**, 70–76.

Greene, D.F. & Calogeropoulos, C. (2002) *Dispersal ecology: measuring and modelling seed dispersal of terrestrial plants*. Blackwell, Oxford.

Greene, D.F., Canham, C.D., Coates, K.D. & Lepage, P.T. (2004) An evaluation of alternative dispersal functions for trees. *Journal of Ecology*, **92**, 758–766.

Grimm, V. & Railsback, S. (2006) Agent-based models in ecology: patterns and alternative theories of adaptive behaviour. *Agent-based computational modelling* (ed. by F.C. Billari, T. Fent, A. Prskawetz and J. Scheffran), pp. 139–152. Physica-Verlag HD, Germany.

Harcombe, P.A., Hall, R.B.W., Glitzenstein, J.S., Cook, E.S., Krusic, P., Fulton, M. & Streng, D.R. (1999) Sensitivity of gulf coast forests to climate change. *Vulnerability of coastal wetlands in the southeastern United States: climate change research results* (ed. by G. Gunterspergen and B.A. Varain), pp. 45–66. USGS, Belvoir, Virginia.

Hastings, A. (1996) Models of spatial spread: is the theory complete? *Ecology*, **77**, 1675–1679.

Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, **8**, 91–101.

Hukui, N. & Ueda, K. (1999) Seed dispersal of Chinese tallow-tree, *Sapium sebiferum*, by birds. *Japanese Journal of Ornithology*, **47**, 121–124.

Jarnevich, C.S. & Stohlgren, T.J. (2009) Temporal Management of Invasive Species. *Management of invasive weeds* (ed. by R.L. Inderjit), pp. 103–122. Springer, Dordrecht.

Jongejans, E., Skarpaas, O. & Shea, K. (2008) Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 153–170.

Klein, E.K., Lavigne, C., Picault, H., Renard, M. & Gouyon, P.-H. (2006) Pollen dispersal of oilseed rape: estimation of the dispersal function and effects of field dimension. *Journal of Applied Ecology*, **43**, 141–151.

Kot, M., Lewis, M.A. & Driessche, P.v.d. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.

Lee, S.K. (1956) Genus *Sapium* in the Chinese flora. *Acta Phytotaxonomica Sinica*, **5**, 111–130.

Lee, A.H., Wang, K. & Yau, K.K.W. (2001) Analysis of zero-inflated Poisson data incorporating extent of exposure. *Biometrical Journal*, **43**, 963–975.

Lin, J., Harcombe, P.A., Fulton, M.R. & Hall, R.W. (2004) Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. *Oecologia*, **139**, 399–407.

Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T. & McMichael, A. (2006) Biological invasions: recommendations for U.S. policy and management. *Ecological Applications*, **16**, 2035–2054.

Merritt, D.M., Nilsson, C. & Jansson, R. (2010) Consequences of propagule dispersal and river fragmentation for riparian plant community diversity and turnover. *Ecological Monographs*, **80**, 609–626.

Miller, J.H. & Schelhas, J. (2008) Adaptive collaborative restoration: a key concept for invasive plant management. *Invasive plants and forest ecosystems* (ed. by R.K. Kohli, J.P. Singh, D.R. Batish and S. Jose), pp. 251–265. CRC Press, Boca Raton, FL.

Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.

Morales, J.M. & Carlo, T.A. (2006) The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology*, **87**, 1489–1496.

Muneepeerakul, R., Bertuzzo, E., Rinaldo, A. & Rodriguez-Iturbe, I. (2008) Patterns of vegetation biodiversity: the roles of dispersal directionality and river network structure. *Journal of Theoretical Biology*, **252**, 221–229.

Murphy, H.T. & Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos*, **105**, 3–14.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.

NOAA (2008) *Climate maps of the United States. Temperature maps*. Available at: http://cdo.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl (accessed 15 June 2008).

Nowak, D.J., Smith, P.D., Merritt, M., Giedraitis, J., Walton, J.T., Hoehn, R.E., Stevens, J.C., Crane, D.E., Estes, M., Stetson, S., Burditt, C., Hitchcock, D. & Holtcamp, W. (2005) *Houston's regional forests: structure, function, values*. Texas Forest Service, Houston, Texas.

Pattison, R.R. & Mack, R.N. (2008) Potential distribution of the invasive tree *Triadica sebifera* (*Euphorbiaceae*) in the United States: evaluating CLIMEX predictions with field trials. *Global Change Biology*, **14**, 813–826.

Pattison, R.R. & Mack, R.N. (2009) Environmental constraints on the invasion of *Triadica sebifera* in the eastern United States: an experimental field assessment. *Oecologia*, **158**, 591–602.

Primack, R.B. & Miao, S.L. (1992) Dispersal can limit local plant distribution. *Conservation Biology*, **6**, 513–519.

Pyšek, P., Jarošík, V. & Kučera, T. (2002) Patterns of invasion in temperate nature reserves. *Biological Conservation*, **104**, 13–24.

Quesada-Moraga, E., Navas-Cortes, J.A., Maranhao, E.A., Ortiz-Urquiza, A. & Santiago-Alvarez, C. (2007) Factors affecting the occurrence and distribution of entomopathogenic fungi in natural and cultivated soils. *Mycological Research*, **111**, 947–966.

Renne, I.J., Gauthreaux, S.A. & Gresham, C.A. (2000) Seed dispersal of the Chinese Tallow tree (*Sapium sebiferum* (L.) *Roxb*.) by birds in coastal South Carolina. *American Midland Naturalist*, **144**, 202–215.

Renne, I.J., Spira, T.P. & Bridges, W.C., Jr (2001) Effects of habitat, burial, age and passage through birds on germination and establishment of Chinese tallow tree in coastal South Carolina. *Journal of the Torrey Botanical Society*, **128**, 109–119.

Renne, I.J., Barrow, W.C., Johnson Randall, L.A. & Bridges, W.C. (2002) Generalized avian dispersal syndrome contributes to

Chinese tallow tree (*Sapium sebiferum, Euphorbiaceae*) invasiveness. *Diversity and Distributions*, **8**, 285–295.

Ribbens, E., Silander, J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.

Rogers, W.E. & Siemann, E. (2005) Herbivory tolerance and compensatory differences in native and invasive ecotypes of Chinese tallow tree. *Plant Ecology*, **181**, 57–68.

Rudis, V.A., Gray, A., McWilliams, W., O'Brien, R., Olson, C., Oswalt, S. & Schulz, B. (2006) Regional monitoring of nonnative plant invasions with the Forest Inventory and Analysis program. Gen. Tech. Rep. WO-70. *Proceedings of the Sixth Annual FIA Symposium* (ed. by R.E. McRoberts, G.A. Reams, P.C.V. Deusen and W.H. McWilliams), pp. 49–64. USDA Forest Service, Denver, CO.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160–3174.

Sebert-Cuvillier, E., Simon-Goyheneche, V., Paccaut, F., Chabrerie, O., Goubet, O. & Decocq, G. (2008) Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. *Landscape Ecology*, **23**, 787–801.

Sheley, R.L., Mangold, J.M. & Anderson, J.L. (2006) Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecological Monographs*, **76**, 365–379.

Siemann, E. & Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters*, **4**, 514–518.

Siemann, E. & Rogers, W.E. (2003) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology*, **91**, 923–931.

Siemann, E. & Rogers, W.E. (2007) The role of soil resources in an exotic tree invasion in Texas coastal prairie. *Journal of Ecology*, **95**, 689–697.

Siemann, E., Carrillo, J.A., Gabler, C.A., Zipp, R. & Rogers, W.E. (2009) Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management*, **258**, 546–553.

Skarpaas, O., Shea, K. & Bullock, J.M. (2005) Optimizing dispersal study design by Monte Carlo simulation. *Journal of Applied Ecology*, **42**, 731–739.

Skellam, J. (1951) Random dispersal in theoretical populations. *Bulletin of Mathematical Biology*, **53**, 135–165.

Smolik, M.G., Dullinger, S., Essl, F., Kleinbauer, I., Leitner, M., Peterseil, J., Stadler, L.-M. & Vogl, G. (2010) Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *Journal of Biogeography*, **37**, 411–422.

Stephenson, C.M., MacKenzie, M.L., Edwards, C. & Travis, J.M.J. (2006) Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecological Modelling*, **193**, 747–758.

Stoyan, D. & Wagner, S. (2001) Estimating the fruit dispersion of anemochorous forest trees. *Ecological Modelling*, **145**, 35–47.

Sutherst, R.W. & Maywald, G.F. (1985) A computerised system for matching climates in ecology. *Agriculture Ecosystems and Environment*, **13**, 281–299.

Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution*, **13**, 329–332.

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.

Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.

Tufto, J., Engen, S. & Hindar, K. (1997) Stochastic dispersal processes in plant populations. *Theoretical Population Biology*, **52**, 16–26.

USDA (2005) *The enhanced forest inventory and analysis program-national sampling design and estimation procedures*. USDA Forest Service, Southern Research Station, Asheville, NC.

USDA (2008a) *FIA data and tools*. Available at: http://fia.fs.fed.us/tools-data (accessed 4 November 2008).

USDA (2008b) *Nonnative invasive plant data tool*. Available at: http://srsfia2.fs.fed.us/data_center/index.shtml (accessed 18 November 2008).

USGS (2009) *1:250,000 and 1:100,000 scale land use land cover (LULC)*. Available at: http://edc2.usgs.gov/geodata/index.php (accessed 16 April 2009).

Walters, C.J. (1986) *Adaptive management of renewable resources*. Macmillan Publishing Company, New York.

Wang, H.-H. (2009) *Occupation, dispersal, and economic impact of major invasive plant species in southern U.S. forests*. PhD Dissertation. Texas A&M University, College Station, TX.

Wilson, J.R.U., Richardson, D.M., Rouget, M., Proches, S., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11–22.

With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**, 1192–1203.

Yantis, J.H. (2006) *Vegetation classification and the efficacy of plant dominance-based classifications in predicting the occurrence of plant and animal species*. PhD Dissertation. Texas A&M University, College Station, TX.

Zedler Joy, B. & Kercher, S. (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, **23**, 431–452.

Zou, J., Rogers, W.E. & Siemann, E. (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Functional Ecology*, **21**, 721–730.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Target ecosystem and invasive plant.

Appendix S2 Model structure, model dynamics, spread within cells: estimation of r_i and HQ_i, and invasion from other cells: estimation of k_{ji}.

Table S1 Landscape features, climatic conditions, and forest conditions (from Table 2) selected, based on the indicated results of logistic regression, to estimate habitat quality (HQ = probability of invasion) for Chinese tallow on forested plots in seven counties in South Carolina.

Figure S1 Increase in percent land cover of Chinese tallow over an approximately 5-year period on forested plots in east Texas sampled by the United States Forest Service (USDA, 2008a).

Figure S2 Effect of the scale parameter representing dispersal velocity [L, in grid-width (4927 m) units] on the lognormal dispersal kernel ($k(D)$), assuming the shape parameter (S) equals 1 (see equation 4). $L = 0.2$ (black line), $L = 0.5$ (gray line), and $L = 1$ (bold black line).

BIOSKETCH

Hsiao-Hsuan Wang is a postdoctoral research associate with the Department of Wildlife and Fisheries Sciences at Texas A&M University, Texas, USA. She received her undergraduate and MS degrees in Forestry from National Taiwan University, and PhD degree in Forestry from Texas A&M University. She is primarily interested in the role of dispersal and habitat selection in producing the spatial distribution of populations across landscapes. She is also interested in the application of ecological theory and knowledge to problems in conservation ecology.

Author contributions: H.-H.W., W.E.G., T.M.S., J.G., W.E.R., T.E.K., J.H.M. and J.W.T. conceived the ideas. H.-H.W., J.H.M. and J.W.T. compiled the data. H.-H.W. and J.G. conducted statistical analyses. H.-H.W., W.E.G., T.M.S. and T.E.K. developed the agent-based, spatially explicit simulation models. H.-H.W., W.E.G and W.E.R. led the writing.

Editor: Bethany Bradley