Title: Facilitation of management plan development via spatial classification of areas invaded by alien invasive plant

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Abstract

Propagule supply and habitat suitability strongly influence the success of invasive alien plants. Thus, an invaded area is likely to have an adequate propagule supply, a suitable habitat, or both for species persistence. Based on this idea, we classified invaded areas into four categories as follows but with establishment still occurring in some cases: Class 1, adequate propagule supply and habitat suitability; Class 2, adequate propagule supply but limited habitat suitability; Class 3, limited propagule supply and adequate habitat suitability; and Class 4, mid- to low-level propagule supply and habitat suitability. We propose a framework for the classification of invaded areas into these four classes and present a case study in which this framework was applied. Classifying target areas in this manner could facilitate more efficient and practical management planning, thereby saving time and resources. We selected the alien shrub *Leucaena leucocephala* L. (Fabaceae) as a model species, which has invaded the Nakodo-jima Island in the Ogasawara Archipelago of Japan. We developed a species distribution model by incorporating proxy variables for propagule supply and habitat suitability as well as submodels for propagule supply or habitat suitability. Using these submodels, we estimated the levels of propagule supply and habitat suitability in each, and classified the current distribution range appropriately. Using these classifications, land managers could set priorities to concentrate their efforts to efficiently control target species.

Keywords: Ecosystem management, habitat suitability, *Leucaena leucocephala*, propagule pressure, resource allocation, species distribution model

Introduction

Biological invasions represent major ecological and economic threats (Vilà et al. 2010). Substantial time and effort have been invested in controlling established alien invasive species populations and preventing range expansions to reduce the negative impacts of alien invasive species (e.g. Pichancourt et al. 2012). Although abundant resources are required for these control programs, funding and manpower are limited (Humston and Mortensen 2005; Shaw 2005; Osawa and Ito 2015; Osawa et al. 2016b) and are generally directed toward reducing the size of existing alien species populations (Masters and Sheley 2001; Kluth et al. 2003). Therefore, a pragmatic option for the attainment of adequate management would be an optimal allocation of limited resources across areas of interest, particularly for controlling invasive species lacking current effective and low-cost management tools (Moilanen et al. 2009; McDonald-Madden and Chades 2011; Kumschick et al. 2012).

Provision of a framework to establish spatially explicit management plans is particularly relevant for invasive species control (Giljohann et al. 2011; Grice et al. 2011; Kumschick et al. 2012). Although previous studies have formulated concepts for establishing these strategies, including the selection of priority areas, methods, and target species (Hauser and McCarthy 2009; Giljohann et al. 2011; Grice et al. 2011; Januchowski-Hartley et al. 2011), most of these studies focus on large spatial scales at which species-specific ecological processes frequently cannot be incorporated into a management plan, including catchment areas with coarse resolution, (Giljohann et al. 2011; Januchowski-Hartley et al. 2011; van Wilgen et al. 2012). Incorporating ecological processes of target species, such as dispersal strategies, into management plans are indispensable for practically prioritizing management actions in the field (Davies and Sheley 2007; Osawa et al. 2016b).

Two sequential processes play important roles in determining the distribution/expansion and persistence of invasive species within a region after its successful establishment: (i) an adequate propagule supply (Murray and Phillips 2010), and (ii) passage through barriers imposed by biotic and abiotic environments (Pyšek and Richardson 2010; Simberloff and Rejmánek 2011). If an alien species disperses adequate numbers of propagules across a landscape and successfully passes through the environmental filtering processes, range expansion is highly likely to occur. Even if only one of the limiting processes is overcome, an invading species may still come to occupy the area. For example, even when habitat conditions are not appropriate for active growth and reproduction, populations may still persist if sufficient propagules are continually supplied (Jiménez-Valverde et al. 2011); these population should also be managed when the alien species strongly affect native communities and ecosystems, regardless whether or not they establish a self-sustaining population. Although the relative importance of propagule supply and environmental filtering in alien plant establishment differs among species and regions, both play some role in determining the occurrence of invasion. Hence, areas within a region occupied by an alien invasive species can be classified into at least four categories: Class 1, adequate propagule supply and habitat suitability; Class 2, adequate propagule supply but limited habitat suitability; Class 3, limited propagule supply and adequate habitat suitability; and Class 4, mid- to low-level propagule supply and habitat suitability, but with establishment still occurring in some cases (Fig. 1). This spatial classification framework could provide guidelines for land managers aiming to develop appropriate plans for the areas under their supervision. For example, for those areas categorized as Class 2, restriction of alien propagule supply would be required before the eradication of extant populations in that area to avoid reinvasion, under the premise that propagule supply and habitat suitability both play roles in determining alien species occurrence. In an area categorized as Class 3, eradication action would be necessary only once in theory, even when vast resources are required to completely eliminate the existing populations.

Classifying target areas in this manner should facilitate the establishment of efficient and practical management plans by selecting the effective order in which to take action, thereby saving time and resources. Simultaneously, establishing efficient and practical management plans should be applicable and easy-to-use for practitioners, as methods that are too complex or require substantial effort for application may not be adopted by practitioners even positive results could be obtained (Prendergast et al. 1999; Knight et al. 2008). Thus, the aim of this study is to propose a framework for classifying areas that have been invaded by alien invasive plants based on estimates of habitat suitability and propagule supply, while considering applicability. We describe a case study applying our framework to detail the procedure. Our study species was the alien invasive plant, white leadtree *Leucaena leucocephala* L. (Fabaceae), a shrub that has invaded the oceanic Ogasawara Islands of Japan.

Methods

Overview

We categorized areas within a region invaded by the target species into four classes (Fig. 1). A schematic of the whole procedure is provided in Fig. 2. We developed a species distribution model (SDM) for the target species using proxies for propagule supply levels and habitat suitability (i.e., environmental explanatory variables) for the modeling exercise (Fig. 2b). After parameter estimation, we subdivided the model into a submodel expressing the relationship between the occurrence of target species and the level of propagule supply, as well as another submodel expressing the relationship between species occurrence and level of habitat suitability (Fig. 2c). Using these two submodels, we estimated propagule supply levels and habitat suitability in each of the units in which the target species occurred (Fig. 2d). Based on the estimations for each unit, we mapped distributions of the four classes for establishment of a management plan.

Study area and target species

The case study was conducted on Nakodo-jima, an oceanic island in the Ogasawara Archipelago, Japan (27°37'N to 27°38'N, 142°10'E to 142°11'E; 1.37 km^2) (Fig. 3). The Ogasawara Islands are registered as a World Natural Heritage Site (UNESCO http://whc.unesco.org/en/list/1362; accessed October 10, 2018). Maintenance of this unique ecosystem urgently requires management due to threats from alien invasive species, including *L. leucocephala* (UNESCO http://whc.unesco.org/en/list/1362; accessed October 10, 2018).

L. leucocephala is an evergreen shrub with a native distribution in South America. It was exported to Southeast Asia, including the southwestern islands of the Ogasawara Archipelago. After the formation of dense monotypic thickets in disturbed areas, *L. leucocephala* prevented the germination of woody and understory herbaceous species on these islands (Hata et al. 2010a, b). Due to its negative impacts on the native ecosystems wherein it has colonized, *L. leucocephala* is listed as one of the 100 World’s Worst Alien Invasive Species (Lowe et al. 2000) and is registered as a cautious invasive species requiring monitoring by the Japanese Invasive Species Act (Ministry of Environment, Japan 2005 https://www.env.go.jp/en/nature/as.html; accessed October 10, 2018). Although over 100 years has passed since the species was first introduced to the island (Funakoshi 1979), expansion of *L. leucocephala* in Nakodo-jima became aggressive after goats, which fed on the species, were eradicated from the island in 1999 (Osawa et al. 2016a). Thus, this plant currently exists in the expansion phase (Osawa et al. 2016a). The local government has been running operations to monitor and control the distribution of *L. leucocephala* since 2003 (Tokyo Prefecture 2013). Currently cutting and/or uprooting with chemical application is one of effective way to local eradication (Tokyo Prefecture 2013). To apply this method for about 400 m^2, 5 hours with 12 laborers are needed (Tokyo Prefecture 2013). However, despite continuous local eradications, this species continues to rapidly recover and reinvade, and its distribution range continues to expand (Tokyo Prefecture 2013). Considering the absence of highly effective and low-cost management tools to control *L. leucocephala*, a practical option to improve this situation could be the development of a spatially explicit and cost-effective management plan (Tokyo Prefecture 2012; 2013).

Data preparation

We used 50 m cell grids (i.e., 50 m grids) as the spatial units for statistical analysis in this case study (Fig. 3). The locations of *L. leucocephala* patches in 2012 were obtained from a published report (Tokyo Prefecture 2013). The 160 original locations of *L. leucocephala* patches were aggregated into 101 grids using Geographic Information System software (ArcGIS 10.1; ESRI, Redlands, CA, USA).

We used neighboring occurrence cells of a chosen focal area as the proxy variable for propagule supply (Appendix Fig. 1), because reliable information on decay by distance of propagules was not available. To define the propagule source, we considered eight potential proxies of propagule supply based on two sources of information regarding the distribution of the target species around a focal cell at four distance thresholds (Appendix Fig. 1). One of the information sources considered only the presence/absence data (hereafter, p/a: Appendix Fig. 1a–d); the second considered the total number of occurrences within a given distance threshold (Appendix Fig. 1e–h). If more than two occurrences exist within the distance threshold, proxies a–d considered the presence but not the number of propagule sources, whereas proxies e–h considered the total number of occurrences, namely the number of propagule sources. We used these values as proxies of propagule supply. The four distance thresholds were as follows: (a, e) four adjacent cells able to provide propagules (diagonally adjacent cells were not regarded as adjacent); (b, f) eight adjacent cells providing propagules (diagonally adjacent cells were regarded as adjacent); (c, g) cells within two units of a focal cell providing propagules; and (d, h) eight adjacent cells and sixteen outer adjacent cells providing propagules (Appendix Fig. 1). These data were also processed using ArcGIS software. When reliable information on decay by distance of propagules is available, the use of a dispersal kernel describing propagule supply may enable a precise description of the dispersal process (Fukasawa et al. 2009; Andrew and Ustin 2010).

We used three physical environmental variables to assess habitat suitability in each of the grids in which *L. leucocephala* occurred: average elevation (Ev), average slope (Sl), and the Euclidean distance from the coast line (Dc). We selected Ev as the variable acting as a proxy of soil condition, because low elevation areas accumulate soil in oceanic islands (Hata et al. in press). Sl acts as a proxy of potential land slide. We included Dc as an environmental variable because plant species on oceanic islands are likely to be strongly affected by maritime influences, such as waves and onshore winds carrying salt spray. In particular, salinity stress is a major abiotic stress limiting the plant growth and productivity (Gupta and Huang 2014). We adopted only these variables as the island has a relatively homogeneous micro environment; therefore, these are considered to be sufficient (see model performance in Results). Same as the proxy variable for propagule supply, when reliable information on habitat suitability is available, the use of a proxies should select according to the ecological characteristics of the target species.

Ev and Sl were derived from a 10 m digital elevation model (Tokyo prefecture 2012). Dc was obtained from island polygon data derived from the Japanese National Land Numerical Information (http://nlftp.mlit.go.jp/ksj/; accessed October 10, 2018). All explanatory variables were averaged within the 50 m grids before further processing (661 grids in total). Ev, Sl, and Dc averages across all 50 m grids were 42.5 ± 34.4 m, 21.7° ± 13.5°, and 88.8 ± 78.7 m, respectively.

Modeling

SDM construction

A generalized linear model (GLM) with a binomial distribution (log-link function) was used to construct an SDM explaining the presence/absence of *L. leucocephala* in the study area. This type of linear model allowed us to readily subdivide the overall effects of the explanatory variables into those attributable to individual factors, because the effects of the explanatory variables were additive in the linear predictor. Thus, the linear model was readily subdividable into partial models.

We first identified the most plausible proxy for propagule supply (Ps) via the following procedures. First, we constructed eight GLMs—including only one of the eight candidate Ps proxies described in the previous section (see also Appendix Fig. 1)—as the single explanatory variable. Then, we selected the Ps proxy with the lowest Akaike information criterion (AIC) value to be used as the proxy for further analyzes in the model. Subsequently, we constructed an SDM using GLM that included the Ps proxy and the three physical environmental variables (Ev, Sl, and Dc) as explanatory variables. In this step, we standardized all variables by subtracting their mean and then dividing by their SD. All variables have zero mean and SD of 1 to enable an estimation of the effect of each variable on the occurrence of *L. leucocephala*, with incorporation of the first order interactions between the Ps proxies and habitat suitability variables into the model. After parameter estimation, we averaged coefficients and standardized error of the coefficients of all possible candidate models generated using the best subset procedure (2^7) based on Akaike weight (Burnham and Anderson 2003) with the “model.avg” function in the R package MuMIn 1.40.4. Expression for the averaged model was as follows:

$$\text{logit}(p/a) \sim \beta0 + \beta1\ Ps + \beta2\ Ev + \beta3\ Sl + \beta4 Dc + I1\ Ps{:}Ev + I2\ Ps{:}Sl + I3\ Ps{:}Dc + \sigma,$$

(1),

where, p/a is the presence or absence of the target species, Ps is the proxy for propagule supply; Ev, Sl, and Dc refer to elevation, slope, and distance from the coastline, respectively; Ps:Ev refers to the interaction between Ps and Ev; Ps:Sl and Ps:Dc are also interaction terms of these two variables; β0 is the intercept value; βm is the estimated coefficient of variable m; In is the estimated coefficient of the interaction term n; and σ is the residual error.

We identified significant terms in the averaged model when the absolute values of the coefficients exceeded standard errors 1.96× of the mean values, namely, within a two-sided 95% confidence interval. We calculated the relative importance of each explanatory variable based on the sum of Akaike weight across all models that included the explanatory variables.

Model evaluation

We examined the predictive performance of the averaged model and two submodels (see below) through a receiver operating characteristic curve analysis (Swets 1988), which included an area under the curve (AUC) value (Lobo et al. 2008). The AUC value ranges from 0 for an inverse model to 0.5 for a random model, with 1 representing a perfect model. We identified an optimal cutoff point when the sensitivity + selectivity value was highest (Greiner 1995). The sensitivity value is the ratio of correctly predicted presence values, whereas the selectivity value is the ratio of correctly predicted absence values. Therefore, we evaluated the model for the omission/commission errors. We also calculated Moran’s I on the residuals to assess spatial autocorrelation. We concluded that our estimates for the averaged model were not biased by spatial autocorrelation because the Moran's I values for the residuals of the averaged model were low and not significant ($I = -0.0472$, $p > 0.05$). When a high spatial autocorrelation was detected in the residuals, spatially explicit models, such as the conditional autoregressive model (Lichstein et al. 2002), would be required for our framework.

Subdividing the model

We divided the averaged model into two submodels: (i) propagule supply, and (ii) habitat suitability. Using these submodels, we estimated the levels of propagule supply and habitat suitability for each grid. The submodels were as follows:

$$\textit{level of propagule supply} = \beta_0 + \beta_1 \text{ Ps} + \beta_2 \text{ average of Ev} + \beta_3 \text{ average of Sl} + \beta_4 \text{ average of Dc} + I_1 \text{ Ps:average of Ev} + I_2 \text{ Ps:average of Sl} + I_3 \text{ Ps:average of Dc},$$

(2),

$$\textit{level of habitat suitability} = \beta_0 + \beta_1 \text{ average of Ps} + \beta_2 \text{ Ev} + \beta_3 \text{ Sl} + \beta_4 \text{ Dc} + I_1 \text{ average of Ps:Ev} + I_2 \text{ average of Ps:Sl} + I_3 \text{ average of Ps:Dc},$$

(3),

For our submodeling exercise, we used average values for variables that were not the foci of the particular submodel in question and treated them as constants [e.g., in the habitat suitability submodel (eq. 3), we used the average but not raw value of Ps and treated it as a constant]. The residual error value was ignored when estimating the levels of propagule supply and habitat suitability for each 50 m grid. R software (ver. 3.2.1; R Development Core Team, Vienna, Austria 2016) was used to perform all the statistical analyzes and calculations.

Classification and mapping

We classified all grids colonized by *L. leucocephala* based on the estimated levels of propagule supply and habitat suitability. We classified colonized grids in which these levels were higher than the 75th percentile value of Class 1 (i.e., the top 25%). We classified colonized grids in which only one level of propagule supply or habitat suitability exceeded the 75th percentile value in Classes 2 and 3, respectively. The remaining colonized grids were assigned to Class 4. We arbitrarily selected the 75th percentile as the threshold for classification to simply demonstrate the procedure. In actual conservation planning exercises, the threshold would be determined by considering the characteristics of the target species, as well as taking into consideration social and economic factors of the study region, such as management aims and levels of available resources. In the final step of our exercise, we mapped the classified areas invaded by *L. leucocephala* using ArcGIS.

Results

SDM

Table 1 lists AIC values for each of the candidate propagule supply models. We were not able to estimate parameters for the model employing the proxy for propagule supply as the explanatory variable, because there was insufficient variance in the values of the explanatory variable (i.e., proxy a) among the grids, with most grids having the same value. A model employing the candidate proxy (Appendix Fig. 1g) had the lowest AIC value among the remaining seven models (Table 1) and was used in subsequent analyses.

The averaged model's AUC value was 0.912, indicative of excellent performance (Zhu et al. 2010). AUC values of the submodels were 0.895 for propagule supply and 0.815 for habitat suitability, indicating good performance for both submodels. Thus, our explanatory variables were appropriate to predict the occurrence of *L. leucocephala* in the area. Both Ps and Dc were positively correlated with *L. leucocephala* occurrence and showed relatively high importance (Table 2). Two interaction terms, Ps:Ev and Ps:Dc, were negatively correlated with occurrence of the species (Table 2). Ps had the largest estimated coefficient and the highest relative importance among the variables used in the averaged model (Table 2), suggesting that *L. leucocephala* occurrence was more regulated by propagule supply. The coefficient of Dc was the largest among the three physical environmental variables (Table 2).

Overall, the estimated level of propagule supply was positively correlated with that of habitat suitability ($r = 0.39$, $p < 0.001$) (Fig. 3). This relationship was similar between that of the presence and absence grids, although the relationship was weaker for presence grids ($r = 0.08$, $p < 0.01$ for presence grids; $r = 0.34$, $p < 0.001$ for absence grids) (Fig. 3). A limited number of grids had relatively high propagule supply and low habitat suitability levels, whereas a large number of grids had relatively low propagule supply and high habitat suitability levels (Fig. 3).

Maps of values and classes

The grids with relatively high propagule supply levels occurred in the northwestern, central, and southern regions of the island (Fig. 4a; Appendix Fig. 2a). Grids with relatively high habitat suitability levels occurred in the midwestern to mideastern regions (Fig. 4b; Appendix Fig. 2b). Among the 101 grids invaded by *L. leucocephala*, 9 were assigned as Class 1, and 16 were assigned to each of Classes 2 and 3 (Fig. 4c). Grids assigned to Classes 1–3 were highly clumped (Fig. 4c; Appendix Fig. 3). Most of the grids classified as Class 1 were surrounded by grids belonging to the other two classes (i.e., Classes 2 or 3, Fig. 4c; Appendix Fig. 3).

Discussion

Spatially explicit management plans must be developed at multiple spatial scales (Hiebert 1997; Shea et al. 2002; Foxcroft et al. 2009). Management plans at large (e.g., national or regional) or middle (e.g., watershed) spatial extents are suitable for guiding management, monitoring activities, and risk and priority assessments, while small spatial extent plans with fine grain are preferred for on the ground management implementations (Foxcroft et al. 2009). Therefore, studies at different spatial scales have complementary roles (Barnett et al. 2007). However, most studies only focus on the development of large spatial plans with a coarse grain size (Giljohann et al. 2011; Grice et al. 2011; Januchowski-Hartley et al. 2011; Jiménez-Valverde et al. 2011; Chiou et al. 2013; Osawa and Ito 2015). Our framework to classify areas based on habitat suitability and propagule supply complements the gap between the large spatial extent and coarse grain plans with on the ground implementation adopted at a fine scale, and thereby supports the establishment of effective management plans.

We classified invaded areas based on the relative strength of propagule supply and habitat suitability using each proxy. The classification could map the relative importance of each process, in other words, it provided a more responsible process for establishment in each spatial unit. When either of the processes is disproportionately responsible for determining species distribution, priority areas for eradication should be set based on the strength of the responsible process, although order direction (i.e., increasing or decreasing) depends on species attributes, such as dispersal strategies and life stages (Grevstad 2005; Pichancourt et al. 2012). Furthermore, even in cases where both processes play some role, information on the relative importance of the process provides a clue to prioritize areas for eradicating established alien invasive plants among the defined Classes of 1–3. In our case, “good” performance in both of the submodels suggests that both processes play a significant role in determining the distribution of the study species. We generally recommend primarily eradicating established individuals in units classified with adequate habitat suitability and limited propagule supply (Class 3) for efficient eradication of focal species. This is because these units are relatively less likely to be recolonized after a single eradication activity due to limited propagule supply, thus, eradicating these areas contributes to suppression of propagule supply to the remaining units. Individuals in units classified as areas with limited habitat suitability and adequate propagule supply (Class 2) should receive lowest priority in such cases, because reinvasion after eradication may become less likely after suppression of propagule supply. This priority may be changed for cases involving species with low dispersal capacity but quickly increased abundance in favorable sites. Our prioritization scheme is also based on the potential “reception” of propagules, which can be estimated from the submodel, and thus do not consider the amount of propagules to be supplied. Thereby, the next challenge of our framework is to incorporate the amount of propagules supplied from the units in the prioritization/classification scheme.

In our case study, propagule supply was by far the most important factor for *L. leucocephala* establishment, although the effect of habitat suitability was also significant. Indeed, based on a field experiment, Hata et al. (2010b) suggested that distance from seed sources, which reflects the amount of propagule supply, is a critical factor for the establishment of *L. leucocephala* in this study area. Therefore, restricting propagule supply is the primal measure required to control *L. leucocephala* in the area, and the prioritization scheme proposed above would be applicable. More specifically, we recommend allocating eradication efforts first in the northwest and central areas of the island, where there is a high density of Class 3 units, while then focusing on the central areas where Class 1 units are aggregated.

In this study we adopted an SDM technique to emphasize the concept and framework underlying this approach. Thereby, the distribution model can be modified/improved depending on specific situations, e.g., we used the DEM-derived static environmental proxy with 50 m resolution for simplicity, but the incorporation of dynamic factors such as vegetation types, use more high resolution of analyzing unit could improve predictive power (Osawa et al. 2013; Aung and Koike 2015). Indeed, *L. leucocephala* in Nakodo-jima tends to invade grasslands rather than forests and bare ground (Osawa et al. 2016a). However, precision of model predictions does not always improve applicability in the real fields. When modeling for management of alien invasive species, applicability of the model may prove to be more important than its precision (Osawa and Ito 2015). If large efforts, including extensive data collection, and conduction of complex and hard to implement analyzes are required to improve model precision, allocating resources to such efforts may not be an effective and efficient option, particularly when resources are limited and/or expansion speed of the invading species is rapid. Management strategies should be developed to account for local circumstances, including the character of target species and the area to be managed, and availability of funding and data (Grice et al. 2011). As in our case study, use of noncomplex (but high performance) models would be a first step for improvement of ongoing management project. After application of the initial model in the field, application would provide further insights for improvement. The concept presented herein serves as a basis for the improvement and development of management strategies.

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Figure captions

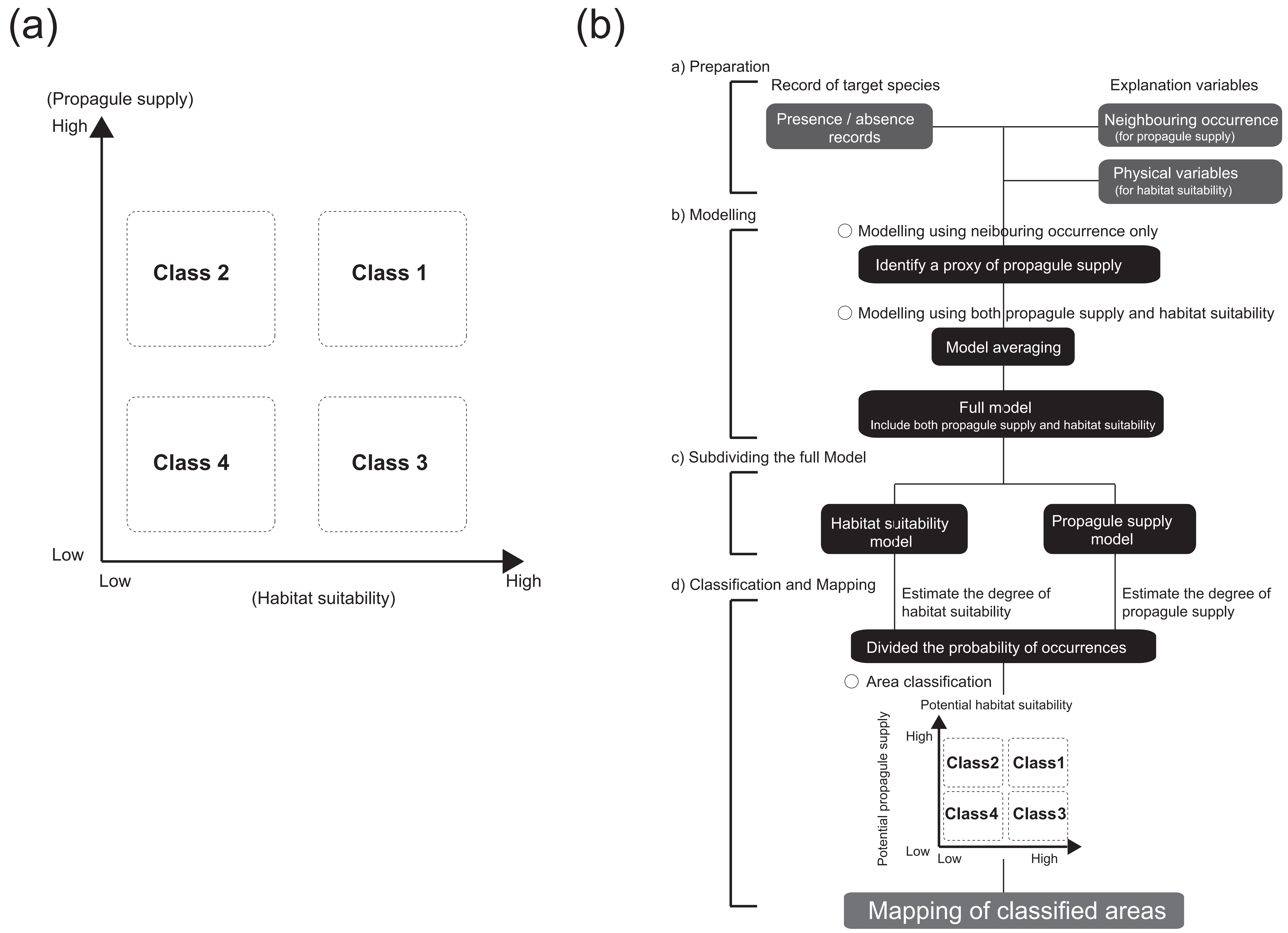
Figure 1. (a) Conceptual diagram of the procedure for the classification of invaded areas and (b) analytical framework of the study.

Figure 2. Study area and units analyzed in the study.

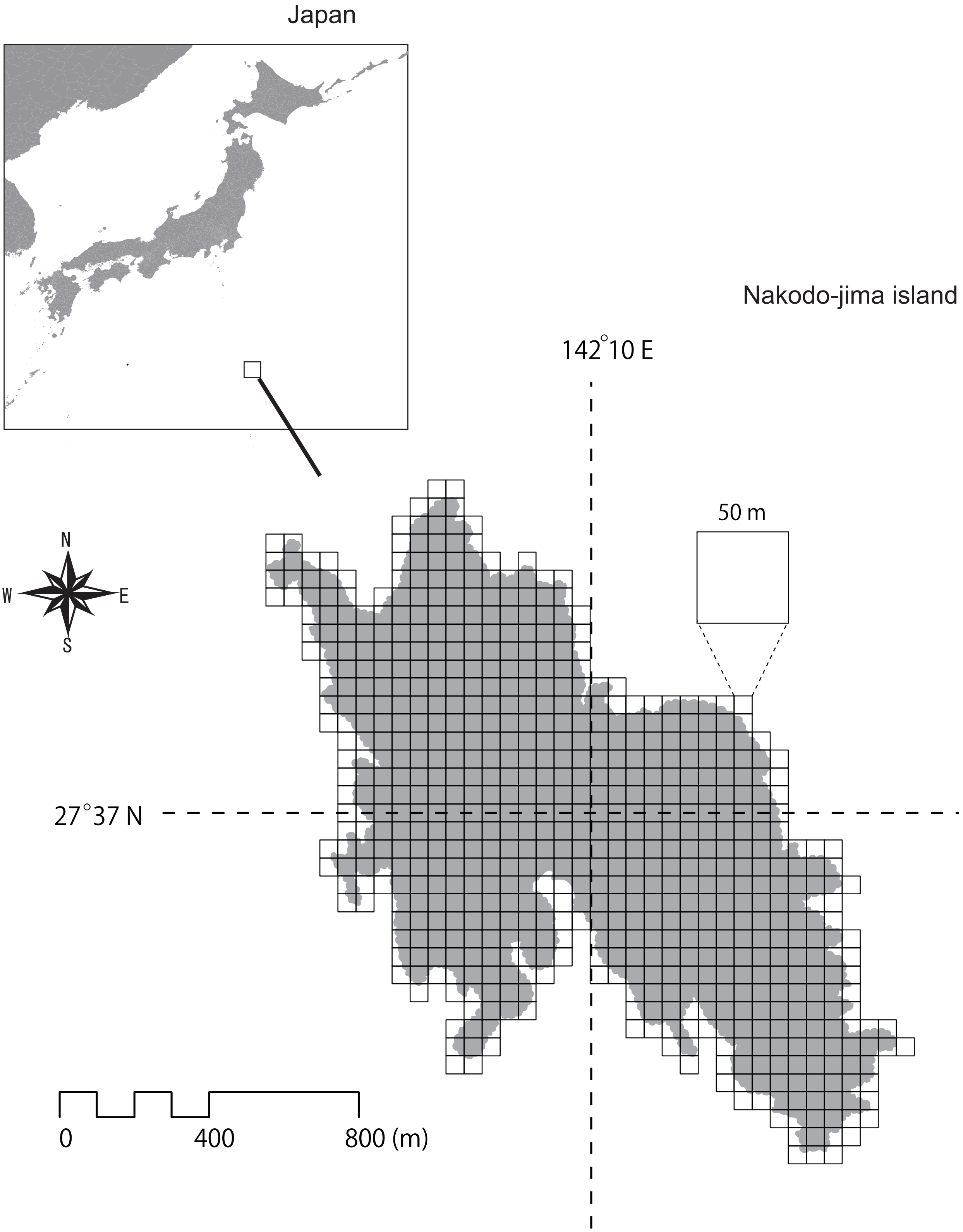
Figure 3. Scatterplot of predicted propagule supply (Ps) values on predicted habitat suitability values.

Figure 4. Maps based on the sub-models. Map (a): distribution of propagule supply values derived from the sub-model; Map (b): distribution of habitat suitability values derived from the sub-model; Map (c): three classes based on classification.

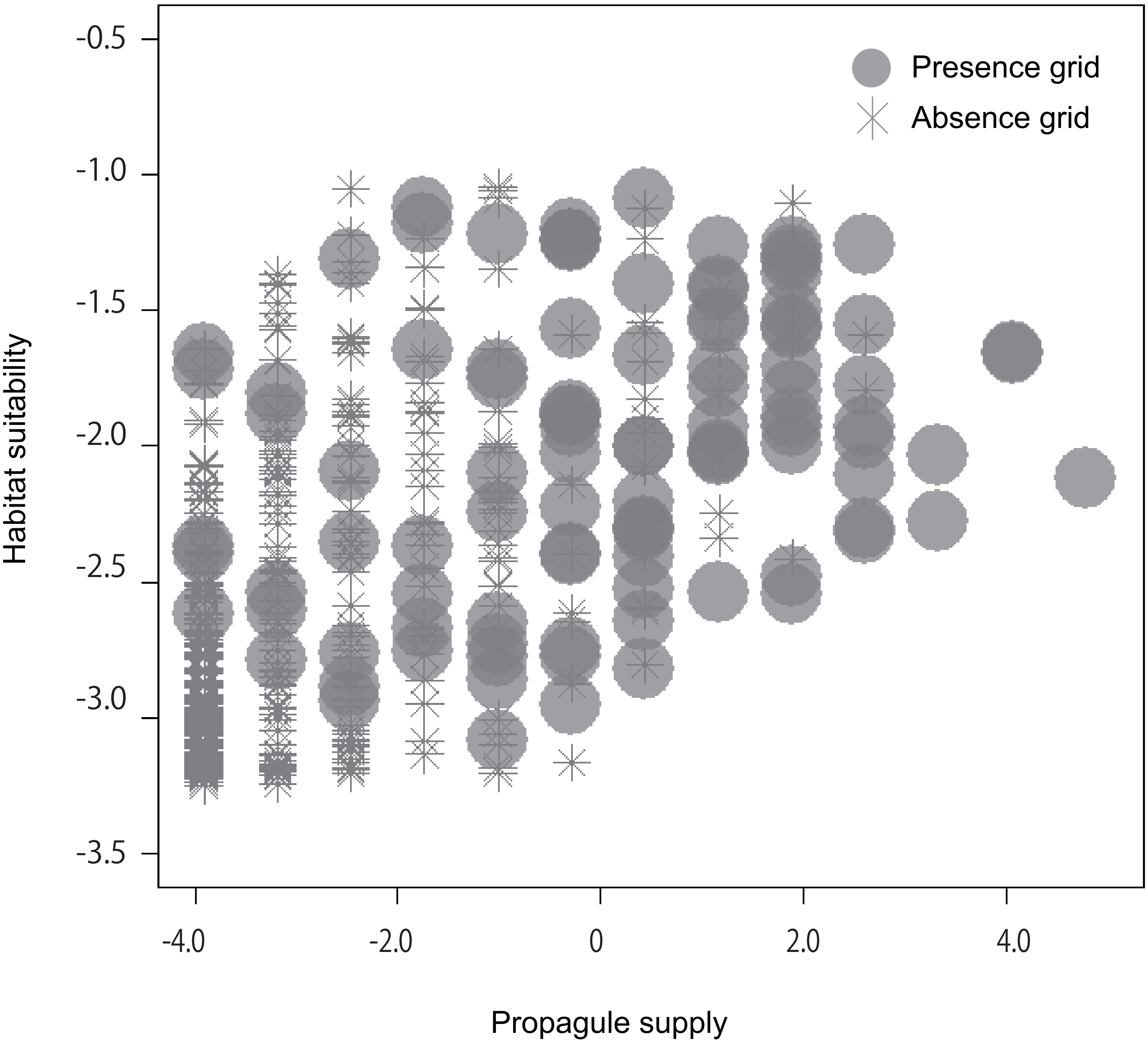
Osawa et al. Fig. 1



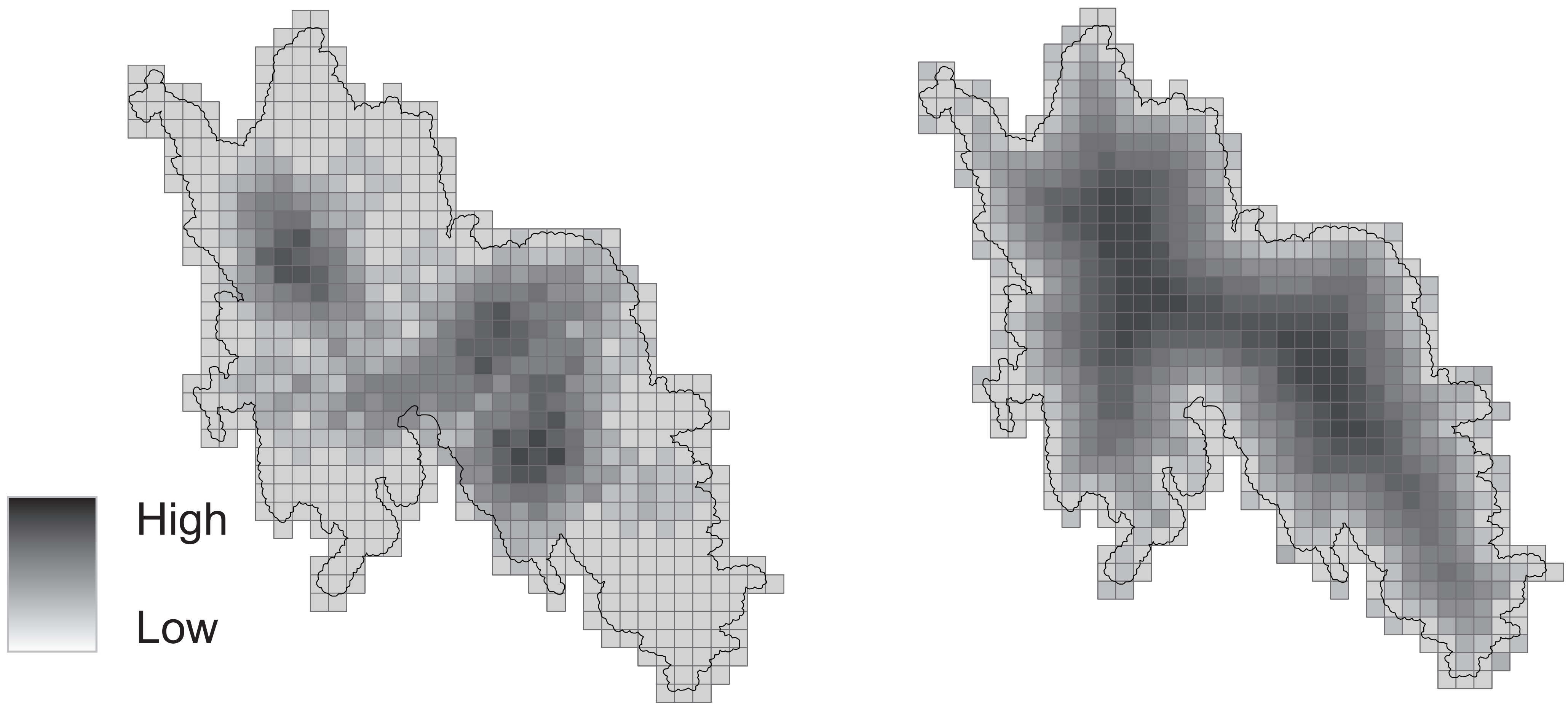
Osawa et al. Fig. 2



Osawa et al. Fig. 3



Osawa et al. Fig. 4


(a) Level of of propagule supply values

(b) Levels of habitat suitability values

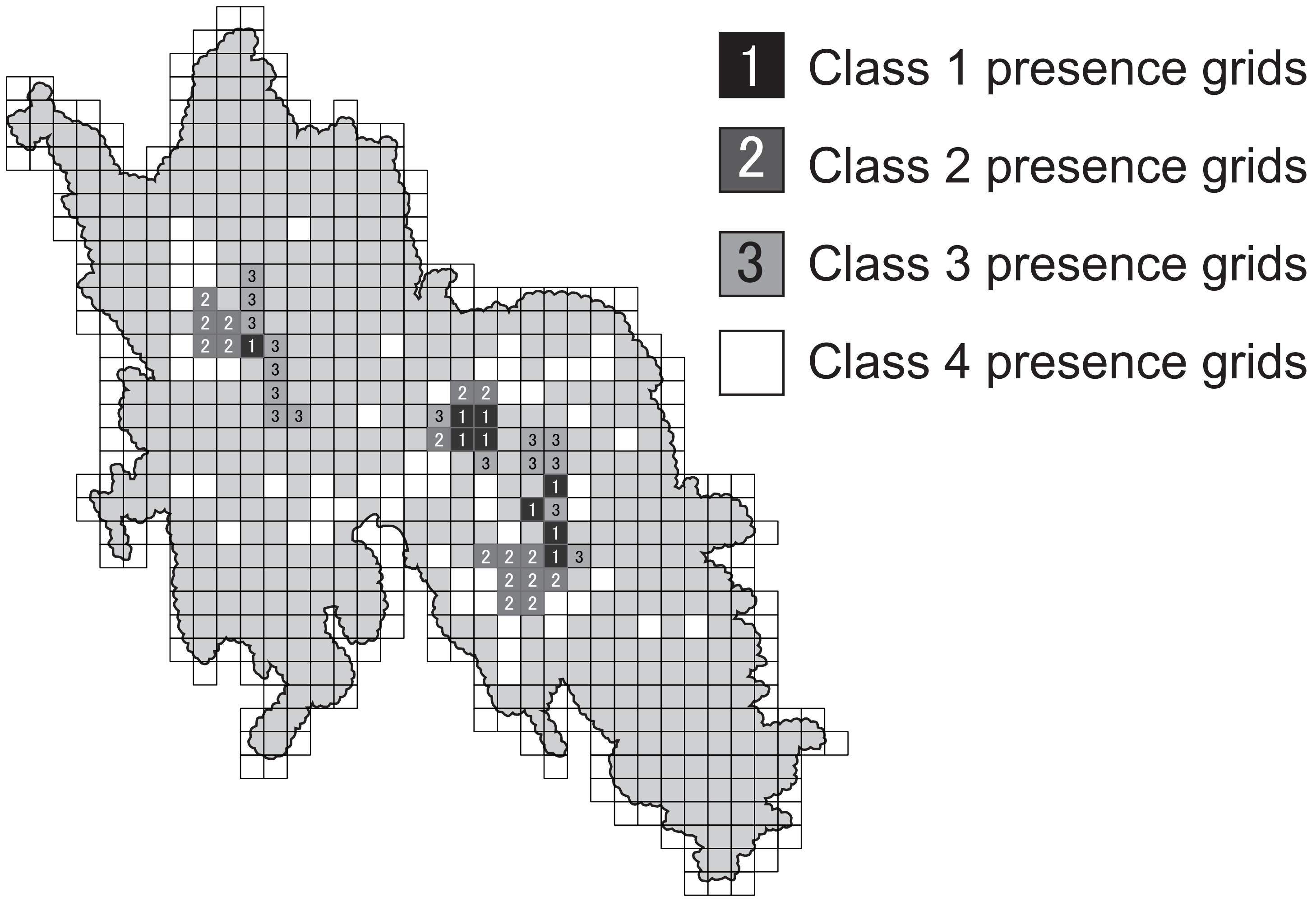

(c) Class 1, 2 and 3 grids

Table.1 Akaike information criterion (AIC) values for generalized linear models (GLMs) based on the presence/absence (p/a) of Leucaena leucocephala and eight candidates proxies of propagule supply (Ps). Details of the configurations are shown in Fig. 4. For Type a (see Fig. 4), only the p/a data could not be fitted to the GLM. The model with the lowest AIC value is identified in bold type.

Neighbouring occurrences	Type	AIC	
Only Presence / Absence	a	n.a.	
	b	407.6	
	c	440.7	
	d	454.5	
With Abundance	a	365.8	
	b	371.0	
	c	**358.7**	**Best model**
	d	371.8	

n.a. means that could not calculated.

Table2. Coefficients of explanatory variables in the average GLM for *Leucaena leucocephala* .
n.s. indicated that explanatory variables were not significant.

	Coefficients	Standard Error		Relative Importance
Neighbouring occurrence cells (Ps)	1.86	0.22		1.00
Elevation (Ev)	0.21	0.22	n.s.	0.62
Slope (Sl)	0.03	0.25	n.s.	0.34
Distance from the coast line (Dc)	0.596	0.21		0.97
Ps:Ev	-0.44	0.21		0.49
Ps:Sl	0.04	0.29	n.s.	0.10
Ps:Dc	-0.49	0.17		0.97
Intercept	-2.59	0.23		-