


Spatially explicit removal strategies increase the efficiency of invasive plant species control

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Abstract. Effective management strategies are needed to control expansion of invasive alien plant species and attenuate economic and ecological impacts. While previous theoretical studies have assessed optimal control strategies that balance economic costs and ecological benefits, less attention has been paid to the ways in which the spatial characteristics of individual patches may mediate the effectiveness of management strategies. We developed a spatially explicit cellular automaton model for invasive species spread, and compared the effectiveness of seven control strategies. These control strategies used different criteria to prioritize the removal of invasive species patches from the landscape. The different criteria were related to patch size, patch geometry, and patch position within the landscape. Effectiveness of strategies was assessed for both seed dispersing and clonally expanding plant species. We found that, for seed-dispersing species, removal of small patches and removal of patches that are isolated within the landscape comprised relatively effective control strategies. For clonally expanding species, removal of patches based on their degree of isolation and their geometrical properties comprised relatively effective control strategies. Subsequently, we parameterized the model to mimic the observed spatial distribution of the invasive species *Antigonon leptopus* on St. Eustatius (northern Caribbean). This species expands clonally and also disperses via seeds, and model simulations showed that removal strategies focusing on smaller patches that are more isolated in the landscape would be most effective and could increase the effectiveness of a 10-yr control strategy by 30–90%, as compared to random removal of patches. Our study emphasizes the potential for invasive plant species management to utilize recent advances in remote sensing, which enable mapping of invasive species at the high spatial resolution needed to quantify patch geometries. The presented results highlight how this spatial information can be used in the design of more effective invasive species control strategies.

Key words: biological invasions; Caribbean; control effort; ecosystem restoration; invasive species management; patch geometry; removal strategy; spatial modelling.

INTRODUCTION

Invasive Alien Species (IAS) are an important ecological driver of global change, exerting profound impacts on biodiversity and the functioning of ecosystems (Olson 2006, Pejchar and Mooney 2009, Bellard et al. 2016, Franklin et al. 2016). Through their adverse impacts on ecosystem functions and concomitant losses of ecosystem services, the economic impact of such invasions is considerable (Pimentel et al. 2005, Xu et al. 2006). Islands, due to their unique evolutionary histories, may be particularly susceptible to IAS and their negative impacts on endemic species (D'Antonio and

Dudley 1995, Sakai et al. 2001, Reaser et al. 2007, Turbelin et al. 2017, but see Vilà et al. 2011). Unfortunately, many island nations and territories lack the information, infrastructure and resources that are needed to adequately respond to the problems caused by IAS (Barnard and Waage 2004, Reaser et al. 2007).

Regarding invasions of alien plant species, the probability of successful eradication decreases rapidly with increasing infestation size (Rejmánek and Pitcairn 2002). More specifically, complete eradication of infestations larger than 10,000 ha is unlikely, and in these cases a management strategy that focuses on control and containment may be more realistic (Mack and Lonsdale 2002, Rejmánek and Pitcairn 2002). Within an infestation, one can distinguish primary patches that were typically established early in the invasion process and have developed to a large size, and nascent satellite patches

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that established later and are still small (Moody and Mack 1988). Whether management strategies should focus on removing primary patches or satellite patches in the invaded range is an ongoing debate (Moody and Mack 1988, Wadsworth et al. 2000, Whittle et al. 2007, Blackwood et al. 2010, Baker 2017, Hoffberg et al. 2018, Weston et al. 2019). Which removal actions comprise the most effective strategy may depend on the specific characteristics of the particular IAS, the phase of the invasion process, and the amount of available control effort considered (Liebhold and Bascombe 2003, Taylor and Hastings 2004, Epanchin-Niell and Hastings 2010).

Previous research has studied how a control effort can be effectively distributed not only over time (Taylor and Hastings 2004, Hastings et al. 2006, Baker and Bode 2016), but also in space (Travis and Park 2004, Hauser and McCarthy 2009, Chades et al. 2011, Giljohann et al. 2011, Guillera-Aroita et al. 2014, Baker and Bode 2016, Baker 2017, Bonneau et al. 2017, Baker et al. 2018). Spatial effects can be included in model frameworks by assuming variable impacts of control efforts throughout the landscape (Hauser and McCarthy 2009, Giljohann et al. 2011, Guillera-Aroita et al. 2014), or by studying control efforts in discrete patches that are connected through dispersal (Travis and Park 2004, Blackwood et al. 2010, Chades et al. 2011). Alternatively, reaction-diffusion models can be used to study whether control efforts are most effectively targeted at suppressing local growth or reducing expansion into surrounding areas (Baker 2017, Bonneau et al. 2017, Baker et al. 2018). These approaches typically do not consider the geometrical shape of individual patches or their relative position in the landscape. Yet, spatial considerations at the patch scale may be important in cases where the current spatial distribution pattern and shapes of patches determine the rate of spread, which in turn determines the future distribution pattern (Caswell and Etter 1999, Eppstein and Molofsky 2007, Tobin et al. 2007, Eppinga et al. 2013; Michaels et al., 2020).

How the specific spatial distribution of invasive plant species mediates spread and the effectiveness of control strategies may depend on the plant traits determining the mode(s) of expansion. The ability to expand clonally is a plant trait typically associated with invasiveness (Kolar and Lodge 2001), and with stronger impacts on native plant species (Vilà et al. 2015). Most perennial clonal plants, however, also possess the ability to reproduce sexually via seeds (Klimeš et al. 1997). Moreover, invasions by plants that can only reproduce sexually are also frequently observed (Vilà et al. 2015). Until now, it is unclear how optimal management outcomes may depend on the dominant mode of reproduction and invasive spread of the IAS, and the spatial characteristics and distribution of invasive species patches. Addressing this question requires a spatially explicit framework that considers both clonal expansion and dispersal via seeds. A potential disadvantage of such detailed spatially explicit models, however, is that they typically provide limited means for analytical analyses, and therefore often constrain the analyses to specific questions

or case studies (Higgins et al. 2000, Grevstad 2005, Eppinga et al. 2006, Baker 2017). On the other hand, empirical data may provide a means to constrain model parameters in a way that enables comprehensive analyses through simulation (Bernik et al. 2018). Hence, spatially explicit simulation models, parameterized with data of the specific IAS population considered, provide a powerful means to study how spatial organization of control efforts may mediate the effectiveness of control strategies targeting a particular IAS within a specific location (Epanchin-Niell and Hastings 2010).

Recent advances in remote sensing data and analyses allow the study of entire IAS populations with the level of detail needed to study processes of invasive spread (Santos et al. 2016, Dronova et al. 2017). This development provides promising, yet largely untested, capacities to increase our understanding of invasion processes and to aid the design of management strategies that optimize the spatial organization of control efforts. There is a wealth of new imaging sensors mounted to airplanes or UAVs, and an increasing number of satellites collect data at very high spatial and temporal resolution, which can be used to map populations of IAS (Alvarez-Taboada et al. 2017, Truong et al. 2017). These output maps can then serve as a basis to calculate spatial properties of established patches in the invaded range and constrain parameters of mathematical models of invasive spread.

In this study, we evaluate effectiveness of IAS control methods using a spatially explicit modelling framework. First, we use this framework to investigate how the efficiency of control methods may depend on whether an IAS spreads asexually via clonal growth or sexually through the production and subsequent dispersal of seeds. Second, we calibrate the model for an IAS capable of both clonal expansion and seed dispersal. Specifically, we use spatial data of high resolution (2×2 m) describing the successful invasion of a vine species (*Antigonon leptopus*), on the northern Caribbean island St. Eustatius (Appendix S1: Fig. S1). In our analyses, we compare different spatially explicit control strategies in terms of their ability to control further spread of the IAS. Control strategies differed from each other with respect to the criteria used to prioritize the removal of invasive species patches from the landscape. These different criteria were related to patch size, patch geometry and patch position within the landscape (i.e., distance to the nearest neighboring patch). We compared the effectiveness of the selected control strategies at different levels of total eradication effort. By comparing eradication strategies for a given effort, our analyses specifically focus on the role of spatial organization of eradication effort on IAS containment.

MATERIALS AND METHODS

Model description

We developed a stochastic cellular automaton model to describe the invasion dynamics of an alien plant

species that can spread both clonally and via seed dispersal. Space was discretized as a square-tiled lattice Ω in which each tile measured 2×2 m and could be either occupied by the invasive plant (state I) or not (state 0). The model used monthly time steps, with occupied cells dispersing seeds at the end of each time step, creating the possibility to colonize new cells according to

$$P_{S,0 \rightarrow I}(x,y;x',y') = G_S(\tau_{x',y'})K(x-x',y-y')p_S \quad (1)$$

in which $P_{S,0 \rightarrow I}(x,y;x',y')$ indicates the probability of the invader establishing at a tile with center location (x,y) , from seeds originating from a parent cell at a tile with center location (x',y') ; $K(x-x',y-y')$ is the dispersal kernel; G_S is a modifying function of propagule pressure (Eppstein and Molofsky 2007) and p_S quantifies the theoretical probability of successful invader establishment if propagule pressure of the parent plant in the absence of modification. Specifically, the modifying function $G_S(\tau_{x',y'})$ describes how propagule pressure increases with time since establishment of the invader at location (x',y') , and is formulated as

$$G_S(\tau_{x',y'}) = 0 \text{ for } \tau_{x',y'} \leq \tau_{0,S} \quad (2a)$$

$$G_S(\tau_{x',y'}) = \frac{\tau_{x',y'} - \tau_{0,S}}{\tau_a - \tau_{0,S}} \text{ for } \tau_{0,S} \leq \tau_{x',y'} \leq \tau_a \quad (2b)$$

$$G_S(\tau_{x',y'}) = 1 \text{ for } \tau_{x',y'} \geq \tau_a \quad (2c)$$

in which $\tau_{0,S}$ is the age at which the invader has produced its first viable seeds (set at 4 months in this study; Table 1). It is assumed that the number of seeds produced increases until the invader cover within the tile has stabilized. The duration of this process leading to the advanced state of invasion is described by the parameter τ_a (set at 16 months in this study; Table 1). We assume a Gaussian kernel K with a standard deviation L to describe dispersal of relatively heavy seeds (Sagnard et al. 2007) from location (x',y') to location (x,y)

$$K(x-x',y-y') = \frac{1}{2\pi L^2} e^{-\left(\frac{\sqrt{(x-x')^2 + (y-y')^2}}{2L}\right)^2} \quad (3)$$

As this kernel is normalized through the first factor in Eq. 3 (i.e., it sums up to one when integrated over the entire region of potential dispersal), it yields the proportion of propagules originating from location (x',y') that arrives at location (x,y) .

As noted above, we assume that the invader is also capable of spreading clonally. In the model, the four neighboring tiles (i.e., the von Neumann neighborhood; e.g., Oborny et al. 2000) of an alien species-occupied tile at location (x',y') could become occupied via clonal expansion according to

$$P_{C,0 \rightarrow I}(x,y;x',y') = G_C(\tau_{x',y'})p_C \quad (4)$$

here, (x,y) is a location within the von Neumann neighborhood of an invader-occupied tile at location (x',y') ; G_C modifies clonal expansion pressure, and is a function of the time since establishment of the invader at location (x',y') , $\tau_{x',y'}$. Specifically, $G_C(\tau_{x',y'})$ is formulated as

$$G_C(\tau_{x',y'}) = 0 \text{ for } \tau_{x',y'} \leq \tau_{0,C} \quad (5a)$$

$$G_C(\tau_{x',y'}) = \frac{c_1(\tau_{x',y'} - \tau_{0,C})^2}{c_2^2 + (\tau_{x',y'} - \tau_{0,C})^2} \text{ for } \tau_{0,C} \leq \tau_{x',y'} \leq \tau_a \quad (5b)$$

$$G_C(\tau_{x',y'}) = \frac{c_1(\tau_a - \tau_{0,C})^2}{c_2^2 + (\tau_a - \tau_{0,C})^2} \text{ for } \tau_{x',y'} \geq \tau_a \quad (5c)$$

in which $\tau_{0,C}$ indicates the age at which the invader can reach the edge of a 2×2 m tile and grow (clonally) into a neighboring cell (set at 4 months in this study; Table 1). In addition, c_1 determines when the maximum clonal expansion pressure is reached. This parameter is a function of the parameter τ_a described above, and c_2 ; the time it takes after the invader reaches a tile edge to exert a clonal expansion pressure of $c_1/2$ (set at 12 months in this study; Table 1). The parameters c_1 , c_2 , and τ_a are set so that $G_C(\tau_{x',y'})$ describes the first part of a sigmoidal function. Through this function, clonal expansion pressure increases slowly at first, then accelerates, and finally decelerates (slightly) when the invader approaches stabilization. The parameter p_C quantifies the theoretical probability of successful establishment of the invader through clonal expansion in the absence of modification by the function $G_C(\tau_{x',y'})$. See Table 1 for parameter names and values, and for function descriptions.

Comparing management impacts for asexually and sexually reproducing IAS

To study the implications of reproduction mode for IAS control, we compared a species only investing in asexual (i.e., clonal) reproduction ($p_C = 0.06$, $p_S/(\tau_a - \tau_{0,S}) = 0$) with a species only investing in sexual (i.e., dispersal via seeds) reproduction ($p_C = 0$, $p_S/(\tau_a - \tau_{0,S}) = 0.0006$). To focus on the effect of reproduction mode, the values for p_C and p_S were chosen so that the different reproduction strategies yielded similar basal rates of spread, i.e., in the absence of a control strategy. To assess the robustness of our results, we performed a sensitivity analysis in which we varied this basal rate of spread (using parameter ranges for p_C and $p_S/(\tau_a - \tau_{0,S})$ of 0.03–0.09 and 0.0003–0.0009, respectively, Table 1; see Appendix S1 for details).

For both the asexual and sexual reproduction strategies, we considered three different levels of control effort,

TABLE 1. Overview of the model parameters and functions. The values of model functions vary between tiles and over time; therefore the symbol “–” is shown, rather than a set of values.

Symbol	Interpretation	Value for asexually reproducing species	Value for sexually reproducing species	Value for case study species (<i>A. leptopus</i>)	Unit(s)
$\tau_{0,S}$	the time it takes the invader to produce its first viable seeds	n.a.	4 [†]	4 [†]	months
$\tau_{0,C}$	the time it takes the invader to reach the edge of a 2 × 2 m area, enabling clonal spread into surrounding area	4 [‡]	n.a.	4 [‡]	months
τ_a	the time it takes the invader to stabilize its cover in a 2 × 2 m area, and its expansion pressure to surrounding areas	16 [‡]	n.a.	16 [‡]	months
L	the standard deviation of the (Gaussian) seed dispersal kernel	n.a.	43 [§]	43 [§]	m
P_C	the maximum theoretical probability of clonal expansion from source tile into neighboring tile (i.e., in absence of modification, see below)	0.03–0.09	0	0.037	month ⁻¹
P_S	the maximum theoretical probability of colonization by seed from source tile (i.e., in absence of modification)	0	$3 \cdot 10^{-4}$ ($\tau_a - \tau_{0,S}$) – $9 \cdot 10^{-4}$ ($\tau_a - \tau_{0,S}$)	$8 \cdot 10^{-5}$ ($\tau_a - \tau_{0,S}$)	month ⁻¹
c_1	parameter determining the relative clonal expansion pressure from a source tile that is reached when the invader age in the tile is τ_a	$\frac{c_s^2 + \tau_a^2}{\tau_a^2}$	n.a.	$\frac{c_s^2 + \tau_a^2}{\tau_a^2}$	unitless
c_2	the time it takes after the invader reaches a tile edge to exert a clonal expansion pressure of $\frac{c_1}{2}$	12	n.a.	12	months
$K(x - x', y - y')$	the normalized Gaussian dispersal kernel quantifying the propagule pressure at location (x, y) exerted by a source tile located at coordinate (x', y')	n.a.	–	–	unitless
$G_S(\tau_{x',y'})$	function modifying the probability of colonization by seeds, as a function of the invader age in the source tile located at coordinate (x', y')	n.a.	–	–	unitless
$G_C(\tau_{x',y'})$	function modifying the probability of colonization by clonal expansion, as a function of the invader age in the source tile located at coordinate (x', y')	–	n.a.	–	unitless
$P_{S,0 \rightarrow I}(x, y; x', y')$	the probability of the tile at location (x, y) getting colonized through establishment of seeds	n.a.	–	–	unitless
$P_{C,0 \rightarrow I}(x, y; x', y')$	the probability of the tile at location (x, y) getting colonized through clonal expansion	–	n.a.	–	unitless

Notes: n.a., not applicable.

[†]Forman and Kesseli (2003)

[‡]Ernst and Ketner (2007)

[§]Calibrated in this study (Fig. 2).

corresponding to annually removing 5%, 10%, or 15% of the original cover, respectively. For each reproduction strategy × control effort combination, we compared seven different types of management strategies to control IAS expansion. These control strategies were partly based on previous studies addressing the removal of primary patches vs. satellite patches (Moody and Mack 1988). Here, we distinguish between primary and satellite patches based on size, labelling large patches as primary patches and small patches as satellite patches. Furthermore, we also considered prioritizing removal of patches based on their degree of isolation (Caplat et al. 2012). Degree of isolation was quantified as the distance to the nearest neighboring patch, using either the absolute distance, or the distance normalized by the patch

area (Moilanen and Nieminen 2002). In addition, we also considered prioritizing removal of patches based on their geometrical characteristics (Murphy et al. 2013, Wilkinson et al. 2018). Specifically, we quantified patch shapes through the ratio between patch perimeter and patch area (Murphy et al. 2013), and their “solidity” (Roitberg and Shoshany 2017, Wilkinson et al. 2018). Patch solidity is calculated as the ratio between a patch area and the area of the smallest convex polygon that contains this patch. This metric quantifies the extent to which a patch contains a core area that is relatively isolated from the surroundings (Wilkinson et al. 2018). Within the context of invasive species patches, the potential of spread from these core areas would thus be relatively limited. Finally, we also considered random

removal of patches as a reference strategy. In summary, control effort in the different strategies was allocated to one of the following: (1) random removal of patches, (2) removal of the largest patches, (3) removal of the smallest patches, (4) removal of the patches with the largest distance to their nearest neighbor, (5) removal of the patches with the largest distance-to-nearest-neighbor:foal-patch-area ratio, (6) removal of the patches with the largest patch-perimeter:area ratio, (7) removal of the patches with the lowest solidity.

For each strategy, 30 replicate simulations were performed (Appendix S1: Fig. S2). We tested for differences in impacts between control strategies with one-way ANOVA and a Tukey HSD post hoc test. This parametric testing procedure was used because the variable ‘remaining cover of the invasive species’ was normally distributed for all reproduction strategy \times control effort combinations (verified with a Jarque-Bera test). Although there was no homoscedasticity of variances between strategies, each group contained an equal number of observations, and for this group size number ($n = 30$), the parametric ANOVA test is relatively robust to effects on the Type I error rate (Kohr and Games 1974, Blanca et al. 2018). These analyses (as well as the further analyses listed below) were carried out in MATLAB (v. 9.0, Mathworks, Natick, Massachusetts, USA), with patch properties being computed with MATLAB’s Image Processing Toolbox. Through these analyses, we obtained a general overview of the role of reproduction strategy in mediating the effectiveness of IAS control efforts. In the following section, we will explain how this framework was also applied to a specific IAS case study.

Case study area

St. Eustatius (17°28' N, 62°58' W) is a northern Caribbean island that is part of the Cenozoic lesser Antilles volcanic island arc (Macdonald et al. 2000, Eppinga and Pucko 2018). The climate is tropical, with a mean annual temperature of 25.7°C and mean annual precipitation of 1,073 mm (Rojer 1997). The lower mountain slopes are covered by dry evergreen forests, (semi-)evergreen, and deciduous seasonal forests, whereas (secondary) rain forest can be found on the highest elevations (Stoffers 1956, Rojer 1997, De Freitas et al. 2012, Van Andel et al. 2016, Eppinga and Pucko 2018). Furthermore, the crater of the Quill volcano harbors a unique type of evergreen forest (Stoffers 1956, De Freitas et al. 2012, Van Andel et al. 2016, Eppinga and Pucko 2018). The central part of the island is relatively flat, and here recent changes in land use have created a disturbance regime facilitating the expansion of multiple invasive plant species (Ernst and Ketner 2007, Axelrod 2017; Haber et al., *unpublished manuscript*). The most successful and aggressive invasive species on the island is *Antigonon leptopus* (Hook. & Arn.; Ernst and Ketner 2007, Van der Burg et al. 2012; Haber et al., *unpublished manuscript*).

Case study species

The herbaceous perennial vine *A. leptopus* has spread from its native range in Mexico throughout global tropics (Burke and DiTommaso 2011). The species tends to grow a network of rhizomes, from which shoots can rapidly grow up to 50 cm in <2 months after mowing (Ernst and Ketner 2007). The species also produces buoyant and relatively heavy seeds (weighing 70% of the total fruit mass; Burke and DiTommaso 2011). *A. leptopus* climbs and smothers higher vegetation such as trees and shrubs (Appendix S1: Fig. S1; Surendra et al. 2013), but it can also expand laterally over bare areas or grasslands, either through propagation of roots underground or stolons aboveground (Appendix S1: Fig. S1; Burke and DiTommaso 2011, Vandebroek et al. 2018). The invasion of *A. leptopus* on St. Eustatius is among the most severe infestations of the species in the world (Ernst and Ketner 2007, Burke and DiTommaso 2011), and this invasion may contribute to vegetation changes that affect organisms at higher trophic levels in the food web (Jesse et al. 2020, Madden and Van Zanten 2020). In a previous study, a high spatial resolution (2 \times 2 m pixels) distribution map of *A. leptopus* on St. Eustatius was produced (Fig. 1a; Haber et al., *unpublished manuscript*). More specifically, a Support Vector Machine (SVM) algorithm was used to classify a multi-spectral Worldview-2 satellite image into *A. leptopus*-invaded and uninvaded pixels with an overall accuracy of >90% (Haber et al., *unpublished manuscript*). The resulting distribution map contains 1,852 patches of *A. leptopus*, with an average size of 345 m² (median size 128 m², range 64 m²–13,544 m², see black dashed lines in Fig. 1b–e).

Model calibration for the case study

We parameterized the dispersal kernel of *A. leptopus* using the distribution map of this species on St. Eustatius (Fig. 1a). Specifically, we calculated for each *A. leptopus* patch the distance from its centroid to the centroid of the nearest neighboring patch, Δ_{patches} . This yielded 1,852 values of Δ_{patches} , to which we fitted the cumulative frequency distribution belonging to the dispersal kernel used (Eq. 3):

$$\text{CDF} = \frac{1 + \operatorname{erf}\left(\frac{\Delta_{\text{patches}}}{\sqrt{2}L}\right)}{2}. \quad (6)$$

Eq. 6 shows that L is the only free parameter to be fitted. Fitting this cumulative frequency distribution to the observed distribution of Δ_{patches} (using the nonlinear least-squares fitting method as implemented in MATLAB), we obtained a value $L = 43$ m (nonlinear least-squares fitting: $R_{\text{adj}}^2 = 0.79$, $\text{df} = 570$, $P < 10^{-16}$). This corresponds to a mean dispersal distance of $\frac{\sqrt{\pi}}{2}L = 38$ m (e.g., Nathan et al. 2012), which is higher than observed for wind-dispersed seeds of other invasive vine

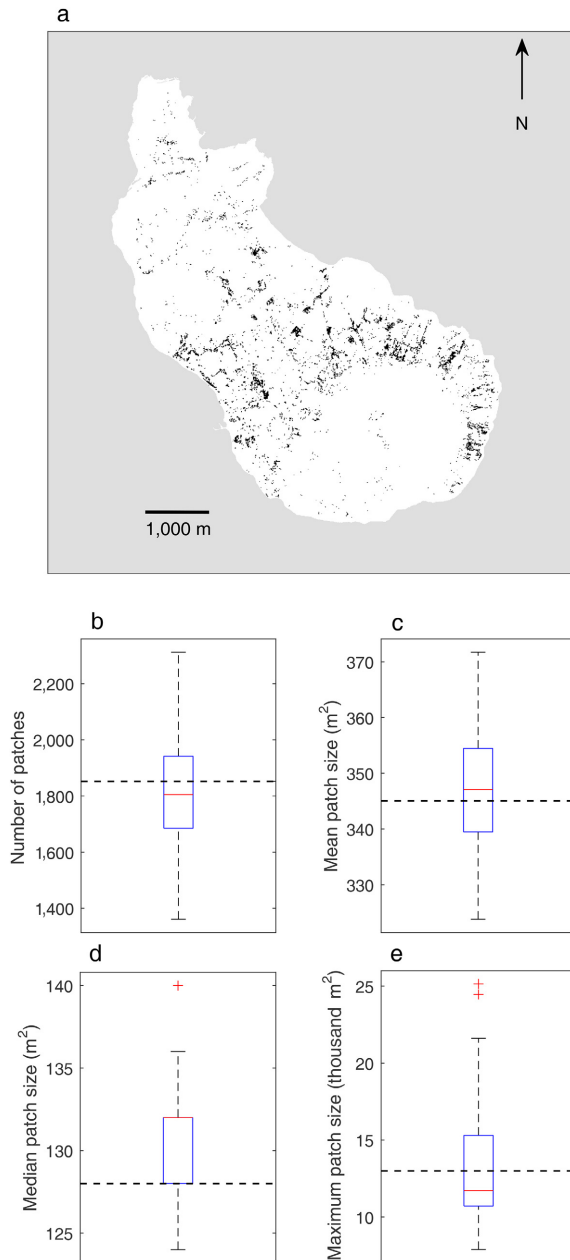


FIG. 1. (a) Spatial distribution (in black) and (b–e) summary statistics (black dashed lines) of the invasive vine *Antigonon leptopus* patches on St. Eustatius. The distribution was obtained through classification of a Worldview-2 image, with a spatial resolution of 2×2 m (Haber et al., unpublished manuscript). In the current study, a cellular automaton model was calibrated to these data; simulated patch statistics from 100 replicate runs shown as box plots in panels b–e). Box plot components show the median (red line) and the 1st and 3rd quartiles (box edges) of each patch statistic. Whisker lengths are constrained either by the most extreme value in the model dataset or by 150% of the interquartile range. Model data points outside of the range spanned by these whiskers are shown as outliers (red crosses).

species *Vinetoicum nigrum* and *V. rossicum* (4–17 m, DiTommaso et al. 2018), but within the dispersal range observed in the same study (0–80 m DiTommaso et al. 2018). The extent of the resulting dispersal kernel is very similar to the dispersal kernel used in a previous study to describe spread of the vine *Pueraria montana* var. *lobata* (Aurambout and Endress 2018). We used this dispersal kernel in all simulations, but varied the value of p_S (see Eq. 1) to simulate either *A. leptopus* in the case study, or we varied this parameter within the sensitivity analysis for asexually reproducing IAS (Table 1; see *Comparing management impacts for asexually and sexually reproducing IAS* and Appendix S1: Fig. S3). For the case study, our objective was to obtain emergent dynamics of simulated species spread that were similar to those observed for *A. leptopus* on St. Eustatius. Although the species has been present on the island for more than a century (Boldingh 1909), aggressive expansion mainly occurred in the last 50 yr, following agricultural abandonment (Ernst and Ketner 2007). Hence, we initialized the model with randomly assigning focal patch points on the lattice (10^{-4} % of tiles), with each initial patch size measuring 192 m^2 . Model simulations were then used to calibrate the values of the parameters of p_S and p_C (see Eq. 4) so that the macroscopic properties of the simulated and observed spatial distribution of *A. leptopus* aligned. Specifically, simulations were run for 50 yr, varying the values of p_S and p_C . The two parameter values were selected so that the distributions of average patch size, patch number and maximum patch size of 100 replicate simulations encompassed the current observed patch size distribution of *A. leptopus* on St. Eustatius (Fig. 1b–e; dashed lines indicate data, box plots indicate simulation results). This procedure yielded parameter values for $p_S/(\tau_a - \tau_{0,S})$ and p_C of 0.00008 and 0.037, respectively (Table 1).

Case study analyses

For the case study, we first studied the role of patch geometry in determining the spread potential of individual patches. Each of the 1,852 *A. leptopus* patches on St. Eustatius (Fig. 1a) was simulated in isolation for a period of 10 yr. By comparing the initial and final invasive species cover within these single-patch simulations, a relative expansion rate could be calculated for each patch (again using 30 replicate simulations for each patch). We then assessed the correlation structure between patches' relative expansion rate and their geometrical properties using a Principal Component Analysis (PCA). All variables in the PCA were standardized to zero mean and unit variance.

Subsequently, we used another set of simulations to study the role of the relative position of patches within the landscape in determining their spread potential. For these analyses, we used the observed distribution of

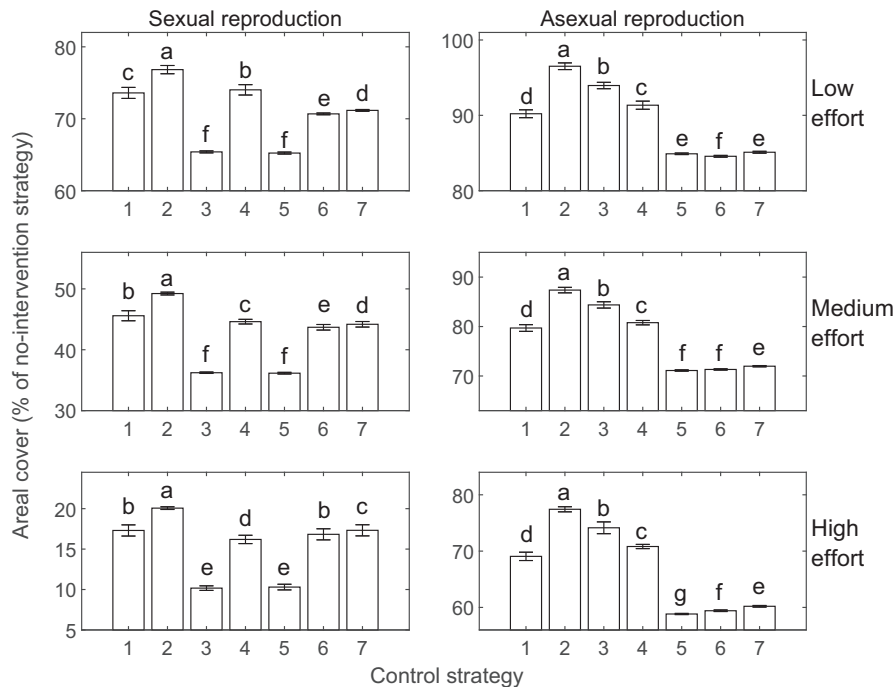


FIG. 2. Comparison of seven different removal strategies' effectiveness in controlling the areal extent of an invasive plant species. The invasive species either reproduced sexually (left column) or clonally (right column), and three different levels of eradication effort were considered: low effort (5% of initial cover removed per month, top row), medium effort (10%, middle row), and high effort (15%, bottom row). Bars indicate different removal strategies: (1) random removal of patches, (2) removal of the largest patches, (3) removal of the smallest patches, (4) removal of the patches with the largest distance to their nearest neighbor, (5) removal of the patches with the largest distance-to-nearest-neighbor:focal-patch-area ratio, (6) removal of the patches with the largest patch-perimeter:area ratio, (7) removal of the patches with the lowest solidity. Bars indicate average remaining cover, based on 30 replicate runs with each run spanning a period of 10 yr; error bars indicate ± 1 standard deviation. Different lowercase letters indicate significant differences between strategies (one-way ANOVA and Tukey post-hoc tests, $P < 0.05$).

A. leptopus on St. Eustatius (Fig. 1a) as the initial condition. In the simulations, we considered the same seven control strategies as described above (see *Comparing management impacts for asexually and sexually reproducing IAS*). We performed two types of analyses. First, we performed a static analysis, in which we considered how each strategy reduced the current number of patches and the current total area under propagule pressure of the invasive species, as a function of a single eradication effort (varied between 0% and 25%, with increments of 1%). Specifically, the total area under propagule pressure was quantified as the area where the invasive species colonization probability (i.e., the combined impact of both colonization processes as described by Eqs. 2 and 3) was equal to or larger than a critical value of 1% per month. Second, we performed an analysis based on dynamic simulations, in which we assessed for each strategy how much it reduced the invasive species' spread over time, as compared to a null simulation (i.e., a no-intervention strategy in which the species could expand unimpeded). Simulations were run for a period of 10 yr, including 10 annual patch removals. Similar to the analyses described above, differences between strategies were compared for low, medium, and high levels of control effort, i.e.,

annually removing 5%, 10%, or 15% of the original cover, respectively.

RESULTS

Management impacts along the reproduction trade-off

Prioritizing the removal of large patches or the removal of patches farthest from a neighboring patch were relatively ineffective IAS control strategies, regardless of the species' reproduction mode or the level of management effort (Fig. 2). Random removal of patches was more effective for asexually reproducing species, while removal of the smallest patches was more effective for sexually reproducing species (Fig. 2). All strategies incorporating patch geometrical properties (i.e., the ratio between patch area and its distance to the nearest neighbor, its perimeter or its solidity) were relatively effective control strategies for asexually reproducing species, and removing patches with the largest distance-to-nearest-neighbor:focal-patch-area ratio was also effective for sexually reproducing species (Fig. 2; Appendix S1: Fig. S4, S5). Finally, we found that in the scenarios with an asexually reproducing

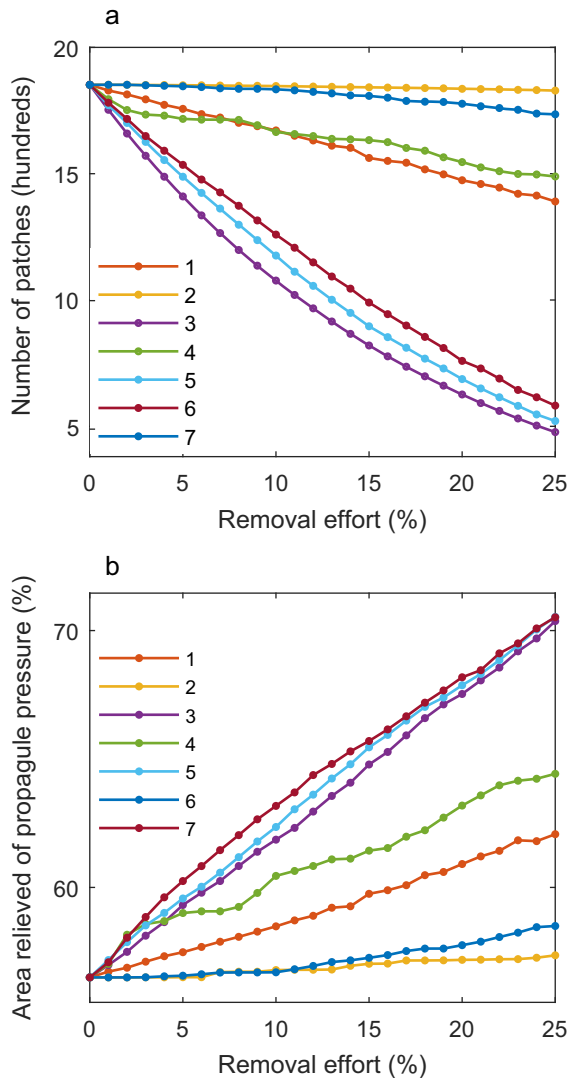


FIG. 3. Impacts of one-time removal of *Antigonon leptopus* on St. Eustatius on (a) number of patches and (b) area relieved from propagule pressure. The intercept on the y-axis indicates the island area that does not experience propagule pressure from the current distribution of *A. leptopus*. Removal effort was defined as percentage of initial cover. Numbers (colors) indicate removal strategies: (1) random removal of patches, (2) removal of the largest patches, (3) removal of the smallest patches, (4) removal of the patches with the largest distance to their nearest neighbor, (5) removal of the patches with the largest distance-to-nearest-neighbor:focal-patch-area ratio, (6) removal of the patches with the largest patch-perimeter:area ratio, (7) removal of the patches with the lowest solidity.

species, the invaded area increased more rapidly than it did in scenarios with a sexually reproducing species. This difference increased with the level of control considered (average cover of an asexually reproducing species remaining was 19%, 72%, and 308% higher for low, medium, and high control efforts, respectively; Fig. 2). A subsequent sensitivity analysis revealed that these results were robust to variation in basal spread

rates of the invasive species considered (Appendix S1: Fig. S4, S5).

Case study: Potential management impacts on A. leptopus' spatial distribution

For the observed patch size distribution of *A. leptopus* on St. Eustatius, a relatively large amount of effort would be required to remove the largest patches from the island. As a result, as control effort increases, the total number of patches decreases very slowly when this effort is directed at removing the largest patches (Fig. 3 a). Although the solidity of patches was not strongly correlated to patch area itself (Spearman's $\rho = -0.52$), patch removal based on this metric also yielded the removal of a mixture of a few large patches and a number of smaller patches (Fig. 3a). Naturally, the number of patches decreases relatively rapidly when effort is directed at removing the smallest patches (Fig. 3a). As the metrics distance-to-nearest-neighbor:focal-patch-area ratio and patch perimeter:area ratio were more strongly negatively correlated with patch area (Spearman's $\rho = -0.69$, $\rho = -0.82$, respectively), it follows that the number of patches removed also declined steeply with increasing control effort (Fig. 3a). When removal efforts were based on the distance to the nearest neighbor only, the decline in patch number is similar to that found under random removal of patches (Fig. 3a).

When focusing on the total area relieved of invasive species propagule pressure, two strategies using geometrical patch properties (distance to nearest neighbor:focal patch area ratio and patch perimeter:area ratio) were more effective in creating areas relieved of propagule pressure, as compared to the strategy removing the smallest patches (Fig. 3b). The largest differences between these strategies occurred at low amounts of eradication effort (Fig. 3b). Removing patches only based on the distance to the nearest neighbor relieved more area of propagule pressure than random patch removal, even though the number of patches removed in these two strategies was relatively similar (Fig. 3). Finally, the strategy prioritizing removal of patches with the lowest solidity relieved a relatively small area of propagule pressure, although more area was cleared under high removal effort, as compared to the strategy removing the largest patches (Fig. 3b).

Case study: Potential management impacts on A. leptopus' spread

The relative expansion rate of individual *A. leptopus* patches most strongly correlated with the patch perimeter:area ratio, with both properties having high weights on the first PCA component (Fig. 4a, explained variance first PCA component, 44%; Fig. 4b, rank correlation expansion rate and perimeter:area ratio: Spearman's $\rho = 0.96$, $P < 10^{-16}$). The second PCA component was associated with the position of the individual patch

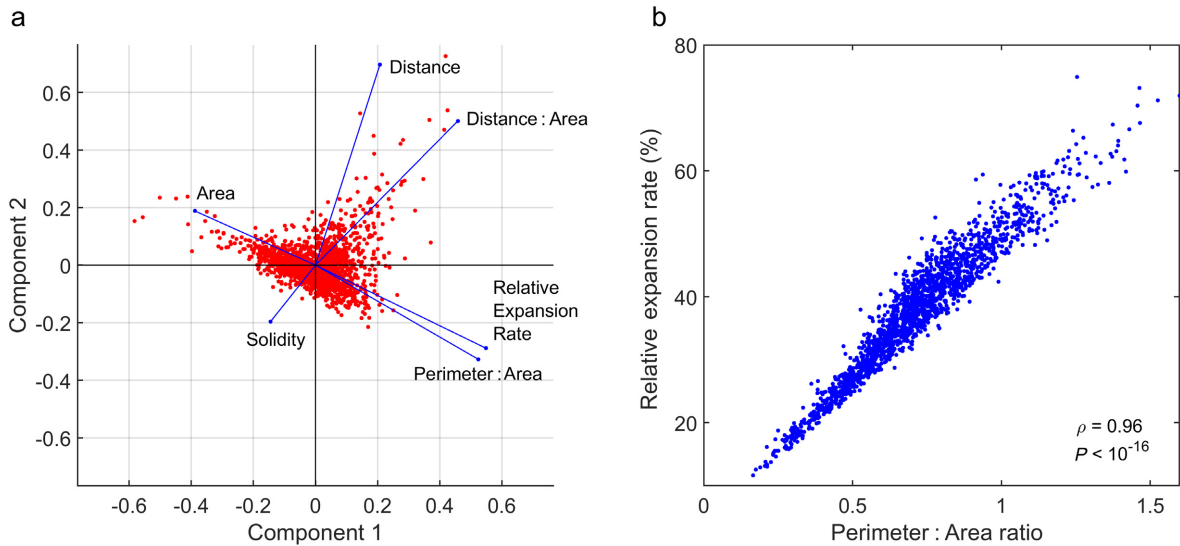


FIG. 4. Results from a Principal Component Analysis (PCA) showing the correlation structure between patch geometrical properties, and the relative rate of spread of patches. Patches were isolated from the landscape (as shown in Fig. 1), and simulated separately for a 10-yr period to calculate the relative increase in invasive species cover. (a) Biplot constructed with data from simulations using model parameters for *A. leptopus* (see Table 1), which spreads both asexually and sexually. (b) Correlation between the perimeter:area ratio of patches and their relative expansion rate during simulations.

within the landscape (explained variance, 26%; Fig. 4a). While these properties did not affect the spread of individual patches considered in isolation (Fig. 4a), they did affect the amount of area under propagule pressure (Fig 3b), the importance of which was considered in the subsequent dynamic simulations.

For the calibrated model parameter values, the invasive species *A. leptopus* would be able to increase its cover by 69% over a 10-yr timespan if no control efforts were undertaken ('no intervention' lines in Fig. 5). Regardless of the amount of control effort invested, prioritizing the removal of patches with the largest distance-to-nearest-neighbor:focal-patch-area was the most effective control strategy (Fig. 5). Although the calibrated model included both asexual and sexual reproduction of *A. leptopus*, the effectiveness of control strategies for the species were similar to those observed for simulated species that only reproduced asexually (i.e., via clonal growth, Fig. 2, 5). Compared to random removal of patches at the same level of effort, the most effective control strategy further reduced invasive species cover after 10 yr by 90%, 47%, and 30% under low, medium, and high removal effort, respectively. This result highlights how the spatial organization of control efforts can mediate the effectiveness of invasive species control strategies.

DISCUSSION

Our model results show how the effectiveness of IAS control strategies may depend on the invader's reproduction strategy and the resulting patch geometries within the IAS population. Prioritizing the removal of small

patches is a relatively effective strategy for sexually reproducing IAS, but not for IAS that expand clonally (Fig. 2). For both types of IAS, an effective control strategy is one that takes into account the distance to the nearest neighboring patch as well as the patch area (Fig. 2). When invasive plant species form circular patches (the least complex shape that can be measured with the patch perimeter:area ratio) that can expand at a constant, density-independent rate through a relatively homogeneous environment, eradications of smaller, satellite patches are always more effective than eradications of larger, primary patches (Moody and Mack 1988). Our results are in agreement with this notion, as the removal of larger patches was never the most effective eradication strategy in any of the scenarios considered in this study (Fig. 2, 5; Appendix S1). In spatially explicit model frameworks as utilized here, it is possible to further refine predictions based on circular patches, as not only patch size, but also patch location (relative to other patches) and patch geometry can be considered (Epanchin-Niell and Wilen 2012). Interestingly, prioritizing removal of patches with low solidity was a relatively effective strategy (Figs. 2,5), as it provides a means to distinguish core patch areas (with limited ability to spread) from edge patch area (with higher ability to spread). Moreover, although perimeter:area ratio was the strongest predictor of the spread potential of individual patches (Fig. 4), the position of patches within the landscape may comprise a more important constraint on patch spread potential (Fig. 5). These findings suggest that the ongoing debate regarding the removal of smaller or larger invasive species patches (Moody and Mack 1988, Wadsworth et al. 2000, Whittle et al. 2007,

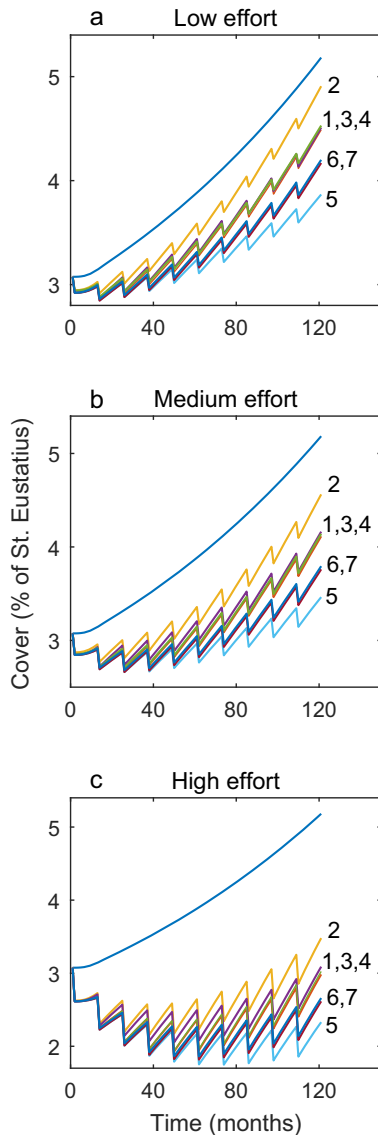


FIG. 5. Model simulations of invasive spread, with parameters calibrated to the spatial distribution of *A. leptopus* on St. Eustatius. The figure shows seven different removal strategies' effectiveness in controlling the species' areal extent, for three different levels of removal effort: (a) low effort (5% of initial cover removed per month, top row), (b) medium effort (10%, middle row), (c) high effort (15%, bottom row). In all panels, colors and numbers indicate different removal strategies: (1) random removal of patches, (2) removal of the largest patches, (3) removal of the smallest patches, (4) removal of the patches with the largest distance to their nearest neighbor, (5) removal of the patches with the largest distance-to-nearest-neighbor:foal-patch-area ratio, (6) removal of the patches with the largest patch-perimeter:area ratio, (7) removal of the patches with the lowest solidity. The smooth teal-blue curves at the upper part of each plot represent the no-intervention scenario.

Blackwood et al. 2010, Hoffberg et al. 2018, Weston et al. 2019) needs to consider the mediating roles of varying patch geometries and the relative positions of patches within the landscape.

While parameterizing our model framework to fit the spatial distribution of *A. leptopus* on St. Eustatius (Fig. 1), we found that the most effective control strategy was the one that worked relatively well for both sexually and asexually reproducing species (Figs. 2, 5). These findings show how a spatially explicit modelling framework can be used to incorporate information about patch geometry and relative positions of patches in the landscape into the design of IAS control strategies (Appendix S1: Fig. S6; see Appendix S1 for additional discussion). The possibilities to obtain the spatial distribution of IAS, and hence the geometry of IAS patches, via high spatial resolution remote sensing products are rapidly increasing (Andrew and Ustin 2009, Hestir et al. 2008, Kettenring et al. 2016, Santos et al. 2016). A high spatial resolution of IAS map is needed in order to accurately assess patch geometry. In the case study considered here (Fig. 1), the average patch size was about two orders of magnitude larger than the pixel size, meaning that patch edges could be quantified with a relatively high level of detail.

It is important to note that the formulation of our spatially explicit modelling framework involved several simplifying assumptions. First, we assumed that colonization of new sites depended only on the vicinity of the IAS (and the time since establishment in these sites). It is likely that colonization probabilities are also dependent on local environmental conditions. For example, *A. leptopus* is unlikely to invade intact forests, and on St. Eustatius the species has not been observed at high elevations (Ernst and Ketner 2007). By not taking into account potential barriers for establishment, our simulations may overestimate projected rates of invasive spread within 'no intervention' scenarios. Second, we assumed that reproduction allocation was constant over time, while investments in asexual and sexual reproduction may vary over time and in response to changes in environmental conditions. For our study species, *A. leptopus*, it has been observed that investment in asexual reproduction is highest after heavy rains, whereas intermittent dry spells within wet seasons stimulate the production of flowers and thus potential seeds (Solomon Raju et al. 2001). Explicitly considering temporal variation in climate and resulting changes in reproductive behavior of the IAS may identify specific windows of opportunity for IAS control (D'Antonio and Chambers 2006). Finally, we assumed a linear relationship between the area of IAS removed and the required effort of this removal. However, this relationship may be non-linear, as the marginal removal effort may either be increasing or decreasing with the size of the IAS removal area (Rejmánek and Pitcairn 2002, Byers et al. 2006, Epanchin-Niell and Hastings 2010). Taking into account such non-linearities may alter the assessment of effectiveness of different IAS eradication strategies (Epanchin-Niell et al. 2012).

As IAS cause substantial ecological and economic impacts (Pimentel et al. 2005, Franklin et al. 2016), and

the number of exotic species introductions is still increasing (Tittensor et al. 2014), there is an urgent need for effective eradication and control strategies (SCBD 2014, Crowley et al. 2017). Previous studies have successfully identified optimal solutions that balance economic costs associated with the control efforts and their ecological success (Sharov and Liebhold 1998, Higgins et al. 2000, Taylor and Hastings 2004), and considered how management effort should be distributed in space (Travis and Park 2004, Hauser and McCarthy 2009, Chades et al. 2011, Baker and Bode 2016, Bonneau et al. 2017). Less attention has been paid, however, to the mediating role of invasive patch geometries and their relative position in the landscape. Using a spatially explicit modelling framework, we showed that even when the total amount of control effort is kept constant, targeting specific patches based on their geometry and/or relative position in the landscape can result in substantial differences in IAS cover (Fig. 2, 5). Recent advances in remote sensing enable the collection of high-resolution spatial distribution data of IAS (Fig. 2; Hestir et al. 2008, Andrew and Ustin 2009, Kettenring et al. 2016, Santos et al. 2016, Bolch et al. 2020; Haber et al., *unpublished manuscript*), providing a promising approach to combine models and observations for the development of spatially explicit management strategies.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2257/full>

DATA AVAILABILITY

Code and data are provided in Supporting Information: Data S1.