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A rapid method for constructing precaution maps based on a simple virtual ecology model: a case study on the range expansion of the invasive aquatic species *Limnoperna fortunei*

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Abstract Before invasion, or in its early stages, information on the invader in target areas is generally extremely limited. In such situations, managers must select focal areas in which to concentrate control and mitigation efforts. Here, we discuss a rapid method for selecting areas in which to control invasive aquatic species based on limited information. We used a simple cellular automata model that does not require species-specific information, but simulates the process of invasive species expansion and includes observed expansion progress to detect keystone areas. As a case study, we simulated the expansion of an invasive aquatic mussel, *Limnoperna fortunei*, in Ibaraki Prefecture, Japan, and detected the areas in which control efforts should be concentrated. To some extent, our model was able to predict the expansion of *L. fortunei* from the initial detected invasion to the current distribution. We predicted areas with a high potential of spreading and areas that would suffer from high propagule pressure. Results revealed a mismatch between areas with high spread potential and those with high propagule pressure. Managers should concentrate their invasion prevention efforts in the former because these are likely to have a greater long-term influence. Additionally, we predicted future expansion from the current distribution and showed that current scattered populations could merge naturally. Our approach is useful for establishing a management plan before or in the early stages of invasion.

Introduction

Invasive species have had negative effects on biodiversity and ecosystems worldwide (Mooney et al. 2005; Ficetola et al. 2007; Vila et al. 2009), and these adverse impacts have resulted in large amounts of time, money, and effort being spent in managing existing invader populations and preventing further spread (Pichancourt et al. 2012). As preventing the introduction and establishment of species with a high invasive potential is considered the most cost-effective way of reducing future problems (Ficetola et al. 2007; Koike and Iwasaki 2011), doing so prior to invasion or during the early invasive stages is very important (Sakai et al. 2001; Wittenberg and Cock 2001).

Several studies have concentrated on predicting new regions of invasion (e.g., Ficetola et al. 2007; Osawa et al. 2013) and future range expansions (e.g., Fukasawa et al. 2009; Koike and Iwasaki 2011). Almost all have focused on methods of locating areas that are likely to be invaded. For example, areas with high propagule pressure (Murray and Phillips 2010) and/or where invasive species are likely to become established (e.g., high habitat suitability: Simberloff and Rejmanek 2011), or both (e.g., combined model: Fukasawa et al. 2009). These models, however, all require detailed information about the target species in specific areas.

However, before or in the early stages of an invasion, information about the target species in target areas is severely limited, making it necessary to predict range expansions based on limited data (Koike 2006). Obtaining

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detailed information can be costly in terms of time, effort, and resources, all of which are generally limited for social and/or economic reasons (Humston et al. 2005; Shaw 2005). Additionally, invasive species can expand and become established in target areas while detailed observations are being made, creating a major logistical challenge for field studies on invasive species.

Aquatic organisms such as fishes and water clams are limited to water habitats. Thus, we can, in theory, predict their potential range expansions based on river, lake, and/or pond distributions. Maps of aquatic habitats, especially rivers, are relatively easy to obtain and are useful in constructing thematic maps for conservation and/or management (Osawa et al. 2011).

Here, we propose a very simple but practical way to predict key invasion areas and prevent future expansions of invasive aquatic species using a virtual ecology approach (Zurell et al. 2010). A virtual ecology approach simulates species dynamics using models that simulate real species and can be "virtually" observed (Zurell et al. 2010; Albert et al. 2011; Pagel and Schurr 2012). Using this approach, we can test target species dynamics under various environmental conditions (Zurell et al. 2010; Albert et al. 2011; Pagel and Schurr 2012). This process can indicate areas in which practitioners should concentrate their efforts and allows for monitoring of founder areas during and after expansion. Thus, it can help identify keystone areas in the expansion process.

We predicted theoretical expansion ranges of aquatic invasive species using a simple virtual ecology model based solely on a river distribution map that required no specific information about the target species. As a case study, we simulated the expansion process of a freshwater mussel, *Limnoperna fortunei* (Dunker 1857), a noxious invasive species in several regions (Boltovskoy 2015). This species is fully aquatic throughout its life cycle and is a typical aquatic invasive species. We developed precaution maps of spread and invasion risks based on virtual simulation results, and conclude by discussing the practicality of our approach.

Methods

Target species

Limnoperna fortunei is an obligately aquatic freshwater mussel originally from China (Magara et al. 2001) and invasive in several regions, including Asia and South America (Boltovskoy et al. 2006; de Oliveira et al. 2006; Morton and Dinesen 2010; Boltovskoy 2015; Ito 2015); in Japan, it is designated as an Invasive Alien Species under the Invasive Alien Species Act (Ministry of environment

2005). Species dispersal within continents (especially in South America) is probably mainly due to boat traffic (e.g., attachment to hulls, in ballast water), and upstream dispersal has also been reported (Darrigran and Pastorino 1995; Boltovskoy et al. 2006; Karatayev et al. 2007). In Japan, however, upstream dispersal has never been reported (Ito 2015), probably because most Japanese rivers host little commercial boat traffic (Masuda 1993; Nakano et al. 2014). Since this species is likely to expand its range in Japan (Ito 2008, 2010, 2015), it is well suited to a case study.

Study area

We conducted a case study in Ibaraki Prefecture, Japan (Fig. 1), where *L. fortunei* is rapidly expanding and where its potential detrimental effects on natural and agricultural environments are becoming a concern (Ito 2007, 2008, 2010, 2015). Thus, effective management plans against *L. fortunei* are particularly important in this area.

Virtual ecology model

We used a modified cellular automata (CA) model. CA models apply flexible mathematical tools to approximate spatiotemporal dynamics and are therefore used for a wide range of ecological problems (Racz and Bulla 2003; Racz and Karsai 2003; Dragićević 2010; Koike and Iwasaki 2011). The digital space in a CA model consists of a rectangular grid of square cells representing a target area. This is the same size as the unit of predicted range expansion. Each cell has three parameters: (*1*) the cell ID, (*2*) the dispersion path vector, and (*3*) the elevation value (Fig. 2a). The Cell ID indicates the spatial location of the area to be analyzed, while the dispersion path involves four variables indicating four directional vectors of adjacent cells (Fig. 2b; we describe this in detail in the next section). The elevation value indicates the relative heights among the analyzed areas. If the target species can only expand according to the elevation value (e.g., passive expansion according to stream water flow), this might act as a barrier to expansion. In fact, freshwater mussel larvae are generally transported passively in rivers (Ito 2008; Lucy et al. 2008; Nakano et al. 2014). We assumed that the cell space was of homogeneous habitat quality for the target species.

In this CA model, the dispersion path of the target species is defined as the possibility of expansion to four adjacent cells: those on the left, right, top, and bottom, often called Neumann model (Neumann and Burks 1966; Dragićević 2010) (Fig. 2b). We used this model because of suitability for dispersal paths. The Moore model, for example, has eight adjacent cells (Dragićević 2010), but it is not suitable because few river connections in four diagonal

Fig. 1 Location of the study area
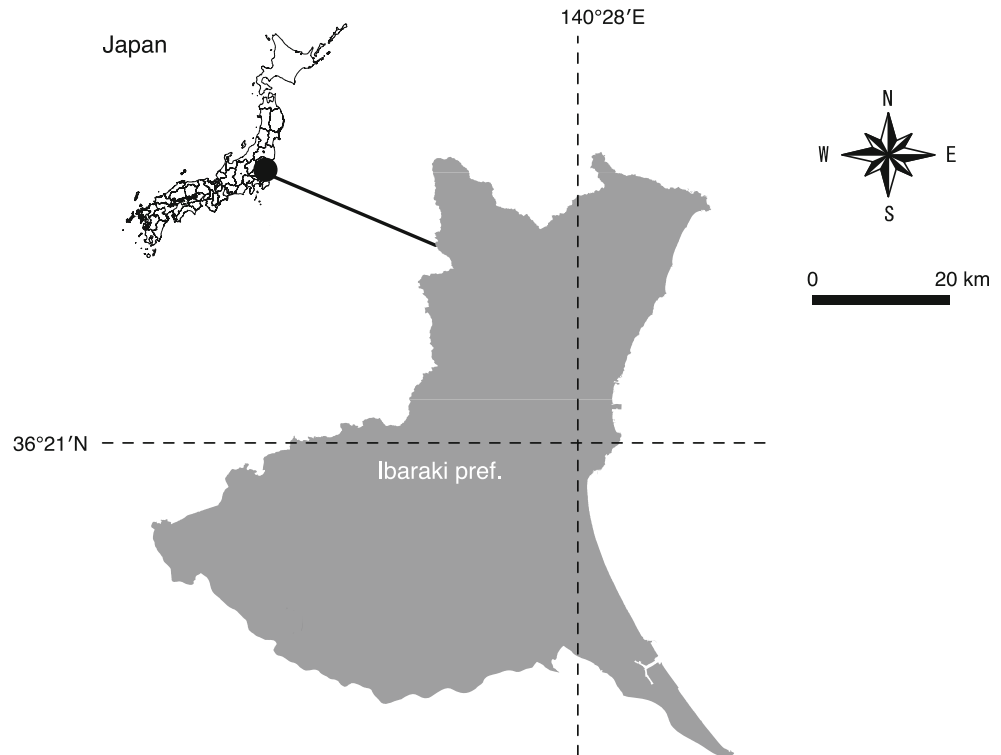
directions exist (Fig. 2c). The dispersion path is defined as a vector with four binomial values,

$$\text{Dispersion path } x = dx(d1, d2, d3, d4) \tag{1}$$

where $d1$, $d2$, $d3$, and $d4$ indicate the dispersion path to the top, left, bottom, and right cells, respectively (Fig. 2b). If all dispersion path values are 0, the invasive species in this cell cannot expand to other cells. The dispersion path is defined based only on habitat, i.e., river continuity. Thus, if the river line crosses two adjacent cells, the target species could move in both directions (Fig. 2c).

In this study, the analysis unit was the local population, so one cell could contain one population. Thus, the model can simulate the potential of population expansion in the target area, and the virtual population can expand only according to the dispersion path. The model processes involve three preconditions: (1) population expansion can occur via the dispersion path according to elevation, i.e., a population can expand only from a high-elevation to a low-elevation cell according to stream flow, even when the cells are in the dispersion path; (2) local population size and extinction are both ignored; and (3) a population can expand only to the four adjacent cells as in the Neumann model because very few diagonal river connections exist.

We used three sizes of grid cells—1, 5, and 10 km—for analysis (Fig. 3a). These are the standard units in Japan used for gathering several kinds of statistics, such as population, land use, and wildlife (Ministry of Internal

Affairs and Communications; Ministry of Environment, Japan). We used grid IDs as cell IDs, a decision derived from Japanese government protocols (1 and 10 km were derived from the National Land Numerical Information download service, Ministry of Land, Infrastructure, Transport and Tourism, and 5 km was based on the Integrated Biodiversity Information System, available at the Biodiversity Center of Japan (J-IBIS), Ministry of Environment, Japan. The elevation value of each cell was taken from a numerical map using 250-m values (The Geospatial Information Authority of Japan). We used minimum rather than average elevation in each cell because we predicted that in our study river habitat, water might occur in both highlands and lowlands. Grid dispersion paths were defined according to the above rule (see Fig. 2c) using national first-class river data derived from the National Land Numerical Information Download Service, Japan (Ministry of Land, Infrastructure, Transport and Tourism, Japan; see Fig. 3b).

Virtual model simulations

Using the model, we restaged and predicted the *L. fortunei* invasion from the past into the future. First, we predicted expansion from the cell of initial detection in Ibaraki Prefecture (Sunoh 2006) to test the accuracy of our model. We also used a simple simulation that cancelled the elevation constraint (the population could expand
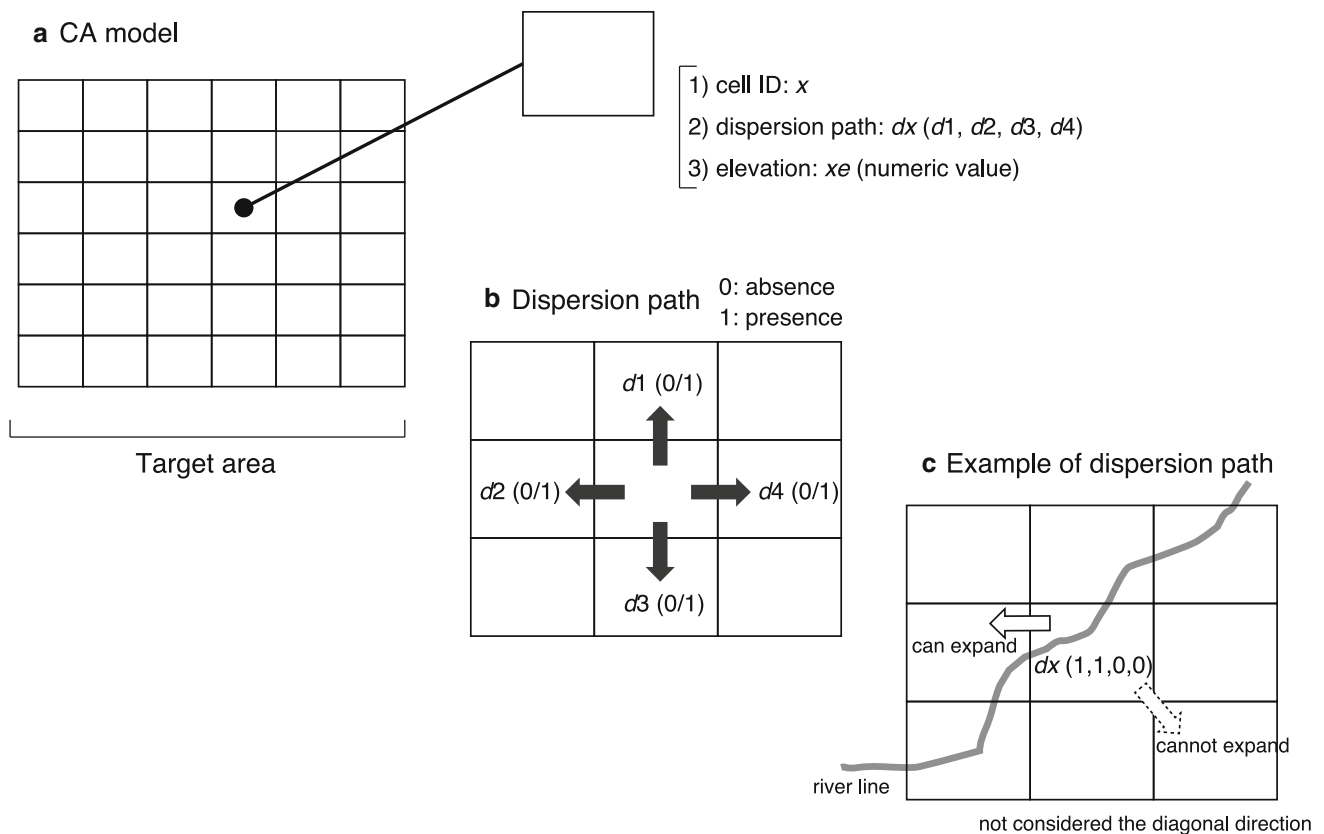
a CA model

Target area

1) cell ID: x
2) dispersion path: dx ($d1$, $d2$, $d3$, $d4$)
3) elevation: xe (numeric value)

b Dispersion path

0: absence
1: presence

$d1$ (0/1)

$d2$ (0/1) $d4$ (0/1)

$d3$ (0/1)

c Example of dispersion path

can expand

dx (1,1,0,0)

cannot expand

river line

not considered the diagonal direction

Fig. 2 Basic structure of the modified cellular automata (CA) model. **a** Each cell has three values; (1) the cell ID x is a unique ID of the cell, (2) the dispersion path dx indicates four directional vectors of adjacent cells (described below), and (3) elevation xe indicates the elevation value in the cell. **b** Values $d1$, $d2$, $d3$, and $d4$ indicate the dispersion path to the *top, left, bottom*, and *right* cells, respectively. If the dispersion path value is 1, the invasive species in this cell can expand to the adjacent cell. **c** If the river line crossed two adjacent cells, the target species could move to the adjacent cells according to the dispersion path. In this CA model, the dispersion paths of the target species are defined as the possibilities of the expansion of four adjacent cells, thus, the target species cannot expand diagonal directions

according to any dispersion path) and a dispersion path (the population could expand into any cell from high to low elevation) to test the accuracy of our model. To validate model accuracy, we compared the predicted results with the current distribution range of the species, derived from Ito (2010). We did not use the 1-km cell size because approximately 60 % of the expansion paths had values of zero (3947 of 6729 cells). We used six results in two cell sizes (5 and 10 km) to test the accuracy of the model, which was used for the next test.

To establish precaution maps, we calculated the theoretical number of cells that could expand from each cell as the potential expansion range for all cells. In other words, this value indicates the risk of spreading from the focal cell when the target species invades. We also calculated the theoretical number of invasions from other cells, namely, the extent of propagule pressure, a value typically used for invasion risk (e.g., Zenni and Simberloff 2013). Thus, we predicted and compiled the expansion ranges from all cells. High value cells indicated that target species could invade

from several other cells, i.e., each cell has several pathways of invasion. In all cases, we ran the model with 100 iterations to reach a static state of expansion because the model is deterministic, not stochastic. Results could reach one static state in all cases by 100 iterations, and thus, we did not use a temporal axis in our study. Finally, we predicted the expansion range from the cell of current distribution to predict future expansion.

Results

Results of simulations in each cell size

Initial detected area (Sunoh 2006) and the current distribution range (Ito 2010) of *L. fortunei* in 10-km cells are presented in Fig. 4a; those in 5-km cells are shown in Fig. 5a. In the 10-km cells, 22 cells already contain *L. fortunei* (Fig. 4a), whereas in the 5-km cells, 47 cells already do so (Fig. 5a).
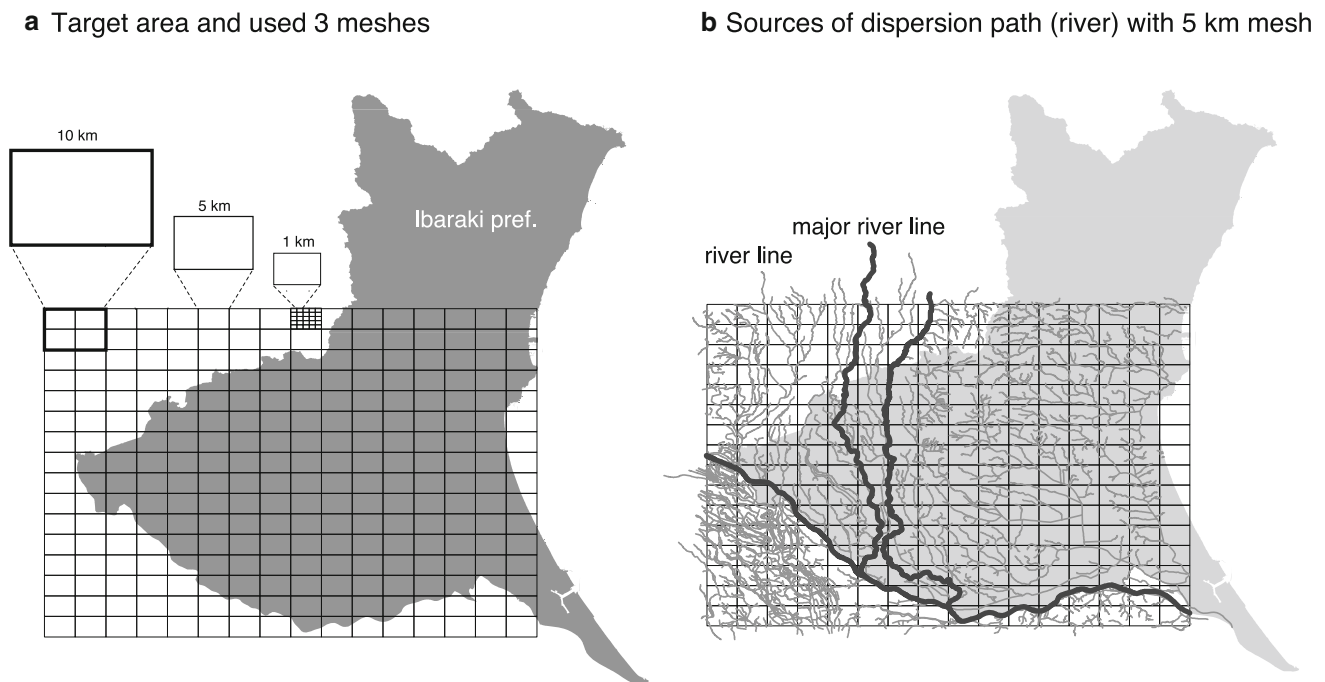
a Target area and used 3 meshes

b Sources of dispersion path (river) with 5 km mesh

Fig. 3 Study area and units for this study. Locations and sizes of all mesh grids are defined by the Japanese government

The simulated expansion of *L. fortunei* from the cell of initial invasion predicted one large population (cohesion) in the current distribution range and excluded other infrequent occurrences (Figs. 4b, 5b). We observed no overestimation in both 10- and 5-km cells (Figs. 4b, 5b). In the 10-km cell model, 7/22 (32 %) cells were predicted correctly, whereas in the 5-km model, 16/47 cells (34 %) were predicted correctly. Without the elevation model, overestimation was common (Figs. 4c, 5c). Without the dispersion path model, the results of the 10-km cells were the same as those using both dispersion path and elevation (Fig. 4d). However, we observed some overestimation in the 5-km cell model (Fig. 5d). We decided to use the 5-km model with both expansion path and elevation to establish precaution maps because it did not overestimate and had the best accuracy.

Precaution maps

We established precaution maps using the 5-km grid cell model with both dispersion path and elevation. Many expansions (cells into which expansion was possible) were located in the upper-middle region of the study area (Fig. 6a). Conversely, many invasions (areas with high propagule pressure) were located in the lower-left and lower-right regions, in agreement with the predicted expansion from the initial invasion area (Figs. 5b, 6b), shown in the map of future expansion from the current distribution (Fig. 6c). All scattered occurrences were connected by virtual expansion (Fig. 6c).
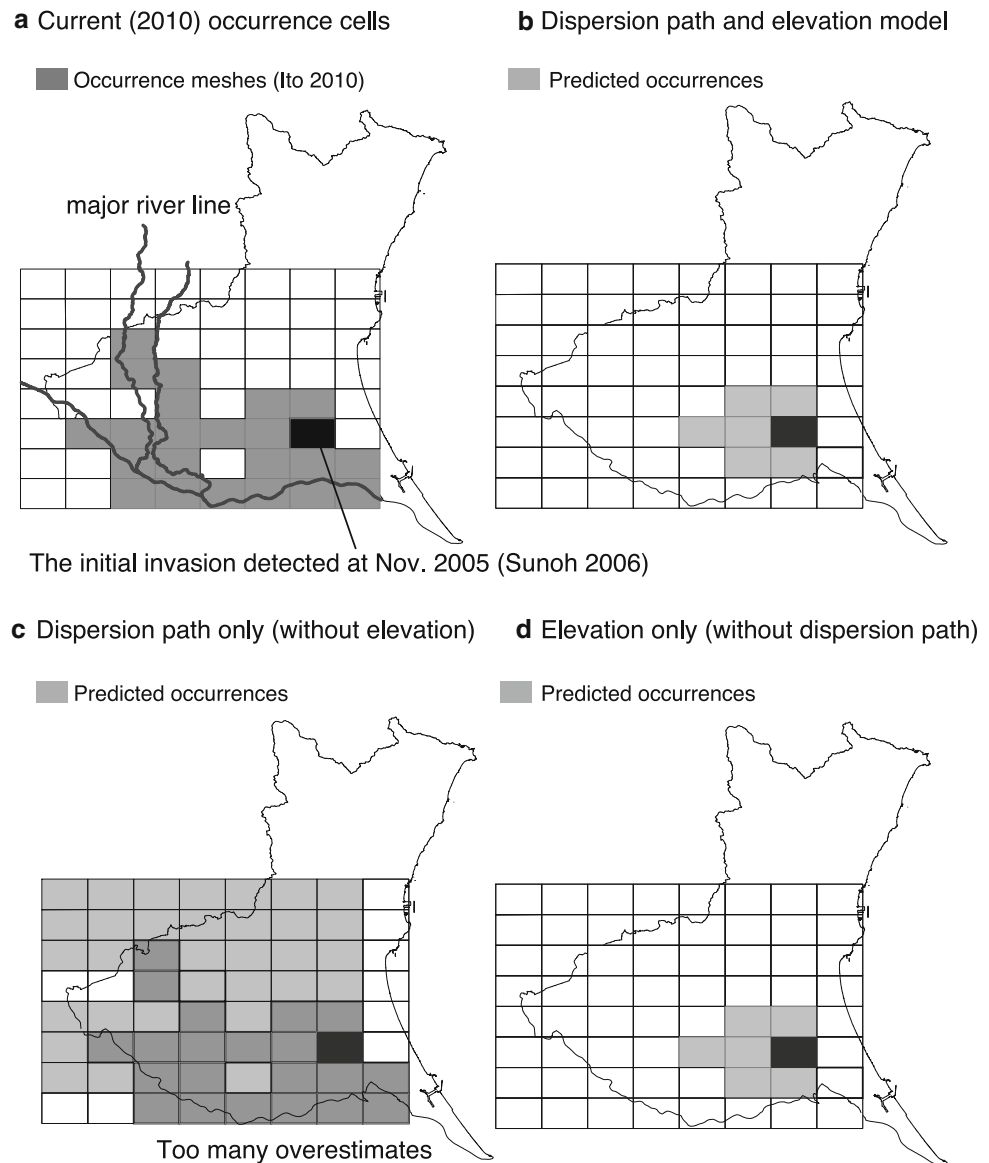
Discussion

We simulated the expansion of *L. fortunei* using a simple CA model that does not require species-specific information. To some extent, our model was able to predict the expansion of *L. fortunei*, and thus, this simple model has the potential for application in an invasive species management plan.

Cell size and dispersion path

We conducted simulations using two cell sizes, 5 and 10 km. Results showed that the 5-km cell model with both dispersion path and elevation best predicted the largest group among the current distribution ranges without overestimating. The 10-km cell models with elevation only and both dispersion path and elevation were also able to predict the largest group among the current distribution range without overestimating. However, these showed relatively low accuracy compared to the 5-km model, which might have been caused by the source of the dispersal path. Only the 10-km models revealed many cells having a perfect dispersion path in four directions (52/64 cells had values of 1). Thus, in the 10-km models, the simulation was mainly regulated by elevation, resulting in identical simulations between elevation only and both dispersion path and elevation. National first-class rivers as sources of the dispersal path, combined with a 5-km grid, were suited for predicting the expansion of *L. fortunei*. If

Fig. 4 Current occurrence cells of *Limnoperna fortunei* in the study area (**a**) and predicted occurrence cells in 10-km cells from the initial area of detection (**b–d**)

a Current (2010) occurrence cells

Occurrence meshes (Ito 2010)

major river line

The initial invasion detected at Nov. 2005 (Sunoh 2006)

b Dispersion path and elevation model

Predicted occurrences

c Dispersion path only (without elevation)

Predicted occurrences

Too many overestimates

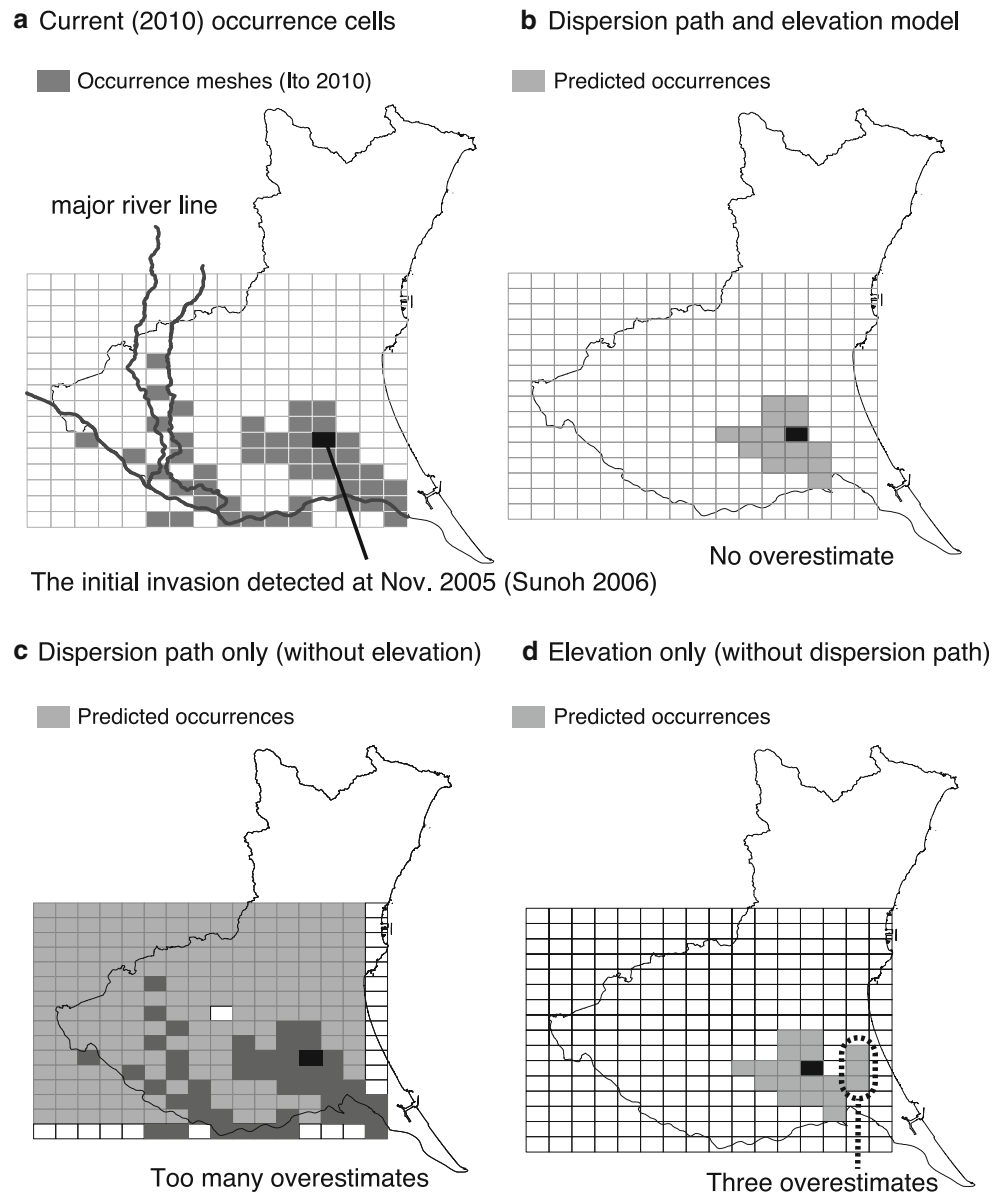**d** Elevation only (without dispersion path)

Predicted occurrences

applying our model to smaller cell sizes, such as 1 km, data on detailed sources of dispersion, such as small rivers, ditches, and irrigation channels should be obtained. Indeed, Nakano et al. (2014) suggested that such paths might be important for expansion of this species. However, obtaining such detailed information would require a large amount of time and money. In contrast, information on large rivers was relatively easy to obtain (Osawa et al. 2011). From an application viewpoint, we propose that the 5-km cell model created with national river data is the best.

Reliability of simulation results

Our model could not predict scattered *L. fortunei* populations, perhaps due to effects of the Kasumigaura Canal,

which has some underground waterways. This is a large artificial waterway for central water use, matching the areas with the largest scattered group of *L. fortunei* to the northeast (Ito 2010). This waterway raises water with a pump from the lowlands to uplands, perhaps allowing *L. fortunei* to expand against stream flow, as predicted by Ito (2008, 2010, 2015). Incorporating these irregular dispersion paths may help to improve the accuracy. Another possible explanation is human-mediated invasion. *Limnoperna fortunei* is thought to have been introduced into various rivers and lakes in Japan by accidental inclusion in shipments of clams imported from China (Nishimura and Habe 1987; Magara et al. 2001; Nakano et al. 2014). The proliferation of imported products is likely to facilitate *L. fortunei* invasion (Nakano et al. 2014). Thus, some areas might be invaded from locations

Fig. 5 Current occurrence cells of *Limnoperna fortunei* in the study area (**a**) and predicted occurrence units in 5-km cells from the initial area of detection (**b–d**)

a Current (2010) occurrence cells

▪ Occurrence meshes (Ito 2010)

major river line

The initial invasion detected at Nov. 2005 (Sunoh 2006)

b Dispersion path and elevation model

▪ Predicted occurrences

No overestimate

c Dispersion path only (without elevation)

▪ Predicted occurrences

Too many overestimates

d Elevation only (without dispersion path)

▪ Predicted occurrences

Three overestimates

other than those used as sources for modeling (Sunoh 2006). Nevertheless, we emphasize that we were able to predict expansion to some degree even without such detailed information.

Detecting high-priority areas based on precaution maps

Simulation results for the 5-km cell model with both dispersion paths and elevation showed interesting trends. Many expansions (cells into which expansion was possible) were located in the upper-middle region of the study area (Fig. 6a). Conversely, many invasions (areas with high propagule pressure) were located in the lower-left and lower-right regions, agreeing with predicted expansion from the initial invasion area (Figs. 5b, 6b). Notably, we found a mismatch between cells with high expansion potential and cells with high propagule pressure (Fig. 6a, b). The distribution of cells with high propagule pressure could reflect the species' current distribution compared to that of cells with a high expansion potential (Figs. 5b, 6b). However, we suggest that managers should concentrate their efforts on areas with high expansion potential, rather than on those with high propagule pressure, because although areas with high propagule pressure are likely to be invaded, they do not always contribute to broader range expansion in the long term. Predicting future distributions of invasive alien species is vital to management decisions,
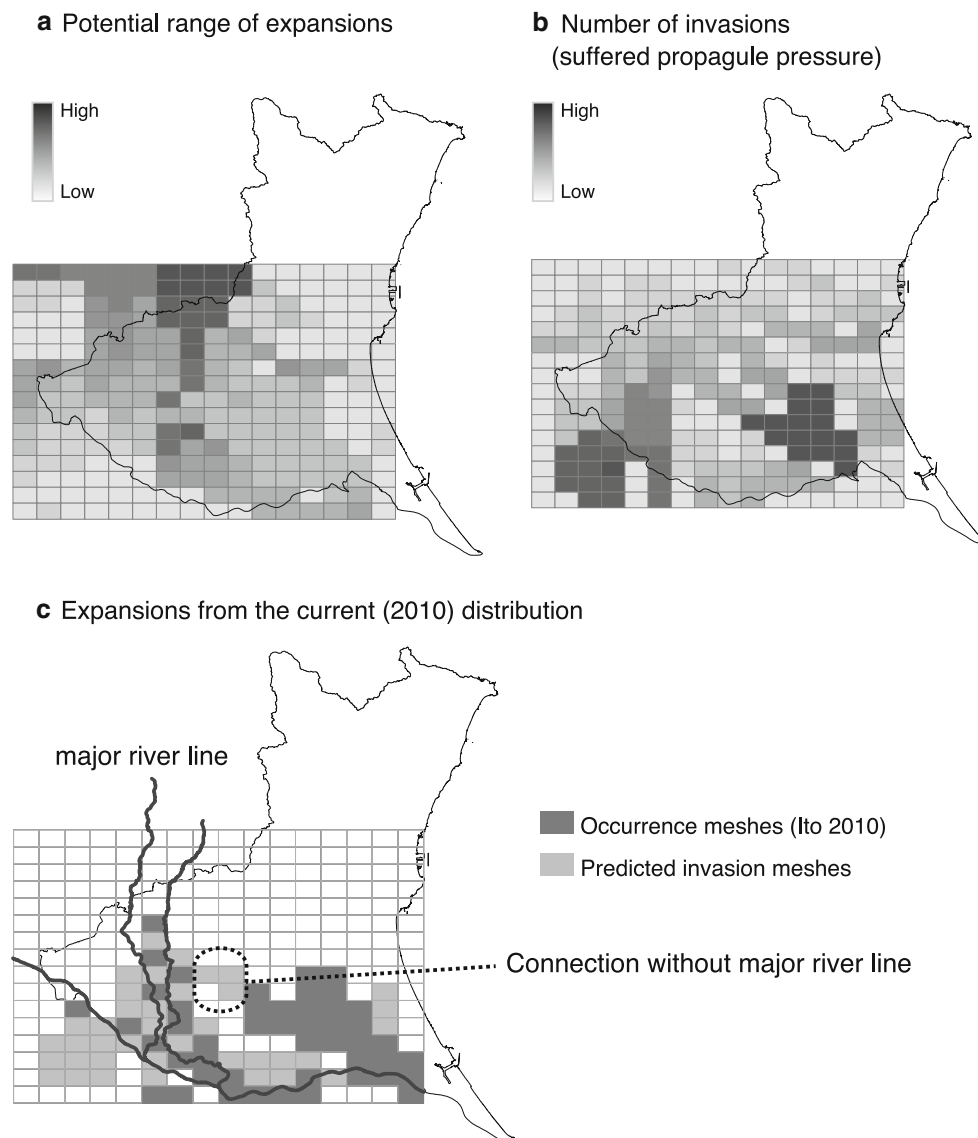
a Potential range of expansions

b Number of invasions
(suffered propagule pressure)

c Expansions from the current (2010) distribution

Fig. 6 Predicted results showing areas with **a** a high potential for spreading elsewhere and **b** areas suffering from high propagule pressure, which are likely to be invaded many times, and **c** future expansion from the current distribution

and impact assessments should be based on future distribution ranges (Koike 2006). Therefore, predicting areas of potential invasion is more important than predicting areas under imminent threat of invasion and establishment.

We also predicted future expansion from current distribution ranges. Results showed that current distribution ranges were mainly connected along major river lines (Fig. 6c). Additionally, we found connection without major river lines in the centers of cells (Fig. 6c), suggesting that current *L. fortunei* populations will connect in the near future. Generally, small populations require a relatively low management cost (Mehta et al. 2007), so managers should prevent *L. fortunei* invasion in areas where our

models predicted the intersections of scattered populations would occur.

Perspectives for application

This study yielded two major implications for management. First, we can predict the expansion of aquatic species such as *L. fortunei* using a very simple model and public data, at least for large populations expanding from a cell of initial invasion. The persistence and expansion of all species are constrained by habitat continuity, so our simple model may be applicable to other invasive species with distinct habitats and dispersal pathways.

Second, high-priority management areas are not always the same for short- and long-term planning, as we found in our case study. Thus, managers should decide on a management term before establishing a concrete plan. Managers could employ our approach as a first, rapid step in developing such a plan.

Conclusion

Predicting future range expansions of invasive species will enable the development of pre-arrival countermeasures and help avoid social issues, such as the need to reach a consensus about those countermeasures (Koike and Iwasaki 2011). Biological Invasions sometimes cause very long-term impacts, whereas practitioners are usually interested in very short-term results. Our approach can (1) predict expansion using a simple model and (2) focus on expansion potential to identify important areas in which to prevent expansion, making it practical for stakeholders.

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