Diversity and Distributions, (Diversity Distrib.) (2014) 1–10

A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

Predicting the invadedness of protected areas

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ABSTRACT

Aim Invasive species management is an expensive priority on many protected areas but the magnitude of invasion can vary drastically from site to site. Conservation planners must consider this variability when they plan for treatment across multiple protected areas. We examine the scope for predicting site invadedness and management costs from common protected area characteristics, a method that could be used to estimate the future management needs of a protected area network.

Location Three hundred and sixty-five protected areas across the state of Florida, USA.

Methods We use data on invasive plant cover and protected area features to predict invadedness and invasive species management funding allocation in a multiple regression framework. We then examine the relationship between invadedness and funding on a subset of 46 of the protected areas.

Results Invadedness (relative proportion of a protected area that is covered by invasive plants) was related to the size of a protected area and the number of surrounding households. However, the explained variation (9–50%) depended on the type of species occurrence data used; with models using approximated data on the area infested able to explain more of the variation than those that included data with GIS-calculated area infested. Cumulative funding investment at a protected area was also predicted by the number of surrounding households and protected area size. Yet, funding and invadedness were not correlated with one another.

Main conclusions Readily available data on protected area features were statistically related to variation in the invadedness of a protected area and were also associated with past management expenditures. This does not translate into a clear relationship between current invadedness and past expenditures, however. Our results suggest that basing predictions of future costs on current funding may not accurately represent budgetary needs.

Keywords

Conservation costs, Florida, invasion, invasive plants, management costs, protected areas.

INTRODUCTION

Managers of protected areas face the difficult exercise of how to plan for treatment of invasive species infestations within budget limitations. Invasive species inhabit protected areas world-wide (Usher, 1988; Allen *et al.*, 2009), and there is both social and ecological justification for their removal if conservation goals are to be met (Gordon, 1998; Simberloff, 2005). Planning for regional treatment and management costs requires an understanding of relative invasion across protected areas, but available data on invasive species presence and cover is often incomplete. One solution is to use site features to predict trends in relative invasive cover (invadedness) across a network of protected areas.

Invasive species presence at a protected area may respond to features that regulate the native community's resistance to invasion (Myers & Ewel, 1990; Hobbs & Humphries, 1995), or to features that influence whether invasive plant

DOI: 10.1111/ddi.12171
http://wileyonlinelibrary.com/journal/ddi

propagules can reach the protected area and become established (Simberloff, 2009; Kuhman *et al.*, 2010). Protected area features that influence plant community composition include those such as protected area size, elevation and temperature, which drive landscape level processes (Pyšek *et al.*, 2002). Meanwhile, protected area features that influence propagule availability and establishment often are directly related to human activities, with human proximity often considered a primary driver of invasion (Stohlgren *et al.*, 2006; Marini *et al.*, 2009). Such activities could include transportation of propagules into protected areas, disturbance that allows for invasive species establishment or provision of source populations.

Invasive species treatment is expensive (Pimentel *et al.*, 2005), and invasive species management on protected areas is no exception (Frazee *et al.*, 2003; Green *et al.*, 2012). Estimates of potential costs vary widely and factors such as infestation levels, species present and treatment technique all influence the estimate (Usher, 1988). In addition, potential costs depend on whether the management objective is eradication, reduction or containment. However, to provide an idea of the magnitude of cost that we are considering, in FL, it costs about 6000$/HA for the initial treatment of cogon grass (*Imperata cylindrica*) (Jubinsky, G., Personal communication), and this grass infests about 1500 HA of protected areas in our dataset (Table 2). Similarly, expert estimates of initial and upkeep treatment costs for individual species of weeds affecting biodiversity conservation in the 30 million HA Kimberly region of Australia are in the millions of dollars (AU) over a 5-year period (Carwardine *et al.*, 2011).

Invasive species management can account for a large proportion of the protected area management budget (Frazee *et al.*, 2003). Because the management budget of a protected area is a significant cost that is of interest to conservation planners (Armsworth *et al.*, 2011), being able to predict relative invasive species extent across a network of protected areas would be a useful first step towards efficient conservation resource allocation (Buchan & Padilla, 2000; Keller *et al.*, 2008). These predictions need to provide results that conservation planners can use to make funding allocation decisions that involve site-scale comparisons across hundreds of protected areas (e.g. for allocating regional funding or evaluating trade-offs with regard to future protected area locations). In addition, they need to be based on readily available data that does not require intensive, in person, survey work. We explore the prediction of invadedness as a representation of infestation that could be used for this purpose. We define invadedness as relative proportional cover by invasive species at a protected area. Because it measures the current invasion at a protected area, it differs conceptually from other indices such as invasibility (potential for invasion) or level of invasion (species richness of the invaders) (Richardson, 2011; Catford *et al.*, 2012).

Here, we develop a model to predict invadedness from protected area features and then use management expenditures to examine the relationship between treatment funding and invadedness. First we ask (1) what features of a protected area are associated with invadedness? We use coarse-grain data for the predictive features in this analysis to correspond with the grain at which planners use data to make site-level decisions (e.g. planning for funding needs across hundreds of protected areas). We then use subsets of the data to ask (2) Does data structure (estimated invaded area vs. calculated invaded area) affect the explanatory power of our model? This question affects land managers because recording invasive species occurrence data is often a trade-off between mapping ease and utility. Some data types may be quicker to collect with basic equipment (e.g. point centroids with estimated area for an infestation) while others require more involved mapping but are useful for issuing contracts for invasive species treatment (e.g. polygons with delineated spatial extent of infestations). Finally, to explore the expected cost of treating an invasion, we ask (3) can protected area features predict invasive plant management funding allocation and is funding related to invadedness? This analysis aims to provide an estimate of relative variation in future management expenditures across a network of protected areas, rather than a cost estimate for an individual protected area.

METHODS

Study system

We used data from publicly owned protected areas in the state of Florida, USA. Florida has more than 1800 publically owned protected areas that range across temperate to tropical climates, urban to rural locations and small to large sites (Median = 78 HA, 5th and 95th percentile = 2 and 7100 HA). Florida is heavily impacted by invasion, and 146 invasive plant species are tracked by the Florida Exotic Pest Plant Council (FLEPPC) because of their documented harm to ecosystems or recent increases in abundance (2009 FLEPPC list). The state spent over $100 million to manage invasive plants on all protected areas between 1999 and 2010 (Cleary, R. unpublished work).

Invasive plant distribution data

We obtained invasive plant distribution data from the FLInv geodatabase, which contains occurrence records for FLEPPC-listed species on all of the public protected areas in Florida. This database was commissioned by the Florida Fish and Wildlife Conservation Commission (FWCC) to improve their prioritization of invasive species management funds and is maintained by the Florida Natural Areas Inventory (FNAI). We chose data that met the following criteria. (1) We used data for only the 28 most prevalent species (each found on more than 100 protected areas throughout the state) to increase reliability of identification. (2) We chose protected areas where all records were single species occurrences with either estimated invaded area (stored as points in dataset) or calculated invaded area (stored as polygons). Generally, points were used to record information on small infestations, and polygons were used to improve treatment utility and to map larger infested areas (Price, 2009). All records included data on observation date, percentage cover (binned for analysis into 2.5%, 15%, 38%, 63% and 88%) and area infested (estimated acreage recorded by surveyor for points, acreage calculated by spatial analysis software for polygons). (3) We chose records from protected areas where all occurrence data were collected by FNAI botanists between the years of 2008 and 2010 to enhance conformity with data collection protocols.

The final dataset includes 365 protected areas across Florida. While a subset of the whole network of protected areas, it was still a large sample spanning gradients of protected areas features (Table 1) albeit slightly skewed towards smaller protected areas. The limitations of this sample must be balanced against the desirability of having all surveys conducted by one agency (FNAI) with standardized reporting protocols.

For each protected area, we calculated 'invadedness' as a measure of relative variation in the extent of invasion across protected areas. To construct our metric, we first calculated the area of invasive cover for each occurrence record by multiplying the acreage infested by the percentage cover bin. We then summed the area covered by focal species at a protected area to calculate the proportion of the protected area infested [(sum of area of 28 species)/(area of protected area), Fig. 1] This value indicates the proportion of the protected area that would be infested by invasive plants if they were all clumped into one area with their leaves touching. Because the area is summed from individual occurrence records, there is the possibility of double counting area where trees and understorey both consist of invasive species. However, because removal effort is likely to be higher in such cases, the relative degree of invasion is represented accurately. For this study, we are interested in identifying the protected areas that are likely to be most invaded, regardless of species.

We were also interested in the question of 'does data structure (estimated invaded area vs. GIS calculated invaded area) affect explanatory power of our model?' For this analysis, we only used data from protected areas where the invadedness was entirely described by estimated data (GIS points only) or entirely described by calculated data (GIS polygons only).

Protected area features

When seeking to predict invadedness from protected area features, we chose predictors that tested specific *a priori* hypotheses motivated from past studies (Table 1). We first examined factors that could relate to ecological function and community composition at a protected area. Protected area size information was obtained from the Florida Managed Areas GIS layer of protected areas managed for conservation within the state (maintained by FNAI). We derived protected area average elevation from USGS NED 1/3 arc second data layers at 1-m resolution. Minimum winter protected area temperature was obtained from WorldClim climate data, December–March values (1950–2000) at 1-km resolution.

Then, we assessed factors that could relate to anthropogenic disturbance at a protected area. We estimated the number of nearby households by weighting the number of households in nearby year 2000 census-tracts by their overlap with a 25 km buffer around the protected area. We also used roads as a proxy of onsite disturbance. For this predictor variable, we divided area of roads by protected area size for all roads that intersected or were adjacent to the protected area, using an average road width of 10 m (USGS 24000:1 roads layer).

Table 1 Protected area features and the hypotheses that led them to be incorporated into the model as predictor variables

Protected area feature	Hypotheses	Variable
Size	We expect smaller protected areas to be less invaded than larger protected areas[1,2,3] because ecological processes that may minimize invasion are more likely in large areas (burning, flooding and population stability).	Total HA
Elevation	We expect lower (wetter) protected areas to be more invaded than higher (drier) protected areas[1,4] (e.g. wet flatwoods vs. scrub). However, the very wettest may be less invaded (floodplain forest).	Average height of protected area(m above sea level)
Household density	We expect that protected areas with more households within 25 km are more invaded[1,5,6,7,8] because urban intensity likely increases dispersal vectors, seed sources and anthropogenic disturbance on site.	Number of households within 25 km of protected area
Average low temperature	We expect tropical protected areas to be more invaded than northern protected areas because lower temperature bounds probably limit the range of many species, and there is an increase in species richness with declining latitude.	Minimum average monthly low winter (Nov–Mar) temp
Roads on protected area	We expect the area of interior and adjacent roads to serve as a proxy for protected area disturbance and thus to increase with invadedness.	Road cover (m^2/m^2) per protected area

1: (Pysek *et al.*, 2002), 2: (Lonsdale, 1999), 3: (McKinney, 2002), 4: (Chytry *et al.*, 2008), 5: (Catford *et al.*, 2011), 6: (Gassó *et al.*, 2012), 7: (Pyšek *et al.*, 2010), 8: (Stohlgren *et al.*, 2006).

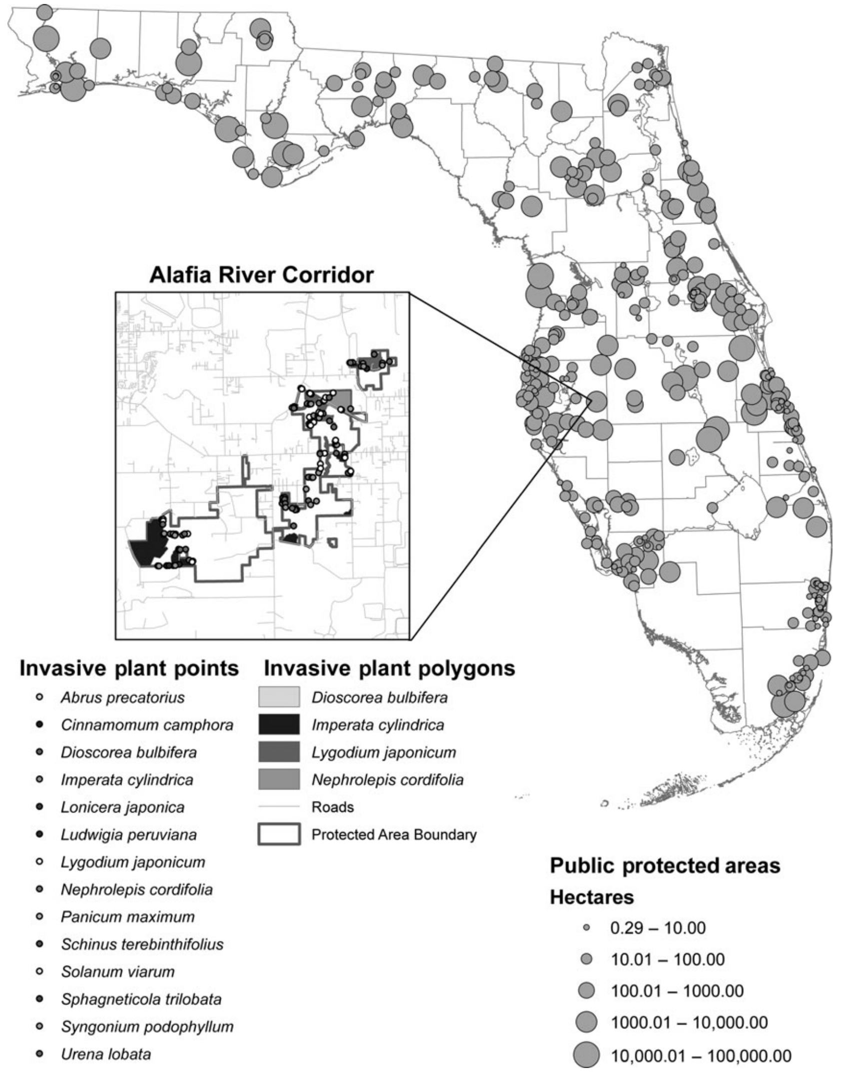

Figure 1 Invadedness study sites: 365 public protected areas in Florida were used in the analysis. Inset map illustrates the set of invasive plant occurrences (points and polygons) at one protected area (Alafia River Corridor). The sum of the area × percentage cover of each occurrence is aggregated into the invadedness metric for a protected area.

Funding for invasive plant management

To address the question 'how is invasive plant management funding allocated across a subset of protected areas, and is it related to invadedness?', we used data on state-allocated funding for terrestrial invasive plant management for 46 protected areas in our primary dataset. Specifically, we examined funding allocation, by the FWC Invasive Plant Management Section, of legislature-mandated funding for invasive plant treatment on public protected areas within the state (Cleary, 2007). Invasive plant management funding on our 46 protected areas totalled almost $50 million and was allocated under the Upland Invasive Exotic Plant Management Program. This constitutes about half of the total program spend over the previous 10-year period. For 42 of the protected areas, this funding was awarded prior to the protected area being surveyed for invasive plants. Funding proposals are permitted for any FLEPPC-listed invasive species, but often projects involving target species or retreatment projects are prioritized for funding by FWCC. Target species include *Lygodium microphyllum*, *Lygodium japonica* and *I. cylindrica* (Jubinsky, G., Personal communication). In addition, larger projects tend to be funded over smaller projects. For each protected area, we summed all state-provided funding and cooperative project funding reported by the protected areas from 1999–2009. We used consumer price index history tables for June of each year to correct dollar values for inflation to 2009 amounts (http://www.bls.gov/cpi/#tables, accessed Jan, 2012).

Analysis

Invadedness

We used a multiple regression framework with AIC model selection in SAS (version 9.2, SAS Institute Inc., Cary, NC, USA) to test for statistical associations between protected area features (Table 1) and invadedness. For each analysis, we Box–Cox-transformed ($\lambda = 0.12$) the response variable (invadedness) and log-transformed all predictor variables, except minimum temperature, to meet assumptions of normality of errors (e.g. model average residuals of the response variable: Kolmogorov–Smirnov $D = 0.03$, $P > 0.2$). We did not include interaction terms because we had no *a priori* reason to prioritize some interactions for examination from among the large number of possible interactions of the variables in Table 1. Tolerance testing indicated that no predictor variable was too dependent on variation in other predictor variables (more than 20%) ensuring that collinearity requirements were adequate to proceed. For the model using all data and the data structure models, we constructed all possible model combinations and then identified the set of parsimonious models with AIC values within two points of the minimum AIC value observed. We then calculated a multimodel average across this parsimonious set using model weights. We tested for spatial autocorrelation in model average residuals by calculating Moran's I statistics for protected area centroids using Euclidean distances across five distance classes (ARC MAP, version 9.3, ESRI, Redlands, CA, USA). Because we found a small but significant amount of spatial autocorrelation across all distance classes (max Moran's I was 0.188 at 10 km lag), we generated simultaneous autoregressive (SAR) versions of each of the AIC +2 models to examine the impact of explicitly accounting for spatially correlated errors within the model. SAR analyses were performed in the SAM package (version 4.0; Rangel *et al.*, 2010).

Funding

To explore patterns of funding allocation for invasive control on protected areas, we performed three analyses. First, we used multiple regression, as above, to examine the relationship between site-level factors and log-transformed funding investment. We did this to see whether factors that might predict invadedness also predict treatment spend. For this analysis, there was no significant spatial signal so we present only the non-spatial model results (Moran's $I < 0.04$ for all lags). Then, we calculated the correlation between log-transformed total funding and observed invadedness. Finally, we used partial correlation to examine the relationship between log-transformed total funding and invadedness while controlling for site-level predictor variables. We performed these correlations to see whether current spending was associated with invadedness across the network.

Results

Invadedness

Overall, 23 455 hectares were infested across the 365 study protected areas (total area of study protected areas = 466 623 HA). *Schinus terebinthifolius* (all species per Wunderlin & Hansen, 2003) was found on about 1% of the total area, and six other species were also found on more than 1000 HA of protected area each (*L. microphyllum, Urena lobata, I. cylindrica, Colocasia esculenta, L. japonicum and Solanum viarum*, Table 2). The number of protected areas that each of the 28 species occurred on ranged from 211 with *S. terebinthifolius* to 25 with *Ardisia crenata* (Table 2). Invadedness of individual protected areas varied widely (Table 3) as measured by the sum of cover by all 28 species

Table 2 Distribution of dominant invasive species across study protected areas

Plant name	HA cover	Number of protected areas
Schinus terebinthifolius	4644	211
Ludwigia peruviana	2754	101
Lygodium microphyllum	2204	41
Urena lobata	2102	154
Imperata cylindrica	1518	120
Colocasia esculenta	1362	56
Lygodium japonicum	1099	77
Solanum viarum	1034	28
Panicum repens	876	94
Melaleuca quinquenervia	787	52
Casuarina equisetifolia	687	60
Leucaena leucocephala	642	56
Urochloa mutica	526	53
Dioscorea bulbifera	406	96
Panicum maximum	377	98
Rhynchelytrum repens	310	64
Cinnamomum camphora	305	87
Ricinus communis	291	44
Nephrolepis cordifolia	263	90
Sphagneticola trilobata	245	72
Sapium sebiferum	240	92
Lantana camara	236	97
Abrus precatorius	235	72
Melia azedarach	223	79
Syngonium podophyllum	52	48
Ardisia crenata	31	25
Lonicera japonica	7	34
Albizia julibrissin	1	51

Table 3 Descriptive statistics of variables

Variable	5th Percentile	Median	95th Percentile
Invadedness (all data)	8 E-06	0.02	0.38
Invadedness (points, $n = 94$)	9 E-07	0.0003	0.18
Invadedness (polygons, $n = 73$)	2 E-05	0.03	0.56
Total HA	2	60	8600
Households within 25 km	10,000	104,000	679,000
Winter min temperature (C°)	4	7	11
Road length (m)	45	2000	82,000
Mean elevation (m)	1	4	32
Funding (\$, $n = 46$)	2500	44,000	582,000

divided by protected area size (relationship between invadedness and species richness, $R^2 = 0.03$, $P < 0.01$; Iacona, unpublished data). But, in general, the protected areas had low invasive plant cover; 67% of protected areas had invadedness proportions < 0.05.

The model using all data (points and polygons, Table 4) suggests that invadedness of a protected area decreases as site size increases and as the number of surrounding houses decreases (Fig. 2). Both of these factors were included in all models in the AIC +2 set, and the confidence limits on the coefficients did not span zero (Table A1). Comparison of the partial r^2 values suggested that the majority of explained variation in invadedness was determined by protected area size and nearby household density (Table A2). Because transformation of variables makes interpretation of our model coefficients less intuitive, we illustrate the predicted relationships using a hypothetical situation where we examine the variation in modelled invadedness when all predictor variables are set to their median value. If we then double protected area size (from 60 HA to 120 HA), back-transformed invaded area only increases by 60%. Similarly, if only the number of surrounding households is doubled from the median, invaded area increases by 61%. However, this model had relatively low explanatory power ($R^2 = 0.20$). There was no relationship between road cover, elevation or temperature and invadedness. Accounting for spatial effects with the SAR model produced similar predictions with regard to magnitude and direction of coefficient values for the protected area size effect (Table A3). Meanwhile, the coefficient value for the nearby households effect decreased, and the model explanatory power increased (R^2 increased by about 30% if space is included in the model). The coefficient values suggest greater variation in the effect of households than that of area when space is accounted for. This suggests that a spatial effect that drives household density, such as coastal clustering, may be impacting the non-spatial regression results.

Protected areas where invaded area was calculated by GIS (polygons) were more invaded than protected areas where invaded area was estimated by surveyor (points) (point protected areas median invadedness = 0.0003%, interquartile range 0.0000–0.0090, polygon protected areas median invadedness = 0.03%, interquartile range 0.00–0.018, Table 4). At protected areas where invasive plant cover was estimated by the surveyor (point data only), the relationship between invadedness and protected area size and surrounding household density were similar to the model with all data but the explanatory power was much greater ($R^2 = 0\ .50$, $n = 94$, Table 4, Table A4). For protected areas where invaded area was calculated by GIS (polygon data only), the predictions were also the same as the model with all data, but with greatly decreased explanatory power ($R^2 = 0.09$, $n = 73$, Table 4, Table A6). This result indicates that the answer to our question 'does data structure affect explanatory power of the model?' is yes, but perhaps not in the way one might have anticipated. Comparison of the partial r^2 values suggested that in both cases, protected area size explained the largest proportion of variation in invadedness (Table A5, Table A7).

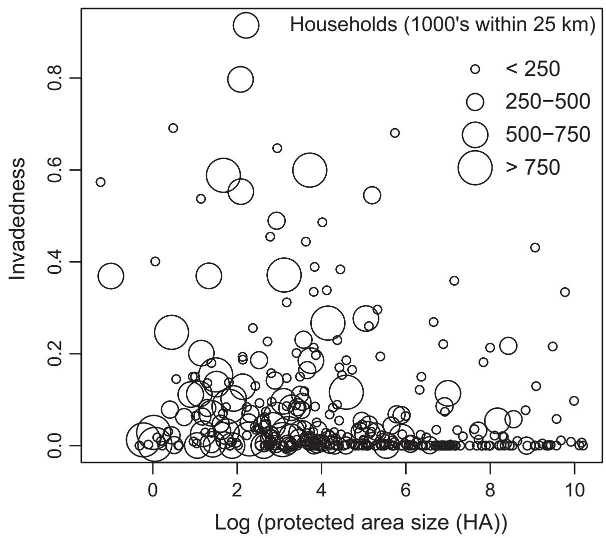

Figure 2 Plot of invadedness (proportional cover of aggregate invasive plant species on a protected area) versus protected area size. Points in the figure are scaled according to the number of households within 25 km of the protected area.

Table 4 Parameter estimates, standard errors and partial r^2 for the model average across the AIC +2 set of parsimonious models for predicting invadedness of protected areas (Box–Cox-transformed) for all of the data, and subsets including only points ($n = 94$), only polygons ($n = 73$) and funding data (log-transformed, $n = 46$)

	Model average	Intercept	log HA	log House density	log Road cover	log elevation	Min. temperature	R^2
All	Coefficient ± 1 SE	−7.89 ± 0.90	−0.15 ± 0.03	0.43 ± 0.07	0.00 ± 0.00	−0.02 ± 0.03	0.02 ± 0.02	0.20
	Partial r^2		0.11	0.09	0.00	0.00	0.00	
Points	Coefficient ± 1 SE	−6.75 ± 1.37	−0.38 ± 0.06	0.32 ± 0.11	−0.01 ± 0.01	0.00 ± 0.03	0.00 ± 0.02	0.49
	Partial r^2		0.44	0.05	0.00	0.00	0.00	
Polygons	Coefficient ± 1 SE	−2.62 ± 0.94	−0.20 ± 0.08	0.03 ± 0.04	0.01 ± 0.01	−0.02 ± 0.03	0.01 ± 0.09	0.09
	Partial r^2		0.08	0.00	0.00	0.00	0.00	
Funding	Coefficient ± 1 SE	0.06 ± 3.03	0.25 ± 0.10	0.73 ± 0.21	0.06 ± 0.06	−0.01 ± 0.04	0.00 ± 0.03	0.31
	Partial r^2		0.10	0.21	0.00	0.00	0.00	

Funding

Funding for invasive plant treatment over a 10-year period varied greatly ($1600 to >$1 million). Protected area features explained 31% of the variation in funding invested in invasive species control across protected areas (Table 4, Table A8). Larger protected areas were allocated more treatment dollars in the 10-year period, as would be expected (Table A9); however, the coefficient on protected area size was < 1, suggesting an economy of scale, an issue we return to in the discussion. More money was also spent at protected areas with higher surrounding household density. If we examine changes in predictor and response variables using a hypothetical situation as above, spending on invasive species management only increases by 19% when protected area size is doubled. Meanwhile, if the number of surrounding households doubles, spending on invasive species management increases by 66%. There was no relationship between funding investment and invadedness (Fig. 3), either alone or when controlling for site-level predictor variables.

DISCUSSION

We show that readily available site-level features are related to protected area invadedness (explaining 9–50% of the variation). This is an important result because the amount of invasive cover impacts the conservation value of a protected area (Martin & Blossey, 2012) and likely the ultimate cost of management. However, studies of invasion of protected areas have tended to focus on species richness of invaders instead of cover (McKinney, 2002; Pysek *et al.*, 2002). Our study also illustrates that the allocation of funding for management of invasive species can be predicted by protected area features, but is not clearly related to invasion across the network. At least in Florida, management investment does not appear to track protected area invadedness. Thus, predictions of long-term costs based on current spending patterns may be inaccurate.

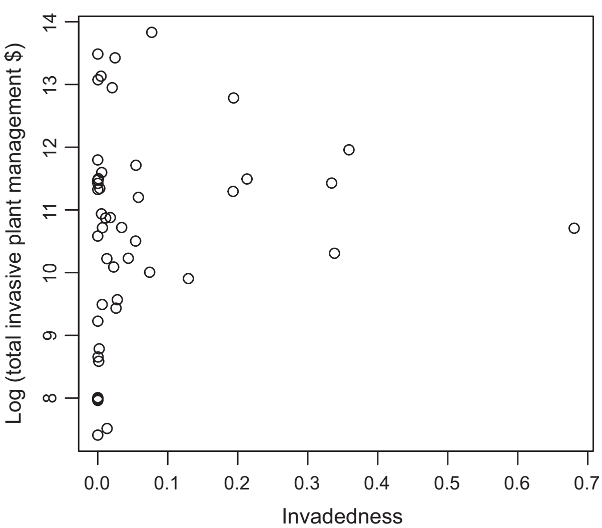

Figure 3 Plot of cumulative spend on invasive plant management (log-transformed) at each protected area over a 10-year period versus invadedness.

Site-level predictors of invadedness

Protected area size and the number of nearby households were the most important predictors of invadedness of the factors that we tested. This result is similar to previous work (Catford *et al.*, 2011; Polce *et al.*, 2011) and illustrates how factors that influence propagule pressure or site disturbance drive invasion at a protected area. The effect of nearby households could be as a seed source as recent studies have shown that propagule pressure is one of the primary drivers of invasion at a site (Von Holle & Simberloff, 2005; Simberloff, 2009). Household density may influence direct disturbance by human visitors such as foot traffic (Mack & Lonsdale, 2001). Meanwhile, the relationship of invadedness to protected area size may indicate the importance of ecological processes, such as fire or flooding, that maintain native community structure and limit invasion success (Hobbs & Humphries, 1995). These processes may be more likely to occur on large protected areas than on small protected areas. Protected area size could also influence invadedness if invasive plants move onto the site from populations around the edge (Morgan, 1998; Yates *et al.*, 2004; Alston & Richardson, 2006). Larger protected areas tend to have lower edge-to-area ratios than smaller protected areas and therefore could have lower levels of invadedness. However, sensitivity tests that added edge-to-area ratio as a predictor variable in the models found that edge effects are an unimportant aspect of the relationship with protected area size (with edge-to-area ratio included, the model average $R^2 = 0.21$; partial $r^2 = 0.001$, Table A12 and Table A13).

Several site-level predictors had no relation to invadedness contrary to our expectations. We expected minimum winter temperature to be important because latitudinal gradients drive patterns of invasion on a world-wide scale (Pysek & Richardson, 2006). The observed lack of relationship may be due to the continuous nature of the variable versus the more binary biological response to subfreezing temperatures. To test this possibility, we ran a sensitivity analysis using a dummy variable that indicated 3 or more frost days per year. This test suggested that protected areas in south Florida may be more invaded because 3 or fewer frost days per year was as good a predictor variable as protected area size and number of surrounding households (Tables A10–A11). We were also surprised that road cover did not relate to invadedness as it is often assumed that roads are an indicator of disturbance and a vector for propagule movement (Von Der Lippe & Kowarik, 2007). This may have been due to our road cover variable not accurately measuring those impacts. Some of the larger protected areas in rural regions of the state have extensive networks of old logging roads yet are relatively invasion-free.

The relatively low predictive power ($R^2 \sim 0.20$) of the model with all the data may result from our aggregation of multiple species for the invadedness metric. We wanted to predict the total invaded area because it is relevant to land managers and conservation planners (Kuebbing *et al.*, 2013), but preliminary results from models of single species invadedness suggest enhanced predictive ability for individual species ($R^2 \sim 0.36$–0.52, Iacona, unpublished results).

The utility of these levels of predictive ability depends on what the predictions are to be used for. If management of invasive plant infestations at a small scale is the objective, then much more detailed knowledge of the location and extent of invasion are necessary. In such a case, the inference supplied by a model such as this would not be at the scale of interest, and site-level surveys would be necessary. However, if the model predictions are intended for conservation decision-making at a regional scale (e.g. if assessing the possible consequences of pursuing agency-wide policies on minimum reserve sizes), it is more important to understand the variation in network wide trends of invadedness. In such cases, a model such as this that uses easily obtainable coarse-grain data to cheaply describe expected variation in invadedness across large scales would be appropriate.

Data structure

The increase in predictive capacity of models for protected areas where invaded area was estimated by surveyors (point data) indicates that our site-level predictive factors may best describe invasion at small protected areas or low densities. This is because, in practice, the invasive plant occurrences on a protected area may be represented as point data, polygon data or both types, depending on surveyor preference and the needs of the managing agency. Generally, a surveyor uses point data when estimation of the size of a hypothetical circle is adequate to represent an infestation such as for small protected areas or protected areas where invasive plant occurrences are widely scattered clumps. Meanwhile, collection of polygon data allow for the GIS calculation of invaded acreage within more realistic infestation shapes, which is useful for large or heavily infested protected areas. Polygon data may be preferred by managing agencies because it better represents the area that needs to be treated. Our result suggests that model inference depends on the type of data collected.

Funding model

Funding allocation increased with surrounding household density, similar to predictions of invadedness. In addition, total funding allocation increased with protected area size. Because the model was constructed as a log-transformed response to a log-transformed predictor, the coefficient value can provide an indication of economies of scale (Armsworth *et al.*, 2011). When back-transformed, these models examine a power law relationship between area and invadedness. If the coefficient on protected area size was 1, there would be a linear relationship between back-transformed funding allocation and protected area size. However, our modelled coefficient is much < 1 (0.25), suggesting a possible invasive plant management economy of scale where less is spent to manage an additional hectare if it is added to a large protected area than if it is added to a small protected area. If previous spend is an accurate indicator of need, these results suggest that larger protected areas in rural areas would be cheaper to manage over the long term and that small protected areas in high population density regions would be the most expensive per relative area.

The previous result suggests that funding may be allocated in a manner that tracks invadedness. However, we found no relationship between invadedness and funding, either overall or after controlling for the effects of protected area features. If total funding were to scale with protected area features (as it seems to) and if spending on management decreased invasive cover, we would expect variation in funding to relate to variation in invadedness. There are two scenarios that would produce an observable relationship. If management funding was adequate to meet treatment needs and the management objective was to eliminate infestations (as opposed to merely preventing an increase), we would expect to see a negative relationship between invadedness and funding allocation. Meanwhile, if funding was spent in accordance with protected area invadedness but had no effect in reducing the extent of existing infestations, we would expect to have seen a positive relationship between invadedness and funding allocation.

We did not observe either of these patterns, but there are many potential explanations for a lack of relationship. For instance, if both of these scenarios were in effect, they could cancel each other out. Alternatively, the lack of relationship could result from inadequate resources to change invadedness on a protected area. However, opportunistic allocation of treatment dollars by the state could also result in the observed patterns, and the current allocation strategy provides funding only to protected areas that apply for it (Cleary, 2007). Our results suggest that these applications for funding may not relate to onsite invasive cover. Finally, this may be an effect of other unaccounted for treatment funding. For instance, maintenance efforts that are not specifically for invasive species treatment, such as burning, can reduce invasive cover and are not included in this analysis. Also, cost sharing can influence prioritization of funds, and our dataset may not represent all funding for invasive treatment at a protected area if local agencies engage in projects without FWCC assistance.

It is tempting to draw conclusions about effectiveness (or the lack thereof) of management treatment funding from our results. However, to do so, we would have to examine changes in invasive species cover over time as management funds are invested. This is not possible with our dataset because it is based on a single visit survey. FNAI aims to perform follow-up invasive species cover surveys on selected protected areas with the objective of assessing effectiveness of treatment spend. Such a study would provide insight into small-scale changes within a subset of these protected areas and the habitats they contain. In the meantime, we present this analysis as a first step towards examining the patterns of invasive species management funding allocation at a larger scale: one that is useful to conservation planners at a state-wide level. In addition, we calculate the covariance between invadedness and funding as a logical complement that explores whether existing data are appropriate for predicting future costs. We conclude that state-wide patterns of treatment funding allocation suggest that current funding is not a meaningful predictor of future need.

Conclusions and implications for conservation

Fragmentation and human density surrounding protected areas are both likely to increase in future. Although conservation planning has long considered protected area size and location to be important for connectivity and species persistence (Simberloff & Abele, 1982), we show that these features also impact invadedness. Larger protected areas are less invaded than small ones, and there is a positive correlation between nearby housing density and invadedness. In addition, more treatment funding is allocated to protected areas with higher nearby housing density and larger protected areas, in a manner consistent with economies of scale. This suggests that more invaded protected areas cost more to manage over time than less invaded protected areas, or they would if the management funding were allocated optimally (Lee *et al.*, 2009). Because we found no relationship between current funding allocation and invadedness, it is possible that current funding allocations do not fully represent management needs. Thus, estimates of future funding requirements for protected area management should be made with caution.

ACKNOWLEDGEMENTS

This research was supported by the Department of Ecology and Evolutionary Biology at the University of Tennessee. Data were provided by the Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory. Thanks to members of the Armsworth laboratory, S. Kuebbing, E. Larson, N. Sanders, R. Cleary, D. Simberloff, L. Gross and several anonymous referees for providing comments that greatly improved this document.

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SUPPORTING INFORMATION

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

Appendix S1 Detailed coefficient tables for all models.

Appendix S2 List of protected areas included in analysis.

BIOSKETCHES

Gwen Iacona is a conservation scientist with specific interests in quantifying and predicting the costs of managing protected areas for biodiversity conservation. Gwen is a PhD student with **Paul Armsworth** whose research group focuses on empirical and theoretical approaches to improving conservation effectiveness. She previously was a botanist at Florida Natural Areas Inventory (FNAI) where she worked with **Frank Price** on data collection for the Florida Invasive Plant Geodatabase (FLInv). Frank currently is the heritage programme data manager and invasive plant project manager at FNAI.

Author contributions: All authors conceived the ideas; F.P. provided data; G.I. performed the data analysis; G.I. and P.A wrote the paper.

Editor: David Richardson