

RESEARCH ARTICLE

10.1002/2014WR015537

Special Section:

Eco-hydrology of Semiarid Environments: Confronting Mathematical Models with Ecosystem Complexity

Key Points:

- We present new simple method to examine spread rate by various dispersal vectors
- Spread by three dispersal vector types quantified by 153 subcounties arrival time
- The extremely fast invasion of a plant species is attributed to dispersal by rivers

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Citation:

Horvitz, N., R. Wang, M. Zhu, F.-H. Wan, and R. Nathan (2014), A simple modeling approach to elucidate the main transport processes and predict invasive spread: River-mediated invasion of *Ageratina adenophora* in China, *Water Resour. Res.*, 50, 9738–9747, doi:10.1002/2014WR015537.

Received 5 MAR 2014

Accepted 22 NOV 2014

Accepted article online 28 NOV 2014

Published online 31 DEC 2014

A simple modeling approach to elucidate the main transport processes and predict invasive spread: River-mediated invasion of *Ageratina adenophora* in China

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Abstract A constantly increasing number of alien species invade novel environments and cause enormous damage to both biodiversity and economics worldwide. This global problem is calling for better understanding of the different mechanisms driving invasive spread, hence quantification of a range of dispersal vectors. Yet, methods for elucidating the mechanisms underlying large-scale invasive spread from empirical patterns have not yet been developed. Here we propose a new computationally efficient method to quantify the contribution of different dispersal vectors to the spread rate of invasive plants. Using data collected over 30 years regarding the invasive species *Ageratina adenophora* since its detection at the Sichuan province, we explored its spread by wind and animals, rivers, and roads into 153 subcounties in the Sichuan, Chongqing, and Hubei provinces of China. We found that rivers are the most plausible vector for the rapid invasion of this species in the study area. Model explorations revealed robustness to changes in key assumptions and configuration. Future predictions of this ongoing invasion process project that the species will quickly spread along the Yangtze River and colonize large areas within a few years. Further model developments would provide a much needed tool to mechanistically and realistically describe large-scale invasive spread, providing insights into the underlying mechanisms and an ability to predict future spatial invasive dynamics.

1. Introduction

Biological invasions—the entry, establishment, and spread of nonnative species—are considered a major cause of human-induced environmental change and have become a pressing problem in every biome on earth [Elton, 1958; Maclsaac et al., 2011; Pimentel et al., 2005; Williamson, 1996]. Biological invasions threaten global biodiversity by altering the structure and functioning of ecosystems [Cook et al., 2007; Levine et al., 2003; Trakhtenbrot et al., 2005] and disrupting key biological interactions [Mitchell et al., 2006; Traveset and Richardson, 2006]. These invasions have also been considered as a major cause of recent extinctions [Thomas et al., 2004] and have had a substantial economic impact [Pimentel et al., 2005].

Invasive species, defined as nonindigenous species that have established and reached widespread distribution in an area far beyond their native range [Colautti and Maclsaac, 2004], undergo a process of spatial spread we termed here as “invasive spread.” Similar to the spread of indigenous species in their native range, the process of invasive spread is shaped by three distinct, yet not mutually exclusive, components: fecundity (the number of seeds produced and dispersed), dispersal kernel (the probability of a dispersed seed to arrive at a given location with respect to its mother plant), and habitat suitability (the probability of a seed to reach reproductive stage). There have been extensive research on the roles of habitat suitability [Evangelista et al., 2008; Ibanez et al., 2014; Morissette et al., 2006; Rouget and Richardson, 2003] and fecundity [Lockwood et al., 2005; Mason et al., 2008; Parker, 2000] in determining invasive spread, and many studies have successfully quantified dispersal kernels of invasive plants over relatively short spatial scales [Buckley et al., 2005; Caplat et al., 2012; Skarpaas and Shea, 2007] or applied dispersal kernels to examine theoretical scenarios over large scales [Bullock et al., 2012; Engler and Guisan, 2009; Nathan et al., 2011a]. Yet, our ability to quantify dispersal kernels underlying actual large-scale spread of invasive species is still rather poor, and

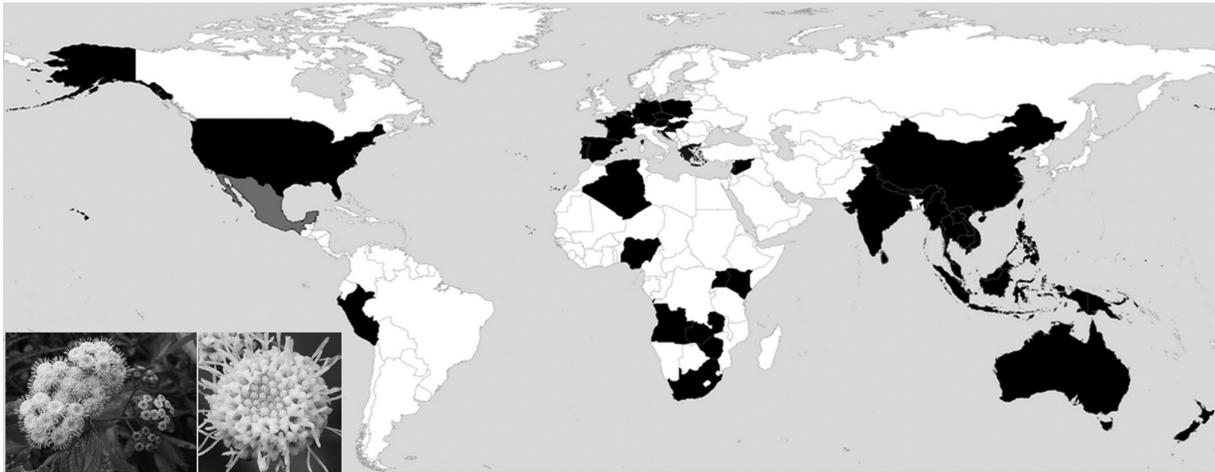


Figure 1. Worldwide distribution of the Crofton weed *Ageratina adenophora*. The species is native in Mexico (gray) but spread to over 40 countries (black) around the globe. Based on Muniappan *et al.* [2009], GBIF (www.gbif.org), and GRIN (www.ars-grin.gov). Spatial resolution is in country level.

the challenge of elucidating the relative contribution of different (and often unknown) dispersal vectors [Nathan *et al.*, 2008] remained largely unresolved. Therefore, progress in understanding and predicting actual large-scale invasive spread still awaits empirically derived mechanistic models capable of incorporating different dispersal vectors, and representing spread at relatively high resolution (e.g., < 1 km) and over large areas (e.g., > 1000 km).

The challenge of quantifying dispersal kernels underlying actual large-scale invasive spread is rather overwhelming, involving extremely rare but critical events that are inherently difficult to quantify and predict [Nathan, 2006], multiple potential dispersal vectors and other interacting, and usually unknown, factors [Higgins *et al.*, 2003a, 2003b; Nathan *et al.*, 2008]. Furthermore, the spread of invasive species is almost always meagerly documented, and the available information typically appears in the form of sparse anecdotal historical snapshots of the invasive process. It has been suggested that due to such difficulties and uncertainties, the process of large-scale spatial spread is doomed to be poorly divulged and unpredictable [Clark *et al.*, 2001]. Without downplaying these difficult fundamental challenges, understanding the underlying mechanisms and developing predictive frameworks for large-scale invasive spread are still of critical importance for both basic and applied research of biological invasions [Jongejans *et al.*, 2008; Trakhtenbrot *et al.*, 2005].

To facilitate addressing these challenges, we aim at developing and testing a simple approach for quantifying dispersal kernels for a typical case of anecdotally and sparsely documented invasive spread, putting aside, at this stage, complexities involved with other components of this complex system and relying on some simplifying assumptions. More specifically, we aim to develop a method to quantify the contribution of various dispersal vectors to the invasion process of plants, focusing on *Ageratina adenophora*, identified as an invasive species in over than 40 countries worldwide [Muniappan *et al.*, 2009] (Figure 1) and in the Sichuan, Chongqing, and Hubei provinces of southwestern China in particular. Using data on the first arrival year of the *A. adenophora* to 153 subcounties (including 37 subcounties where the species was absent) of these three provinces (Figure 2a), we developed a spatially explicit grid model to explore the (effective) dispersal kernel via three main dispersal vectors. The first, the isotropic dispersal vector (associated with speed variable $t_{isotropic}$), represents all dispersal mechanisms not affected by roads or water resources, mainly dispersal by wind or animals. Dispersal by wind is a common dispersal mechanism used by plants and the most advanced in terms of mechanistic modeling [Cousens *et al.*, 2008; Kuparinen, 2006; Nathan *et al.*, 2002; Nathan *et al.*, 2011b]. Similarly, dispersal by animals, both epizoochory and endozoochory, has been a subject of extensive research [Schupp, 1993; Spiegel and Nathan, 2007]. Even though both dispersal by animals, and, moreover, dispersal by wind are known to be anisotropic [Nathan *et al.*, 2002], they are likely to be considerably less directional than the two other dispersal mechanisms we considered. In addition, the directionality of winds and animal activity are expected to be highly variable in a mountainous area such as our study site; therefore, we made the assumption that for the entire study area they act in

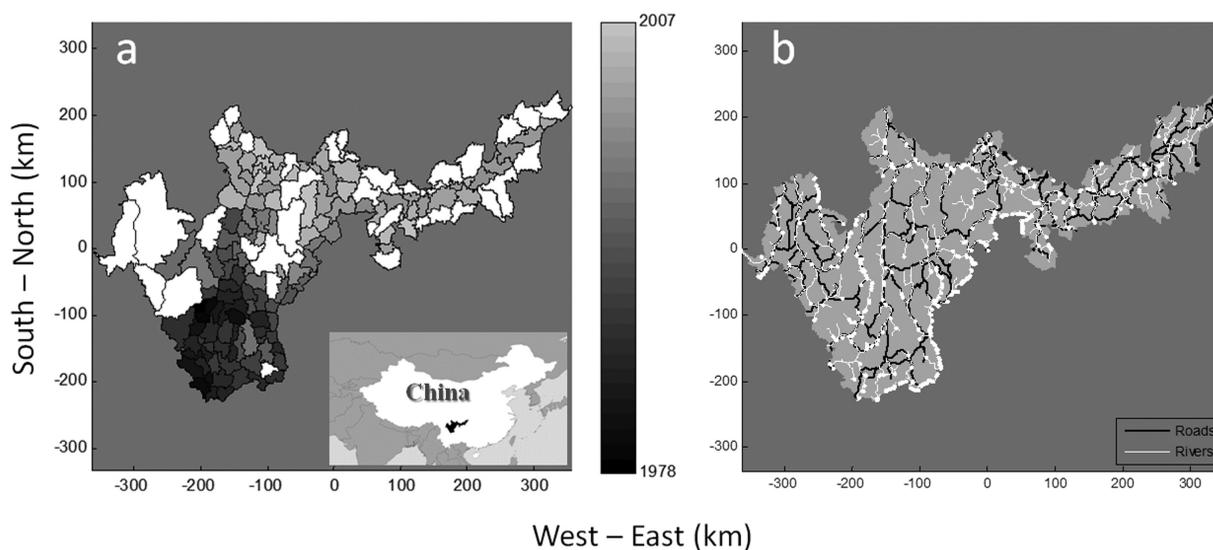


Figure 2. Earliest observed year of *Ageratina adenophora* (grayscale bar in the middle) in each subcounty in Sichuan, Guizhou, and Chongqing provinces. (a) Earliest arrival year for 153 subcounties included in this study. White area represents non invaded subcounties. (b) Rivers (white lines) and roads (black lines) considered in our analysis. The central (0,0) point is located at 28.143°N, 103.754°E.

an isotropic manner. We note, however, that this assumption may be relaxed in future studies, for example by incorporating directionality of dispersal based on wind measurements.

The second mechanism we consider in our study is dispersal by rivers (associated with speed variable t_{river}). Dispersal by rivers was studied broadly throughout many taxa and disciplines [Bertuzzo *et al.*, 2007; Boedeltje *et al.*, 2003; Guppy, 1892; Konar *et al.*, 2013; Mari *et al.*, 2014] and shown to have an important role in long-distance dispersal (LDD) of plants [Hampe, 2004; Johansson *et al.*, 1996; Nathan *et al.*, 2008] and in *A. adenophora* in particular [Wang *et al.*, 2011]. The third dispersal mechanism we consider is via various transportation means associated with roads (associated with speed variable t_{road}). This mechanism was extensively studied, mostly quantifying the travel distance of seeds by cars [Hodkinson and Thompson, 1997; Veldman and Putz, 2010; von der Lippe and Kowarik, 2007; von der Lippe *et al.*, 2013], but without assessing the probability of a seed to be transported by a car. Thus, even though the mechanism of dispersal by human transportation is widely accepted as a major contributor to long-distance dispersal of plants [Nathan *et al.*, 2008], we are still short handed in making predictions about its quantitative contribution to invasive spread.

Following Wang *et al.* [2011], we predict that the isotropic and river vectors will be found to play a major role in the spread process of *A. adenophora*, while the contribution of roads will be less notable. We tested this prediction by comparing the best fitted parameters of the model (i.e., we predict that $t_{isotropic}$ and t_{river} will be much faster than t_{road}), and also checked the proportion of distance each vector contributed to *A. adenophora* spread across the study area (See 2.4). We also used sensitivity analysis to evaluate model robustness to small changes in configuration (see subsection 2.5). Finally, we produced a prediction map for the future spread of *A. adenophora* across the Guizhou, Chongqing, Sichuan, Hunan, and Hubei provinces.

2. Methodology

2.1. Study Species

Crofton weed (*Ageratina adenophora* Sprengel) is a perennial herbaceous plant of the composite family native to Mexico [Cronk and Fuller, 1995]. The species has invaded more than 30 countries and regions of tropical and subtropical regions and has become one of the worst invasive weeds in the world [Cronk and Fuller, 1995]. In China, it was first noticed in the Yunnan Province in the 1940s and since 1978 has spread along the upper Yangtze River [Wang and Wang, 2006]. Mean seed production per plant is high (7000–10,000 seeds year⁻¹; [Parsons and Cuthbertson, 2001]), seed mass is 0.4 mg [Parsons and Cuthbertson, 2001] and its bristle pappus structures facilitate dispersal by wind and water. Seeds can also be dispersed as an

impurity in agricultural products, in sand and gravel used for road making, in mud sticking to animals, machinery, and other vehicles, and by adhering to footwear or clothing [Parsons and Cuthbertson, 2001]. Vegetative propagation can occur from fragmented stems carried by water in rivers and, particularly, in flooding events [Wang et al., 2011].

2.2. GIS and Modeling Resources

Highway data were obtained from CHGIS site (<http://www.fas.harvard.edu/~chgis/data/dcw>). Rivers data were downloaded from the HydroSHEDS site (<http://hydrosheds.cr.usgs.gov>). To focus only on major streams, we used only rivers with an “Up_cells” attribute (a proxy for mean annual flow, see <http://hydrosheds.cr.usgs.gov/hydro.php>) higher than 1000. The dispersal model was compiled in Visual C++ version 11 (Microsoft Corporation, Redmond, WA, USA). All other analyses were performed using Matlab version 7.14 (MathWorks Inc, Natick, MA, USA).

2.3. Dispersal Model

We divided the invaded area into 1 km by 1 km cells (Figure 2b). For each grid cell, we assigned the subcounty that contains the largest portion of the cell area. We considered three types of dispersal vectors: (1) the isotropic vector—allowing dispersal from each cell to its eight neighbor cells; (2) the rivers vector—allowing dispersal from each cell to any neighboring cell downstream from it; and (3) the roads vector—allowing dispersal between each neighboring cell connected by major roads. Neighboring cells in the nondiagonal direction are considered connected by river (or road) if there is a river (road) crossing their mutual edge. Neighboring cells in a diagonal direction were considered connected if the same river (road) was flowing through the two half of nearest edge of their mutual corner. For example, if cell A is north-east to cell B, they were considered connected by river if the same river flows through the eastern half of the north edge or northern half of the east edge of cell B and also flows through the western half of the south edge or southern half of the west edge of cell A. For each model iteration, three parameters describing time to spread from one cell to its neighbor for the isotropic ($t_{isotropic}$), rivers (t_{river}), and roads (t_{road}) vectors were assigned. Vector speed in diagonal direction was multiplied by a factor of $\sqrt{2}$. If a neighbor cell was connected by more than a single vector type, the overall time to spread to this cell was calculated as the inverse of the sum of the inverse of speed for each separate vector connecting it. All grid cell values were initialized to infinite, except for the cells of the earliest invaded subcounty (i.e., Shuhe subcounty), which were set to 1978, the year of first observation. At each iteration, we calculated for each cell the earliest year of plant arrival and set this year as the cell value. For each subcounty i , we then calculated the first arrival time to any of its grid cells (m_i). The resulting sum of square differences (SSD) for the input parameters was defined as the sum of square of differences between the observed subcounty arrival time (o_i) and m_i , that is,

$$SSD = \sum_i (m_i - o_i)^2.$$

SSD represents the goodness of fit, with lower SSD values indicating a better fit. For each model configuration, we choose the best fitting parameters of the three vectors by selecting the parameters that minimizing SSD.

We set o_i for subcounties with no observed plants as the year following to the last year of observed arrival to subcounty (i.e., 2008, last year of data collected).

2.4. Contribution of Each Vector to Spread

We calculated the contribution of each of the three vectors to the spread from the invasion origin to each grid cell as the proportion of distance carried by each vector from the spread origin to this grid cell. For a specific grid cell, we first back-tracked the spread from the grid cell to the first invaded subcounty cells. This was done by taking the grid cell and its eight neighbor cells, and identifying from which of those eight neighbor cells the plant invaded into the grid cell. After identifying through which neighbor cell the plant invaded, we took that neighbor cell and identified from which of its eight neighbors the plant had spread. We continued this process until we reached a cell within the first invaded subcounty.

The above procedure yielded the full track from the first invaded subcounty to each cell, used to calculate the distance each vector contributed to the spread. For instance, for one step s (i.e., movement from a cell to its neighbor), the distance carried by the isotropic vector is calculated by

$$d_{s, isotropic} = D_s \frac{t_{isotropic}^{-1}}{t_{isotropic}^{-1} + I_{s, river} t_{river}^{-1} + I_{s, road} t_{road}^{-1}}$$

where D_s is the distance between the center of the grid cell to its follower along the track and $I_{s, river}$ ($I_{s, road}$) is 1 if the two cells are connected by river (road) and 0 otherwise. For cells connected by river, $d_{s, river}$ was calculated the same way, by replacing $t_{isotropic}$ by t_{river} in the numerator. Otherwise $d_{s, river}$ is 0. The same calculation was done for $d_{s, road}$. The proportion of distance carried by the isotropic vector across all track is

$$d_{isotropic} = \frac{\sum_s d_{s, isotropic}}{\sum_s D_s}$$

and likewise for d_{river} and d_{road} .

2.5. Sensitivity Analysis

We analyzed the sensitivity of our model to three possible changes in its configuration. First, we examined how changes in grid cell size could affect the model predictions. We ran the model with cell sizes ranging from 1 to 5 km with 1 km intervals and checked for trends in the best fitted speeds for the three vectors. Second, we evaluated the sensitivity of the model to our arbitrary decision to set the earliest arrival time of subcounties with no observed plant as one year after the last observed subcounty occupation year. We compared best fitted parameters when our assumption for arrival year of plant-free subcounties was changed from 1 to 10 years after the latest observed subcounty arrival time.

Since the observed arrival year for each subcounty might be overestimated (i.e., in the case where the plant had actually invaded the subcounty prior to the first observation) but cannot be underestimated, we also checked how the model predictions changed when a penalty p_{late} was introduced for subcounties for which the model predicts arrival after the actual observed invaded time. SDD equation in this case is

$$SSD = \sum_{\{i|m_i < o_i\}} (m_i - o_i)^2 + \sum_{\{j|m_j > o_j\}} [p_{late}(m_j - o_j)]^2$$

We changed p_{late} between 1 and 2 with increments of 0.1. Third, we checked the change in SSD while holding two of the best fitted parameters constant and changing the third by 10% to 1000% of its original value. This procedure was repeated for each of the three vector speed parameters.

3. Results

The best fitted speed parameters of the model were $t_{isotropic} = 3.24 \text{ km yr}^{-1}$ (i.e., 0.3082 years km^{-1}), $t_{river} = 270.4 \text{ km yr}^{-1}$, $t_{road} = 5.30 \text{ km yr}^{-1}$, and SDD = 7568 (an average of 4.35 years difference per subcounty between modeled and observed earliest arrival year). Modeled invasive spread is presented in Figure 3. For each track from the first invaded subcounty to the first invaded cell of each other subcounty, we calculated the portion of distance each vector contributes to the track (Figure 4a). The mean contribution of the isotropic vector was 17.9%, the rivers vector contributed 67.8%, and the roads vector 14.3% of the distance traveled to the earliest occupied cell of each subcounty. Examining tracks to all cells (Figure 4b), the mean contribution of the isotropic, rivers, and roads vectors were, respectively, 19.8%, 65.3%, and 14.9% of the distance travel to all grid cells. In both cases, there was no notable trend in the relative contribution of the three vector across years, except even larger proportion of the river vector in very early stages of invasion (Figure 4). There was no significant effect on best fitted parameters with increase in cell size ($p > 0.3$ for all three vectors; Figure 5a). The isotropic and rivers vectors best fitted parameters decreased ($t_{isotropic}^{-1} = 3.08 + 0.24 * p_{late}$ and $t_{road}^{-1} = 5.04 + 0.41 * p_{late}$; $p < 0.001$ for both) with increasing penalty for late arrival (see subsection 2.5), while the river vector speed ($p = 0.18$) did not show any significant change (Figure 5b). All vector speeds were decreasing with an increase in the assumed noninvaded subcounties invasion year (subsection see 2.5; Figure 5c). The effect on the isotropic and roads vectors was significant ($t_{isotropic}^{-1} = 3.33 - 0.03 * \text{years}$ and $t_{road}^{-1} = 5.45 - 0.05 * \text{years}$; $p < 0.001$ for both) while the effect on rivers vector was marginally significant ($t_{river}^{-1} = 228.82 - 6.72 * \text{years}$; $p = 0.09$). Holding two of the vectors at their best fitted values while changing the third, we found that 95% confidence bounds (Figure 5d) for the isotropic vector: 2.88–3.66 km yr^{-1} (0.88–1.13 of the optimal value), for rivers vector: 152–2700 km yr^{-1} (0.1–1.77 of

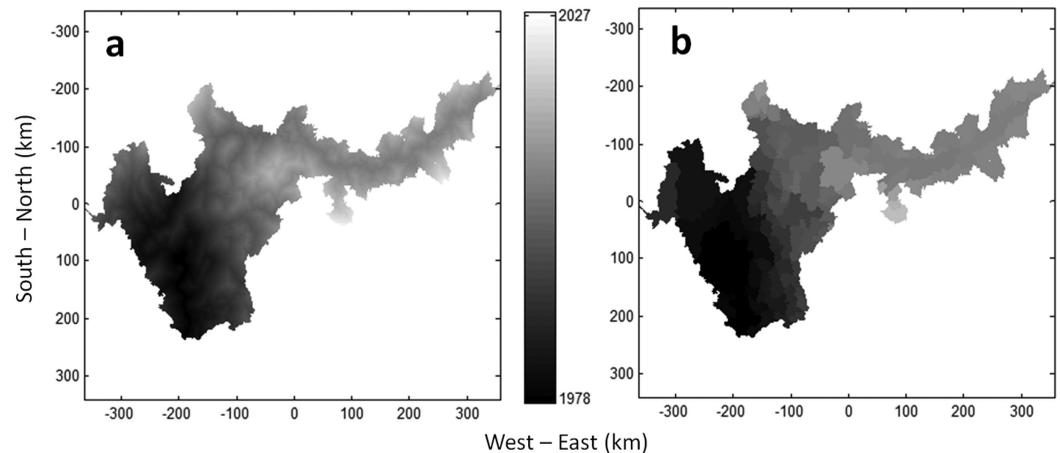


Figure 3. Results of the model with best fitted parameters. The isotropic vector speed is 3.24 km yr^{-1} , river vector speed is 270.4 km yr^{-1} , and road vector speed is 5.3 km yr^{-1} . (a) Map colors represent plant earliest arrival to each grid cell in the simulated area (see grayscale bar for years). (b) Map colors represent plant earliest arrival to each subcounty in the simulated area. The central (0,0) point is located at 28.143°N , 103.754°E .

the optimal value), and for roads vector: $4.18\text{--}6.40 \text{ km yr}^{-1}$ ($0.83\text{--}1.27$ of the optimal value). Model prediction for future invasion process into Guizhou, Chongqing, Sichuan, Hunan, and Hubei provinces is presented in Figure 6.

4. Discussion

The growing number of alien species invading novel environments worldwide, especially species like *A. adenophora* that threaten native species [Xie *et al.*, 2001], possess a major threat to both biodiversity and global economy [Elton, 1958; MacIsaac *et al.*, 2011]. Controlling the spread of invasive species and preventing the successful establishment of newly introduced species, necessitates a thorough understanding of the invasion process, as well as reliable tools to predict invasive spread. A major challenge in addressing these needs is the difficulty of quantifying dispersal kernels underlying large-scale invasive spread in a way that is both mechanistically sound (e.g., incorporating multiple rather than a single dispersal vector) and linked to empirical data. In this paper, we presented a simple method to quantify the contribution of different

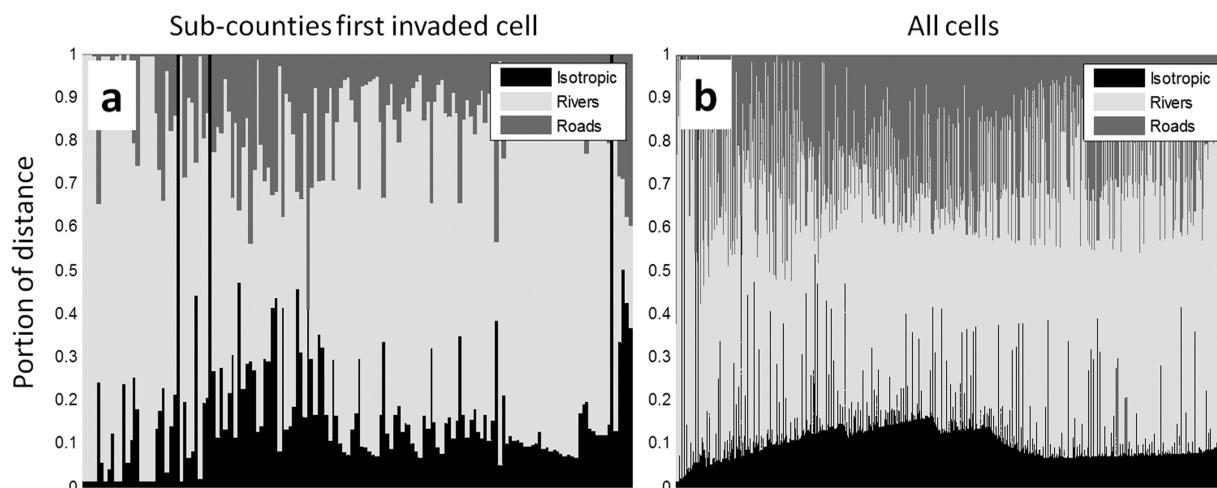


Figure 4. Relative contribution of different dispersal vectors to the invasion of *Ageratina adenophora* in the study area. Colors indicate the relative contribution of the isotropic (black), rivers (light gray), and roads (dark gray) vectors, as the proportion of the calculated invasion tracks over which the plant was estimated to be dispersed by each vector, averaged for each time interval. The invasion tracks are presented synchronically from left (start time) to right (end time) in both plots. All tracks start at the first invaded subcounty in 1978 and end in either (a) the first occupied cell in any other subcounty projected until 2017 or (b) any other grid cell projected until 2027. The mean contribution of the isotropic vector, rivers, and roads is, respectively, 17.9%, 67.8%, and 14.3% for (a), and 19.8%, 65.3%, and 14.9% for (b).

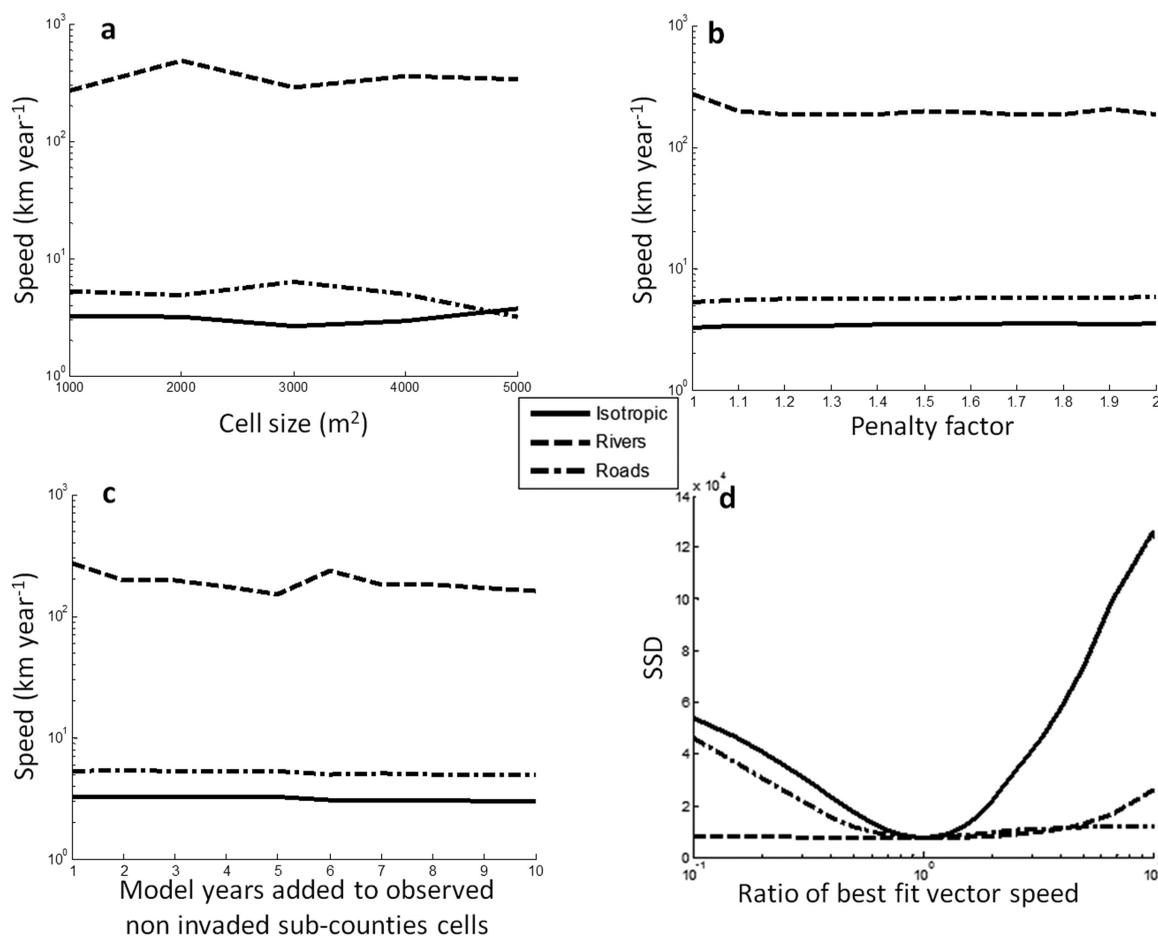


Figure 5. Sensitivity analysis of the model. (a) Changes in best fitted parameters with increasing cell size. Cell size does not significantly affect neither the isotropic ($p = 0.63$), rivers ($p = 0.97$) nor the roads ($p = 0.31$) vectors speed. (b) Changes in best fitted parameters with changing penalty factor for subcounties with arrival time later than observed. For the isotropic and roads vectors ($t_{\text{isotropic}}^{-1} = 3.08 + 0.24 \cdot p_{\text{late}}$ and $t_{\text{road}}^{-1} = 5.04 + 0.41 \cdot p_{\text{late}}$; $p < 0.001$ for both), speed increases with increasing penalty factor, while for the rivers vector variation in penalty factors does not induce a change in speed ($p = 0.18$). (c) Changes in best fitted parameters when changing the assumed time of arrival for non invaded subcounties. The x axis describes the years added to the latest year of observed newly invaded subcounty, changing from 1 (year assigned to noninvaded subcounties is 2008) to 10 (years assigned to non invaded subcounties is 2017). The isotropic and roads vectors ($t_{\text{isotropic}}^{-1} = 3.33 - 0.03 \cdot \text{years}$ and $t_{\text{road}}^{-1} = 5.45 - 0.05 \cdot \text{years}$; $p < 0.001$ for both) show significant decrease in speed when more years are added. For the rivers vector, decrease in speed is marginally significant ($t_{\text{river}}^{-1} = 228.82 - 6.72 \cdot \text{years}$; $p = 0.09$). (d) Effect of changes in one of the best fitted parameters. Changes in the resulting sum of square differences (SSD) are less than 5% when the speed is 2.88–3.66, 152–2700, and 4.18–6.40 year km⁻¹ for the isotropic, rivers and roads vectors, respectively.

dispersal mechanisms to the invasive spread of *A. adenophora* in three provinces at southwestern China. We found the model adequately revealed the contribution of three different dispersal mechanisms (Figure 4), and was robust to small changes in configuration or initial assumptions (Figure 5).

We found that rivers play the most important role in the observed rapid spread, while the isotropic and roads vectors were less imperative (Figure 4). Our findings only partially match those of Wang *et al.* [2011] who applied join-count spatial statistics with reproduction mode examination to the same data set. They found that the best model fitting the spread is the one combining wind and rivers as dispersal mechanisms, suggesting a negligible role for roads. Our results suggest that rivers are overwhelmingly important for the spread of this species, but suggest comparable roles for dispersal by isotropic (which includes winds) and roads vectors. Wang *et al.* [2011] examined dispersal between specific locations of plant observations, hence emphasized the role of local scale dispersal mechanisms (e.g., wind), especially between locations that are neither near rivers nor roads. In contrast, our model used data on first arrival time to subcounties, placing stronger emphasis on mechanisms contributing to the large-scale invasion spread.

The spread rate estimated for the isotropic vector (3.24 km yr⁻¹) is much higher than those suggested for dispersal by wind [Bullock *et al.*, 2012; Nathan *et al.*, 2011a], though higher rates may be achieved by a few, rare, extreme atmospheric conditions [Nathan *et al.*, 2011b]. Previously published results of seed dispersal

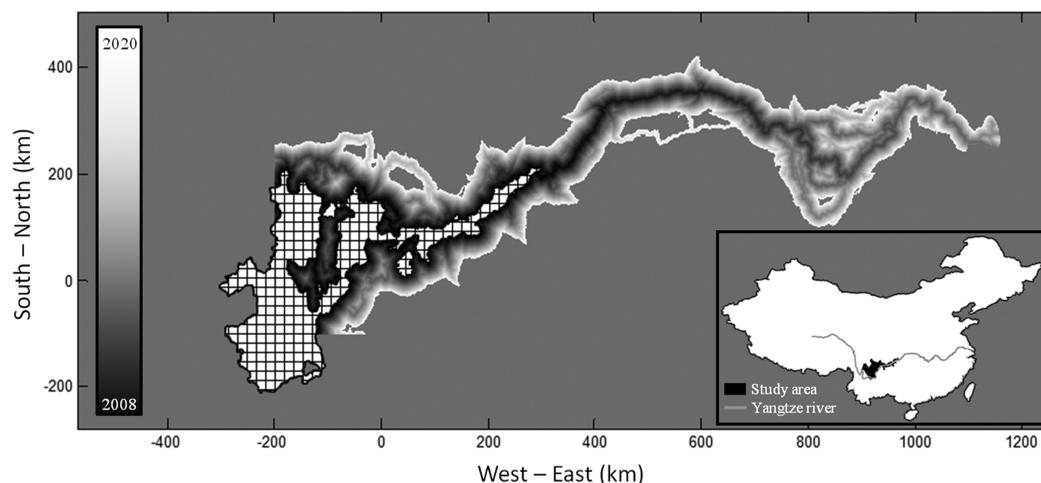


Figure 6. Prediction of future invasion of *Ageratina adenophora* in southwestern China. Projection of the best fitted model for the invasive spread of the species around our study area. By 2020, the species is expected to spread very locally in northern part of the area (Sichuan, Guizhou, and Chongqing provinces) but very rapidly to the east (Hunan and Hubei provinces) along the Yangtze River. Grid cells of previously observed invaded subcounties (mesh) were initialized to year 2008 (last year of observations). The central (0,0) point is located at 28.143°N, 103.754°E.

distances by animals can account for spread rates of a few kilometers per year [Kremer *et al.*, 2012; Spiegel and Nathan, 2007]. We thus suggest that the isotropic vector is more likely to represent dispersal by animals than dispersal by wind.

Dispersal by rivers plays the most important role in the observed spread. The significance of hydrochory to plant LDD is long known [Guppy, 1892; Nathan *et al.*, 2008; Nilsson *et al.*, 1991]. We quantified the spread rate by rivers to be approximately 270 km yr⁻¹. Past studies examining dispersal distances by rivers found much lower rates [Boedeltje *et al.*, 2003]. This is probably due to their use of data from trapped seeds downstream, limiting the data to only a few kilometers (i.e., the distance between seeds release sites and traps locations), overlooking rare events of very long distance dispersal.

Constructing the dispersal kernel of human-mediated transport is probably the most challenging task of all dispersal mechanisms, due to the highly stochastic nature of this process. We found that spread by the roads vector is approximately 5.3 km yr⁻¹. Even though previous studies did not quantify the rate of spread by cars, several studies provide a rough estimation of the distance a seed is expected to be carried by a car, ranging from 250 m [von der Lippe and Kowarik, 2007] and at least 500 m [Veldman and Putz, 2010], to 3–40 km [Hodkinson and Thompson, 1997]. Thus, our estimation of speed of invasion along roads is well within the observed rates.

We used our findings to construct a map of predicted future spread into Guizhou, Chongqing, Sichuan, Hunan, and Hubei provinces (Figure 6). Our predictions suggest that *A. adenophora* will spread east along the Yangtze River and reach the eastern border of Hubei by 2020. Expansion of this species to the north through Sichuan province is predicted to be much slower, probably due to the elevation increase in this direction, hence upstream of rivers, thereby diminishing the key LDD vector of this species. We note that the species has been recorded in other parts of China, far away (> 300 km) from our study area [Wang *et al.*, 2011], hence neglecting these populations in the present study. Our predictions suggest that attempts to control the spread of *A. adenophora* should focus around major rivers. Indeed, a monitoring program operated by the Chinese government since 2003 has effectively eradicated *A. adenophora* along the Yangtze River. To our knowledge, no new population has established in the study area outside the expansion boundaries of 2008, implying effective prevention of a potential spread of over 1000 km eastward predicted by our model.

Our focal plant species, *A. adenophora*, is native to Mexico and been declared as an invasive species in many countries around the world ([Muniappan *et al.*, 2009]; Figure 1). In the United States, it was found in California around 1849 [Muniappan *et al.*, 2009] but has yet to be observed in any other state [The PLANT Database, <http://plants.usda.gov>]. Moreover, it has not been observed in the northern third of California or in any noncoastline county aside from San Bernardino. The high disparity between rapid spread in China and the slow spread in the U.S. suggests that the invasive potential is not only affected by plant traits, but

also on the external conditions. In China, the plant spread rapidly toward the east because of many rivers flowing in this direction in the region of invasion. On the contrary, the streams in western California are flowing west into the Pacific Ocean, limiting the plant dispersal toward the nonshoreline counties. Overall, our study highlights the critical importance of the location of the initial introduction of an invasive species and, consequently, the need to identify high-risk hotspots from which rapid invasion is more likely as targets for intensive monitoring and management. Yet, such measures necessitate identifying the major dispersal mechanism facilitating rapid invasion, since the identification of such invasion hotspots inherently depends on the identity of the main LDD vectors.

Seeds of *A. adenophora* have a bristle pappus that facilitates dispersal by wind. Yet, we found that the main vector of LDD in our study area is rivers. The disparity between the morphology of the dispersal unit and its actual LDD agent has been described for many species [Higgins *et al.*, 2003a], highlighting the difficulty of predicting which plants species are prone to become invasive. Plant LDD agent might be inscrutable at the plant native habitat. For example, if its LDD agent was rivers, but no rivers flowed through its native habitat. Additionally, the task of predicting plant LDD potential is difficult to accomplish using field experiments because those are usually restricted to small distances, over which LDD cannot be observed [Higgins *et al.*, 2003a].

The simplicity of our model, allowing it to quantify the spread rate by different mechanisms in a rather naive way, at relatively small spatial resolution (i.e., 1 km) over a large area (i.e., over 100,000 km²), may also be its Achilles heel. Our model overlooks many important attributes of the species and the environment that might significantly affect its result. Our assumption that *A. adenophora* is capable of colonizing all modeled area leads to simulated dispersal into unsuitable habitats. For example, predicted invasion to the north or south of the Yangtze River in Hubei (Figure 6) might be improbable because the mountains possess a dispersal barrier unsuitable for establishment [Wang and Wang, 2006; Wang *et al.*, 2011]. Our model also does not take into account variation in dispersal mechanisms throughout the study area. Varying wind speeds and heterogeneous wind directions might strongly affect the wind vector. Likewise, variation in flow rate and width of rivers, or the number of cars on the roads, could alter our predictions. We also assume spatially continuous dispersal (i.e., each cell can only disperse to its neighbors), whereas rapid invasion such as that observed in our study is more likely to advance through long jumps. Our model compensates for this effect by focusing on the first arrival time to any cell within a subcounty, yet this practice might also lead to overcompensation, hence also requires careful sensitivity analysis.

In conclusion, we introduced a simple model to discern the contribution of different dispersal mechanisms to the spread of invasive alien plant into new environments. Our main motivation was to fill the critical gap in assessing the mechanisms of large-scale invasive spread and to develop a predictive capacity to guide management control projects of invasive species. Future work should integrate species traits, habitat attributes, and empirical data to model invasion, in order to further elucidate the mechanistic drivers and to, thereby, minimize the detrimental consequences of biological invasions.

Acknowledgments

This research was supported by grants from the Israel Science Foundation (ISF-474/02, ISF-150/07 and ISF-FIRST-1316/05), the National Basic Research and Development Program of China (2009CB119200), the National Nature Science Foundation of China (31000883, 31471827), the State Scholarship Fund of China (201203250061), the Special Fund for Scientific Research in Environmental Protection Public Interest (201409061), and the Nonprofit Applied Technology Research Project from Zhejiang Province (2010C34003). R. Nathan also acknowledges support from the Minerva Center for Movement Ecology, and the Adelina and Massimo DellaPergola Chair of Life Sciences. We would like to thank Chaim Brickman for his useful remarks. Nir Horvitz and Rui Wang contributed equally to this work.

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