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The economic costs and ecological benefits of protected areas for biodiversity conservation

Gwenllian D. Iacona
University of Tennessee - Knoxville, giacona@vols.utk.edu

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To the Graduate Council:

I am submitting herewith a dissertation written by Gwenllian D. Iacona entitled "The economic costs and ecological benefits of protected areas for biodiversity conservation." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Paul R. Armsworth, Major Professor

We have read this dissertation and recommend its acceptance:

Louis Gross, Daniel Simberloff, Donald Hodges

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Gwenllian D. Iacona
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The economic costs and ecological benefits of protected areas for biodiversity conservation

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Gwenllian D. Iacona
August 2014

For Megan and Mason

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Abstract

Conservation science acknowledges that economic cost and ecological benefit information is important for effective biodiversity conservation decision making. Obtaining this information for protected areas has proven difficult, however. This dissertation explores various aspects of obtaining information on the costs and benefits of protected areas in an effort to support applied conservation. Here I present a set of studies that 1) examine the threat and cost of plant invasion on protected areas, both for cumulative invasion and 2) across species that differ in their management priority, 3) provide a method for measuring the benefit of forest conservation, and 4) describe the conservation benefit implications from multiple conservation organizations working in the same region. The first two studies show that while conservation needs and prior costs can be estimated, there is no evidence that past expenditures relate to future budget requirements. This result is the impetus for the next study, where I develop a method to estimate the conservation benefit of forest protection using satellite imagery so that conservation professionals can better assess the relationship between conservation actions and outcomes. The final study reveals that competition for limited funding affects how conservation organizations allocate their resources, resulting in variation in benefit that depends on the organizations' priority alignment. Overall, my dissertation reinforces the importance of properly accounting for costs and benefits in conservation planning and provides insight and tools to help achieve that outcome.

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Chapter 1

Introduction

A primary goal of conservation science is to counteract human imposed ecological impacts and allow species and communities to persist into the future. Establishment of protected areas is the primary strategy that has been used to counteract ecological degradation, but it has yet to stem the tide of biodiversity loss (Gaston et al., 2008). Systematic conservation planning has promise for increasing the effectiveness of protected area establishment (Margules and Pressey, 2000), however, cost and benefit information is instrumental to the approach (Underwood et al., 2008). The problem is that both cost (Armsworth, 2014) and benefit (Maron et al., 2013) information is difficult to obtain. This dissertation approaches this problem by examining some of the details of obtaining economic cost and ecological benefit information that relate to protected areas for biodiversity conservation.

Ecological communities are assemblages of interacting species whose identity and function are influenced by their dynamic environment. Ecologists have long been interested in the interactions and processes that shape these communities, but have often failed to account for the activities of a species with tremendous recent impact. Human activities have affected every ecosystem on the planet (Sanderson et al., 2002), driven many species extinct (Barnosky et al., 2011), and disrupted important regulatory processes such as climate (IPCC, 2007), fire regime (Bowman et al., 2011), and hydrology (Fernald and Purdum, 1998). This has resulted in a global biodiversity crisis.

The number of protected areas worldwide has drastically increased in the past 100 years as we attempt to counteract the human impacts on biodiversity (Naughton-Treves et al., 2005). However, the protection level is still not adequate (Gaston et al., 2008). This could be because protected area establishment was often opportunistic (Pressey, 1994), and in many cases ended up protecting marginal lands that were not ideal for biodiversity conservation (Scott et al., 2001; Groves et al., 2000).

Systematic conservation planning is an attempt to resolve the problems that arose from opportunism by using quantitative methods to target protected areas to the places where the species that need protecting actually reside (Margules and Pressey, 2000; Moilanen et al., 2009). Modern methods suggest that the threat of habitat conversion or species loss must also be incorporated into the planning process (Margules and Pressey, 2000; Newburn et al., 2005; Carwardine et al., 2012). In addition, a consideration of the costs of establishing (Ando et al., 1998; Wilson et al., 2006) and/or maintaining (James et al., 1999; Naidoo et al., 2006) protected areas is important for cost effective conservation (Withey et al., 2012).

Spatial optimization techniques allow for the maximization of expected conservation benefits when there is a cost constraint (Moilanen et al., 2009). The solutions to these optimizations suggest rules-of-thumb for ranking potential protected areas for effective conservation (Wilson et al., 2006). The ranked projects can then be prioritized for funding and protection. An example of a ranking metric follows (adapted from Newburn et al., 2005):

$$\frac{\text{Avoided threat * Benefit}}{\text{Cost}}$$

Here the relative conservation importance of a protected area within a network can be assessed by quantifying the biodiversity benefit and threat reduction that it provides. This value is then divided by the cost of acquiring those benefits to allow for equivalent comparisons across protected areas. Ranking conservation projects using this approach has been applied in conservation initiatives such as the Investment Framework for Environmental Resources in Western Australia (Pannell et al., 2012) and the Project Prioritization Protocol as applied in New Zealand (Joseph et al., 2009). The problem is that estimates of the cost, benefit, and threat values that should be entered into the ranking are not easy to obtain (Pannell et al., 2013).

For this dissertation, I designed a suite of studies to examine various understudied aspects of protected area costs, benefits and threats. I chose two areas of specific focus: 1) how to predict the threat and costs of invasive species treatment on protected areas, and 2) how to measure the benefit of conservation spending on protected areas.

Invasive exotic species can disrupt ecological processes in their introduced range (Gordon, 1998). They have been responsible for species extinctions throughout the world (Simberloff, 2005) and are widely considered to be a primary threat to biodiversity conservation. Most protected areas face biological invasion, and a major focus of land management is to control the impacts of these species (Tempel et al., 2004). In chapter 2, I develop a method for predicting the threat of invadedness (relative proportional cover) across protected areas by using features of the protected areas themselves. I then use ten years worth of invasive plant management data to examine whether funding allocation can be predicted from site level features and if it covaries with invadedness. I show that the size of a protected area and the surrounding household density can predict variation in both invadedness and funding allocation. However, I also find that cumulative treatment funding does not relate to current invadedness across the study sites. Based on these results I suggest that estimates of management need can be related to protected area features, but that past funding levels cannot provide an indication of future costs.

I expand my invadedness model in chapter 3, to examine how predictions of both presence and invadedness vary across species. In particular, I am interested in whether site level predictive features of presence and invadedness differ between species that are prioritized for management versus those that are not. I find that predictors of presence and invadedness differ both across and within species. Predictors of presence are not necessarily the same as those that predict cover, which has implications for management planning. Meanwhile, there are no clear predictors of either presence or invadedness that relate to management priority. However, several predictors are common to multiple species suggesting that general predictions of invasion can be appropriate.

I then move on to two studies that examined the benefit of conservation spending. Planners need to know the outcomes of spending in order to maximize the value of conservation expenditures (Parrish et al., 2003). However, there is some worry that conservation spend is not being allocated as efficiently as possible (Ferraro and Pattanayak, 2006). This could be because the benefit of conservation spending is difficult to assess. When the desired outcome of conservation spending is biodiversity protection, a measure of benefit needs to examine the direct outcomes of spending and compare them to outcomes where no spending occurred (Gaston et al., 2008). This approach has been hindered in practice because it is difficult to quantify outcome (Geldmann et al., 2013), data on the counterfactual is usually unavailable (Maron et al., 2013), and the measurement of benefit in general has not been a priority for conservation science (Naughton-Treves et al., 2005)

In chapter 4, I test a set of models to estimate attributes of forest structure and composition that would be important for assessing the benefit of management on a PA. I show that some forest attributes are able to be explained using remote sensing imagery. I find that about half of the variation in both tree size and the proportion of pine trees can be explained by my approach, and lesser amounts of variation in several other forest attributes is also explained by my models. I then use two of the models to explore example applications that examine the relationship between PA size and forest change over time as a demonstration of how these models could be used by conservation professionals. Example applications that examine predictions of dbh at acquisition and changes in pine species density over time do not suggest that these attributes were related to PA size on my study sites.

Chapter 5 uses a theoretical framework to analyze the impact on biodiversity benefit of strategic interactions between multiple conservation organizations. In my other work on quantifying costs and benefits, I noticed a discrepancy between the academic writing on these concepts and what actually occurred in the real-world. The literature almost exclusively considers cost and benefit accounting from the perspective of a single organization, but my work with practitioners demonstrated that multiple organizations were involved in almost every conservation project. This chapter is an examination of how current conservation theory is not appropriately accounting for benfit by ignoring interactions between organizations. Here I show that measurements of the benefit of conservation spend need to consider the strategic actions of other organizations in the region. Depending on the amount of priority alignment across organizations, conservation funders can actually do much better or worse than their expected returns if they do not consider the actions of other organizations.

Overall, this dissertation explores some of the many aspects of the costs and benefits of protected areas. It provides a method for quantifying an avoided threat, some insight into obtaining a specific management cost, and a method and consideration for measuring benefit. Although there is much work left to be done, these studies provide results that can be used by conservation professionals to enhance the conservation planning process.

Chapter 2

Predicting the invadedness of protected areas

The following section is a slightly modified version of a paper published in the journal *Diversity and Distributions.* It is reproduced here under permission from Wiley and Sons, license number 3411980201544

Iacona, G.D, Price, F., and P.R. Armsworth. 2014. Predicting the invadedness of protected areas. *Diversity and Distributions.* 20: 430-439

The use of "we" in this chapter refers to me and my co-authors. As the lead author of this article I was responsible for this paper. G.D.I, F.P, and P.R.A. designed the research, G.D.I and P.R.A wrote the paper.

Abstract

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. We use data on invasive plant cover and protected area features from 365 protected areas across the state of Florida, USA 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. We find that invadedness (the 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 (8 - 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. Our results suggest that basing predictions of future costs on current funding may not accurately represent budgetary needs.

2.1 Introduction

Managers of protected areas (PAs) face the difficult exercise of how to plan for treatment of invasive species infestations within budget limitations. Invasive species inhabit protected areas worldwide (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 PA, but available data on invasive species presence and cover is often incomplete. One solution is to use site-level features to predict trends in relative invasive cover (invadedness) across a network of PAs.

Invasive species presence at a PA may respond to features that regulate the native community's resistance to invasion (Myers and Ewel, 1990; Hobbs and Humphries, 1995), or to features that influence whether invasive plant propagules can reach the PA and become established (Simberloff, 2009; Kuhman et al., 2010). Protected area features that influence plant community composition include those such as PA size, elevation, and temperature, that drive landscape level processes (Pyšek et al., 2002a). Meanwhile, PA 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 PAs, 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 PAs 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 Florida it costs about 6 000$/HA for the initial treatment of cogon grass (Imperata cylindrica) (Jubinsky, G., *Personal communication*) and this grass infests about 1 500 HA of PAs in our dataset (Table 2.2). 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 five year period (Carwardine et al., 2011).

Invasive species management can account for a large proportion of the PA management budget (Frazee et al., 2003). Because the management budget of a PA 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 PAs would be a useful first step towards efficient conservation resource allocation (Buchan and 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 PAs (eg. for allocating regional funding or evaluating tradeoffs with regard to future PA 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 PA. Because it measures the current invasion at a PA, 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 PA features, and then use management expenditures to examine the relationship between treatment funding and invadedness. First we ask 1) what features of a PA 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 (eg. planning for funding needs across hundreds of PAs). 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 PA 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 PAs, rather than a cost estimate for an individual PA.

2.2 Methods

Study system

We used data from publicly-owned PAs in the state of Florida, USA. Florida has more than 1800 publicly-owned PAs 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 dollars to manage invasive plants on all PAs between 1999 and 2010 (Cleary, R. *unpublished work*).

Invasive plant distribution

We obtained invasive plant distribution data from the FLInv geodatabase which contains occurrence records for FLEPPC-listed species on all of the public PAs in Florida. This database was commissioned by the Florida Fish and Wildlife Conservation Commission (FWC) 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 PAs throughout the state) to increase reliability of identification. 2) We chose PAs 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, percent cover (binned for analysis into 2.5%, 15%, 38%, 63%, 88%), and area infested (estimated acreage recorded by surveyor for points, acreage calculated by spatial analysis software for polygons). 3) We chose records from PAs 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 PAs across Florida. While a subset of the whole network of PAs, it was still a large sample spanning gradients of protected areas features (Table 2.1) 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 PA, we calculated “invadedness” as a measure of relative variation in the extent of invasion across PAs. To construct our metric we first calculated the area of invasive cover for each occurrence record by multiplying the acreage infested by the percent cover bin. We then summed the area covered by focal species at a PA to calculate the proportion of the PA infested (sum of area of 28 species/ area of PA, Figure 2.1). This value indicates the proportion of the PA 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 understory 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 PAs 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 PAs 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 PA features, we chose predictors that tested specific *a priori* hypotheses motivated from past studies (Table 2.1).We first examined factors that could relate to ecological function and community composition at a PA. Protected area size information was obtained from the Florida Managed Areas GIS layer of PAs managed for conservation within the state (maintained by FNAI). We derived PA average elevation from USGS NED 1/3 arc second data layers at 1 m resolution. Minimum winter PA 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 PA. 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 PA. We also used roads as a proxy of onsite disturbance. For this predictor variable, we divided area of roads by PA area for all roads that intersected or were adjacent to the PA, using an average road width of 10 m (USGS 24000:1 roads layer).

Funding for invasive plant management

To address the question "how is invasive plant management funding allocated across a subset of PA, 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 PAs within the state (Cleary, 2007). Invasive plant management funding on our 46 PAs totalled almost $50 million dollars and was allocated under the Upland Invasive Exotic Plant Management Program. This constitutes about half of the total program spend over the previous ten year period. For 42 of the protected areas, this funding was awarded prior to the PA being surveyed for invasive plants. Funding proposals are permitted for any FLEPPC-listed invasive species, but often projects involving target species or re-treatment projects are prioritized for funding by FWC. 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 PAs from

1999 to 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) to test for statistical associations between PA features (Table 2.1) 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 2.1. 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 2 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 5 distance classes (Arc Map, version 9.3). 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 PAs 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 if 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 if current spending was associated with invadedness across the network.

2.3 Results

Invadedness

Overall, 23 455 hectares were infested across the 365 study PAs (total area of study PAs = 466 623 HA). *S. terebinthifolius* (all species per Wunderlin and Hansen, 2003) was found on about 1% of the total area and six other species were also found on more than 1 000 HA of PA each (*L. microphyllum, Urena lobata, I. cylindrica, Colocasia esculenta, L. japonicum,* and *Solanum viarum*, Table 2.2). The number of PAs that each of the 28 species occurred on ranged from 211 with *S. terebinthifolius* to 25 with *Ardisia crenata* (Table 2.2). Invadedness of individual PAs varied widely (Table 2.3) as measured by the sum of cover by all 28 species divided by PA size (relationship between invadedness and species richness, $R^2 = 0.03$, $p < 0.01$; Iacona, unpublished data). But, in general, the PAs had low invasive plant cover; 67% of PAs had invadedness proportions less than 0.05.

The model using all data (points and polygons, Table 2.4) suggests that invadedness of a PA decreases as site size increases and as the number of surrounding houses decreases (Figure 2.2). 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 2.5). Comparison of the partial r^2 values suggested that the majority of explained variation in invadedness was determined by PA size and nearby household density (Table 2.6). 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 PA 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 regards to magnitude and direction of coefficient values for the PA size effect (Table 2.7). 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 PAs where invaded area was estimated by surveyor (points) (point PAs median invadedness = 0.0003%, interquartile range 0.0000 - 0.0090, polygon

PAs median invadedness = 0.03%, interquartile range 0.00 - 0.018, Table 2.4). At PAs where invasive plant cover was estimated by the surveyor (point data only), the relationship between invadedness and PA 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 2.4, Table 2.8). For PAs 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 ($R^2 = 0.08$, n = 73, Table 2.4, Table 2.10). 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 PA size explained the largest proportion of variation in invadedness (Table 2.9, Table 2.11).

Funding

Funding for invasive plant treatment over a ten-year period varied greatly ($1 600 - >$1 million). Protected area features explained 31% of the variation in funding invested in invasive species control across PAs (Table 2.4, Table 2.12). Larger PAs were allocated more treatment dollars in the ten-year period, as would be expected; however, the coefficient on PA size was less than 1, suggesting an economy of scale, an issue we return to in the discussion (Table 2.13). More money was also spent at PAs 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 PA 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 (Figure 2.3), either alone or when controlling for site-level predictor variables.

2.4 Discussion

We show that readily available site-level features are related to PA invadedness (explaining 8 - 50% of the variation). This is an important result because the amount of invasive cover impacts the conservation value of a PA (Martin and Blossey, 2012) and likely the ultimate cost of management. However, studies of invasion of PAs have tended to focus on species richness of invaders instead of cover (McKinney, 2002; Pyšek et al., 2002a). Our study also illustrates that the allocation of funding for management of invasive species can be predicted by PA features, but is not clearly related to invasion across the network. At least in Florida, management investment does not appear to track PA invadedness. Thus, predictions of long-term costs based on current spending patterns may be inaccurate.

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 PA. 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 and Simberloff, 2005; Simberloff, 2009). Household density may influence direct disturbance by human visitors such as foot traffic (Mack and Lonsdale, 2001). Meanwhile the relationship of invadedness with PA size may indicate the importance of ecological processes, such as fire or flooding, that maintain native community structure and limit invasion success (Hobbs and Humphries, 1995). These processes may be more likely to occur on large PAs than on small PAs. 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 and Richardson, 2006). Larger PAs tend to have lower edge-to-area ratios than smaller PAs 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 PA size (with edge-to-area ratio included, the model average $R^2 = 0.21$; partial $r^2 = 0.001$, Table 2.16, Table 2.17).

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 worldwide scale (Pyšek and Richardson, 2006). The observed lack of relationship may be due to the continuous nature of the variable versus the more binary biological response to sub-freezing 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 PAs in south Florida may be more invaded because 3 or fewer frost days per year was as good a predictor variable as PA size and number of surrounding households (Table 2.14, Table 2.15). 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 and Kowarik, 2007). This may have been due to our road cover variable not accurately measuring those impacts. Some of the larger PAs in rural regions of the state have extensive networks of old logging roads yet are relatively invasion-free.

The relatively low predictive power ($R^2 \approx 0.20$) 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 models of single species invadedness suggest enhanced predictive ability for individual species (chapter 3, this dissertation).

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 is 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 PAs where invaded area was estimated by surveyors (point data) indicates that our site-level predictive factors may best describe invasion at small PAs or low densities. This is because, in practice, the invasive plant occurrences on a PA 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 PAs or PAs 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 PAs. 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 PA 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 PA size was 1 there would be a linear relationship between back-transformed funding allocation and PA size. However, our modelled coefficient is much less than one (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 PA than if it is added to a small PA. If previous spend is an accurate indicator of need, these results suggest that larger PAs in rural areas would be cheaper to manage over the long term and that small PAs 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 PA features. If total funding were to scale with PA 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 have seen a negative relationship between invadedness and funding allocation. Meanwhile, if funding was spent in accordance to PA 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 PA. 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 PAs 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, etc., 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 PA if local agencies engage in projects without FWC 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 PAs with the objective of assessing effectiveness of treatment spend. Such a study would provide insight into small scale changes within a subset of these PAs 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 PAs are both likely to increase in the future. Although conservation planning has long considered PA size and location to be important for connectivity and species persistence (Simberloff and Abele, 1982), we show that these features also impact invadedness. Larger PAs 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 PAs with higher nearby housing density and larger PAs, in a manner consistent with economies of scale. This suggests that more invaded PAs cost more to manage over time than less invaded PAs, 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 PA management should be made with caution.

Acknowledgements

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2.5 Appendix: Figures

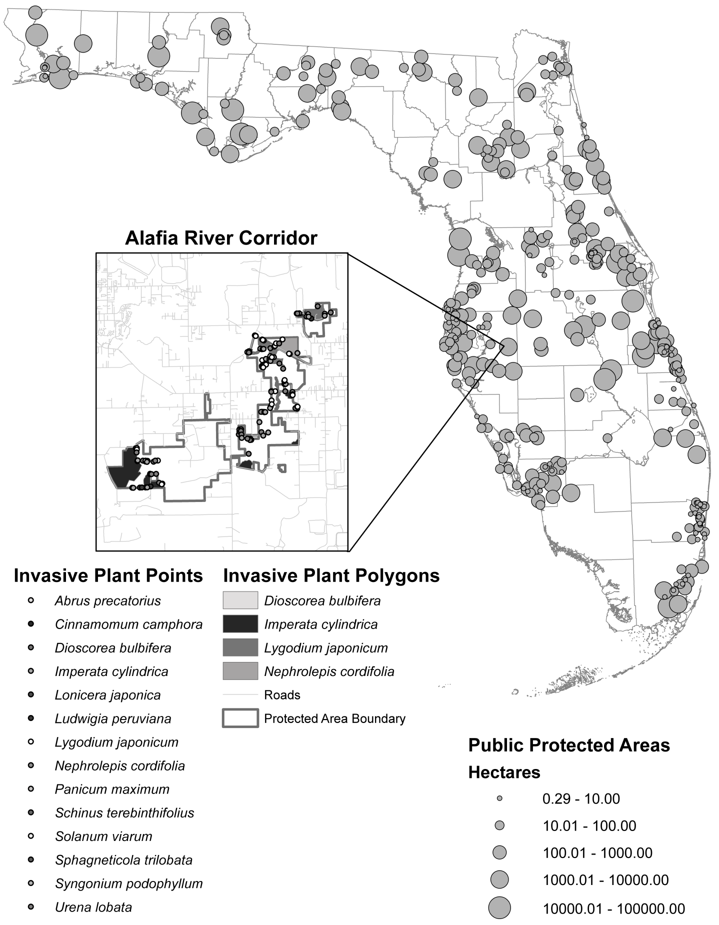

Figure 2.1: Invadedness study sites: 365 public protected areas in Florida were used in the analysis. Inset map illustrates the set of invasive plant occurrences (points and polygons) at one protected area (Alafia River Corridor). The sum of the area*percent cover of each occurrence is aggregated into the invadedness metric for a protected area.

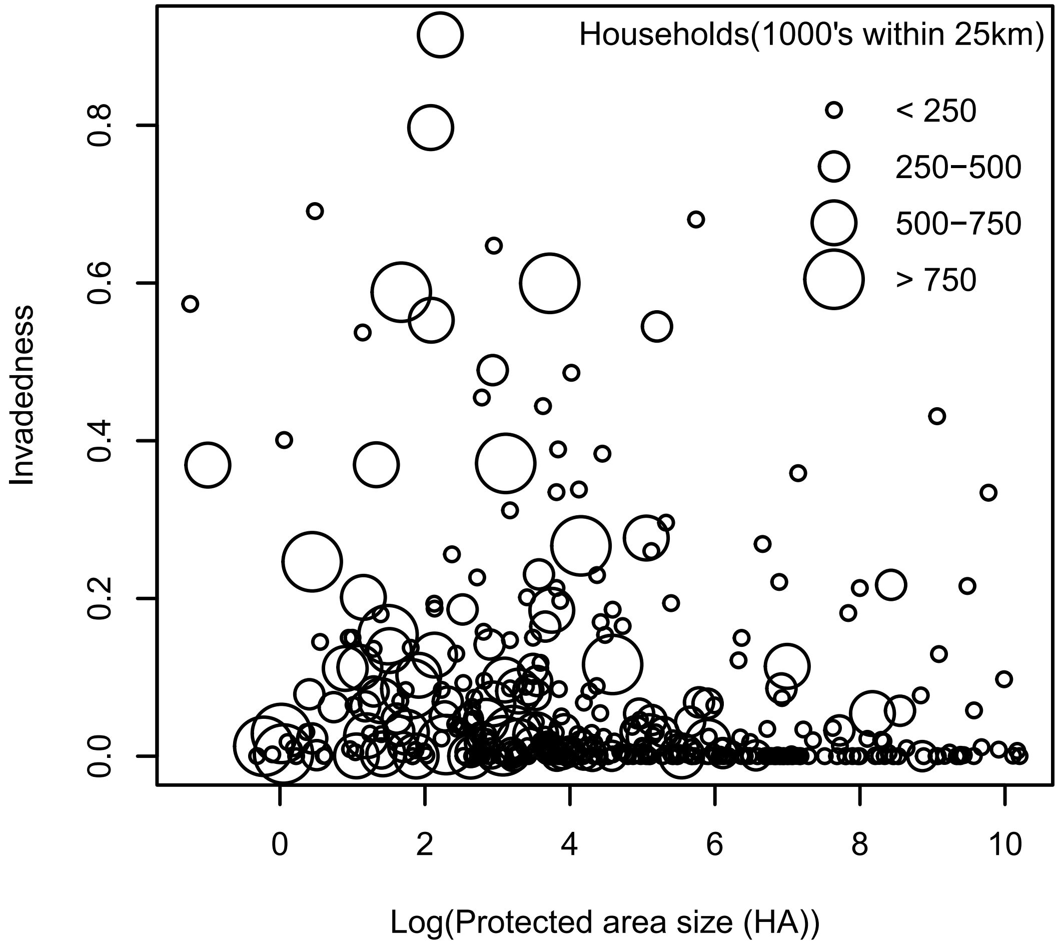

Figure 2.2: Plot of invadedness (proportional cover of aggregate invasive plant species on a protected area) versus protected area size. Points in the figure are scaled according to the number of households within 25 km of the protected area

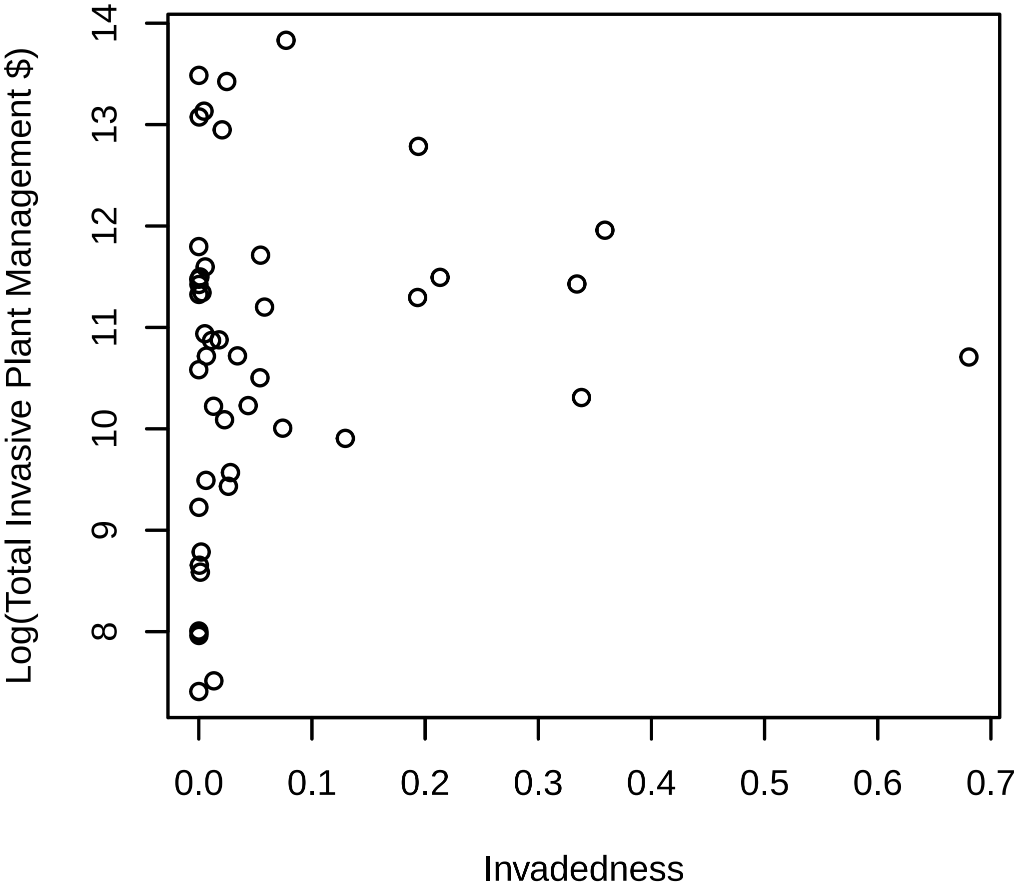

Figure 2.3: Plot of cumulative spend on invasive plant management (log transformed) at each protected area over a ten year period versus invadedness

2.6 Appendix: Tables

Table 2.1: 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 more invaded than larger protected areas (Pyšek et al., 2002a; Lonsdale, 1999; McKinney, 2002) because ecological processes that may minimize invasion are more likely in large areas (burning, flooding, population stability)	totalHA
Elevation	We expect lower (wetter) protected areas to be more invaded than higher (drier)protected areas(Pyšek et al., 2002a; Chytrý et al., 2008)(eg: 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 (Pyšek et al., 2002a; Catford et al., 2011; Gasso et al., 2012; Pyšek et al., 2010; Stohlgren et al., 2006) 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 would increase with invadededness.	Road cover (m^2/m^2) per protected area

Table 2.2: 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 2.3: Descriptive statistics of variables

Variable	5^{th} **percentile**	**Median**	95^{th} **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	8 600
Households within 25 km	10 000	104 000	679 000
Winter Min Temperature (C)	4	7	11
Road Length (m)	45	2 000	82 000
Mean Elevation (m)	1	4	32
Funding ($, n=46)	2 500	44 000	582 000

Table 2.4: 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=42).

	Model average	Intercept	log HA	log house density	log road cover	log elevation	min. temperature	R^2
All	Coefficient±1 s.e.	-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 s.e.	-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 s.e.	-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 s.e.	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	

2.7 Appendix: Supplementary Information

Table 2.5: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed)from all data on 365 protected areas .

MODEL	Intercept	log HA	log house density	log road cover	log elevation	min. temperature
1	-7.89±0.86	-0.15±0.03	0.44±0.07	0.00±0.00	0.00±0.00	0.00±0.00
2	-8.10±0.88	-0.15±0.03	0.42±0.07	0.00±0.00	0.00±0.00	0.05±0.04
3	-7.69±0.91	-0.15±0.03	0.43±0.07	0.00±0.00	-0.05±0.07	0.00±0.00
4	-7.91±0.92	-0.15±0.03	0.41±0.07	0.00±0.00	-0.05±0.07	0.05±0.04
5	-7.84±0.93	-0.15±0.03	0.44±0.07	0.00±0.02	0.00±0.00	0.00±0.00
model average	-7.89±0.90	-0.15±0.03	0.43±0.07	0.00±0.00	-0.02±0.03	0.02±0.02

Table 2.6: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from all data on 365 protected areas.

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elevation partial r^2	Min temp. partial r^2
1	0.20	316.85	0.32	0.11	0.09	0.00	0.00	0.00
2	0.20	317.06	0.28	0.11	0.09	0.00	0.00	0.00
3	0.20	318.32	0.15	0.11	0.09	0.00	0.00	0.00
4	0.20	318.59	0.13	0.11	0.09	0.00	0.00	0.00
5	0.20	318.83	0.12	0.11	0.09	0.00	0.00	0.00
model average	0.20			0.11	0.09	0.00	0.00	0.00

Table 2.7: Regression coefficients, standard errors, and coefficients of determination (R^2) of multiple regression models predicting invadedness on public protected areas in Florida (Box-Cox transformed). Values from AIC +2 parsimonious models (OLS details in Table A2) and SAR models. Significant values at $\alpha = 0.05$ are bold font.

MODEL	Intercept	log HA	log house density	log road cover	log elevation	min. temperature	R^2
1 OLS	**-7.89±0.86**	**-0.15±0.03**	**0.44±0.07**	0±0	0±0	0±0	0.20
SAR	**-6.36±1.06**	**-0.11±0.04**	**0.24±0.10**	0±0	0±0	0±0	0.28
2 OLS	**-8.10±0.88**	**-0.15±0.03**	**0.42±0.07**	0±0	0±0	0.05±0.04	0.20
SAR	**-6.48±1.09**	**-0.11±0.04**	**0.23±0.10**	0±0	0±0	0.02±0.04	0.28
3 OLS	**-7.69±0.91**	**-0.15±0.03**	**0.43±0.07**	0±0	-0.05±0.07	0±0	0.20
SAR	**-6.70±1.09**	**-0.11±0.04**	**0.25±0.10**	0±0	0.11±0.08	0±0	0.28
4 OLS	**-7.91±0.92**	**-0.15±0.03**	**0.41±0.07**	0±0	-0.05±0.07	0.05±0.04	0.20
SAR	**-6.83±1.12**	**-0.11±0.04**	**0.25±0.10**	0±0	0.11±0.08	0.02±0.04	0.28
5 OLS	**-7.84±0.93**	**-0.15±0.03**	**0.44±0.07**	-0.00±0.02	0±0	0±0	0.20
SAR	**-6.53±1.11**	**-0.11±0.04**	**0.24±0.10**	0.01±0.02	0±0	0±0	0.28

Table 2.8: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from point data on 94 protected areas.

MODEL	Intercept	log HA	log house density	log road cover	log elevation	min. temperature
1	-7.00±1.31	-0.37±0.06	0.32±0.10	0.00±0.00	0.00±0.00	0.00±0.00
2	-6.03±1.49	-0.39±0.06	0.31±0.10	-0.05±0.04	0.00±0.00	0.00±0.00
3	-6.98±1.34	-0.37±0.06	0.33±0.11	0.00±0.00	0.00±0.00	-0.01±0.07
4	-7.00±1.34	-0.37±0.06	0.32±0.11	0.00±0.00	0.00±0.13	0.00±0.00
model average	-6.75±1.37	-0.38±0.06	0.32±0.11	-0.01±0.01	0.00±0.03	0.00±0.02

Table 2.9: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from point data on 94 protected areas.

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elevation partial r^2	min. temp. partial r^2
1	0.49	36.01	0.38	0.44	0.05	0.00	0.00	0.00
2	0.50	36.17	0.35	0.44	0.05	0.01	0.00	0.00
3	0.49	37.99	0.14	0.44	0.05	0.00	0.00	0.00
4	0.49	38.01	0.14	0.44	0.05	0.00	0.00	0.00
model average	0.49			0.44	0.05	0.00	0.00	0.00

Table 2.10: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from polygon data on 73 protected areas.

MODEL	Intercept	log HA	log house density	log road cover	log elevation	min. temperature
1	-2.05±0.42	-0.21±0.08	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
2	-2.53±0.62	-0.22±0.08	0.00±0.00	0.04±0.04	0.00±0.00	0.00±0.00
3	-3.96±2.36	-0.19±0.09	0.16±0.19	0.00±0.00	0.00±0.00	0.00±0.00
4	-2.61±0.88	-0.20±0.08	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.47
5	-1.96±0.44	-0.20±0.08	0.00±0.00	0.00±0.00	-0.11±0.17	0.00±0.00
model average	-2.62±0.94	-0.20±0.08	0.03±0.04	0.01±0.01	-0.02±0.03	0.01±0.09

Table 2.11: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from polygon data on 73 protected areas.

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elevation partial r^2	min. temp. partial r^2
1	0.08	78.49	0.32	0.08	0.00	0.00	0.00	0.00
2	0.10	79.39	0.21	0.08	0.00	0.01	0.00	0.00
3	0.09	79.79	0.17	0.08	0.01	0.00	0.00	0.00
4	0.09	79.94	0.16	0.08	0.00	0.00	0.00	0.01
5	0.09	80.07	0.15	0.08	0.00	0.00	0.01	0.00
model average	0.09			0.08	0.00	0.00	0.00	0.00

Table 2.12: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting funding on 46 protected areas (Log transformed).

MODEL	Intercept	log HA	log house density	log road cover	log elevation	min. temperature
1	0.96±2.40	0.24±0.10	0.73±0.20	0.00±0.00	0.00±0.00	0.00±0.00
2	-2.67±4.65	0.29±0.11	0.74±0.21	0.22±0.24	0.00±0.00	0.00±0.00
3	1.01±2.46	0.24±0.10	0.72±0.21	0.00±0.00	-0.02±0.14	0.00±0.00
4	0.93±2.60	0.24±0.10	0.73±0.21	0.00±0.00	0.00±0.00	0.00±0.13
model average	0.06±3.03	0.25±0.10	0.73±0.21	0.06±0.06	-0.01±0.04	0.00±0.03

Table 2.13: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting funding on 46 protected areas (Log transformed).

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elevation partial r^2	min. temp. partial r^2
1	0.30	33.23	0.43	0.10	0.21	0.00	0.00	0.00
2	0.32	34.33	0.25	0.10	0.21	0.01	0.00	0.00
3	0.30	35.21	0.16	0.10	0.21	0.00	0.00	0.00
4	0.30	35.23	0.16	0.10	0.21	0.00	0.00	0.00
model average	0.31			0.10	0.21	0.00	0.00	0.00

Table 2.14: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from all data on 365 protected areas when frost-bin is used as a predictor instead of minimum temperature. Frost-bin is a binary predictor with a value of 1 for protected areas that have three or less frost days per year and 0 if more than 3.

MODEL	Intercept	log HA	log house density	log road cover	log elevation	frost-bin
1	-6.70±0.86	-0.12±0.03	0.23±0.07	0.00±0.00	0.16±0.07	1.43±0.19
2	-6.58±0.90	-0.12±0.03	0.23±0.07	-0.01±0.02	0.17±0.08	1.44±0.19
model average	-6.64±0.88	-0.12±0.03	0.23±0.07	-0.01±0.01	0.17±0.07	1.43±0.19

Table 2.15: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting predicting invadedness (Box-Cox transformed) from all data on 365 protected areas when frost-bin is used as a predictor instead of minimum temperature. Frost-bin is a binary predictor with a value of 1 for protected areas that have three or less frost days per year and 0 if more than 3.

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elevation partial r^2	frost-bin partial r^2
1	0.31	266.60	0.71	0.11	0.09	0.00	0.00	0.11
2	0.31	268.40	0.29	0.11	0.09	0.00	0.00	0.11
model average	0.31			0.11	0.09	0.00	0.00	0.11

Table 2.16: Regression coefficients and standard errors for the AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed) from all data on 365 protected areas when the ratio of protected area edge-per-area is included as a predictor.

MODEL	Intercept	log HA	log house density	log road cover	log elevation	frost bin	log(edge/area)
1	-8.07±0.89	-0.16±0.04	0.46±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
2	-8.28±0.90	-0.16±0.04	0.44±0.07	0.00±0.00	0.00±0.00	0.05±0.04	0.00±0.00
3	-7.88±0.93	-0.16±0.04	0.45±0.07	0.00±0.00	-0.05±0.07	0.00±0.00	0.00±0.00
4	-8.40±1.11	-0.20±0.07	0.46±0.07	0.00±0.00	0.00±0.00	0.00±0.00	-0.09±0.18
5	-7.99±0.95	-0.16±0.04	0.46±0.07	-0.01±0.03	0.00±0.00	0.00±0.00	0.00±0.00
6	-8.10±0.95	-0.16±0.04	0.43±0.07	0.00±0.00	-0.05±0.07	0.05±0.04	0.00±0.00
model avg.	-8.12±0.96	-0.17±0.04	0.45±0.07	0.00±0.00	-0.02±0.02	0.02±0.01	-0.02±0.03

Table 2.17: R^2, AIC, and partial r^2 for AIC +2 set of parsimonious models and the model average predicting invadedness (Box-Cox transformed)from all data on 365 protected areas when the ratio of protected area edge-per-area is included as a predictor

MODEL	R^2	AIC	Akaike Weight	log HA partial r^2	log house density partial r^2	log road cover partial r^2	log elev. partial r^2	frost bin partial r^2	edge/area partial r^2
1	0.20	337.07	0.29	0.11	0.09	0.00	0.00	0.00	0.00
2	0.21	337.44	0.24	0.11	0.09	0.00	0.00	0.00	0.00
3	0.21	338.63	0.13	0.11	0.09	0.00	0.00	0.00	0.00
4	0.21	338.82	0.12	0.11	0.09	0.00	0.00	0.00	0.00
5	0.20	339.02	0.11	0.11	0.09	0.00	0.00	0.00	0.00
6	0.21	339.06	0.11	0.11	0.09	0.00	0.00	0.00	0.00
model avg.	0.21			0.11	0.09	0.00	0.00	0.00	0.00

2.7.1 Appendix S2: List of study protected areas (from 2010 FLMA GIS layer, FNAI)

1. Alafia River Corridor
2. Alafia Scrub Preserve
3. Allen David Broussard Catfish Creek Preserve State Park
4. Allen's Creek Management Area
5. Alligator Creek Conservation Area
6. Alligator Lake Management Area
7. Anclote Gulf Park
8. Anclote Islands Management Area
9. Annutteliga Hammock
10. Ansin Tract
11. Apalachicola River Water Management Area
12. Apalachicola River Wildlife and Environmental Area
13. Atlantic Ridge Parcels
14. Austin Cary Memorial Forest
15. Bay Bluffs Park
16. Baycliff Preserve
17. Bear Creek Nature Trail
18. Big Hickory Island Preserve
19. Bivens Arm Nature Park
20. Black Hammock Trail Head
21. Black Hammock Wilderness Area
22. Blackburn Point Park and Addition
23. Blackwater Hammock
24. Blue Cypress Conservation Area
25. Bocilla Preserve
26. Bowditch Point Park
27. Boyd Hill Nature Park
28. Brohard Beach and Paw Park
29. Brooker Creek Buffer Preserve
30. Brooker Creek Headwaters
31. Brooker Creek Preserve
32. Brooksville Plant Materials Center
33. Buck Lake Conservation Area
34. Bull Creek Wildlife Management Area
35. Bulow Creek State Park

36. Cabbage Key Management Area
37. Caloosahatchee Regional Park
38. Cameron Preserve
39. Canaveral Marshes Conservation Area
40. Captain Forster Hammock Preserve
41. Carlton Village Park
42. Carver Preserve
43. Cayo Pelau Preserve
44. Cecil Field Conservation Corridor
45. Cedar Point
46. Chain of Lakes Stormwater Park
47. Charles Lee Property
48. Charlie's Marsh Preserve
49. Chassahowitzka National Wildlife Refuge
50. Chinsegut Hill Conference Center
51. Chipola River Greenway
52. Choctawhatchee River Water Management Area
53. Clam Bayou
54. Clear Springs
55. Colt Creek State Park
56. Columbus G. MacLeod Preserve
57. Cone Ranch
58. Coontie Hatchee Landing
59. Cooper's Point
60. County Line Scrub
61. Cow Branch Management Area
62. Crandon Park
63. Crews Lake Wilderness Park
64. Cross Bayou North
65. Crystal River Preserve State Park
66. Curry Island
67. Cutler Wetlands
68. Cypress Creek Sand Pine Preserve
69. Cypress Lakes Preserve
70. Cypress Point Park
71. Daniels Preserve at Spanish Creek
72. De Leon Springs State Park
73. Dead Lakes Park
74. Deep Creek Conservation Area (SRWMD)
75. Deer Lake State Park
76. Devil's Hammock

77. Dicerandra Scrub Sanctuary
78. Dupuis Reserve
79. Eagle Lake Preserve
80. Eagle Point Park
81. East 417 Property
82. East Lake Management Area
83. Easterlin Regional Park
84. Econ River Wilderness Area
85. Econfina River State Park
86. Eden Gardens State Park
87. Edward Ball Wakulla Springs State Park
88. Edwards Bottomland
89. Elinor Klapp-Phipps Park
90. Escambia Bay Bluffs
91. Estero Marsh Preserve
92. Falling Creek Park
93. Fanning Springs State Park
94. Faver-Dykes State Park
95. Fellsmere Water Management Area
96. Fern Prairie Preserve
97. Ferndale Preserve
98. Fickett Hammock Preserve
99. Flat Island Preserve
100. Flatwoods Conservation Area
101. Flinn Tract Conservation Area
102. Flint Pen Strand
103. Fort Desoto Park
104. Fort Matanzas National Monument
105. Four Mile Cove Ecological Preserve
106. Fowlers Bluff Conservation Area
107. Fox Creek
108. Fox Lake Sanctuary
109. Frog Pond/L-31 N Transition Lands
110. Gamble Place
111. Garcon Point Water Management Area
112. Golden Aster Preserve
113. Golden Sands Park
114. Gopher Tortoise Preserve (Broward County)
115. Goulds Pineland and Addition
116. Graham Swamp Conservation Area
117. Grassy Point Preserve

118. Grassy Waters Preserve
119. Grayton Beach State Park
120. Green Salt Marsh
121. Greenbriar Swamp Preserve
122. Grissom Parkway
123. Gulf Islands National Seashore
124. Gum Root Park
125. Hackberry Hammock
126. Half Moon Island Preserve
127. Hallandale City Beach
128. Hallstrom Farmstead
129. Hamilton Reserve
130. Harden Hammock
131. Harmony Oaks Conservation Area
132. Hathaway Park
133. Haw Creek Preserve
134. Haw Creek Preserve State Park
135. Haynes Creek Park
136. Headwaters at Duette Park
137. Helwig (456)
138. Herman and Dorothy Shooster Preserve
139. Hidden Lake Project
140. Highland Scrub Natural Area
141. Hillsboro Pineland Natural Area
142. Hixtown Swamp Conservation Area
143. Hogtown Creek Headwaters Nature Park
144. Holland Park
145. Hollywood North Beach Regional Park
146. Holton Creek Conservation Area
147. Homeland
148. Honey Creek Research Natural Area
149. Imperial River Preserve
150. Indian River Lagoon Preserve State Park
151. Ingram Pineland
152. Inland Groves
153. Jack Creek
154. James E. Grey Preserve
155. Jerry Lake
156. Jim Wingate Park
157. Joe's Creek Management Area
158. Joe's River Park

159. John David Patton Wildlife Park

160. John Mahon Park

161. John Williams Park

162. Kendall Indian Hammocks Park

163. Key Vista Nature Park

164. King Islands Management Area

165. Kissimmee Chain of Lakes

166. Kissimmee Prairie Preserve State Park

167. Kissimmee River

168. Lake Griffin State Park

169. Lake Harney Wilderness Area

170. Lake Jackson Mounds Archaeological State Park

171. Lake Jesup Conservation Area

172. Lake Lotus Park

173. Lake Runnymede Conservation Area

174. Lake Seminole Management Area

175. Lake Stone Fish Management Area

176. Lake Talquin State Park

177. Lake Tarpon Management Area

178. Lake Tarpon West Management Area

179. Lake Thomas Cove Park

180. Lake Woodruff National Wildlife Refuge

181. Lakes Regional Park

182. Lathrop Bayou Tract

183. Letchworth-Love Mounds Archaeological State Park

184. Little Manatee River

185. Little Manatee River (SWFWMD)

186. Lochloosa Wildlife Conservation Area

187. Lonesome Camp Ranch Conservation Area

188. Long Branch Management Area

189. Lost Tree Islands Conservation Area

190. Lower Alapaha Conservation Area

191. Lower Escambia River Water Management Area

192. Lower Peace River Corridor

193. Lower Wekiva River Preserve State Park

194. Lucas Tract

195. Lucille Hammock
196. Ludlam Pineland
197. Lyonia Preserve
198. Madison Blue Spring
199. Mallory Heights Park #3
200. Manatee Park
201. Mangrove Preserve
202. Marianna Greenway
203. Mariner's Point Management Area
204. Marjorie Kinnan Rawlings Historic State Park
205. Marsh Park and Boat Ramp
206. Mashes Sands Park
207. Matanzas Pass Preserve
208. Matheson Hammock Park
209. Mikes Donation
210. Military Trail Natural Area
211. Mills Pond Park
212. Miramar Pineland Natural Area
213. Mobbly Bayou Preserve
214. Model Lands Basin
215. Morningstar Parcel
216. Morsani Conservation Easement
217. Morsani Ranch
218. Mullock Creek Preserve
219. Murdock Point Cayo Costa
220. Natural Bridge Battlefield Historic State Park
221. Navarre Beach Park
222. New Tampa Nature Park
223. North Buck Lake Scrub Sanctuary
224. North Fork Riverwalk
225. North Peninsula State Park
226. North Sebastian Conservation Area
227. North/Walk-in-Water Creek
228. Northwest 39th Avenue Park
229. Oak Hammock Park
230. Oak Island Nature Preserve
231. Ollie's Pond Park
232. Olustee Experimental Forest
233. Orange River Parcel
234. Orange River Preserve
235. Ordway-Swisher Biological Station
236. Oslo Riverfront Conservation Area

237. Overlook Park
238. Oyster Bar Salt Marsh
239. Ozona Management Area
240. Palatka-Lake Butler State Trail
241. Palatlakaha Environmental and Agricultural Reserve Park
242. Palatlakaha River Park
243. Palmetto Estuary Preservation Project
244. Pasco Palms Preserve
245. Paynes Prairie Preserve State Park
246. Peck Sink Preserve
247. Pendarvis Cove Park
248. Pepper Ranch Preserve
249. Pine Glades Natural Area
250. Pine Island Conservation Area
251. Pine Island Preserve
252. Pine Island Ridge Natural Area
253. Ponce de Leon Springs State Park
254. Pond Apple Slough
255. Prairie Creek Preserve (Charlotte County)
256. Prairie/Shell Creek
257. Prange Islands Conservation Area
258. Price Park
259. Princess Place Preserve
260. Punta Rassa Preserve
261. Ravine Gardens State Park
262. Reddie Point Preserve
263. Ribault River Preserve
264. River City Nature Park
265. River Lakes Conservation Area
266. River Tower Restoration Site
267. Robert K. Rees Memorial Park
268. Rodney Kroegel Homestead
269. Rotunda Community Park and Preserve
270. Round Island South Conservation Area
271. Russell Grove
272. Ryall Parcel
273. Sailboat Bend Preserve
274. Sal Taylor Creek Preserve
275. Salinas Park
276. San Carlos Bay - Bunche Beach Preserve

277. San Felasco Hammock Preserve State Park

278. Sand Hill Trailhead

279. Santa Fe Swamp Conservation Area

280. Saw Palmetto Natural Area

281. Sea Oats Park

282. Sebastian Harbor Preserve

283. Sebastian Inlet State Park

284. Sebastian Scrub Conservation Area

285. Secret Woods Buffer and Nature Center

286. Seminole Ranch Conservation Area

287. Seminole Wayside Park

288. Shadowbrook Tract

289. Shell Bluff

290. Shell Creek Preserve

291. Shell Key Preserve

292. Sheridan Oak Forest

293. Shoreline Park South

294. Silver Palm Hammock

295. Six Mile Cypress Slough Preserve

296. Snipe Island Unit

297. South Lake Jesup Property

298. South Marianna Trail and Canoe Launch

299. Southern Glades

300. Spessard Holland North Beach Park

301. Spessard Holland South Beach Park

302. St. James Creek Preserve

303. St. Marks Headwaters

304. St. Marks River State Park

305. St. Sebastian River Preserve State Park

306. St. Vincent National Wildlife Refuge

307. Subtropical Agricultural Research Station

308. T. H. Stone Memorial St. Joseph Peninsula State Park

309. T. M. Goodwin Waterfowl Management Area

310. Tall Cypress Natural Area

311. Tampa Bay Estuarine Ecosystem - TECO Tract and Fulkerson Road Shell Pit

312. Tampa Bay Estuarine Ecosystem - Terra Ceia

313. Tate's Hell Wildlife Management Area
314. Temple Terrace Riverfront Park
315. Tenoroc Fish Management Area
316. The Hammock
317. Thomas Creek Preserve
318. Timer Powers Park Conservation Area
319. Tippecanoe Environmental Park
320. Tivoli Sand Pine Park
321. Tomoka State Park
322. Tradewinds Regional Park
323. Trailhead Park
324. Travatine Island Management Area
325. Turkey Creek Sanctuary
326. Twin Rivers 2 Preserve
327. Tyndall Air Force Base
328. University of Central Florida East Parcel
329. University of Central Florida McKay Tract
330. University of Central Florida Pond Pine
331. University of Central Florida Riparian Area
332. Upper Alapaha Conservation Area
333. Upper Aucilla Conservation Area
334. Upper Chipola River Water Management Area
335. Upper Little Manatee River
336. Upper Pithlachascotee River Preserve
337. Valkaria Expansion
338. Valkaria Scrub Sanctuary
339. Varn Parcel
340. Verdie Forest
341. Vilano Oceanfront Park
342. Vinkemulder LAPC
343. Wabasso Scrub Conservation Area
344. Wacissa Conservation Area
345. Walsingham Park
346. Warbler Wetland Natural Area
347. Ward Creek West
348. Washington Oaks Gardens State Park
349. Watson Island Parcel

350. Weedon Island Preserve

351. West Creek Pineland Natural Area

352. West Marsh Preserve

353. Westmoreland

354. Whispering Pines Hammock Preserve

355. Wild Turkey Strand Preserve

356. Wildcat Cove

357. William J. Kelly Rookery

358. Wilson's Landing

359. Windmiller Parcel

360. Windswept Acres Park

361. Withlacoochee State Trail

362. Woodmont Natural Area

363. Yellow Jacket Conservation Area

364. Yellow River Water Management Area

365. Yellow River Wildlife Management Area - Escribano Point

Chapter 3

Predicting invadedness of invasive plant species of management concern

A version of this chapter will be submitted for publication after modification during internal and external review.

Iacona, G.D, and P.R. Armsworth (XXXX). Predicting invadedness of invasive plant species of management concern. *Biological Conservation*

The use of "we" in this chapter refers to me and my co-author. As the lead author of this article I was responsible for developing the ideas for this paper, conducting the analysis, and writing the manuscript. P.R.A. is a co-author of this work and he was responsible for feedback at early stages of the research and editing the manuscript.

Abstract

Predictions of invasive plant infestation are important when conservation managers are budgeting for protected area acquisition and future management efforts. However, many plant species are invasive and different species are often not prioritized equally for management. In addition, many studies predict the presence of invasive species, but they rarely predict cover, which is more relevant to management. Here we examined how predictors of invasive plant presence and cover differ across species that vary in their prioritization for management. To do so we used data on management effort and cover of invasive plant species on Florida protected areas to select three study species that are prioritized for management and three that are not. Using a zero-inflated multiple regression framework, we showed that protected area features can predict the presence and cover of the focal species, but the same features rarely explain both. There were several predictors of either presence or cover that were important across multiple species. Protected areas with three days of frost per year or

fewer were more likely to have occurrences of five of the six focal species. Meanwhile, larger protected areas were related to decreased invadedness (proportional cover) for all of our focal species, and an increase in the number of nearby households was related to invadedness for four of our six focal species. None of the predictive features were clearly related to management priority. These results suggest that while some protected area features are related to invadedness across species, predictors of cover and presence differ and do not covary with management priority.

3.1 Introduction

Invasive plant control causes a significant management cost on many protected areas (PAs) worldwide (Frazee et al., 2003; Goodman, 2003; Reinhardt et al., 2003; Pimentel et al., 2005; Pfennigwerth and Kuebbing, 2012; Cleary, 2013). Predictions of the relative cover of invasive plant species across PAs are necessary if conservation managers must plan for the costs of both protected area acquisition and future management efforts (Martin and Blossey, 2012). Yet, many of the current predictive models continue to focus primarily on species presence without considering cover (Pyšek et al., 2002a,b; Foxcroft et al., 2011). Additionally, many invasive plant species may co-occur on protected areas (Allen et al., 2009; Kuebbing et al., 2013), but they may not all be management priorities. If conservation planners want to predict variation in invasion so they can estimate management needs, they need predictions of presence and cover that are robust across species of management priority while being cost effective to develop and parameterize.

Predictions of invasive plant cover are necessary for managers to estimate impact and costs of treatment, yet most current research focuses only on presence (Higgins et al., 1999; McKinney, 2002; Spear et al., 2013, and many others). Presence and cover of invasive species on PAs are both relevant to conservation planning. Predictions of presence are most useful for identifying possible invaders and planning for monitoring (Catford et al., 2012) and are less helpful for estimating management costs. Meanwhile, predictions of cover provide an indication of the relative effort required to manage invasion, either through eradication or reduction to proportional cover. However, in the few studies that consider cover (Alston and Richardson, 2006; Catford et al., 2011; Polce et al., 2011; Seabloom et al., 2013), there is little consideration of how predictions of presence relate to cover (but see Kuhman et al., 2010). This critical shortage in the literature hinders the applicability to management of existing studies that examine the prediction of invasion.

The desired scale of prediction is likely to matter for both cover and presence. If 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 cheap, easily obtainable coarse grain data to describe expected variation in cover at the scale of a PA would be appropriate. Similarly, predictions of presence at the scale of a PA are relevant for decisions regarding identification and eradication of early invaders. Meanwhile, if the desired inference is of treatment needs at finer scales, the spatial distribution of species on the ground would be a more important consideration. For example, location of invasive plants within a PA can affect treatment cost on large PAs, such as the 64,000 HA Everglades National Park (Committee on independent scientific review of Everglades restoration progress, 2014).

Another issue with current predictions of invasion is that all invasive species cannot be considered equivalent when planning for treatment. Managers tend to prioritize species management effort towards certain focal species (Abella, 2014), even if non-focal species are present that have similar threat rankings (e.g., Florida Exotic Pest Plant Council (FLEPPC) ranking). There are several reasons that managers may focus treatment effort on only certain species. Cost constraints can limit the total management effort available to a PA (D'Antonio et al., 2004; Tempel et al., 2004). Managers may thus choose to focus on treatments they know are effective. For instance, they could focus on species that respond better to treatment or focus on small areas that are limited enough for feasible control. Alternatively, managers could aim to minimize invasive species impact and prioritize treatment of species that are negatively affecting species or communities of conservation interest. Finally, managers may prioritize species that have historically been treated at the PA or whose management is specifically mandated in management plans (Pullin and Knight, 2005).

The potential variation across predictors of presence and cover and the need to predict species that are a management priority suggest that comparisons of predictors of invasion across species must consider three potential contrasts (Figure 3.1). The first contrast is an examination of predictor variables across species. The second contrast is the difference between predictors of presence and cover for a single species. The final is a comparison of shared predictors for species that are a high management priority (those that are likely to be treated) with shared predictors of species that are low management priority. We are interested in this last comparison because predictions that include species that are less likely to be treated (see Chapter 2) could potentially result in overestimates of management cost.

In Chapter 2 of this dissertation, we described a model that relates aggregate invasive species invadedness to features of the PAs on which they are found. This model was developed using plant distribution data from the Florida Natural Areas Inventory (FNAI) FLInv Geodatabase. It included predictors of invasion that describe ecological attributes of the PA that can influence invasibility, as well as predictors chosen because they relate to human disturbance on the PA. The features that best predicted how invaded a PA was likely to be were PA area and the number of surrounding households (other variables tested include minimum temperature, road density, and elevation).

We now expand this model to examine how PA-level predictive features vary when describing both presence and invadedness of individual species that differ in how they are prioritized for management. We expect variation in PA-level predictors of invadedness because species have different life histories and distributions. However, we are seeking common predictors across species of management concern so that we can understand how generalizable predictions of invasion are.

We expect there might be differences in PA features that predict the presence of a species versus those that predict cover. For instance, we expect the probability of presence of a species could increase with PA area because of species area effects (McKinney, 2002), with surrounding households because of human introductions (Gavier-Pizarro et al., 2010), and with road density because of transport (Von Der Lippe and Kowarik, 2007). We also expect that presence may be more likely in southern PAs with less frost (Marini et al., 2009). Finally, in our models, elevation is a proxy for habitat type, which could potentially influence presence (Chytrý et al., 2008). In contrast, based on previous work we expect proportional cover to decrease with PA area, increase with household density, and potentially vary with winter temperature (Chapter 2, this dissertation).

We also expect that some predictive features may be more similar for species that are management priorities than for those that are not. For instance, PA area is a predictor that could relate to management priority if species that are more likely to be found on small PAs, because of disrupted ecological processes, are also more likely to be managed because they are large, obvious, or noxious. Alternatively, species that are introduced as ornamentals may be more likely to be invaders in natural areas than species that are agricultural pests (Richardson, 2011; Zenni, 2014); thus species of management priority may be more likely on PAs close to human development. We do not expect a difference in predictive ability of winter temperature that relates to management priority because FWC allocates funding statewide.

Here we develop models that concurrently predict presence and cover for six species that differ in management priority. We ask:

1. Are predictors of presence and cover similar for a species?
2. Do predictors of invasion vary across species, and does it matter whether they are prioritized for management?

3.2 Methods

Study system

As in chapter 2, we used data from 365 publicly-owned PAs in the state of Florida, USA, to address these questions. Florida is heavily impacted by invasive plant species, and there are 146 species on the Florida Exotic Pest Plant Council (FLEPPC) list that are ranked as either Category I (documented ecological damage) or Category II (increasing in abundance or frequency but no demonstrated ecological damage) for prioritization purposes (FLEPPC list 2009). The more than 1800 publicly-owned PAs within the state range from temperate to tropical climates, urban to rural locations, and small to large area (FNAI, Florida Managed Areas database). In addition, the state spend more than 100 million dollars to manage invasive plants on publicly-owned PAs between 1999 and 2010 (Cleary, R. unpublished data).

Management effort across species

To select focal species that differed in their priority for management, we examined the distribution of management effort across the FLEPPC listed species using an operations database from the Florida Fish and Wildlife Conservation Commission (FWC) upland habitat management program (Cleary, 2007). This database included information on the acreage and numbers of individuals for 96 different FLEPPC-listed species that were treated on PAs throughout the state over ten years (Cleary, R., unpublished data). We calculated the proportion of effort applied to each species (by acreage or by number of individuals treated, depending on PA) to rank the FLEPPC listed species by treatment effort (Supplementary Table 3.5). We then compared effort with data from the FLInv Geodatabase on the statewide distribution of the 28 most common species on our 365 study PAs (see Chapter 2 for species selection details). Figure 3.2 shows how effort relates to cover (Panel 3.2a) and occurrences (Panel 3.2b) across our PAs. Management effort was highly skewed in its distribution across species with 70% of the total management effort focused on only ten species and 24% of total effort on *Schinus terebinthifolius* (Brazilian pepper) alone (Table 3.1). *S. terebinthifolius* is also the most widespread (found on the most PAs) and the most abundant (most area invaded) of all of the species in the occurrence dataset (Table 3.1). Other abundant species that received considerable management effort were *Imperata cylindrica* (cogon grass) and *Lygodium microphyllum* (Old World climbing fern). However, several notably widespread and abundant species were not prioritized for management. For instance, *Ludwigia peruviana* (Peruvian primrose-willow) and *Urena lobata* (Caesar's weed) were the second and fourth most abundant species in our dataset, while *Panicum maximum* (Guinea grass) was the fifth most common invasive species in the state in terms of the number of PAs it occupies. However, these species received 1% or less of the total management effort in the state.

Predicting invadedness of individual species

We used the effort and cover data distributions to choose six study species as highlighted in Figure 3.2. Three of our test species were chosen because they are targeted by state effort and funding for treatment (*S. terebinthifolius*, *I. cylindrica*, and *L. microphyllum*), and three species were chosen because they are widely prevalent on public conservation lands but are a lower management priority (*L. peruviana, U. lobata*, and *P. maximum*). Data on the cover of invasive plants at each PA were used to calculate invadedness for species of management concern for the 365 study PAs (see Chapter 2 for details on PA choice). Invadedness is a metric we developed to compare relative cover of invasive species across PAs, and is calculated as the area of a PA invaded by the invasive species divided by the area of the PA. For each species, we chose PAs for analysis where all records for that species were GPS point data with surveyor-estimated area of coverage (see Chapter 2 for justification, Figure 3.3).

Because each species was present on only some of the PAs in our dataset, many observed records were zeros. This required us to model both the probability of occurrence of a species at a PA and its abundance if it was present. To model the two processes concurrently, we used a zero-inflated negative binomial model (Zeileis et al., 2008) to predict expected invadedness at a PA in relation to PA features. We used a negative binomial model because our observed variance in invasive plant cover was greater than the mean (overdispersion) and because AIC comparisons across additional models tested during the model-fitting process indicated that this error structure was the most appropriate.

Our modeling strategy considers the entire dataset to be binary data and models the probability of the species presence at a given PA, assuming a binomial distribution ($\text{probability of presence} = \pi_i = 1 - (\frac{e^{\alpha+\beta_1 X_{1i}+\ldots\beta_n X_{ni}}}{(1+e^{\alpha+\beta_1 X_{1i}+\ldots\beta_n X_{ni}}}))$.Our model also uses the observed cover measurements and some of the zero cover records to relate the probable mean cover of a species at a PA to site-level features, assuming a negative binomial distribution ($\text{mean cover if present} = \mu_i = e^{\alpha+\beta_1 X_{1i}+\ldots\beta_n X_{ni}}$). We could then calculate the expected value of the mean cover at a PA while accounting for the zero-inflated process ($\text{mean cover} = E(Y_i) = \mu_i * \pi_i$). This prediction of cover at a PA estimates expected cover weighted by the probability of the species being present.

To construct our response variable, we binned invadedness for each species into thousandth of a percent bins to meet model assumptions of a discrete data distribution (Table 3.2). Predictive factors tested were PA area, number of surrounding households, elevation, onsite road density, and a binary variable (frost-bin) indicating three days of frost per year or not (see Chapter 2 for details on predictor variable choice). We constructed separate models for each of the six species using the pscl package in R (Zeileis et al., 2008; R Development Core Team, 2010; Jackman, 2012). In all cases, we used a log link function for modeling the underlying invadedness distribution, and a logit link function for modeling the excess zeros. We log transformed all the predictor variables except frost-bin. Tolerance testing indicated that none of the predictor variables were more than 20% dependent on variation in other predictor variables, ensuring that collinearity requirements were adequate to proceed (Quinn and Keough, 2001). Finally, examination of semivariance plots of residuals from each model indicated that spatial autocorrelation was not a concern in this dataset.

3.3 Results

We assessed predicted invadedness for each focal species using a zero-inflated modeling technique that considered records of zero cover for that species as being one of two types. If a species was not present, it could be due to characteristics of the PA that precluded that species being there in the first place (i.e., outside its range of temperature tolerance), or it could be due to characteristics of the PA that are related to low amounts of cover (i.e., low propagule pressure minimizing establishment). For these reasons, we present the results in two sections even though they were produced in a single modeling process. The first section describes the predictive features that relate to the probability that the species of interest is present at the PA. The second section describes the predictive features that relate to the expected cover of the species if it is present. For a prediction of total expected invasive plant cover for a species at a PA, multiply the estimated mean cover (predictions from Table 3.3) by the probability of the PA having more than zero cover present (predictions from Table 3.4).

The presence of four of our six focal species could be predicted with PA-level features, although the significant predictors varied across species (Table 3.3). Features that relate to geographic range of a species or its habitat preferences appeared to be most important for predicting species presence. For instance, PAs with three days or fewer of frost per year (frost-bin binary variable) were more likely to have occurrences of *S. terebinthifolius, L. peruviana, I. cylindrica,* and *L. microphyllum.* The only species that was not more likely to be present if there were fewer than three frost days per year was *P. maximum.* In addition, the probability that *I. cyclindrica, L. peruviana,* and *L. microphyllum* were present increased as PA mean elevation increased. Meanwhile, PA features that relate to human disturbances were less important in predicting the presence of a species. Although *I. cylindrica* and *L. microphyllum* were more likely to be present as the PA area increased, households and roads were not significant predictors of presence for any tested species. Finally, no PA features predicted *P. maximum* or *U. lobata* presence.

Predictions of cover also varied across species, but in contrast to predictors of presence alone, the important PA-level predictive features included both those that related to ecological processes and those that related to human disturbance (Table 3.4). All six species decreased in invadedness as PA area increased. However, the species differed in their relationship to household density. *S. terebinthifolius* and *I. cylindrica* decreased in cover as the number of nearby households decreased. Meanwhile, *P. maximum* and *L. microphyllum* invadedness decreased as PA area increased but was not related to household density. Finally, *L. peruviana* decreased in invadedness as surrounding household density increased. Invadedness of some species also was related to PA-level predictive features other than area and surrounding households. Frost-bin was a significant predictor of invadedness for *S. terebinthifolius* and *P. maximum*, with higher cover at PAs with three or fewer frost days per year. Road density was related to increased invadedness for *I. cylindrica* and decreased invadedness for *L. microphyllum*.

Outliers were present in the models of each species, but we determined that the information provided by these highly invaded PAs was meaningful (very low invadedness outliers were absorbed by the zero-inflated process). Therefore we present the results with all data included in the model.

3.4 Discussion

The objective of this study is to examine the implications of species identity when estimating invasive plant management needs for PAs. We find that predictive features differ for presence and cover within and across species. These results suggest that predictions of presence and cover are not interchangeable. In addition, although we identify predictors that are important across multiple species, no predictors related to management priority species specifically.

There are many possible metrics of invasion, but we have chosen to focus on cover and presence because of their management implications. Predictors of the presence of a species were often quite different than predictors of cover. For instance, in several models, the probability of presence of a species increased with PA area, but the amount of cover decreased. This result suggests that the two predictions are not interchangeable and reinforces the call for predictions of cover as well as presence for management applications (Catford et al., 2012; Bradley, 2013; Seabloom et al., 2013). The conservation implications of this discrepancy is relevant for management priorities in Florida because some species (e.g. early detection and response of species such as *L. microphyllum* on the invasion front, Hutchinson et al. (2006)) are managed to minimize presence on PAs and others (e.g. *Melaleuca quinquenervia* in the Florida Everglades, Committee on independent scientific review of Everglades restoration progress (2014)) are managed to minimize cover. Notably, predictors of presence tended to be those PA features related to potential underlying ecological characteristics and processes. This suggests that if a PA is within the geographic range of a species and has the appropriate habitats, invasive species are prevalent enough in Florida that they will likely occur on the PA. In contrast, the invadedness (cover) of the species was more likely to relate to predictive features that indicated human disturbance on a PA. This is an important management implication, suggesting that, even if a species is present, the impact of the invasion may not be severe unless human disturbances promote their spread.

These differences in PA-level predictors of presence and cover across species are important if a land manager or conservation planner aims to produce management recommendations for a particular species. However, several predictive features were common across many of our species, and we suggest that models including those predictors are appropriate for predictions of likely invadedness of a PA regardless of species. For estimates of cover, these factors were PA size and the number of houses within 25 km of the protected area. Meanwhile, the most important predictor of presence was simply whether there were three or fewer frost days per year at the PA. These predictors are the same as those suggested by our previous model on aggregate invadedness (Chapter 2, this dissertation).

Finally, we show that invasion by species of high management priority in general is not predictable by different features of protected areas than those that are low management priority. Instead, both presence and cover of all six of the species were related to slightly different predictive factors. These predictions made sense based on the physiology and life history of the individual species, but there were no clear grouping factors related to management prioritization within the state.

Species specific results

Schinus terebinthifolius is the highest priority invasive species in Florida regardless of which metric is used. It is a documented statewide management priority (Cuda et al., 2006). It is found on the most PAs throughout the state, covers the most area, and is allocated the most effort and funding (Table 3.1). Its presence at a PA is almost entirely related to frost free days. If present, the invadedness of *S. terebinthifolius* decreased as PA area increased and as household density decreased. Invadedness of *S. terebinthifolius* is also sensitive to frost bin. These relationships are similar to those described by our aggregate model of species invadedness in chapter 2 and may be driving those predictions.

Imperata cylindrica is also a very high priority species for management in Florida. Our model suggests that the invadedness of this species is correlated with road density. This is not surprising because *I. cylindrica* is a perennial rhizomatous grass that is thought to be primarily dispersed by vegetative means (Dozier et al., 1998). The species is common along roadsides, as the rhizomes are often transported in road fill and by grading equipment (Jose et al., 2002). In addition, the positive relationship between the presence of *I. cylindrica* and elevation is possible because this species is able to tolerate hot, dry conditions and is one of the few species that will invade upland pine (Yager et al., 2010) and scrub communities.

The presence of *Lygodium microphyllum* was also positively related to elevation. This may be similarly related to prevalence on large inland protected areas (Ferriter and Pernas, 2006). Its invadedness also decreases with increased road cover. This may be due to the fact that it is a statewide management priority (Hutchinson et al., 2006) and, as such, is more likely to be intensively treated in easy-to-access areas. However, this species was present on only 18 PAs in our study, so these results should be interpreted with care.

The predictions for *Ludwigia peruviana* were less intuitive. Our model suggests that the invadedness of this species decreases with proximity to human households. This wetland species is prevalent in the types of large, shallow wetlands that result from water control projects in south Florida (Toth, 2010). These types of projects may be less common in high density developed areas. In addition, the probability of presence of *L. peruviana* is positively related to elevation. This seems counterintuitive for a wetland species, but if it prefers the types of wetlands that are present in the interior of the state, where there is higher elevation and greater distance from the human development along the coast, both of these patterns would hold.

Finally, the presence of both *Panicum maximum* and *Urena lobata* was not strongly related to specific PA features. In addition, the cover of neither of these species was particularly well explained by the density of surrounding households, although they both did decrease in cover as PA area increased. This is probably due to their both being common ruderal species often found on roadsides, trails, and old field areas, resulting in their near ubiquitous presence on PAs statewide (Austin, 1999).

Caveats

Here we used an FWC operations database to estimate the relative management effort allocated to invasive plant species in the state of FL. This operations database describes the actions enacted with state-allocated funding between 1999 and 2009. However, this does not describe all management actions on state PAs during that time, because managing agencies also perform treatment actions without FWC assistance. Despite these limitations, this database describes the largest single source of management activity within the state, and allocation by FWC is likely to be related to allocation within managing agencies.

Conclusions

Invasive plant species management is often a priority for biodiversity conservation, and we confirm that all species cannot be considered equal from a planning perspective. This is important because conservation funding is limited, and invasive species are present on protected areas worldwide (Usher, 1988; De Poorter et al., 2007; Foxcroft et al., 2013). Until species can be ranked by treatment priority based on ecological impact (Hulme et al., 2013), or on the costs and benefits of outcomes, the most likely source of cost estimation is current species rankings. Our work suggests that certain PA features robustly predict invadedness across species, at least in Florida. However, if the desire is estimates of invadedness for only those species that are management priorities, then species-specific models may be necessary.

Acknowledgements

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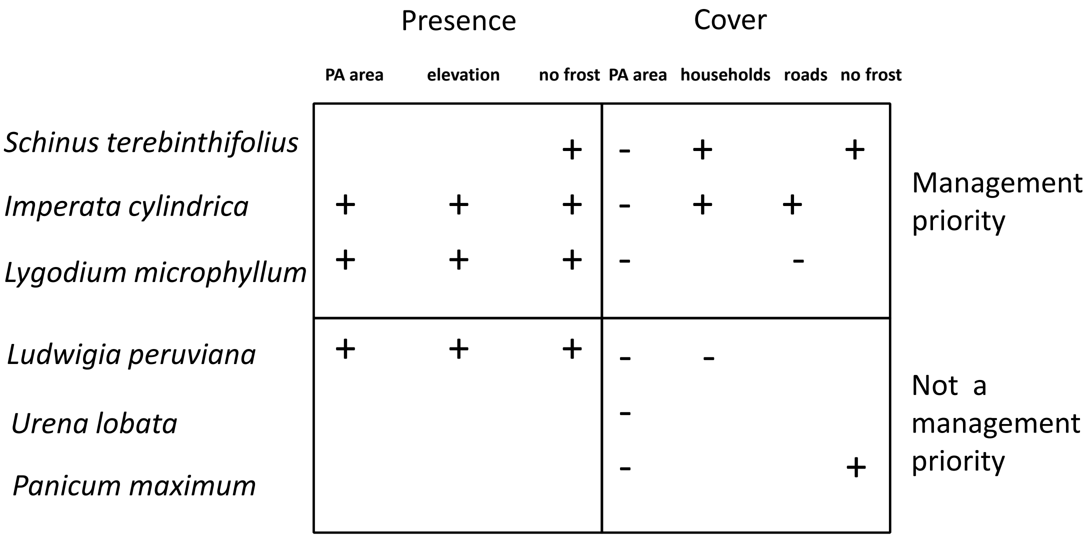
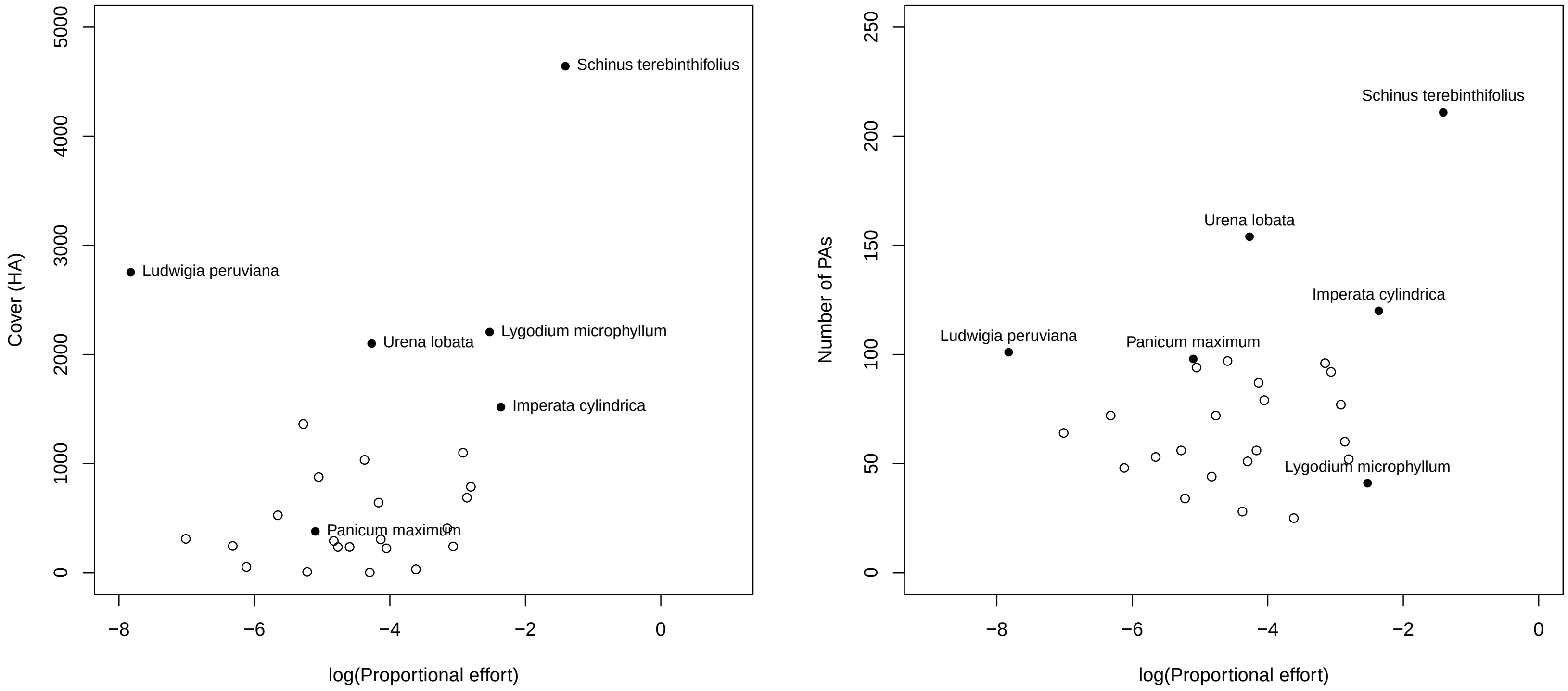
3.5 Appendix: Figures



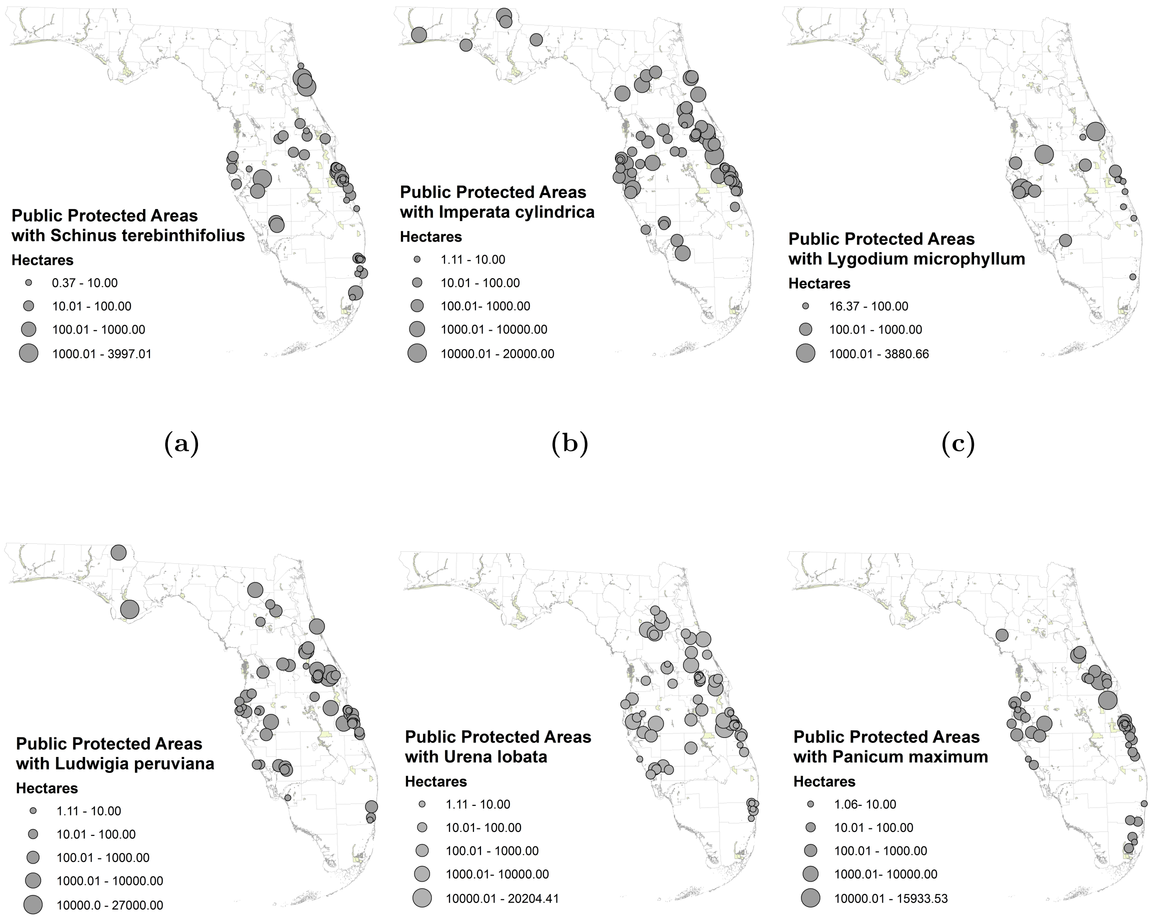
	Presence			Cover				
	PA area	elevation	no frost	PA area	households	roads	no frost	
Schinus terebinthifolius			+	-	+		+	Management priority
Imperata cylindrica	+	+	+	-	+	+		
Lygodium microphyllum	+	+	+	-		-		
Ludwigia peruviana	+	+	+	-	-			Not a management priority
Urena lobata				-				
Panicum maximum				-			+	

Figure 3.1: Diagram outlining study design and results. We examine the site-level features that predict the presence and cover of six different invasive plant species in Florida. These species were chosen based on their abundance and management priority. The sign in the table indicates the relationship described by significant predictors in the multiple regression models relating invasive presence and cover to site-level features. The relevant site-level features are listed along the top of the table. See Table 3.3 for model coefficient values.



(a) **(b)**

Figure 3.2: Variation in effort and cover across the 28 species in our occurrence database. For this study we chose six focal species (filled circles) that differ in the amount of effort that is allocated to their treatment on PAs across Florida. This figure displays effort for each species in relation to (a) cover on our 365 PAs and effort in relation to (b) the number of PAs it occurs on. *Schinus terebinthifolius, Lygodium microphyllum* and *Imperata cylindrica* are high priority species for management and also have high levels of cover across the state. *Ludwigia peruviana, Urena lobata* and *Panicum maximum* are low priority for management but have high cover. *Panicum maximum* is a low priority for management and has relatively low cover but is present on many PAs



(a) (b) (c)

(d) (e) (f)

Figure 3.3: Distribution of study species across sample protected areas. Circles indicate a protected area with the focal species present. Size of the circle corresponds with area of the protected area (HA).

3.6 Appendix: Tables

Table 3.1: Species which we have occurrence records for, the total cover of those species across the 365 study protected areas, and the relative effort expended on treating each species. Species in bold font were case study species used for predicting cover.

Plant name	**HA cover**	**Number of protected areas**	**Proportion effort**
Schinus terebinthifolius	**4644**	**211**	**0.2446**
Ludwigia peruviana	**2754**	**101**	**0.0004**
Lygodium microphyllum	**2204**	**41**	**0.0800**
Urena lobata	**2102**	**154**	**0.0140**
Imperata cylindrica	**1518**	**120**	**0.0944**
Colocasia esculenta	1362	56	0.0051
Lygodium japonicum	1099	77	0.0539
Solanum viarum	1034	28	0.0126
Panicum repens	876	94	0.0064
Melaleuca quinquenervia	787	52	0.0605
Casuarina equisetifolia	687	60	0.0571
Leucaena leucocephala	642	56	0.0155
Urochloa mutica	526	53	0.0035
Dioscorea bulbifera	406	96	0.0427
Panicum maximum	**377**	**98**	**0.0061**
Rhynchelytrum repens	310	64	0.0009
Cinnamomum camphora	305	87	0.0160
Ricinus communis	291	44	0.0080
Nephrolepis cordifolia	263	90	0.0000
Sphagneticola trilobata	245	72	0.0018
Sapium sebiferum	240	92	0.0466
Lantana camara	236	97	0.0101
Abrus precatorius	235	72	0.0085
Melia azedarach	223	79	0.0174
Syngonium podophyllum	52	48	0.0022
Ardisia crenata	31	25	0.0269
Lonicera japonica	7	34	0.0054
Albizia julibrissin	1	51	0.0136

Table 3.2: Descriptive statistics

Variable	Invadedness			n	HA invaded	Proportion effort
	5^{th} percentile	Mean	95^{th} percentile			
Schinus terebinthifolius	0	7.42E-03	1.57E-02	207	4644	0.25
Imperata cylindrica	0	1.16E-04	3.94E-04	312	1518	0.09
Lygodium microphyllum	0	3.88E-05	1.00E-07	342	2204	0.08
Ludwigia peruviana	0	4.94E-05	1.57E-04	326	2754	0.00
Urena lobata	0	2.96E-04	6.25E-04	277	2102	0.01
Panicum maximum	0	1.69E-04	4.58E-04	311	377	0.01
Total HA	2	62	8,600	365		
Households within 25 km	9,900	104,000	679,000	365		
Frost bin	NA	NA	NA	365		
Road Length (M)	45	2,139	81,800	365		
Mean Elevation (M)	1	4	32	365		

Table 3.3: Parameter estimates and standard errors (Coefficient ± 1 SE) for the model component that predicts the presence of an invasive species on a protected area (P(Y=0)). The probability that a species is present at a protected area is calculated as (1 - the logit of the linear combination of these coefficients) multiplied by the predictor variable values for that protected area. See text for the equation. Values in bold font are statistically significant at $p \leq 0.05$.

	Intercept	log HA	log house density	log road cover	log elevation	frost-bin
Schinus terebinthifolius	-11.65±8.52	-0.06±0.25	1.15±0.68	-0.18±0.11	0.76±0.58	**-2.69±1.17**
Imperata cylindrica	-4.29±5.75	**-0.70±0.19**	0.26±0.28	0.45±0.29	**-0.86±0.28**	**-1.46±0.65**
Ludwigia peruviana	12.34±4.71	**-0.68±0.17**	-0.55±0.35	-0.05±0.07	**-0.94±0.33**	**-1.60±0.72**
Lygodium microphyllum	13.72±6.32	**-1.13±0.33**	0.00±0.43	0.10±0.09	**-1.42±0.58**	**-7.25±2.75**
Panicum maximum	6.33±4.54	-0.56±0.31	0.06±0.36	-0.32±0.21	0.69±0.39	-0.98±0.94
Urena lobata	-14.51±48.45	-1.29±0.78	0.89±0.72	-1.10±1.00	-3.85±1.97	26.49±50.29

Table 3.4: Parameter estimates and standard errors (Coefficient ± 1 SE) for the model component that predicts invadedness of an invasive species at a protected area if the species is present ($P(Y>0)$). The mean invadedness at a protected area follows a binomial distribution and thus is calculated as e to the linear combination of these coefficients multiplied by the predictor variable values for that protected area. See text for the equation. Values in bold font are statistically significant at $p \leq 0.05$.

	Intercept	log HA	log house density	log road cover	log elevation	frost-bin	dispersion
Schinus terebinthifolius	-5.16±3.26	**-0.58±0.21**	**0.71±0.26**	-0.11±0.08	0.00±0.44	**4.68±0.97**	5.34±1.17
Imperata cylindrica	-11.17±3.67	**-0.33±0.09**	**0.40±0.20**	**0.60±0.18**	-0.07±0.16	0.42±0.38	1.26±0.41
Ludwigia peruviana	11.51±5.38	**-0.51±0.10**	**-0.56±0.29**	-0.19±0.19	-0.15±0.19	0.70±0.47	2.08±0.71
Lygodium microphyllum	10.77±5.66	**-0.69±0.20**	-0.22±0.41	**-0.22±0.06**	-0.48±0.37	-0.90±2.80	0.52±0.63
Panicum maximum	8.60±4.67	**-0.73±0.17**	-0.41±0.35	-0.15±0.29	0.28±0.46	**2.32±0.86**	3.75±2.36
Urena lobata	-1.86±2.82	**-0.46±0.09**	0.41±0.21	-0.09±0.08	0.22±0.21	0.95±0.56	6.41±1.21

3.7 Appendix: Supplementary Information

Table 3.5: The effort values are sums of proportional effort per protected area (PA). For instance, if all of the treatment effort at a PA was focused on a single species it would receive a value of 1 for that PA. We summed these proportions of effort per species across all PAs. If only one species was managed across all PAs it would receive an effort ranking of 365. In our dataset, *Schinus terebinthifolius* has an effort ranking of 225 which would be equivalent to *Schinus terebinthifolius* being the only species treated on 225 of our 365 PAs. Case study species are in bold font. Florida Exotic Pest Plant Council (FLEPPC) category I species are those documented as impacting native plant communities. FLEPPC category II species have been observed to have increased in abundance or frequency in natural areas.

	Effort	Prop.	Common name	Scientific name	Cat.
1	224.99	0.24	**Brazilian pepper**	**Schinus terebinthifolius**	I
2	86.84	0.09	**cogon grass**	**Imperata cylindrica**	I
3	73.57	0.08	**Old World climbing fern**	**Lygodium microphyllum**	I
4	55.68	0.06	melaleuca, paper bark	Melaleuca quinquenervia	I
5	52.49	0.06	Australian pine	Casuarina species	I
6	49.60	0.05	Japanese climbing fern	Lygodium japonicum	I
7	42.89	0.05	Chinese tallow, popcorn tree	Triadica sebifera	I
8	39.31	0.04	air-potato	Dioscorea bulbifera	I
9	31.14	0.03	Unidentified species	NA	NA
10	24.76	0.03	coral ardisia	Ardisia crenata	I
11	16.03	0.02	Chinaberry	Melia azedarach	I
12	15.15	0.02	skunk vine	Paederia foetida	I
13	14.71	0.02	camphor tree	Cinnamomum camphora	I
14	14.27	0.02	lead tree	Leucaena leucocephala	II
15	13.94	0.02	Bay Biscayne creeping-oxeye	Sphagneticola trilobata	II
16	12.91	0.01	**Caesar's weed**	**Urena lobata**	II
17	12.54	0.01	mimosa, silk tree	Albizia julibrissin	I
18	11.58	0.01	tropical soda apple	Solanum viarum	I
19	9.29	0.01	lantana, shrub verbena	Lantana camara	I
20	8.80	0.01	bowstring hemp	Sansevieria hyacinthoides	II
21	7.85	0.01	rosary pea	Abrus precatorius	I
22	6.61	0.01	shoebutton ardisia	Ardisia elliptica	I
23	5.85	0.01	torpedo grass	Panicum repens	I
24	5.63	0.01	**Guinea grass**	**Panicum maximum**	II
25	5.11	0.01	lather leaf	Colubrina asiatica	I
26	4.98	0.01	Japanese honeysuckle	Lonicera japonica	I
27	4.87	0.01	downy rose-myrtle	Rhodomyrtus tomentosa	I
28	4.74	0.01	wild taro	Colocasia esculenta	I
29	4.64	0.01	seaside mahoe	Thespesia populnea	I
30	4.03	0	guava	Psidium guajava	I
31	3.88	0	scaevola, beach naupaka	Scaevola sericea	I
32	3.88	0	aquatic soda apple	Solanum tampicense	I
33	3.84	0	paper mulberry	Broussonetia papyrifera	II

Table 3.5: (continued)

	Effort	Prop.	Common name	Scientific name	Cat.
34	3.78	0	nandina, heavenly bamboo	Nandina domestica	I
35	3.55	0	kudzu	Pueraria montana	I
36	3.20	0	Par grass	Urochloa mutica	I
37	2.75	0	Burma reed, cane grass	Neyraudia reynaudiana	I
38	2.00	0	arrowhead vine	Syngonium podophyllum	I
39	1.93	0	tung oil tree	Aleurites fordii	II
40	1.91	0	white-flowered wandering Jew	Tradescantia fluminensis	I
41	1.72	0	cat's claw vine	Macfadyena unguis-cati	I
42	1.64	0	wedelia	Wedelia trilobata	II
43	1.49	0	Chinese brake fern	Pteris vittata	II
44	1.48	0	mahoe, sea hibiscus	Hibiscus tiliaceus	II
45	1.48	0	strawberry guava	Psidium cattleianum	I
46	1.25	0	bischofia	Bischofia javanica	I
47	1.24	0	life plant	Kalanchoe pinnata	II
48	1.09	0	sapodilla	Manilkara zapota	I
49	1.06	0	purple sesban, rattlebox	Sesbania punicea	II
50	0.90	0	carrotwood	Cupaniopsis anacardioides	I
51	0.80	0	Natal grass	Rhynchelytrum repens	II
52	0.76	0	woman's tongue	Albizia lebbeck	I
53	0.76	0	Chinese or hedge privet	Ligustrum sinense	I
54	0.76	0	castor bean	Ricinus communis	II
55	0.75	0	winged yam	Dioscorea alata	I
56	0.71	0	confederate jasmine	Trachelospermum jasminoides	NA
57	0.51	0	sweet autumn virginsbower	Clematis terniflora	NA
58	0.48	0	thorny eleagnus	Elaeagnus pungens	II
59	0.46	0	twin-flowered passion vine	Passiflora biflora	II
60	0.44	0	earleaf acacia	Acacia auriculiformis	I
61	0.42	0	West Indian marsh grass	Hymenachne amplexicaulis	I
62	0.41	0	**Peruvian primrose-willow**	**Ludwigia peruviana**	I
63	0.38	0	arrow bamboo	Pseudosasa japonica	NA
64	0.34	0	schefflera, umbrella tree	Schefflera actinophylla	I
65	0.29	0	oyster plant	Tradescantia spathacea	I
66	0.25	0	flamegold tree	Koelreuteria elegans	II
67	0.24	0	Surinam cherry	Eugenia uniflora	I
68	0.24	0	pothos	Epipremnum pinnatum	II
69	0.20	0	malanga, elephant ear	Xanthosoma sagittifolium	II
70	0.19	0	rose Natal grass	Melinis repens	I
71	0.18	0	climbing or Christmas cassia	Senna pendula	I
72	0.14	0	alligator weed	Alternanthera philoxeroides	II
73	0.13	0	coconut palm	Cocos nucifera	NA
74	0.13	0	flamevine	Pyrostegia venusta	NA
75	0.12	0	rubber vine	Cryptostegia madagascariensis	II
76	0.09	0	bush morning-glory	Ipomoea fistulosa	II
77	0.08	0	common asparagus fern	Asparagus setaceus	NA
78	0.07	0	umbrella plant	Cyperus involucratus	II
79	0.07	0	glossy privet	Ligustrum lucidum	I
80	0.06	0	Senegal date palm	Phoenix reclinata	II
81	0.05	0	Napier grass	Pennisetum purpureum	I

Table 3.5: (continued)

	Effort	Prop.	Common name	Scientific name	Cat.
82	0.05	0	sisal hemp	Agave sisalana	II
83	0.04	0	rose-apple	Syzygium jambos	II
84	0.04	0	Egyptian grass	Dactyloctenium aegyptium	NA
85	0.04	0	Mexican petunia	Ruellia brittoniana	I
86	0.04	0	tropical almond	Terminalia catappa	II
87	0.04	0	coral vine	Antigonon leptopus	II
88	0.04	0	red sandalwood	Adenanthera pavonina	II
89	0.03	0	jambolan, Java plum	Syzygium cumini	I
90	0.03	0	solitary palm	Ptychosperma elegans	II
91	0.03	0	orchid tree	Bauhinia variegata	I
92	0.03	0	Taiwanese cheesewood	Pittosporum pentandrum	II
93	0.02	0	Puerto Rico silver palm	Coccothrinax barbadensis	NA
94	0.02	0	queen palm	Syagrus romanzoffiana	II
95	0.01	0	Arabian jasmine	Jasminum sambac	II
96	0.01	0	laurel fig	Ficus microcarpa	I
97	0.01	0	asparagus-fern	Asparagus densiflorus	I
98	0.01	0	limpo grass	Hemarthria altissima	II
99	0.00	0	Washington fan palm	Washingtonia robusta	II
100	0.00	0	puncture vine, bur-nut	Tribulus cistoides	II
101	0.00	0	santa maria, mast wood	Calophyllum antillanum	I
102	0.00	0	white cypress-pine	Callitris glaucophylla	NA
103	0.00	0	Indian rosewood, sissoo	Dalbergia sissoo	II
104	0.00	0	governor's plum	Flacourtia indica	II
105	0.00	0	wood-rose	Merremia tuberose	II
106	0.00	0	susumber, turkey berry	Solanum torvum	II
107	0.00	0	simpleleaf chastetree	Vitex trifolia	II

Chapter 4

Assessing changes in forest structure and composition over time to estimate the benefit of protected areas

A version of this chapter will be submitted for publication after modification during internal and external review.

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The use of "we" in this chapter refers to me and my co-authors. As the lead author of this article, I was responsible for developing the ideas for this paper, conducting the analysis, and writing the manuscript. P.R.A. and E.R.L are co-authors of this work and they were responsible for feedback at early stages of the research and for helping to edit the manuscript. M.J.H and D.H. provided the spectral imagery data.

Abstract

Conservation planners and land managers are searching for a cost-effective method to assess the variation in benefit across different types of protected areas (small vs. large, urban vs. rural, managed vs. not managed, etc.). Because measures of benefit must describe specific protected areas over many years, in many cases the only feasible method for obtaining the relevant data in a timely and cost effective manner is to use remotely sensed spectral imagery. Spectral imagery has been used in assessing the benefits of terrestrial protected areas, but primarily to gauge rates of deforestation and recovery. Here we evaluate whether a similar approach can be used to examine more resolved aspects of the benefit of forest protection. We aim to identify a method to determine a baseline of forest attributes from a time prior to the conservation action and to recreate the history of how the forest has varied over the time since protection.

To do so, we examine our ability to relate six different measures of forest structure and composition on existing protected areas to freely available Landsat satellite imagery. We show that the forest attributes differ in the amount of variation that is able to be detected remotely, with some models outperforming others in predictive capacity. We then illustrate the utility of our forest structure and composition models by examining two relationships between modeled forest growth and protected areas of different sizes.

4.1 Introduction

Conservation scientists and practitioners have been calling for cost effective and efficient methods to measure the benefits of protected area (PA) establishment and management (Naughton-Treves et al., 2005; Ferraro and Pattanayak, 2006; Sutherland et al., 2009). Protected area establishment is the most common biodiversity conservation strategy, but the ability of individual PAs to provide a benefit over time may vary. It is important to quantify this variation in order to assess the benefit of individual PAs and to determine if some types of PAs (differing by area, location, level of protection, type of management, etc.) provide more benefits than others.

An assessment of PA benefits should compare the relevant attributes from before establishment with the same attributes up to the present. This is because the benefit a PA provides has many aspects, but in general it describes the effect of establishing and managing a PA on some objective (Gaston et al., 2008). When biodiversity conservation is the objective, the most important function of a PA is to counteract threats and allow focal species and communities to persist over time (Pressey et al., 2007). Ideally, we would know the history of how indicators of these species and communities have changed over time and would thus be able to identify the influence of PA establishment and presence.

The problem is that change over time data are difficult to obtain. Information on PA attributes prior to protected area acquisition is the most problematic. On-the-ground ecological sampling efforts tend to occur only over short time periods, and many locations that are current or potential protected areas were never sampled in the past (Timko and Innes, 2009). Establishing long term monitoring studies can counteract this limitation for future applications, but the cost of such effort can be prohibitive and it would be decades before meaningful temporal information could accrue. This difficulty in acquiring appropriate data suggests that strategies using remotely sensed spectral imagery, even if imperfectly, may offer the greatest promise to examine the changes over time (Wiens et al., 2009).

Methods that use satellite imagery to remotely sense changes over time have become more accessible for application by practitioners. Landsat data have recently become freely available via the United States Geological Survey, providing decades worth of spectral imagery across the globe (Wulder et al., 2012). Recent advances in computing and pre-processing have made it feasible for conservation professionals to use these data (Wiens et al., 2009). These data sources have been used in recent analyses that examine the effectiveness of protected area establishment in counteracting deforestation in the Brazilian Amazon and elsewhere (Andam et al., 2008, 2013). In addition, researchers have used remote sensing techniques to assist in PA management and conservation efforts as varied as assessing rare species habitat extent (Stabach et al., 2012), monitoring PA effectiveness in remote areas (Ayebare et al., 2012), and quantifying surrounding land use encroachment (Wang, 2012). Although The Nature Conservancy (TNC) has used this spectral imagery to monitor forest re-growth after PA acquisition (Sutter et al., 2009), conservation practitioners have not yet used these data to their full capacity for assessing the benefit of PAs.

The benefit of terrestrial protected areas is often related to their ability to protect forests. In virgin forests, where logging is the greatest threat to species persistence, estimates of changes in forest cover are an appropriate measure of benefit (Andam et al., 2008; Joppa and Pfaff, 2010, 2011; Blackman, 2013). In regions like the eastern US, however, the vast majority of PAs occur on forest lands that have already been harvested at least once (Pan et al., 2011). Thus, PAs contain forests that are in various stages of regrowth and that may be managed for certain tree species (e.g. valuable hardwoods selectively harvested, pines planted for pulp, invasive species removed). Consequently, the benefit of PA establishment is more than the simple retention of forest cover, and instead depends on the persistence and recovery of mature individuals of species that are characteristic of desired forest communities. A small amount of prior research has attempted to quantify forest growth and re-growth but has primarily used proportional cover as a proxy for forest dynamics (Triantakonstantis et al., 2006; Andam et al., 2013; Htun et al., 2013). However, these proxies do not provide sufficiently resolved information to inform forest management. For instance, in forests in the Appalachian mountains of the eastern USA, a high-benefit protected area could be one that contains widely spaced mature individuals of the many tree species present in forest types such as Appalachian Cove Forest, Cumberland Dry Oak Forest, or Appalachian Montane Pine Forest (all forest types per NatureServe, 2011; Anderson et al., 1999). To understand changing benefit over time for PAs that protect Appalachian mountain forests, land managers must understand how the forest structure (e.g. tree age, size, density, etc.) is changing as well as the identity and distribution of dominant species.

In this study we have two objectives. First, we test a method to relate field measured forest structure and composition to contemporary spectral imagery. We are particularly interested in assessing the utility of remote sensing imagery for applications that require more resolved aspects of forest conservation than the variation in forest cover that has already been embraced by conservation professionals. Specifically, we examine how simple models describing the forest features that could relate to TNC's conservation objective of "forest intactness" differ in their explanatory power. We then illustrate how these model results can be projected back in time to evaluate forest conditions prior to PA establishment that would otherwise be impossible to study. Such models could be applied to answer many questions of relevance to conservation professionals. Accordingly, our second objective is to demonstrate their utility with two illustrative examples (tree size and fire-tolerant pine species as a function of PA area). We approach these objectives by addressing the following questions:

1. How well do attributes of forest structure and composition that could proxy for conservation benefit relate to spectral imagery?
2. How do predicted changes in benefit (forest structure and composition) differ on large versus small protected areas?

As discussed above, benefit has many meanings and must be defined for use, but, in the context of Appalachian forest conservation, benefit could be quantified with metrics that describe forest structure and composition change in relation to the desired future condition of the site. For instance, a hypothetical desired future condition for a PA could aim for forest that had 10% cover of fire-maintained species(pine), that was an uneven aged stand with many mature trees (dbh >40 cm), and had high species richness (5-6 species per 10 trees). For such a conservation objective, PAs where the forest structure and composition change to be more similare to the desired future condition can be considered to provide a greater benefit than those that do not (assuming that the desired future condition is appropriately chosen and similar for both PAs). In this example the comparative metric would be a sum of three forest attribute estimates at a point in time.

Estimates of changes in benefit are useful for relating to PA attributes, such as area, to enhance conservation planning decisions. For instance, the relationship between PA area and biodiversity conservation effectiveness is a classic and organizing question in conservation planning (Simberloff and Abele, 1982). The widely accepted answer is "it depends," and conservation organizations have been grappling with ways to prioritize funding across possible acquisitions. In our study region, it is possible that there are fundamental differences in the forest structure and composition of fragments of different sizes and these differences should be considered during the planning process. For instance, occasional high quality tracts of remnant old trees and rare community types are still present, but they may be more prevalent on small privately owned tracts that were possibly never commercially timbered. Meanwhile, large forested tracts also occasionally become available for purchase as the forest products industry continues to divest of its assets in the region (Wear and Greis, 2013). These large tracts can provide cornerstone preserves for regional conservation landscapes and possibly garner strong political and donor base support, but may have been more recently harvested.

Protected area characteristics, such as area, could also be associated with species composition. For instance, contemporary Appalachian forests are primarily dominated by deciduous hardwoods. There is evidence, however, that this dominance is a recent occurrence that has developed as a result of the extensive logging in this area about 150 years ago and the subsequent fire suppression policies (Nowacki and Abrams, 2008). Prior to European settlement, indigenous residents and lightning would have ignited frequent fires on the ridges and dry slopes of the region. Under these environmental conditions, fire adapted forest types dominated by pine (*Pinus*) species and thick barked oaks such as chestnut oak (*Quercus montana*) and white oak (*Quercus alba*) were abundant (Brose et al., 2001). Fire scar analyses (Flatley et al., 2013), soil carbon dating (Fesenmyer and Christensen, 2010), historical accounts, and the presence of pyrogenic understory species (Hoss et al., 2008) have convinced many land managers that the restoration of these communities is a valid conservation goal for the region (Southern Appalachian Man and the Biosphere, 1996b; The Nature Conservancy, 2000, 2003).

4.2 Methods

Study sites and region

To examine variation in current forest structure and composition across PAs, we sampled forest attributes on 27 PAs that were recently acquired by TNC. These PAs were a subset of a Conservation Lands System (CLS) database query from 2010, which called for all TNC land transactions that occurred between 2000 and 2009 in the Central Appalachian Forest (The Nature Conservancy, 2001), Southern Blue Ridge (The Nature Conservancy, 2000), and Cumberland and Southern Ridge and Valley

(The Nature Conservancy, 2003) ecoregions of the Eastern USA. These ecoregions constitute the Appalachian Mountains of the Eastern United States, an ancient mountain chain with rough topography, high deciduous tree diversity, and typically low human population densities (Southern Appalachian Man and the Biosphere, 1996a). In some cases, land transactions resulted in stand-alone PAs, but in other cases the transactions are tracts that were additions to larger PAs. From here on, we call these land transactions PAs regardless of whether the transaction included the entire current PA extent; a choice we revisit in the discussion. We selected PAs to visit for field sampling based on 1) a stated TNC conservation objective for forest protection or "intactness" from internal documents ("deal abstracts") completed in advance of the land transactions, 2) size large enough to accommodate our sampling protocol (PAs larger than $\approx$ 8 HA; see below), and 3) fee simple acquisition. All PAs were owned by TNC at the time of the CLS query, but six had been transferred to government agencies (e.g., North Carolina State Parks, Maryland State Forest, Thomas Jefferson National Forest) by the survey date. The 27 PAs that were sampled ranged in area from 8 to 885 HA, and were distributed across 10 US states (Figure 4.1, Table 4.4).

Field sampling for forest structure and composition

We recorded forest structure and composition information at 20 random sample points per PA. We chose to sample the same number of points per PA because we wanted to obtain inference at the scale of a PA. The sampling locations were determined using Geographic Information System (GIS) software prior to site visits (ArcMap version 10.1, ESRI, Redlands, CA, USA). Sample point locations at a PA were stratified so that half of the points were edge points located within 100 m of a PA boundary, and half of the points were interior. No random points were allowed to fall within 30 m of another random point, consistent with the grain size (30 x 30 m) of pixels from Landsat spectral imagery (see below). Due to this constraint, the smallest PA where we could sample 20 random points was roughly 8 HA in size (see above).

At each sampling point, we recorded canopy openness using a hand held densiometer, identified the 10 closest trees to species, measured the distance to each from the sampling point, and recorded the diameter-at-breast-height (dbh) of each of the ten trees. We considered trees to be any woody shrub with a dbh greater than 10 cm. We made an exception to the 10 cm dbh minimum for scrub oak (*Quercus illicifolia*) because it is a dominant species in the scrub oak-heath community that is a conservation priority at some of our PAs (The Nature Conservancy, 1998), and it rarely exceeds 10 cm dbh. All tree species nomenclature follow Kirkman et al. (2007), except for species we found only in the states of Pennsylvania and West Virginia which follow Elias (1987). All *Crataegus* and *Amelanchier* were identified to genus only. Field surveys were performed between May and September of 2013.

Remote sensed predictor variables

We used 2011 imagery from the Landsat 5 thematic mapper (TM) sensor to fit models of forest structure and composition and imagery from 1985 to 2010 for the example applications. Cloud-free summertime means were generated from multiple TM scenes and path/rows for each year using SPARCS (Hughes and Hayes, 2014) for imagery covering each of our plot locations. We then used the tasseled cap transformation to convert the six chanels of spectral imagery into three minimally correlated predictor variables (Crist and Cicone, 1984). Several bands of Landsat channel data are highly correlated, but data in the six dimensional Landsat band space can be described in terms of three uncorrolated dimensions on a rotated axis (Kauth and Thomas, 1976). The tasselled cap transformation extracts these three orthogonal components from the correlated data. The coefficients from the tasseled cap axis rotation can then be linearly combined with the Landsat channel data to provide three metrics that relate to vegetation reflectance (brightness), chlorophill content (greenness), and moisture (wetness) (Kauth and Thomas, 1976). We calculated brightness, greenness, and wetness values from the imagery for the 30x30 m pixel containing each random point. Three sample points were discarded due to data processing errors. The final dataset contained casseled cap values for 537 plot locations describing the spectral properties of the forest plot. We scaled the relationship to correct for shadows due to time of day and aspect by dividing the value for each Landsat band by the summed value of all bands.

We also included several abiotic covariates in the model to account for underlying environmental effects or gradients that could influence the forest attributes of interest. For each sampling point we obtained data on elevation, northness, slope, and latitude. Elevation data were from the NASA National shuttle radar topography mission (Version 2.1, Rodriquez et al., 2006). Using this dataset, we calculated northness and slope using spatial analyst tools in Arc Map (version 10.1). Northness scales from north (1) to south (-1) and is the cosine of aspect in radians. Latitude was recorded at the point by handheld GPS (Garmin E-Trex 20).

Analysis

Model specification

We developed models for six different forest attributes: mean dbh, % canopy openness, tree density (mean distance from random point), species richness, pine density, and red maple (*Acer rubrum*) density. These response variables were chosen because they represent measures of forest structure and composition that are aligned with conservation objectives common to this region (see introduction and discussion). The first four variables are measures of forest structure. Changes in tree size (dbh) over time can be a proxy for tree age within a forest, and also loosely relate to time since harvest within a stand. Canopy openness is related to how large and close together trees are. This variable must be interpreted with care because some forest types (eg. pine dominated savannas, dry oak forests, scrub oak bald, cedar glades) are characterized by widely spaced trees, so increases in conservation benefit do not necessarily correlate with canopy closure. Tree density was calculated as the mean distance to the ten closest trees from each random point. The expectation is that more mature (and thus greater conservation benefit) forests have large, widely spaced trees, although this depends on community type.

The other three response variables are indicators of forest community composition. We first model species richness of the ten trees at a point. Appalachian forests contain very high tree species diversity, and although the absolute diversity differs across community types, maintaining species richness in general is a common conservation objective. We model the proportion of pines, out of the ten at a point, as a proxy for the presence of the fire maintained community types that are a current conservation focus for many management agencies in the region. Finally, we model the proportion of red maple because it is a species that has recently become dominant in the eastern deciduous forests (Abrams, 1998; Hanberry, 2013) and land managers are concerned about how it is replacing the prior oak (*Quercus* species) dominants.

We used linear mixed models and generalized linear mixed models to relate current forest condition to remote sensing predictors. This approach is appropriate because it allows us to specify modeled distributions as suggested by the data. In addition, it allows us to account for an error structure that includes error due to model specification as well as error due to similarities in forest condition measurements that are related to protected area identity. We illustrate the model specifications below using canopy openness as an example response variable.

$$\%\text{ canopy openness} = \alpha + \beta_1(\text{greenness}) + \beta_2(\text{wetness}) + \beta_3(\text{brightness}) + \beta_X \text{Covariates} + \epsilon_{site} + \epsilon_{pixel}$$

Our approach, relating forest attributes to spectral imagery, is conceptually similar to calculations of indices like NDVI that have been widely employed to quantify change in vegetation structure and status at large scales (e.g. Kennedy et al., 2012). We are, however, harnessing the technique to predict more customized differences in forest condition at the scale of a protected area or regional protected area network.

We fit linear models with random effects using restricted maximum likelihood (package nlme in R, Pinheiro et al., 2009), a choice justified by the design of the data collection and this model framework outperforming simpler models in AIC competition. For modeling % canopy openness, log transformation of the response variable improved model fit and compliance with model assumptions. Meanwhile, we used a generalized linear model with a binomial distribution and a logit link (Bates et al., 2011, package lme4 in R,) for pine and red maple. In all cases, tolerance testing indicated that no predictor variable was more than 20 % dependent on variation in other predictor variables ensuring that collinearity requirements were adequate to proceed (Quinn and Keough, 2001). We specified the full model in all cases for model portability and comparability across measures.

Example applications

These models of forest structure and composition were developed for applications that need predictions of change over time to understand the benefit of attributes of the PAs and their establishment. We illustrate their use with two example applications that examine forest change over time and its relationship to PA area on our Appalachian study sites.

Our first example application uses one of our models to recreate historical conditions. We examine whether the average size of trees in the forest at acquisition differs across PA sizes, using our dbh model. We would expect to see larger trees on smaller tracts as hypothesized above. We calculate the estimated dbh at acquisition by using the coefficients from our dbh model and Landsat channel data for the year of acquisition of each PA. We then regress these predictions of mean dbh per PA at acquisition against PA area (HA). The relationship between PA area and predicted tree size at acquisition would then be represented by the value and significance of the β_1 parameter in the model specified below.

$$\text{Predicted dbh at acquisition} = \alpha + \beta_1(\log(\text{PA area})) + \epsilon$$

Using this model, we can explore the predicted variation in a measurement that is unavailable: how big the trees were when each PA was acquired. Records from a consistently implemented field survey on each PA would clearly be better, but they are not available for any of our study sites. This is a situation we anticipate being quite common in conservation practice.

In the next example, we develop estimates of forest condition prior to acquisition. We are interested in whether there has been a change in pine density over time across PAs and if the change varied with PA area. Only two of our study sites (Floyd, GA, and Blair, PA) have enacted a fire reintroduction program so far, but we are curious about whether trends in the density and extent of remnant fire maintained community types differ with land parcel area across our study PAs. We might expect a difference with area if larger PAs were more likely to retain natural processes such as lightning ignited fire movement through the landscape. To examine changes in fire maintained communities over time on our PAs, we paired the coefficients from our pine density model with Landsat channel data from our sample points for every year since 1985 (the earliest year of Landsat 5 availability, Wulder et al., 2012). We then regressed predicted pine density against time, PA area, and the interaction between time and PA area to assess the relative importance of PA area on pine density. To do so, we used a mixed modeling approach that allowed the intercept of pine density change over time to vary for each PA. Eg:

$$\text{Predicted pine density} = \alpha + \beta_1(\text{PA area}) + \beta_2(\text{year}) + \beta_3(\text{year * PA area}) + \epsilon_{site} + \epsilon_{pixel}$$

Here we are most interested in the significance of the β_3 parameter which indicates whether the slope of the relationship between pine density and time varies for PAs of different sizes.

4.3 Results

Our field-collected forest structure and composition data described a range of forest conditions across the Appalachian mountains. The forests in general had small trees with a mean dbh across our sample sites of 22.71 cm; although mean dbh ranged from 0.50 cm at PAs with scrub oaks to 62.30 cm at a PA with large oaks and hickories (*Carya* species; Table 4.1). There was also a generally high level of canopy closure with a distribution of % openness measures that was skewed towards low values and had a mean value of 18.84 % open. Our sampled Appalachian forests were dense with a mean distance to the ten closest trees of 5.5 m. There was high species richness across the study region with a mean of 4.1 species per 10 trees sampled, 19.3 species per PA, and 95 total species of trees recorded. Finally, the proportions of pine and red maple were both skewed towards zero, with both having a mean value of less than 1 of the 10 trees per sample point (0.85 for pines and 0.99 for red maple).

Forest structure and composition models

Forest structure attributes varied in how well they were explained by our modeling approach and in some cases were not related to the spectral imagery as well as they were related to the covariates (Table 4.2, Table 4.3). Variation in the size of the trees (mean dbh) across the 537 sample points was the forest structure attribute that was best explained by our models (pseudo R^2 = 0.48). This variation was significantly related to the tasseled cap wetness band. Meanwhile, the openness of the forest canopy was explained by wetness and increased with slope (pseudo R^2 = 0.34). Finally, tree density decreased slightly with elevation and could not be discerned using spectral imagery alone (pseudo $R^2 = 0.26$).

Forest composition attributes were also predictable to some extent, but they were more strongly related to covariates than spectral attributes (Table 4.2,Table 4.3). Species richness was not related to the spectral bands but it decreased with latitude, northness, and elevation (pseudo $R^2 = 0.36$). The proportion of the ten nearest trees that were a pine species was related to brightness, greenness and wetness bands and also decreased with latitude (pseudo $R^2 = 0.49$). Meanwhile, very little of the variation in the proportion of red maple out of ten trees was predicted by our model (pseudo $R^2 = 0.10$), but the proportion predicted did increase with latitude.

Example applications

The results of our example applications suggest that the forest structure and composition of our study PAs has not changed drastically in the decade or so since protection or in the 28 years of Landsat data availability. The dbh predictive model suggests that tree size at acquisition does not differ across site sizes for our study PAs. A plot of the predicted values against PA area might suggest a decreasing trend in dbh as PAs increase in area, but the relationship was not significant (Figure 4.2, Table 4.5). There were several outliers at low predicted dbh values that appear to be influencing the relationship, however.

In the second illustrative example, we tested whether PA area relates to variation in pine density over time. We found no relationship between pine density at a sample point and either time or PA area for our 27 study sites (Table 4.5).

4.4 Discussion

The primary objective of this research was to explore the feasibility of using remote sensing data to model attributes of forest structure and composition that are important for biodiversity conservation management objectives. Conservation professionals have embraced the use of remote sensing data for assessment of changes in forest cover (e.g. Sutter et al., 2009), but here we examine the application of these data to measure more resolved aspects of forest conservation benefit. We show that it is possible to describe the variation in several forest attributes that can provide more insight into conservation benefit than forest cover alone. In particular, reasonably large amounts of the variation in dbh and pine density can be explained by the spectral imagery in our models, suggesting that these might be useful proxies for PA benefit calculations in our ecoregions, whereas other responses like red maple density could not be effectively modeled from spectral imagery. Researchers in other regions/ecoregions may similarly need to evaluate which measures of forest structure and composition can be effectively represented by spectral imagery, but our results suggest this approach provides a feasible method to evaluate additional PA benefits affordably and rapidly over large spatial scales and through historic time periods.

We also used two of our models to demonstrate the application of spectral imagery to questions of potential conservation effectiveness over time. We did not see clear differences in tree size that were consistently related to land parcel area at time of purchase, contrary to our hypothesis. We also found that the prevalence of potential fire maintained community types (e.g. those containing pine trees) is not related to PA area and does not appear to have systematically changed over the past 28 years. In both cases, however, the time frame of our comparison may have been limiting.

For example, Landsat data are only available back to 1985, but pine (or other fire maintained community) declines may have greatly preceded this imagery by as much as a century (Nowacki and Abrams, 2008).

Our models were able to explain moderate amounts of variation in some of the forest structure and composition attributes that we examined. This is encouraging for conservation managers because it suggests that it is relatively straightforward to model meaningful variation in forest attributes of conservation interest over large scales using freely available satellite data. However, the variation in some attributes was better described than in others. Tree size (dbh) and proportion pine were the two variables that were best explained by our models with about half the variation explained for each of them. In contrast, the proportion of red maple explained by spectral attributes and covariates was minimal (pseudo $R^2 = 0.10$). These results illustrate that attributes of interest must be chosen carefully and it is probably wise to test the explanatory capacity of several forest attributes when attempting to assess benefit.

Finally, our example applications demonstrate that these types of models can provide meaningful information that relates to conservation planning. Although there was no significant difference in dbh at acquisition, our model suggests that there might be a trend towards larger trees on smaller sites, potentially reflecting a history of variation in management. We would expect to see the hypothesized difference, given the patterns of land tenure and forest harvest in this region. The differences across PAs, however, would not be something as clear as saplings vs. old growth. Instead, it is probably on the order of a decade or two of extra growth on some of the smaller parcels. This region has been highly impacted by logging (Yarnell, 1998), and across the 27 PAs we encountered few trees that displayed old growth characteristics. Meanwhile, the lack of change in predicted pine density across PAs of different sizes or over time is disappointing but not particularly surprising. In some landscapes (e.g. the Southeastern coastal plain of the USA), larger sites have been historically less impacted by fire suppression because of their natural flammability and frequent lighting strikes. We did not observe this pattern in Appalachia. It appears that pine density is similar on PAs regardless of area and that it has not changed consistently in the 28 years of Landsat data availability. This could be because fire suppression in this region is a century rather than decades old and the declines in pine occurred long before 1984 (Nowacki and Abrams, 2008). Our pine change over time model is still useful for land managers, however, because many of these PAs aim to begin reintroducing prescribed fire in the future. Our model could be used to assess the benefit or effectiveness of these management efforts from the perspective of mesic tree suppression and pine species promotion into the future.

Assumptions and caveats

Our models were developed using field data collected on TNC preserves across Appalachia that had a stated objective for forest protection. One consequence of this approach was that our three northernmost sites were dominated by scrub oak. This species is a large shrub that is the dominant tree species in the scrub oak summit (scrub oak-heath) community that was a conservation priority of the northernmost preserves (The Nature Conservancy, 1998, 2001). It is also found in smaller patches on other preserves throughout the region. This means that, in some cases, the explanatory ability of latitude and potentially some of the spectral sensors is responding to this species alone. Inspection of model residuals suggested that the mixed modeling approach corrected for much of the effect of these outliers, but we also performed a sensitivity test by re-fitting the above models while excluding data from sampling locations that were dominated by scrub oak. To do so, we removed 36 data points describing sampling locations where the trees had a mean dbh of less than 10 cm. The resulting sensitivity test models displayed fitted coefficients that were similar in significance, magnitude and direction to the models using the full dataset (Supplementary Table 4.6). However, removing the scrub oak dominated data points resulted in a change in explained variation that ranged from a 43% decrease in explanatory capacity for forest density measurements (Pseudo R^2 changed from 0.26 to 0.15) to a 110% increase in explanatory capacity for red maple density measurements (Pseudo R^2 changed from 0.10 to 0.22). These sensitivity test results suggest that the explained model fit can be influenced by the spatial organization of one species, although the magnitude of the effect varies across the modeled forest attributes. We chose to keep these data in our analysis because the scrub oak heath community is an important community type that is a conservation priority in the region.

For this analysis, we used individual conservation land transactions as the unit of replication as opposed to jurisdictional PA boundaries. This is because the individual deal is the grain at which conservation decisions are usually made, and thus is the relevant scale for purchase benefit assessment. In many of our study cases, the deal is an in-holding or addition to an existing PA. Because of this, many of the classic predictions of the conservation impacts of PA area (e.g. increased edge effects, extinction vs colonization) may not hold for our study sites. Nevertheless, this paper illustrates a method that can be used to directly test whether these types of impacts do actually differ when we consider deals as opposed to entire PAs.

There are also situations where back-casting with a parameterization based on current forest attributes, such as we perform here with our reconstruction of historic forest attributes, may be impossible. Such would be the case if the historic forest attributes were no longer present across any of the current field sites. For instance, 100 years ago, these forests would have been dominated by the American chestnut (*Castanea americana*). Due to widespread extermination by a blight, that species is almost never present in contemporary forests and if it is, it rarely attains canopy height (Stephenson, 1986). Our current day parameterized models have no equivalent combination of signature and covariates that could explain the signature of dominance by that species. We are not suggesting that American chestnut is likely to hinder our historic reconstructions, but, we acknowledge that our method cannot explain all possible forest characteristics.

Application recommendations and conclusions

The scale of decision making is an important consideration when designing tools for benefit measurement. In this case, we consider variation in forest attributes that can be measured at the level of a PA. For instance, average tree size (dbh) on a PA, or average species richness across a PA. Thus our models provide inference about relative variation in forest attributes across different PAs and are appropriate for supporting decisions at the PA scale (e.g. what types of PAs should be established or managed to provide the desired benefit). However, our models were not designed to provide information at finer scales (e.g. how much additional timber does a forest hold).

For this study, we model forest structure and composition attributes that are potential measures of conservation benefit in the Appalachian mountains of the US. Our model coefficients are appropriate for conservation professionals to use directly if they want to model attributes of forested PAs in this region. With appropriate processed Landsat imagery (Hughes and Hayes, 2014) and covariate data (NASA Shuttle Radar Imagery) for the location and time frame of interest, the desired forest attribute estimates can be estimated with a linear combination of the appropriate model covariates. For general use within the Appalachian region, the model intercept value should be calculated as the sum of the random effects (intercept and residual in Table 4.2) and the provided model intercept. This method of presenting model coefficients is due to our mixed modeling approach whereby each study PA has a tailored intercept (random effect). For model application to the PAs where we obtained field data, the average random effects can be disregarded and replaced with the specific random intercept values we provide in the supplementary information (Table 4.8).

Protected area effectiveness is a critical question in conservation science. We develop models of different attributes of forest structure and composition to explore methods of quantifying protected area benefit that are more resolved than simply cover. Our aim is to produce tools that expand the utility of data sources that land managers and conservation practitioners are already using and to providing benefit estimates that can enhance conservation practice. This study is a step towards being able to cost effectively and efficiently estimate the relative benefit of protected areas.

Acknowledgements

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4.5 Appendix: Figures

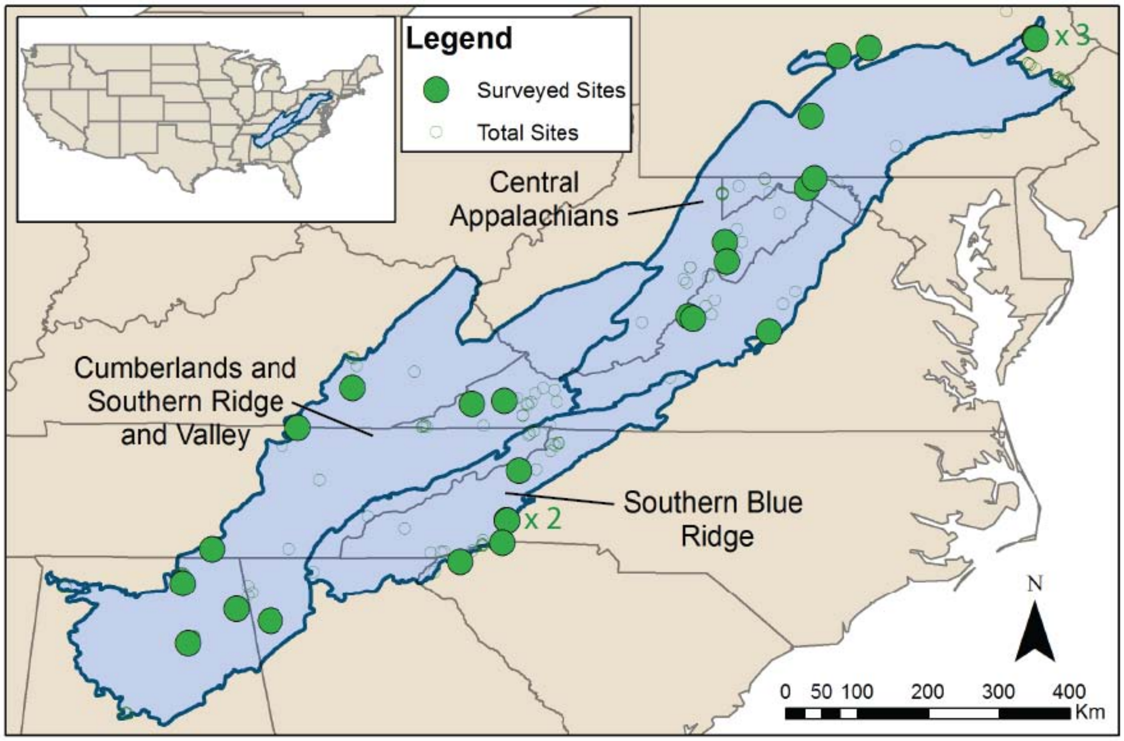

Figure 4.1: Forest structure and composition data were collected from 27 protected areas established by The Nature Conservancy across the Appalachian ecoregions, USA.

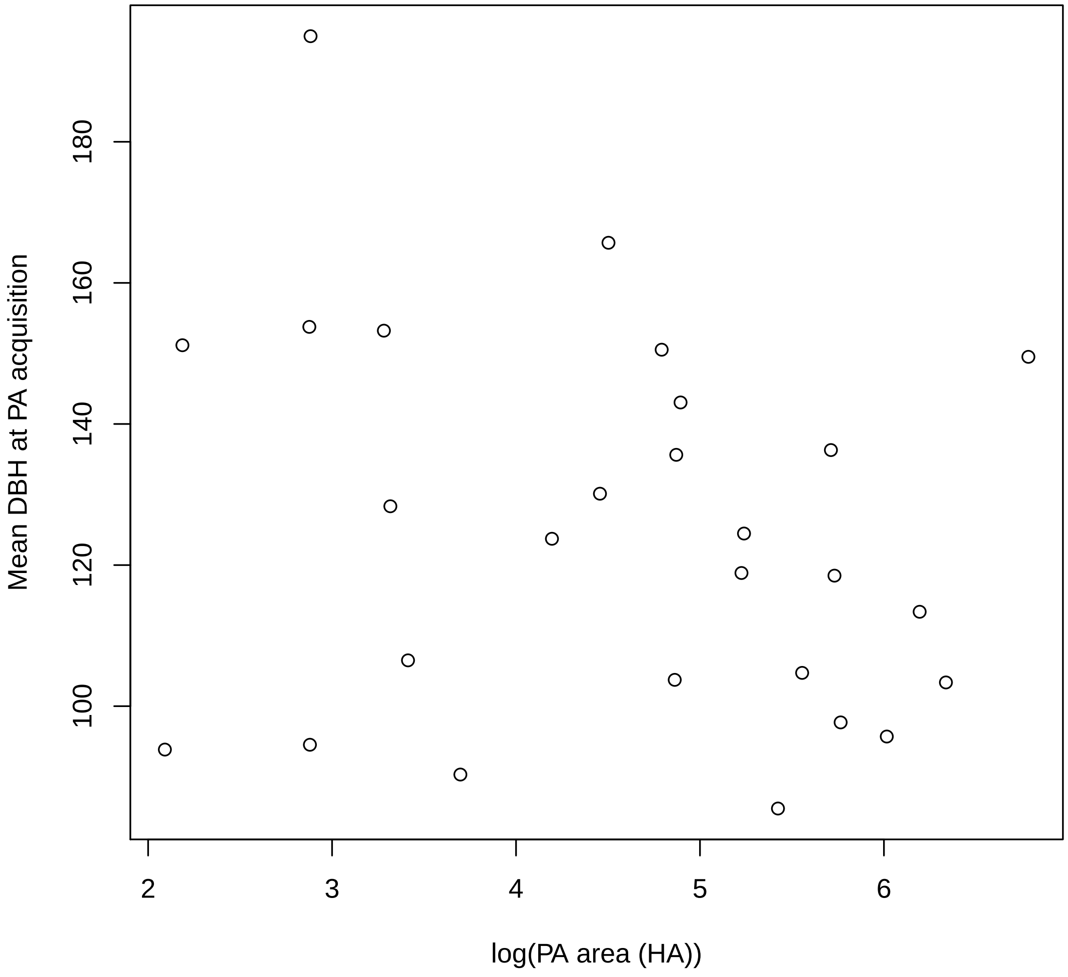

Figure 4.2: Predicted mean tree diameter at breast height (dbh) at the time when each of the 27 protected areas (PA) was acquired. The relationship between dbh and PA area is not statistically significant.

4.6 Appendix: Tables

Table 4.1: Field collected forest structure and composition data descriptive statistics. These descriptive are for the average value of ten trees at each point except for % openness which is a single measurement at the sampling point.

	Min	Mean	Max.
DBH (cm)	0.50	22.71	62.30
Openness (%)	0.00	18.84	99.84
Distance (m)	0.200	5.469	17.060
Spp. Richness	1.00	4.132	8.00
Pines (proportion of 10)	0.00	0.8454	10.00
Red maple (proportion of 10)	0.00	0.99	10.00

Table 4.2: Regression coefficients models relating forest structure and composition to spectral imagery and covariates. Each forest structure measurement was fit separately using mixed effects multiple regression models fit by REML. The full model is reported in each case for comparability across models. Site level influences were modeled as a random effect. Significant fixed effects indicated by bold font ($p < 0.05$).

	Fixed Effects							
	(Intercept)	Brightness	Greenness	Wetness	Latitude	Northness	Elevation	Slope
DBH	-93.39±98.05	357.26±251.66	-91.95±70.28	**56.71±23.62**	-0.60±0.42	0.57±0.46	-0.4E-03±2.7E-03	0.04±0.05
Log(%open +1)	13.93±10.68	-32.78±27.68	7.99±7.79	**-8.27±2.58**	0.04±0.03	-0.01±0.05	-1.8E-04±2.3E-04	**0.01±0.01**
Density	-7.08±24.39	50.19±63.23	-17.09±17.80	1.72±5.89	-0.13±0.08	-0.02±0.12	**-1.0E-03±5.4E-04**	0.02±0.01
Spp. Richness	-6.67±18.50	46.10±48.09	-11.28±13.58	2.84±4.47	**-0.18±0.05**	**-0.22±0.10**	**-1.4E-03±3.8E-04**	0.02±0.01
Pine	**110.7±51.22**	**-266.5±135.6**	**77.9±39.6**	**-25.3±12.53**	**-0.37±0.13**	-0.38±0.29	-7.9E-04±1.0E-03	-0.03±0.03
Red maple	-38.43±35.81	77.38±93.23	-22.42±26.86	8.26±9.08	**0.20±0.08**	-0.00±0.02	-3.1E-04±6.0E-04	-0.01±0.02

	Random Effect	
	(Intercept)	Residual
DBH	5.12	6.19
Log(%open +1)	0.37	0.74
Density	0.84	1.69
Spp. Richness	0.57	1.33
Pine	1.09	1.05
Red maple	0.05	0.23

Table 4.3: AIC and pseudo R^2 for models relating forest structure and composition to spectral imagery and covariates

	AIC	logLik	Efron's pseudo R^2	Link	Distribution
DBH	3551	-1765	0.48	identity	Gaussian
Log(% openness +1)	1279	-630	0.34	identity	Gaussian
Density	2157	-1068	0.26	identity	Gaussian
Spp. Richness	1896	-938	0.36	identity	Gaussian
Pine	157	-70	0.49	Logit	Binomial
Red maple	143	-63	0.10	Logit	Binomial

Table 4.4: Features of protected areas where forest structure and composition data were collected

	State	Area (HA)	Ecoregion	Conservation priority
1	Alabama	885	Cumberlands and Southern Ridge & Valley	Riparian and continuous forests
2	Alabama	8	Cumberlands and Southern Ridge & Valley	Dry mixed pine-hardwood forest
3	Alabama	130	Cumberlands and Southern Ridge & Valley	bottomland hardwood and forest, riparian
4	Georgia	28	Cumberlands and Southern Ridge & Valley	Mesic slope forest, dry pine/oak woodland and limestone cliffs and bluffs.
5	Kentucky	134	Cumberlands and Southern Ridge & Valley	Riparian hardwood forest
6	Maryland	86	Central Appalachian Forest	Riparian Forest
7	Maryland	9	Central Appalachian Forest	Riparian forest
8	North Carolina	319	Southern Blue Ridge	Woodlands
9	North Carolina	30	Southern Blue Ridge	Hardwood forest
10	North Carolina	189	Southern Blue Ridge	Broadleaf and mixed forest, headwater streams
11	Pennsylvania	27	Central Appalachian Forest	Riparian forest
12	Pennsylvania	121	Central Appalachian Forest	Forest
13	Pennsylvania	18	Central Appalachian Forest	Forest
14	Pennsylvania	490	Central Appalachian Forest	Forest
15	Pennsylvania	259	Central Appalachian Forest	Forest
16	Pennsylvania	302	Central Appalachian Forest	Forest
17	South Carolina	18	Southern Blue Ridge	Forest
18	South Carolina	227	Southern Blue Ridge	Forest/rock outcrop
19	Tennessee	186	Cumberlands and Southern Ridge & Valley	upland hardwoods
20	Tennessee	410	Cumberlands and Southern Ridge & Valley	limestone karst terrain, forested headwaters
21	Virginia	565	Central Appalachian Forest	montane pine barren, eastern hemlock forest
22	Virginia	308	Central Appalachian Forest	hardwood forests
23	Virginia	66	Cumberlands and Southern Ridge & Valley	aquatic site, limestone/dolomite barren communities, old growth forest communities
24	Virginia	90	Central Appalachian Forest	montane pine barren, eastern hemlock forest
25	Virginia	18	Cumberlands and Southern Ridge & Valley	hibernaculum for indiana bat, mesic forest community
26	West Virginia	40	Central Appalachian Forest	Red spruce forest
27	West Virginia	129	Central Appalachian Forest	Grass bald, red pine forest, sandstone cliff and ledge

4.7 Appendix: Supplementary Information

Table 4.5: Model coefficients and pseudo R^2 for two example applications. Significant fixed effects indicated by bold font ($p < 0.05$).

Model	intercept	log(PA area)	year	year*PA area	random effect	R^2
dbh at acquisition	**146.13±18.78**	-4.69±3.96	N/A	N/A	N/A	0.05
Pine density over time	0.01±0.03	-0.00±0.01	-0.00±0.00	-0.00±0.00	1.4E-3±4.4E-3	0.09

Table 4.6: Regression coefficients for models relating forest structure and composition to spectral imagery and covariates for sensitivity test when sample points dominated by scrub oak (Quercus illicifolia) are removed from the analysis. The full model is reported in each case for comparability across models. Site level influences were modeled as a random effect. Significant fixed effects indicated by bold font (p <0.05).

	Fixed Effects							
	(Intercept)	Brightness	Greenness	Wetness	Latitude	Northness	Elevation	Slope
DBH	-72.26±92.14	257.15±239.26	-65.08±67.72	**44.02±22.14**	-0.10±0.31	0.66±0.45	-0.1E-03±2.1E-03	0.04±0.04
Log(%open +1)	14.09±9.93	-28.51±25.92	6.93±7.39	**-7.96±2.38**	0.01±0.03	-0.03±0.05	-2.3E-04±2.0E-04	0.01±0.00
Density	-5.99±22.27	40.92±58.40	-16.49±16.77	0.86±5.31	-0.03±0.06	0.06±0.12	**-1.1E-03±4.0E-04**	0.01±0.01
Spp. Richness	-13.80±18.43	60.98±48.25	-16.39±13.81	3.31±4.40	**-0.13±0.05**	**-0.20±0.10**	**-1.3E-03±3.4E-04**	0.02±0.01
Pine	**108.3±52.00**	**-260.3±137.6**	**75.9±40.2**	**-25.4±12.6**	**-0.37±0.14**	-0.41±0.30	-7.6E-04±1.0E-03	-0.03±0.03
Red maple	-40.99±38.79	83.11±101.6	-25.90±29.49	8.82±9.56	**0.24±0.08**	0.00±0.23	-4.43E-04±6.0E-04	-0.02±0.02

	Random Effect	
	(Intercept)	Residual
DBH	3.56	5.96
Log(%open +1)	0.30	0.69
Density	0.54	1.66
Spp. Richness	0.49	1.33
Pine	1.14	1.07
Red maple	0.14	0.38

Table 4.7: AIC and pseudo R^2 for models relating forest structure and composition to spectral imagery and covariates when we perform a sensitivity test that drops 36 data points for which scrub oak is the dominant species (the mean field measured dbh is less than 10 cm)

	AIC	logLik	Efron's pseudo R^2	Link	Distribution	Change in explained variation
DBH	3263	-1622	0.28	identity	Gaussian	40% decrease
Log(% openness +1)	1122	-551	0.27	identity	Gaussian	27% decrease
Density	1983	-982	0.15	identity	Gaussian	43% decrease
Spp. Richness	1769	-875	0.28	identity	Gaussian	23% decrease
Pine	153	-67	0.50	Logit	Binomial	0%
Red maple	130	-56	0.22	Logit	Binomial	100% increase

Table 4.8: Random effects (model intercept) for each forest attribute and study protected area. To reconstruct a predictive model for a study protected areas, add the random effect to the desired forest attribute model intercept from Table 4.2

Protected area	dbh	%openness	distance	species richness	pine	red maple
Allegany	4.74	-0.10	0.86	0.64	-0.13	-0.07
Bath1	-0.96	-0.14	-0.21	-0.04	1.58	-0.01
Bath2	-0.73	-0.01	0.49	0.16	1.31	-0.04
Blair	7.32	-0.30	0.98	0.04	0.05	0.21
Cherokee	-3.76	0.43	-0.77	-1.14	1.80	0.03
Clinton1	-9.05	0.51	-1.62	-0.60	-0.14	-0.02
Clinton2	8.71	-0.17	0.76	0.19	1.17	-0.06
Floyd	-3.49	0.08	-1.01	-0.25	0.37	-0.02
FortunesCove	1.79	0.32	0.50	0.09	-0.43	-0.05
Franklin	-3.09	0.48	0.19	0.44	-0.45	-0.06
Greenville	1.69	0.11	0.15	0.16	0.03	0.08
Jackson	0.85	0.20	0.55	-0.92	-1.13	-0.04
Laurel	2.98	-0.64	0.21	0.08	-0.84	-0.02
LittleYellowMtn	0.98	0.02	0.75	0.31	-0.58	-0.03
Moosic1	-9.88	0.56	-1.38	-0.74	0.09	-0.02
Moosic2	-7.43	0.18	-1.13	-0.37	-0.07	0.03
Moosic3	-2.68	0.46	0.30	-0.38	-0.19	0.02
MtPorteCrayon	-1.36	-0.61	-0.03	-0.19	-0.24	-0.07
Pickens	-0.96	-0.16	-0.26	0.10	0.39	0.02
Pickett	-3.26	0.06	-0.01	0.06	0.28	0.11
PikeKnob	2.43	-0.18	-0.11	0.53	0.76	0.08
RumblingBald1	-2.91	-0.20	-0.57	0.50	0.37	0.00
RumblingBald3	1.63	-0.02	-0.57	-0.23	0.27	0.09
Russell	1.01	-0.11	0.87	0.75	-0.52	-0.04
StClair	1.52	-0.05	-0.33	-0.19	-0.06	0.00
Washington	8.60	-0.48	0.62	0.50	-0.48	-0.05
Wise	5.29	-0.24	0.74	0.49	-0.52	-0.04

Chapter 5

Strategic interactions between multiple conservation players can hinder the effectiveness of biodiversity conservation

A version of this chapter will be submitted for publication after modification during internal and external review.

Iacona, G.D, Bode, M., and P.R. Armsworth.(XXXX). Strategic interactions between multiple conservation players can hinder the effectiveness of biodiversity conservation. *Conservation Biology*

The use of "we" in this chapter refers to me and my co-authors. As the lead author of this article I was responsible for developing the ideas for this paper, building the models, and writing the manuscript. M.B, and P.R.A. helped designed the research and edit the paper.

Abstract

Biodiversity conservation organizations often spend money to acquire or manage protected areas that contain species of interest to their organization. Conservation science aims to improve the cost-effectiveness of how this money is spent, but usually assumes that a single entity is making the decision to buy or manage. In practice, multiple conservation organizations can be acting in the same region, often pursuing similar or identical objectives. As a result, organizational strategy is a balance between the desire to secure their own objectives and their need to outcompete rival organizations for funding. Conservation investment strategy can therefore be considered a game, where each actor maximizes their own objective while considering the strategy of the others.

We developed a game theoretic framework to examine the biodiversity conservation outcomes of different funding strategies in a multiplayer context with three organizations. Our model system uses a funding source and two local land trusts to examine how biodiversity outcomes are influenced by the strategic decisions made by the players regarding their own spending and their interactions with other conservation organizations. In our model, the objectives of a local land trust overlap to some extent (but not completely) with those of the other local land trust, and those of the funder. This modeling framework is a contribution that allows for the exploration of new questions and issues in conservation science. As a first step, we use the framework to explore the simplified scenario in which institutional objectives are constant. Our results show that when institutional adaptation is constrained, the funder is unable to incentivize its desired conservation outcome by offering additional funding. Instead, the biodiversity outcomes are dependent on the priority alignment across the organizations. We find that strategic interactions result in improved biodiversity conservation outcomes when priorities are well aligned, but they decrease conservation benefit when priorities are misaligned. Contractually targeted funding and cost-share mechanisms can counteract these inefficiencies to some extent. Our results also illustrate how strategic interactions between conservation organizations change both the decisions and the overall benefits of each individual organization. This suggests that estimates of conservation outcomes that ignore these interactions may be incorrect.

5.1 Introduction

Because conservation funding is limited, conservation science aims to identify projects that cost-effectively provide biodiversity protection (Murdoch et al., 2010; Cullen, 2013). However, most of these studies assume that a single organization makes a decision to spend and then undertakes a conservation project according to its objectives (Ando et al., 1998; Blom, 2004; Polasky et al., 2008; Frazee et al., 2003, and many others). This is a critical shortcoming in conservation theory because conservation projects usually involve many organizations, and strategic interactions among them may affect the expected biodiversity outcomes.

In reality, most biodiversity conservation outcomes result from the coordinated effort of many different organizations aligning their actions to enact a conservation project. Multiple organizations interact in the landscape and they coordinate actions, compete for funding, or collaborate on strategy to produce conservation outcomes that promote both individual and shared conservation priorities (Kark et al., 2009; Labich et al., 2013; Macdonald, 2002, etc.). To provide a concrete example, one such project is the Greater Cumberlands deal in east Tennessee, USA. This 130, 000 acre project was completed in 2007. State and federal government agencies and two private conservation forestry companies partnered with The Nature Conservancy (TNC), bringing together a complicated set of funding sources to produce a patchwork of conservation outcomes. This example is characteristic of the direction of modern conservation projects and demonstrates that the assumption of a single decision making entity is not very realistic.

In this study we examine the outcomes when multiple agents are working to produce on the ground biodiversity conservation. We ask "how do strategic interactions between a given configuration of pre-existing organizations influence the biodiversity outcomes of a funder's investment?" We ask this question from the perspective of a regional conservation organization that acts by providing funding to local land trusts that perform on-the-ground conservation. To do so, we use a game-theoretic modeling framework to examine scenarios that represent common configurations of funding and action.

This type of research is necessary because there will always be multiple conservation organizations interacting in the real world. Economic theory suggests that the number of conservation organizations is a balance between the vast number that would be present if there were no transaction costs and conservation organizations specialized in every different conservation need, and the reduced number that results from coordination among agencies for cost effectiveness (Economides and Rose-Ackerman, 1993; Albers and Ando, 2003). As they work towards fulfilling their individual objectives, these conservation organizations interact with each other to an extent that ranges from not at all (they do not even know the others exist) to merging to pursue the same objectives (Bates, 2005). Here we focus on the non-profit sector; however similar principles would also likely apply to governmental agencies. Environment-focused charities are one of the fastest growing sectors of the non-profit world (Blackwood et al. 2012), and the focus of these organizations overlaps in many aspects (Armsworth et al., 2012).

The small amount of research that has considered conservation outcomes when there are multiple organizations working on biodiversity conservation in a region suggests that the measured benefit can be very different when strategic interactions are accounted for (Albers et al., 2008; Bode et al., 2011; Punt et al., 2012; Gordon et al., 2013). However, this research has so far only considered strategic interactions between two organizations and has primarily looked at the conservation benefit of cooperation under situations for which conservation organizations pooled their resources. In contrast, we are interested in how strategic interactions influence the conservation outcomes when multiple organizations are acting in their own best interest. We particularly focus on the biodiversity outcomes that can be gained from the perspective of a funding organization investing in a region where conservation organizations are strategically pursuing their priorities while considering the other organizations' actions. The assumption that real-world organizations would act in their own best interest is valid because they each pursue objectives that are likely to be slightly different while they compete for limited pools of conservation funding. We also examine the utility of contracting mechanisms such as cost sharing, that aim to align biodiversity outcomes with the funding organization's priorities.

5.2 Modeling Approach

One way to approach this problem is to use game theory. Game theory is a branch of mathematics that studies strategic behavior in complex systems for which the actions of each entity affects the outcomes of the other entities (Von Neumann and Morgenstern, 1944; Morris, 1994). A game can be viewed as a set of players (in this case local land trusts and a conservation funder), each of whom has an available set of actions (here the proportion of a budget that is spent on conservation in a region). The combination of all the players' actions result in a payoff to each player (in this case, the protection of species that they care about). The equilibrium solution to the game is the set of actions that produce the likely payoff for each player once they all make their choices. Such solutions are known as the Nash equilibria, and they describe the set of choices under which no individual player can unilaterally increase their payoff by adopting a different strategy (Nash, 1950).

To model the type of interactions that could be present in a conservation deal, we use a simple system of a regional conservation organization (Funder) that acts by providing additional funding to two local land trusts (Figure 5.1, Box 1). This configuration represents a common scenario in land trust financing, as we discuss below, and also could represent other conservation situations in which funding entities work with on-the-ground agencies. In our model, the two local land trusts have conservation priorities that are related, to some extent, to the priorities of the funder and each other. Land Trust 1 (LT1) has a set of priority species that it aims to protect. For instance, it could specifically target protection of bird species that are found in a tributary watershed in its region. Land Trust 2 (LT2) also has a set of priority species and, for instance, they could target general wildlife protection in a different watershed. These types of differing objectives are common across land trusts within a region (Foti and Jacbos, 1989; Chang, 2011). Meanwhile, the Funder has yet a different set of priority species that it is focused on protecting. For instance, it could target species that provide ecosystem services in the downstream river valley system that these two watersheds feed. Each land trust works to protect their species of interest in their individual priority regions (A and C). They can also invest in projects in the downstream region (B) that is a protection priority of the Funder, and by doing so they may protect some of their priority species but may also attract additional investment from the Funder. Each land trust decides what proportion (ϵ) of their total budget (β) to allocate toward Funder priorities with the remainder allocated to its own priority region. The Funder decides how to proportionally (p) allocate its budget(α) across the two land trusts. Therefore, the total budget available to a land trust is its unsupplemented budget (γ) plus the amount it receives from the Funder. A number of species (S) are protected from each priority region's species list in accordance with the species area relationship and funding allocated to the region, but there is some amount of species overlap across regions ($\Gamma_{AB}, \Gamma_{BC}, \Gamma_{AC}$, see Supplementary Information for details). We use this overlap in species sets to represent how the conservation priorities of the different organizations are aligned. Here we use species protection as the benefit of interest, but this modeling framework could be easily adapted to quantify other potential benefits. For instance, it could be used to examine the implications of priority overlap and competition between organizations that focus on ecosystem services as compared to those that focus on biodiversity conservation (e.g. Goldman et al., 2008). However, to do so, an appropriate functional relationship between benefit and cost would have to be specified, and we would have to understand the relevant priority overlap across organizations. In this study, we chose to focus on species protection because there are accepted relationships between species and cost, and the priority overlap was straightforward to conceptualize.

Our model provides a framework for examining the understudied implications of interactions between multiple conservation organizations. The described configuration of organizations, their choices, and their underlying priorities, provides the flexibility to examine many aspects of these interactions. As a first step, this chapter describes a set of scenarios where we adjust only the priority overlap parameter. Although this approach does not allow for institutional adaptation to be considered (a choice we revisit in the discussion), it provides insight into the measurement of the conservation benefit of spend in the most basic situation in which organizations operate under known, set objectives.

5.3 Illustrative Examples

We examine possible outcomes of multiplayer interactions among conservation organizations by developing scenarios that illustrate common real-world strategies. First we use two opposing scenarios to study how the overlap in conservation priorities among the organizations influence the benefit the Funder obtains from its spending. Then we expand the model to explore two scenarios where contracting mechanisms are used to counteract reductions in benefit that occur when there is low priority overlap.

Scenario 1: Regional conservation funder supplements the budgets of land trusts according to conservation priority alignment

In this scenario, we study the response of land trusts to the offer of grant support from the Funder. In our model, the land trusts understand that the choice of how much money the Funder is willing to provide to them is based on the proportion of their total budget that will be spent on Funder priorities.

We examine two extremes of this scenario: in the first, the priorities of the Funder and the land trusts are strongly aligned. In the second, there is minimal alignment.

1a) Priority alignment

When priorities are well aligned across conservation organizations, funding allocation is seemingly straightforward. In such a case, external funders (such as a foundation) often promote biodiversity protection by providing grants to local conservation organizations (Emerton et al., 2006; McBryde and Stein, 2011; Gunter, 2004). This funding model is especially common for organizations such as land trusts that aim to protect land from urban development (Hopper and Cook, 2004; McQueen and

McMahon, 2003). One example of this situation is the re-granting strategy of the New York state, USA, based Open Space Institute (OSI). This regional conservation organization provides funding to local land trusts in the Appalachian and Cumberland regions of the USA through their Southern Cumberland Land Protection Fund (David Ray, *personal communication*). The fund was developed with endowments from three different foundations as well as OSI's own funds. It is targeted towards land conservation through fee simple acquisition or easement purchases within focal areas that had been previously identified in their "Southern Appalachians Assessment." Local land trusts in the focal regions apply for funding matches for projects that meet predetermined conservation criteria. Current recipients include the Land Trust for Tennessee, The Tennessee River Gorge Trust, The Land Trust of Northern Alabama, Georgia Department of Natural Resources, and The Nature Conservancy of Tennessee.

In our model of a scenario that is similar to the real world example above, the conservation objectives of the local land trusts are well aligned with the conservation objectives of the Funder but their priorities, while similar, do not completely overlap with each other. The Funder can potentially double the budget of one land trust, although it may choose to allocate the money across both land trusts.

To illustrate how dynamics might play out for such a situation, we consider the case for which each organization (Funder, LT1 and LT2) has a budget that could protect 10% of their region of interest ($\alpha = \gamma_1 = \gamma_2 = 0.1$). We also set the priority alignment to 50% to represent organizations that focus a large proportion of their effort towards similar objectives ($\Gamma_{AB} = \Gamma_{BC} = \Gamma_{AC} = 0.5$)

Our modeling strategy generates benefit estimates for every combination of choices that the three organizations can make. As a strategy for identifying choice combinations that the organizations would be justified in taking, we focus on the Nash equilibrium (See Box 2 for details). These equilibrium solutions describe the choices that rational players are likely to take, in situations where they all have perfect information, because no one organization can improve its outcome by unilaterally changing its strategy. The Nash equilibrium choices for the three organizations indicate that, because of the large amount of priority overlap, both LT1 and LT2 will do best if a little more than the smallest increment from one of their budgets is spent on Funder priorities. The Funder will give its entire budget to the LT that spends on its priorities (Three player Nash equilibria $(\epsilon_1, \epsilon_2, p) = (0.1, 0, 1)$ or $(0, 0.1, 0)$.

The Funder would obtain the greatest benefit if it gave all of its money to a land trust that was willing to spend its entire budget on the Funder's priorities. However, that is counter to either land trust's best strategy so they will continue to spend primarily on their own priorities and only spend on Funder priorities in relation to gain due to overlap. Because of the 50% overlap in objectives, all of the organizations do better than they would if there were no other conservation organizations working in the region. The land trust that spends on the Funder priorities but also obtains the additional budget is able to protect 80% of their species of interest, while the one that does not get the additional funding still is able to protect 76% of their species (Figure 5.2). The Funder is able to protect 70% of their species of interest. This is about a 25% greater benefit from giving money to the land trusts than it would get if it engaged in an on-the-ground conservation activity by itself (where it would get 56% of its species protected). Meanwhile, 75% of the total species in the region are protected (Figure 5.3).

1b) Reduced priority alignment

We next examined the case where the priorities of the Funder and the land trusts were not well aligned. Minimal overlap in organizational priorities is not uncommon in conservation deals. This is because priorities can cover a broad spectrum, even under the heading of biodiversity conservation, and in some cases, conservation projects have unlikely partners. For instance, In 2010, TNC Australia orchestrated The Fish River Station conservation project in the Northern Territory, near Darwin (Fitzsimons and Looker, 2012, James Fitzsimmons, *personal comment*). This 180,000 HA project was completed because TNC was able to provide additional funding and enable the Indigenous Land Corporation (ILC) to buy the site for eventual transfer to an indigenous group. ILC is a local non-government organization (NGO) whose objective is to assist indigenous people in acquiring land. This project took advantage of the Australian government's Caring for Our Country program which provided 2/3 of the necessary funding. TNC then provided 1/6, and the remainder was supposed to come from ILC. ILC had secured the promise of a grant from the Pew Environment Group, but the deal almost fell apart because Pew could not give to a government agency (which ILC is). TNC convinced Greening Australia to step in as a partner and receive the money from Pew and put it into the project. In this example, TNC brokered a large land conservation project by working with an NGO that does not have a biodiversity conservation objective. Thus, significant biodiversity outcomes were a result of coordinated efforts by organizations with minimal institutional priority alignment.

We now model a scenario where the objectives of the conservation organizations are minimally aligned by changing the amount of objective overlap between the Funder and the local land trusts, while holding all other model parameters as above.

Here, each organization (Funder, LT1 and LT2) still has a budget that could protect 10% of their region of interest ($\alpha = \gamma_1 = \gamma_2 = 0.1$). However, we reduce the amount of priority alignment to 10% to represent organizations with mismatched objectives ($\Gamma_{AB} = \Gamma_{BC} = \Gamma_{AC} = 0.1$)

The Nash equilibrium choices for the three organizations indicate that LT1 and LT2 will now do best if one of them spends only the smallest proportion of its budget that it can on Funder priorities. Both LTs obtain the greatest benefit when one of them spends a small amount on Funder priorities, regardless of what the Funder does. However, the Funder will give its entire budget to the LT that makes the choice to spend in its region. The LT that does not receive the extra funding does not secure as large a benefit as the LT that does. However, it still is able to protect more species than it would be able to by acting alone because of spend by the other LT on Funder priorities. (Three player Nash equilibria $(\epsilon_1, \epsilon_2, p) = (0.05, 0, 1)$ and (0, 0.05, 0)).

Despite minimal alignment of priorities, LT1 and LT2 have an incentive to spend a small amount on the Funder's objectives due to overlap, but the Funder cannot coerce the LTs to spend more on its priorities by providing additional funding. The Funder is able to obtain some benefit (40% of its species of interest are protected) from the money it spends, although it does worse than if it engaged in an on-the-ground project of its own where it would get 56% of its priority species protected (Figure 5.2). The land trust that receives the funding (LT2 in Figure 5.2) doubles its budget and is able to obtain a greater benefit than it would have been able to on its own by protecting 69% of its species of interest. Meanwhile, the land trust that receives no additional funding (LT1 in Figure 5.2) still obtains a small improvement in benefit over simply considering its own investment (60% of species protected) due to species gains from the small overlap in priority species with the Funder. Finally, 53% of the total number of species in the region are protected.

The scenarios modeled above show how the effectiveness of conservation spending by the Funder is highly dependent on the amount of priority alignment between it and the land trusts. The Funder's investment cannot incentivize either of the land trusts to spend more on its priorities because they cannot compete with each other for additional funding by offering to increase their spend on Funder priorities. This is because the other land trust can always offer more. Only the amount of priority overlap determines the benefit that the Funder recieves. However, priority alignment is difficult to gauge in reality, and foundations often struggle with this task (Gronbjerg et al., 2000). We next examine two common strategies the Funder can take to reduce benefit inefficiencies that are due to priority misalignment.

Scenario 2: Regional conservation funder supplements the budgets of land trusts, but the funding is contractually targeted

In the next two cases, we examine the effectiveness of the Funder's contractual targeting of funds when there is misalignment in priorities such that there is only a 10% overlap in conservation priorities between the Funder and either local land trust ($\Gamma_{AB} = \Gamma_{BC} = \Gamma_{AC} = 0.1$).

2a) Funder allocates money that is targeted at overlapping priorities

This model parameterization is similar to the common funding mechanism for which the Funder allocates money that is targeted to very specific priorities. For example, this strategy is used by the National Fish and Wildlife Foundation (NFWF) when allocating their funding for management and restoration projects. Their Cumberland Plateau Stewardship Fund was developed under consultation from OSI, to allocate money from the International Paper Forestlands Stewards Initiative (David Ray, *personal comment*). This funding is targeted towards using working forests as conservation tools, and a 2014 funding cycle requested proposals calling for short leaf pine (*Pinus echinata*) forest restoration projects and riparian projects. This call for proposals aims to fund conservation non-profits, government agencies, and/or academic institutions and is particularly interested in projects that propose work on private lands.

In such a scenario, land trusts submit proposals with a cost estimate to do the project, and then the Funder selects among the projects and funds them in line with its conservation goals. The land trusts have to consider their own mission as they select these projects and apply for funding opportunities that forward their own goals.

We now model such a case for which LT1 and LT2 still each have a budget that could protect 10% of their region of interest ($\alpha = \gamma_1 = \gamma_2 = 0.1$) and there is priority misalignment ($\Gamma = 0.1$). However, we set the LT budgets so that although they can choose to spend a proportion of their internal budget on Funder priorities, any money obtained from from the Funder must be spent on Funder priorities. Because the Funder now always has all of its money spent on its priorities, the method of displaying results that we used in the previous scenarios would not be meaningful.

Instead, we compare the Funder's benefit between the case in which it spends no money in the region ($\alpha = 0$) and the case in which it spends the same amount as the LTs ($\alpha = 0.1$)

Baseline condition where there is no spending by the Funder

When LT1 and LT2 do not have the possibility of supplemental funding ($\alpha = 0$), one or the other will allocate the smallest increment of its budget that it can to the Funder's priorities (ϵ_1, or $\epsilon_2 = 0.05$). This is because there are diminishing returns for obtaining benefit under the species area relationship. The Funder will obtain protection of 35% of its species of interest even if it does not invest in the region, due to this spending choice by the LTs and priority species list overlap. The LT that spends a proportion of its budget on the Funder priorities will obtain protection of 59% of its species of interest. The other LT will obtain protection of 60% of its species. Only 48% of all species will be protected.

Compare with benefit when there is spend by Funder

Meanwhile, if the Funder's budget is available and is spent on Funder priorities ($\alpha = 0.1$), neither of the LTs will choose to allocate anything toward Funder priorities. This is because the rapid gains in species accumulation have already been secured and there is no additional benefit to allocating more budget towards Funder priorities. In this case, the Funder and each of the LTs all obtain protection of 61% of their species. In addition 57% of the total species are protected.

Despite the fact that the Funder dollars are only spent on Funder priorities, the LTs are able to obtain a greater benefit when there is Funder investment into the system. This is partially due to additional species gain from overlap (1.2% more species) and partially due to a crowding out effect in which the LT shifted what it previously spent on the Funder's priorities towards its own priorities instead (0.7% more species). Crowding out is a theoretically justified response of conservation players to additional investment although it is usually considered only in the case for which private land trusts under-invest in regions where governmental acquisition is occurring (Albers et al., 2008).

This small gain that a LT obtains by shifting its spend corresponds with a loss for the Funder. We calculate the Funder's loss to crowding out as the difference between the expected Funder's species protected and the actual Funder's species protected. Expected species protected is the proportion that would be protected with the original spending by the local land trust, plus the species protected by the new money (details in Supplementary Information). In our case, this leads to an expectation of 61.70% of Funder species protected. However, when crowding out shifts the previous spending away from the Funder's priorities, the actual Funder species protected is 61.07%. This corresponds with a loss due to crowding out of approximately 1% of potential Funder species protected.

2b) Funder requires cost-matching

Cost-matching can potentially counteract crowding out effects for any Funder allocated money by requiring the LT to dedicate some additional budget to the matching priorities if they are to be funded. This is a common requirement of most foundation provided grants. For instance, the international branch of TNC pursues its conservation objectives in Australia solely through partnerships with local conservation groups. The high profile "David Thomas Challenge" was a ten million dollar conservation initiative that took the form of a challenge grant (James Fitzsimmons, *personal communication*). Local organizations (primarily the land trusts; Bush Heritage, Australian Wildlife Conservancy, Trust for Nature, and Greening Australia) could apply for up to a 50% match from TNC for projects that met certain criteria. One of the more unique criteria that TNC stipulated was that the funding that the local organizations brought in must have been obtained from new donors in increments of at least \$ 10,000 AU. This requirement was because one of the objectives of TNC was to enhance the fund-raising capacity of the local conservation non-profits.

Here we model such a cost sharing strategy. In this scenario, the baseline budgets of each local land trust is again enough to protect 10% of their conservation priorities. The Funder has enough money available to potentially double their budget ($\alpha = \gamma_1 = \gamma_2 = 0.1$) and targets the funding to the overlapping priorities using a contracting mechanism as above. However, we now explore the case in which the LT has to match some level of the Funder's offer in order to receive the funding. To do so, we add a cost share parameter (CS) which indicates that any additional funding (p) will be only supplied in increments of existing spend (formulation details in Supplementary Information). We examine the effectiveness of the Funder's cost share requirement when there is misalignment in priorities such that there is only a 10% overlap in conservation priorities between the Funder and either local land trust ($\Gamma_{AB} = \Gamma_{BC} = \Gamma_{AC} = 0.1$).

A cost share requirement can incrementally improve the Funder's benefit but in our model can only counteract the crowding out effect if they offer a 20.1:1 match (Table 5.2). However, that amount is slightly more than the available Funder budget ($\alpha = 0.1$). The best the Funder can do is offer at 20:1 match which will protect a tenth of a percent less priority species than in the scenario above that includes crowding out (Figure 5.4). In this case, the amount necessary to counteract the crowding out is essentially just replacing the shifted funding, and the cost share does not incentivize different behavior from the land trusts. This is because the 10% overlap in objectives means that ten times the funding must be spent on the Funder's priorities for LT1 or LT2 to get the same amount of benefit as spending on their own priorities. The saturating species accumulation relationship counteracts this effect but only once the benefit of spending less money in the local land trusts' regions is equal to the benefit of spending more money on the Funder's priorities. In the scenarios that we examine, because the budget of all the organizations is relatively small, priority species are still accumulating quickly from local land trust spend in their own regions. There is never a cost share amount that is large enough to provide a benefit that induces the land trusts to change their allocation behavior.

Synthesis

The Funder has the greatest benefit when there are multiple players and there is high priority overlap, as compared to if it spent the money itself and did not consider other players in the system. In the high priority overlap scenario, the Funder obtains a greater benefit than any other scenario even though the LTs do not spend extra on the Funder's priorities. In addition, both LT1 and LT2 obtain a greater benefit when there is high priority overlap. Meanwhile, if the Funder is faced with priority misalignment between itself and potential grantees, the Funder recieves less benefit than if it had spent the money itself. This situation can be partially resolved by contractual targeting of funds, but the benefit can be less than expected due to crowding out. Cost sharing can counteract this effect but it is inefficient in scenarios with low priority alignment. Finally, the local land trusts always receive a greater benefit with multiple players because they gain from overlap and Funder spend.

5.4 Discussion

In this study we asked how strategic interactions between a given configuration of pre-existing organizations influence the biodiversity conservation outcomes of their spend. We develop a modeling framework that allows for the exploration of these types of questions in conservation science. As a first step, we use the framework to explore the simplified scenario in which institutional objectives are constant. We show that the ability of a conservation funder to obtain the biodiversity protection outcome it is interested in is dependent on the strategic interactions between multiple players. These interactions shape outcomes in several ways. First, they prevent the Funder from being able to incentivize local land trust spend on Funder priorities. Second, the presence of multiple players can provide both positive and negative benefit for the Funder but the outcome is due to underlying priority overlap and not strategic choices. Finally, contracting mechanisms can improve Funder benefit but they vary in effect. Overall, we find that multiplayer interactions can drastically change the effectiveness of spend and thus should not be ignored by conservation scientists.

Our observation that the conservation Funder cannot incentivize local land trust behavior was surprising because we expected that competition between local land trusts for funding would provide increased benefit for the Funder. This effect would be observed if there were multiple on the ground organizations working on the Funder's objectives such that they were willing to compete for funding by adjusting their allocation towards Funder priorities. In our model, because there are two Local Land Trusts with similar budgets, neither Land Trust is able to outbid the other in competing for the Funder's investment, so they are as well off just pursuing their own objectives. They never have an incentive to spend more on the Funder's priorities than the amount that corresponds with their personal gain due to objective overlap, so no amount of budget incentive can increase the Funder's gain. Our work suggests that when neither local organization can ultimately offer more to the Funder than the other organization, they both refrain from cooperating with the Funder and essentially force it to give one, or both, of them funding for "free."

Meanwhile, our model suggests that the effectiveness of a Funder's spend is highly dependent on its priority alignment with LT1 and LT2. When there is high priority alignment, the biodiversity outcome of funding is greater when multiple players are acting strategically. However, when there is low priority alignment, the funding organization's spend is much less effective when there are strategic interactions between multiple players. This is unfortunate from the Funder's perspective, because it is difficult to gauge priority alignment in the real world. Philanthropic organizations aim to fund projects that further their own objectives, yet often there may not be well aligned local organizations that can receive the funding. If the Funder can not incentivize LT1 and LT2 to align their spending with its own priorities through offers of budget increase (at any level of local spending on the Funder's priorities) then its hands are tied with regards to increasing spending effectiveness through market forces alone.

Alternative mechanisms such as contracts, can increase the funding effectiveness, but the outcomes vary. Our model suggests that agreements that closely target new funding to shared priorities are effective, but that cost sharing may not be efficient at promoting Funder outcomes. Because priority alignment is the sole influence on what outcome the Funder gets for its spend, conservation organizations in the real-world can minimize funding inefficiencies by focusing on a very tight mission. For instance, Island Conservation International (ICI) is an NGO which tends to get funding that is targeted expressly towards its objective, because its objective is one which other NGOs and governments are willing to pay for (Daniel Simberloff, *personal communication*). ICI's mission is "protecting biodiversity by eradicating invasive vertebrates on islands." The staff are primarily operational and the majority of organizational budget supports dropping people off on islands with the materials they need to eradicate the pest species. Because of this highly targeted mission, as well as the effectiveness of their approach, much of ICI's funding comes from contracts with governments of the USA and elsewhere, and other NGOs.

Caveats and Assumptions

A primary simplifying assumption of our model is that each organization is a static entity with a known conservation objective that does not change over time. Under this assumption, we interpret the results in the context of a worldview where conservation organizations pursue funding if it forwards their stated objective. An alternative formulation could include the ability for organizations to shift their priorities to better position themselves for funding as they pursue conservation goals by increasing their capacity. These two alternatives represent competing theories of goal maximization versus budget maximization. The approach of non-profit organizations in the real world likely includes a mix of both (Steinberg, 1986; Hewitt and Brown, 2000; Brooks, 2005). However, for the purposes of this study, we are taking the viewpoint that conservation organizations are solely pursuing their existing objectives and these objectives do not change.

The Funder's inability to incentivize land trust behavior could also potentially be due to the Funder being constrained to spend its budget to one land trust or the other. In the model, the Funder is not given the ability to choose to allocate zero dollars to both LTs and essentially walk away from the conservation priority region. The modeled scenario is not an unreasonable assumption for real world conservation funders. However, we performed a sensitivity test that examined the robustness of these results when the Funder has the option of limiting how much it spends according to a benefit to cost ratio criteria. Figure 5.6 shows possible increments of Funder spend, up to the budgetary levels we tested, plotted against a ratio of the benefit that the Funder obtains versus the cost of the action. This figure illustrates that, for the budget range we examine the Funder always obtains a benefit from additional spending, but the benefit is reduced as the Funder's spending in the system increases. It also demonstrates that the Funder's willingness to spend its entire budget in the system depends on what level of benefit to cost it is willing to accept. In our models we examine the scenario where the Funder is willing to spend if it obtains any benefit for the money it spends. At this budget level ($\alpha = 0.1$) the Funder will always spend all of its money in the system unless it insists on having a benefit to cost ratio of return of 3.1 or above.

It is also important to note that the effectiveness of conservation spend is a concept that is perspective dependent. For the purposes of this study, we have examined scenarios from the perspective of a conservation funder who is working towards a conservation outcome that it perceives to be important. However, the relative effectiveness of different strategies varies if you consider the outcome from the perspective of other organizations. We can also step back and examine the outcomes of the scenarios in terms of total species protection. This could be interpreted as total biodiversity protected by all of the conservation organizations working in a region. Our results show that total species protection does not necessarily covary with species of interest to the Funder.

Conservation Implications

Because this study demonstrates that strategic interactions between conservation organizations can influence the effectiveness of spend, it suggests that conservation professionals need to consider the influence of those interactions on biodiversity outcomes. In the real world, this means acknowledging the potential effects of cooperation or competition between local organizations on funding outcomes and designing conservation planning projects appropriately. In practice, conservation organizations operate with professional respect for other organizations that they are aware of, but they do acknowledge that competition for funding is a driving force (Alex Wyss, *personal communication*). In particular,our results show that the possibility of competition for funding among local organizations can reduce a Funder's abililty to use financial incentives to obtain its desired outcome.

Acknowledgments

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5.5 Box 1: Model Formulation

The Funder's goal is to protect the maximum number of species from the list of species that provide ecosystem services in region B, by choosing a proportional distribution(p) of its total budget (α).

$$\max_{p} S_B(p, \epsilon_1, \epsilon_2)$$

Land Trust 1 aims to maximize the number of protected bird species from region A. It does so by choosing an amount (ϵ_1) of its total budget to allocate towards the Funder's priority region to receive additional funding. It must consider the competing amount the other Land Trust is willing to allocate towards the Funder's priority region, and the amount the Funder is willing to commit.

$$\max_{\epsilon_1} S_A(p, \epsilon_1, \epsilon_2)$$

Similarly, Land Trust 2 aims to maximize the number of protected wildlife species from priority region C by choosing an amount of its total budget (ϵ_2) to allocate towards the Funder's protected region.

$$\max_{\epsilon_2} S_C(p, \epsilon_1, \epsilon_2)$$

In all regions, the conservation benefit is estimated as the number of species protected in the amount of area that there is funding to protect, assuming a standard species area relationship.

$$S = cA^z$$

For each organization, total benefit is the sum of the estimated number of priority species protected by spending on land conservation in their own region plus the number of species protected by any organization's spending in regions where there is priority (species list) overlap. We subtract out double counted species from all regions We use z = 0.25 as a species area relationship scaling constant. Here, c is a scaling constant that drops out in all calculations. We also calculate the total number of species protected across all regions.

5.6 Box 2: Solution methods

The three species maximization functions in Box 1 describe the benefit that each player will receive from each choice of budget allocation, given the choices of the other players. Simultaneously solving the three functions for the three unknown variables p, ϵ_1 and ϵ_2 provides p*, ϵ_1* , and ϵ_2*; the location(s) where the benefit functions intersect. This solution describes the Nash equilibrium condition where no player can increase protection of species from their region of interest by unilaterally changing their funding allocation strategy. The Nash equilibrium gives us the long run set of choices that each of the three players will make assuming rational behavior. This is because any player is unable to improve its benefit by making a different choice and we assume that each player is working to maximize its own benefit. We chose to focus on the Nash equilibrium because it is commonly used to study strategic decisions (Morris, 1994), and it allows us to select a manageable set of study choices from the more than 9000 possible choices generated by our model.

We can visualize this approach by considering the species maximization functions as reaction surfaces that describe the best choices that each organization could take given the other organizations' choices (Figure 5.5). In this figure, the Funder's budget allocation choice (p) is plotted on the vertical axis and every point on the surface corresponds with the budget allocation choice that maximizes the Funder's benefit (Figure 5.5a). All three choice surfaces are plotted in each panel, but two are transparent for ease of interpretation. The color of the surface corresponds with the benefit that is obtained by making that budget allocation choice, with white being the most species protected and black being the least. The red and blue lines illustrate where surfaces intersect. For ease of interpretation we display a scenario with minimal overlap ($\Gamma = 0.01$)).

Box 2 continued: Solution methods

In Figure 5.5a, the Funder chooses to give its entire budget to one local land trust or the other according to their choices, but attains a larger benefit if they choose to spend more on its priorities. If they both choose to spend close to the same amount, the Funder will split the budget across them. The Funder is quick to give its entire budget to one or the other because of the small amount of priority overlap (0.01). Meanwhile, the choices of the two local land trusts are plotted as surfaces on the horizontal axes (Figure 5.5b and 5.5c). The local land trusts have no incentive to spend anywhere other than in their own regions, yet their benefit will increase if the Funder supplements their budget.

For this study, we used a discrete set of 21 choices of proportional budget allocation to generate reaction surfaces for each player (see supplemental information for details). Using these reaction surfaces, we could identify the Nash equilibrium conditions by identifying the intersection of the three surfaces for a given scenario. To do so, we used a relaxation algorithm (Krawczyk and Uryasev 2000; Conteras et al. 2004) based on the Nikaido-Isoda function (Nikaido and Isoda 1955) and implemented in Matlab to iteratively identify the Nash equilibria. This process starts with an initial guess for the Nash equilibrium and then the funding allocation choice that provides the greatest biodiversity conservation benefit for one player is identified (i.e., identify the surface coordinates along that player's axis) while the choices of the other two are held at the value from the previous iteration. The process is repeated while cycling through the players until we arrive at the set of three choices where none of the players can improve their outcomes by making a different choice given what the other players have chosen (Convergence to Nash equilibrium occurred 82-95 % of the runs depending on Γ choice and first mover choice). The benefit (ie. number of species protected) that can be obtained by each player at the Nash equilibrium set of choices, is the expected solution of the multiplayer game. The Nash equilibrium is noted in the figure by a large black circle.

5.7 Appendix: Figures

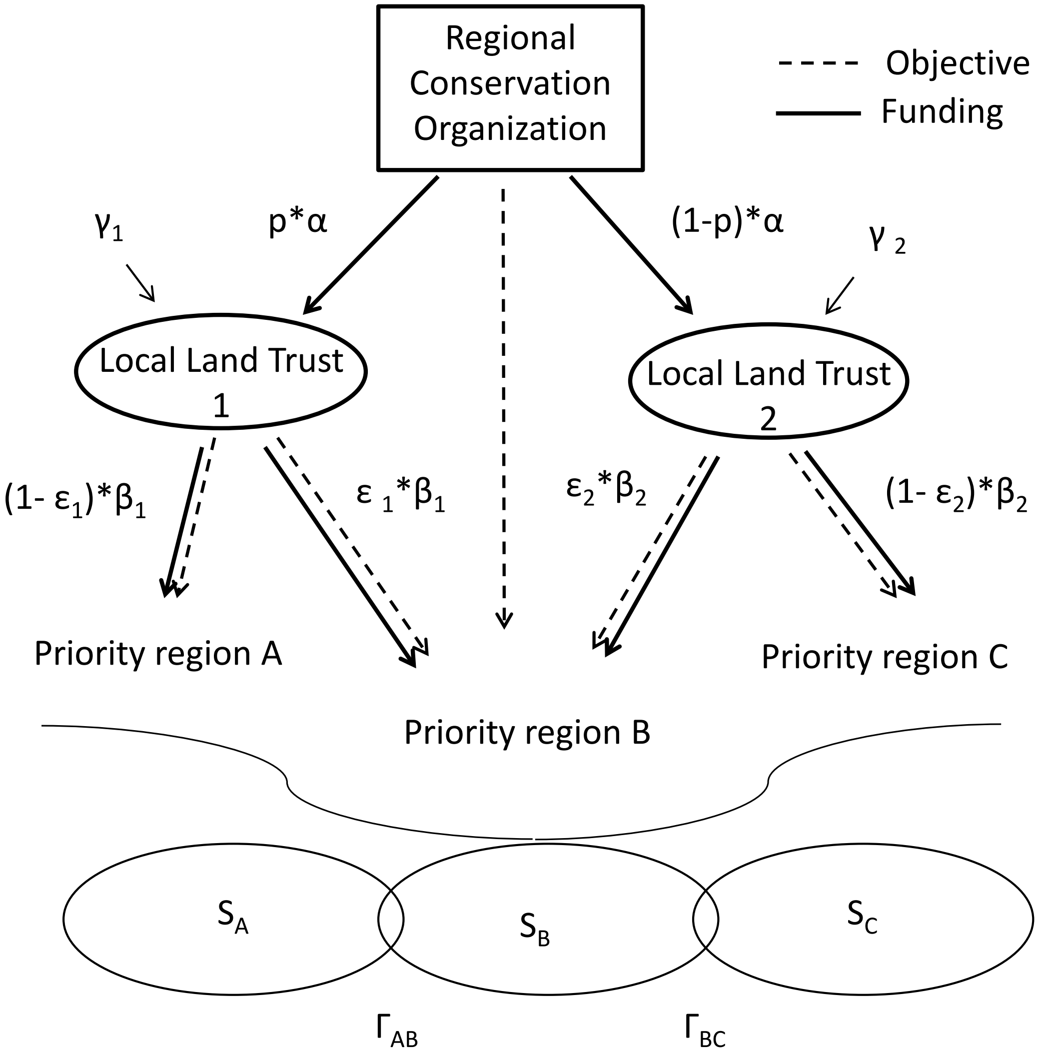


Figure 5.1: Conceptual model of multiplayer system. The regional conservation organization has an objective to protect species in region B but does not have any on-the-ground operations of its own. It obtains a conservation benefit by funding local land trusts that work in the region. These local land trusts decide what proportion of their budget (ϵ) to allocate toward funder priorities in order to incentivize the regional conservation organization's decision of how to proportionally allocate its budget (p). Species (S) are protected according to the spending in each region, but there is some overlap (Γ) across the different organization's priority species.

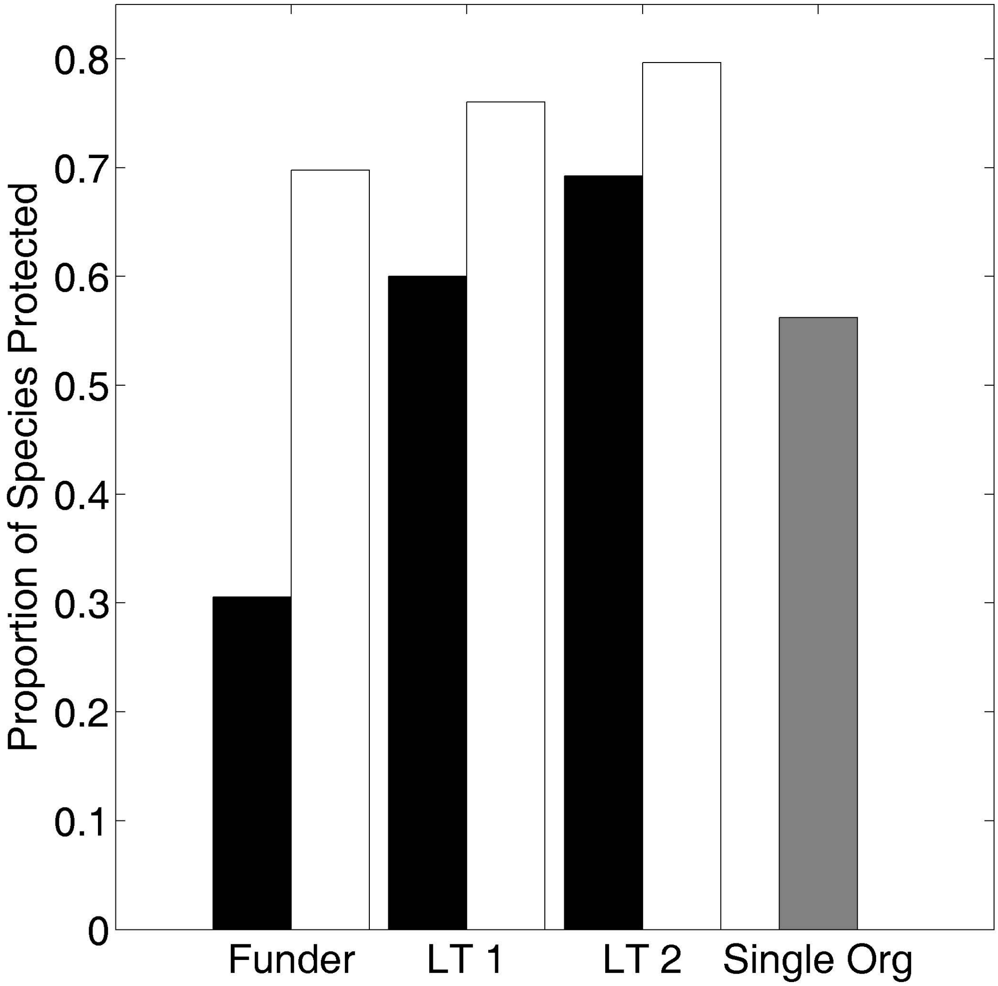


Figure 5.2: Nash equilibrium benefit per organization when there is objective misalignment (black bars) or alignment (white bars). The grey bar indicates the benefit the funder would obtain from this budget if it spent the money itself

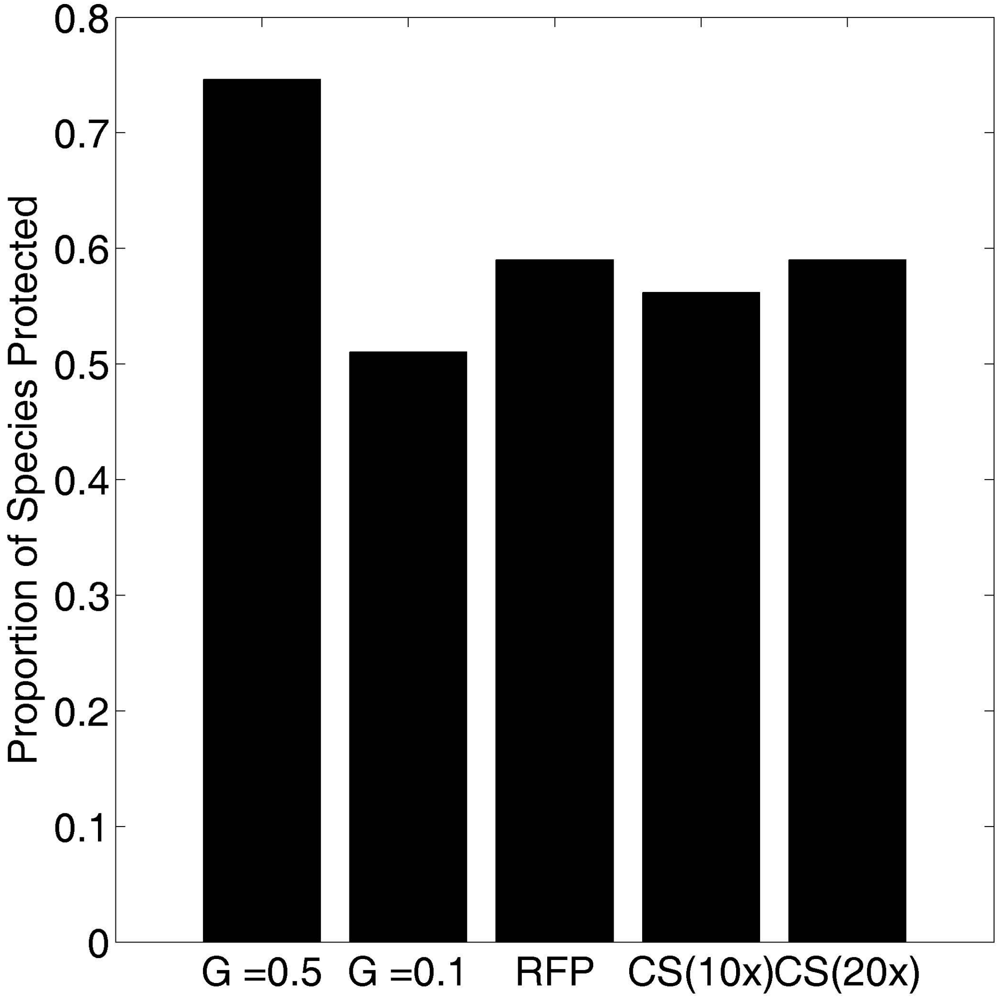


Figure 5.3: The proportion of total species that would be protected by the action of all of the players under the different scenarios. G = 0.5 is the priority alignment scenario. G = 0.1 is the misalignment scenario. “Request for Proposals” (RFP) shows the total benefit when the Funder targets all of its spend towards its own priorities. The two cost share (CS) scenarios illustrate total benefit under Funder investment strategies of 10 and 20 times local land trust investment

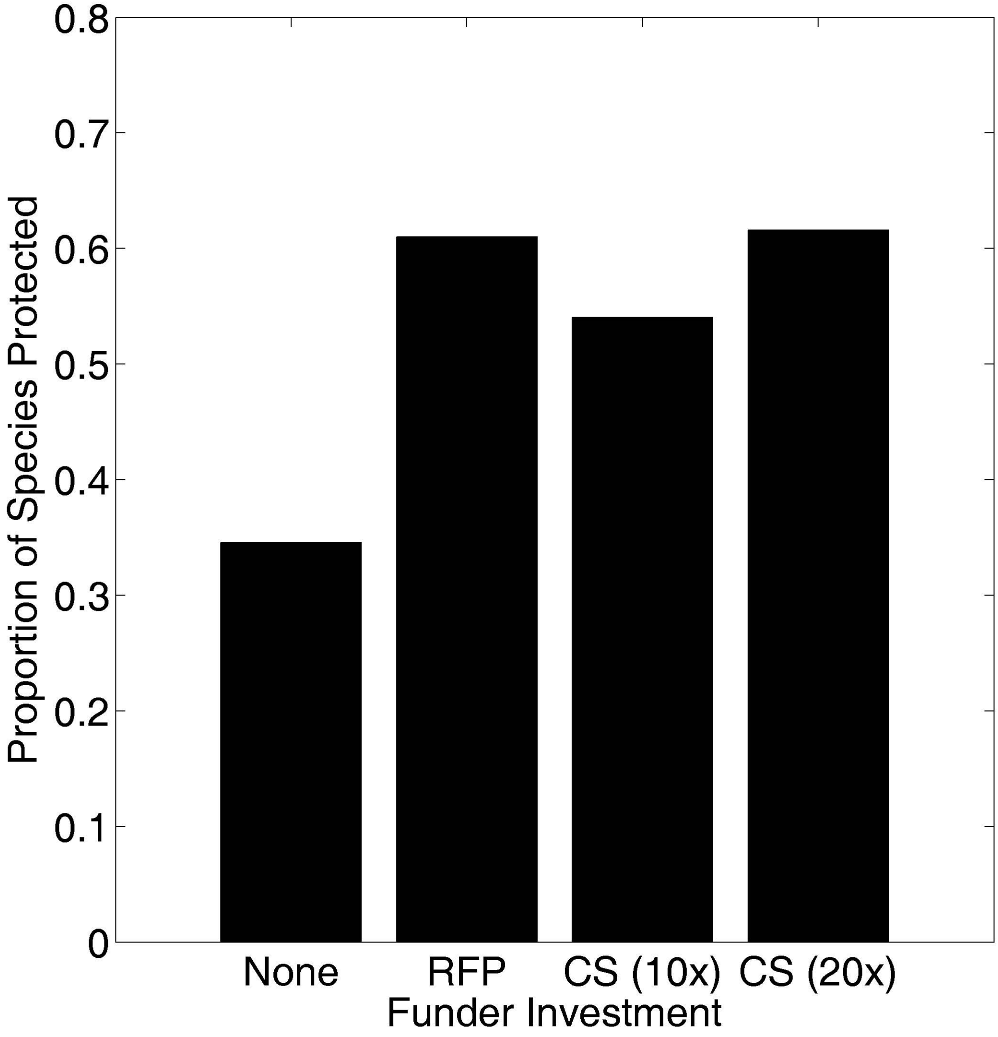
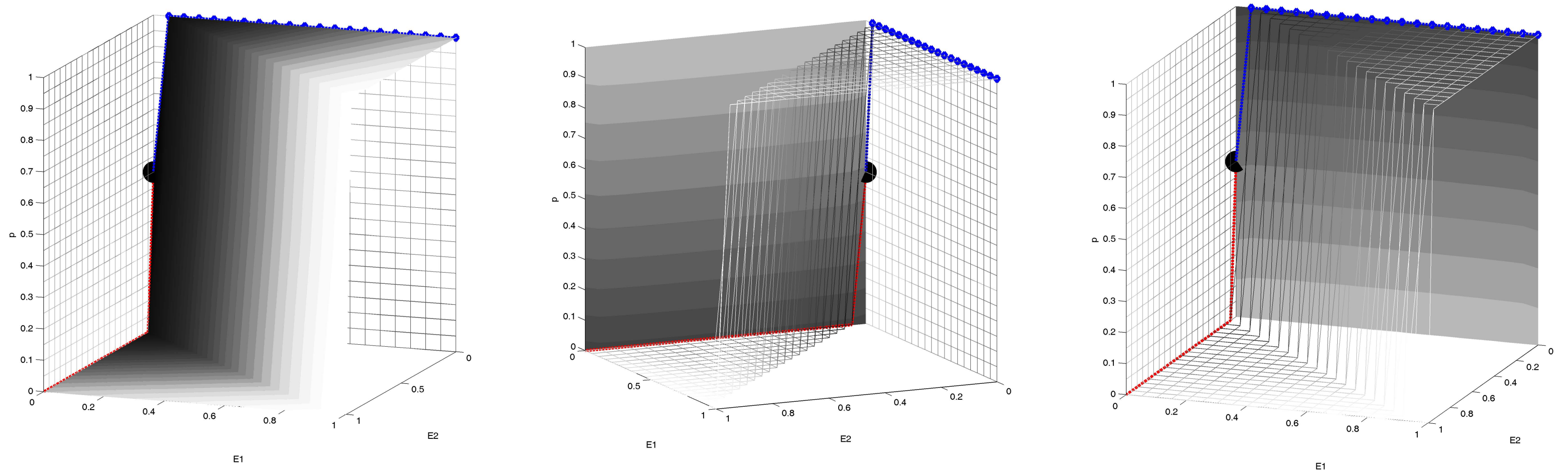


Figure 5.4: Funder benefit across different investment strategies. None is when the Funder does not invest at all. "Request for Proposals" (RFP) is the Funder's benefit when it targets all of its spend towards its own priorities. The two cost share (CS) scenarios illustrate Funder benefit under investment strategies of 10 and 20 times local land trust investment.



(a) (b) (c)

Figure 5.5: Three dimensional visualization of the choices that (a)the Funder, (b)local land trust 1 (LT1), and (c)local land trust 2 (LT2) will make to maximize their own benefit, given the choices of the other players. The location of each solid surface represents a budget allocation choice, and the color of the surface illustrates the benefit that the player will receive from making that choice with white being the greatest benefit and black the least. The colored lines show the intersection between surfaces and the black circle marks the Nash equilibrium location.

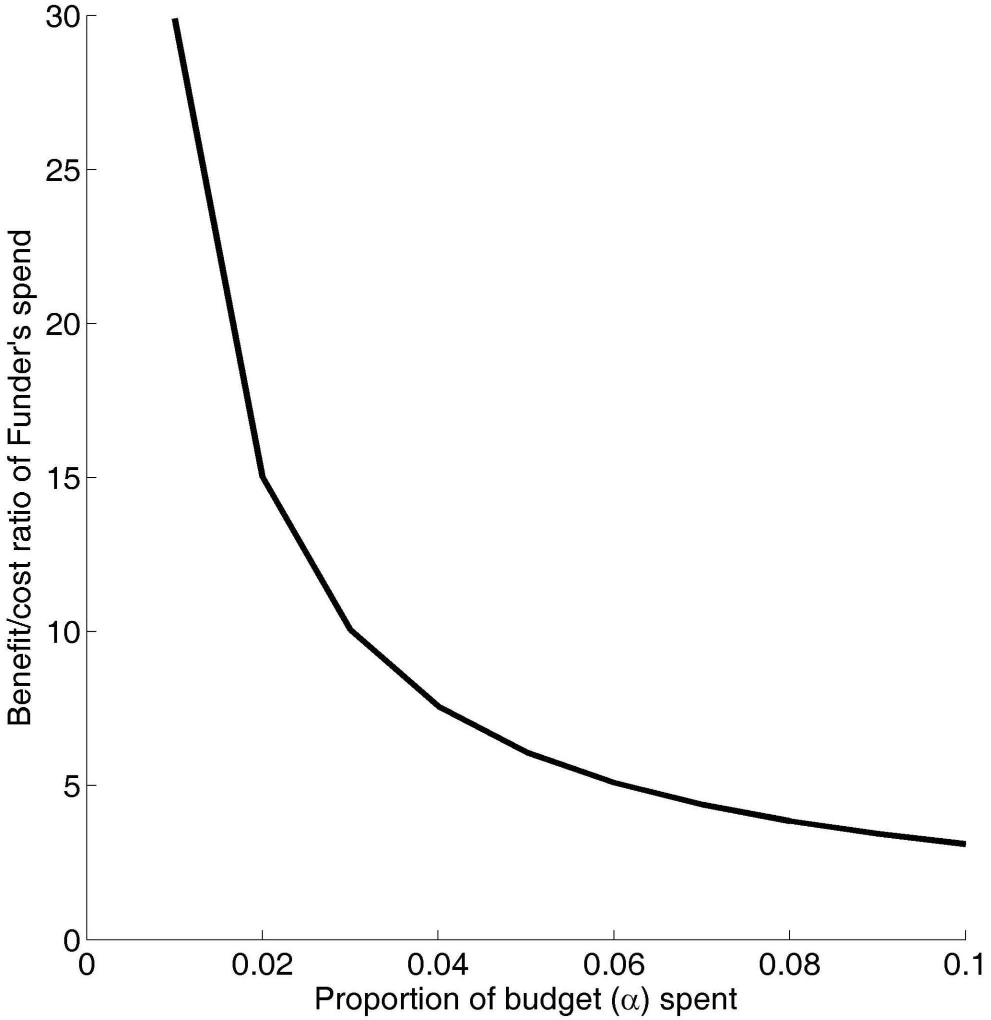


Figure 5.6: Funder benefit to cost ratio plotted versus Funder investment (α) into region

5.8 Appendix: Tables

Table 5.1: Model variables and parameters

		variables	units
p	=	Funder budget allocation decision	% of budget
ϵ_1	=	Local Land Trust 1 budget allocation decision	% of budget
ϵ_2	=	Local Land Trust 2 budget allocation decision	% of budget
		parameters	units
α	=	Funder budget	\$
γ_1	=	Local Land Trust 1 budget without Funder grant	\$
γ_2	=	Local Land Trust 2 budget without Funder grant	\$
Γ_{AB}	=	Objective overlap between Funder and Local Land Trust 1	% of species
Γ_{BC}	=	Objective overlap between Funder and Local Land Trust 2	% of species
Γ_{AC}	=	Objective overlap between Local Land Trust 1 and Local Land Trust 2	% of species

Table 5.2: Funder benefit from cost share

CS	Funder species protected
0(no funder $)	35.0%
1	39.1%
2	42.1%
3	44.4%
10	54.0%
20	61.6%
20.1	61.7%

5.9 Appendix: Supplementary Information

Solution Details

This multiplayer model has 7 different parameters that can be adjusted, so a complete description of system dynamics is outside the scope of this paper. Instead, as a first look at what can be understood using this framework, we chose a few sets of parameter choices to examine based on real-world scenarios and ease of computation.

We used a numerical approach to examine system dynamics and to identify equilibrium solutions in a three dimensional, discrete, choice space. To do so, we set the number of budget increments for the possible budget allocation choices that each player (Funder, LT1, LT2) could make. Here we use 21 choice increments (in equal increments from 0 to 100 percent of the budget) to balance adequate insight into system dynamics with computational speed.

For every combination of possible choices, we calculated the payoff to each player using the benefit functions provided below and the stated parameter choices. The budget parameters $(\alpha, \gamma_1, \gamma_2)$ were set to 0.1 (enough to purchase 10% of each organization's priority region) because this was a reasonable representation of the resources of a midsize conservation organization. We examine scenarios with variation in priority overlap, but we constrain the maximum overlap to 0.5. This maximum level of overlap seems representative of real-world organizations, but also because priority overlap greater than 0.5 resulted in additional Nash equilibria (identified by mapping response surfaces in preliminary exploration of the system dynamics).

There are many ways to examine system dynamics once we obtain this set of benefit calculations. In this study we have chosen to focus on the benefit obtained by each player at the Nash equilibrium set of choices. We used an iterative process (detailed in Box 2) to step through the three dimensional choice space and identify the Nash equilibrium solutions in which no player could improve their benefit by making a different choice. The iterative process requires a set starting point in choice space and then alternates through the players' choices, stepping through the choice space if an increased benefit is possible. Because this is a symmetrical model, in most cases there are two Nash equilibrium solutions. For the parameter choices that we present here, we ran 1000 randomly assigned initial condition choices for each first mover choice and found that convergence to the Nash equilibrium occurred more than 82 % of the time (Table 5.3). The nonconverging runs appeared to result from random seed values that were very close to the upper boundary (1) and may have been unable to converge due to flatness of the benefit surface in those regions. In addition, there are parameter choices not discussed in this paper(eg $\Gamma = 0.3$) for which certain starting points lead to nonconvergence because alternating maximum benefit value choices result in the solver getting stuck in a loop. We identify and discuss all the stable equilibria for our parameter choices. Although unstable equilibria may be present in some scenarios, we do not identify them because they are less relevant for informing conservation organization behavior.

Table 5.3: Convergence diagnostics for 1000 randomly assigned starting positions of the choice maximization process and Nash equilibrium iterative solver

Γ	**Funder plays first**	**LT1 plays first**	**LT2 plays first**
0.5	0.82	0.85	0.82
0.1	0.93	0.95	0.93

Basic priority overlap (Scenarios 1a and 1b)

Each player has a total available budget that they can spend. Choice variables are ϵ_1, ϵ_2, and p. Refer to Figure 5.1 for the identity of the parameters $(\gamma_1, \gamma_2, \alpha)$:

$$\begin{aligned}\text{Total Budget LT1} &= \beta_A = (1-\epsilon_1)(\gamma_1 + p\alpha)\\ \text{Total Budget Funder} &= \beta_B = \epsilon_1(\gamma_1 + p\alpha) + \epsilon_2(\gamma_2 + (1-p)\alpha)\\ \text{Total Budget LT2} &= \beta_C = (1-\epsilon_2)(\gamma_2 + (1-p)\alpha)\end{aligned}$$

Species lists from each region and total species are protected according to the species area relationship. We scale budget (β) between 0 and 1, such that a budget of 1 could protect all of the area (Area), and then calculate the proportion of the area protected. In this formulation, area cancels out and the possible species protected are calculated from the budget alone.

$$S = c(\frac{\beta * Area}{Area})^z = c\beta^z$$

In all instances $c_A = c_B = c_C = 1$ so they are omitted from the statements below and z = 0.25. In this study, we chose to emphasize the role of Γ and hence ignored cost heterogeneity. However, this framework could accomodate variation in costs and it would be interesting to explore in future work.

Γ_{AB} is the priority species that overlap between LT1 and the Funder, Γ_{BC} is the species overlap between LT2 and Funder, Γ_{AC} is the priority species that overlap between LT1 and LT2.

The conservation benefit of each organization's actions is the number of species that obtain protection. Protection of species of interest to LT1 is calculated by summing their species protected by spend in region A, their species protected by spend in region B that are not protected in A, and their species protected by spend in C that are not protected by spend in A. We then subtract out the double count of A species that are protected in both B and C but not A.

$$\begin{aligned}\text{LT1 Species} = S_A = &\beta_A^z \\ &+\Gamma_{AB}\beta_B^z(1-\beta_A^z) \\ &+\Gamma_{AC}\beta_C^z(1-\beta_A^z) \\ &-\Gamma_{AB}\Gamma_{AC}\beta_B^z\beta_C^z(1-\beta_A^z)\end{aligned}$$

We use the same formulation for calculating protected species of interest to the Funder, except now we consider species present in region B.

$$\begin{aligned}\text{Funder Species} = S_B = &\beta_B^z \\ &+\Gamma_{AB}\beta_A^z(1-\beta_B^z) \\ &+\Gamma_{AC}\beta_C^z(1-\beta_B^z) \\ &-\Gamma_{AB}\Gamma_{BC}\beta_A^z\beta_C^z(1-\beta_B^z)\end{aligned}$$

For LT2 we consider species in region C.

$$\begin{aligned}\text{LT2 Species} = S_C = &\beta_C^z \\ &+\Gamma_{BC}\beta_B^z(1-\beta_C^z) \\ &+\Gamma_{AC}\beta_A^z(1-\beta_C^z) \\ &-\Gamma_{BC}\Gamma_{AC}\beta_B^z\beta_A^z(1-\beta_C^z)\end{aligned}$$

Finally, to calculate total species protected, we sum the species protected by spend in each region and then subtract out the overlap between regions. Then we add the overlapping species they all care about back in because they had been deleted with the overlap.

$$\begin{aligned}\text{Total Species} = S_S = &\beta_A^z + \beta_B^z + \beta_C^z \\ &- \Gamma_{AB}\beta_B^z\beta_A^z \\ &- \Gamma_{BC}\beta_B^z\beta_C^z \\ &- \Gamma_{AC}\beta_A^z\beta_C^z \\ &+ \Gamma_{AB}\Gamma_{BC}\beta_B^z\beta_A^z\beta_C^z\end{aligned}$$

Targeted funding: request for proposals

We modify the budget equations for the targeted funding scenarios as follows:

In the request for proposals case (Scenario 2a), funder money is contractually obligated to be spent on funder priorities.

$$\begin{aligned}\text{Total Budget LT1} &= \beta_A = (1-\epsilon_1)\gamma_1 \\ \text{Total Budget Funder} &= \beta_B = \epsilon_1\gamma_1 + p\alpha + \epsilon_2\gamma_2 + (1-p)\alpha \\ \text{Total Budget LT2} &= \beta_C = (1-\epsilon_2)\gamma_2\end{aligned}$$

Priority species of interest to each player are protected according to the benefit functions described above.

The total species of interest that can be protected by the funder ($S_{Bactual}$) are less than expected due to crowding out (as LTs move spend to their own regions).

Crowding out is calculated as

$$S_{Bpotential} - S_{Bactual}$$

where $S_{Bpotential}$ is S_B with a budget that includes the money from the ϵ choice that each LT would make if the funder did not spend any money in the system.

The Funder's expected species to be protected if they invest in a region and the LTs continue to spend as they had previously = (current budget spend in the region + new budget)^z + overlapping Funder species from existing spend in other regions - double counted overlapping species.

Targeted funding: request for proposals + cost share

We examined the potential for the Funder to capture benefit lost to leakage by using cost sharing mechanisms in their contract with the LTs. To do so, we added a cost share parameter (CS) which added budget to be spent on Funder priorities in increments of what the LT was already spending (assumption that cost sharing is possible for both LTs). Now:

$$\begin{aligned}
\text{Total Budget LT1} &= \beta_A = (1 - \epsilon_1)\gamma_1 \\
\text{Total Budget Funder} &= \beta_B = \epsilon_1\gamma_1 + CS * \epsilon_1\gamma_1 + \epsilon_2\gamma_2 + CS * \epsilon_2\gamma_2 \\
\text{Total Budget LT2} &= \beta_C = (1 - \epsilon_2)\gamma_2
\end{aligned}$$

Priority species for each organization are once again protected according to the benefit functions above.

We then calculate the funder's benefit for different values of the cost share parameter to find the match that would recapture the loss due to crowding out.

Chapter 6

Conclusions

Conservation science has acknowledged that estimates of the costs and benefits of protected areas (PAs) are necessary for efficient biodiversity conservation. In this dissertation I examined two aspects of this large topic. I first provided some insight into the management needs and costs of PAs by focusing on the single topic of invasive plant management. I found that I could use the features of PAs to predict invasive plant presence and cover, as well as the allocation of existing funding. However, I also suggest that past funding is not a good indication of future management need. I then tackled the measurement of conservation benefit from two perspectives. In one study, I develop a method that conservation practitioners can use to remotely assess changes over time in forest attributes that relate to conservation benefit. I find that some forest attributes are well suited to remote assessment and I demonstrate potential applications of these models. Then, I use a theoretical model to show how the benefit of conservation spending is dependent on strategic interactions between conservation organizations, and suggest that these interactions need to be considered by conservation planners.

Several overarching conclusions can be drawn from the synthesis of these four studies. 1) This work suggests that cost and benefit measurements that are aggregated to the level of a PA are both feasible and meaningful for conservation practice. Many ecological studies are performed at scales that are much smaller than that of a PA (i.e. quadrat based plant sampling, etc.). In contrast, I study both cost allocation and ecological features (plant occurrences and forest attributes) at the scale of a PA and find meaningful variation that can enhance conservation decision making. 2) In the $\frac{\text{threat avoided * benefit}}{\text{cost}}$ conceptual framework of systematic conservation planning (Newburn et al., 2005), valid estimates of cost may actually be the most difficult to obtain. My work with invasive species management data suggested that the actual costs of effective management were not easily estimated from existing funding. This is likely a result of insufficient spending on invasive species management across the PAs, but it demonstrates that even with access to the best existing datasets, the true costs demanded by the above equation are elusive. Finally, 3) conservation practice does not happen in a vacuum and therefore organization interactions and perspective is important when interpreting results. This consideration is particularly apparent when considering cost and benefit accounting for invasive species managment. For instance, the invadedness models in Chapters 2 and 3 provide estimates of costs and averted threats, but those values are from the perspective of the organizations that manage the individual PAs. Meanwhile the prioritization of funding towards certain species illustrates that the funding organization values slightly different outcomes.

These studies are a valuable contribution to conservation science, but there is still much work to be done. The two studies presented here provide a first step towards estimating invadedness for conservation planning purposes. However, prior land use history or disturbance at a PA is a potential driver of invasion that we were unable to test for due to data limitations. A valuable future line of study would be to examine the improvements in prediction of invadedness that could be obtained by estimating historic disturbances at the PA using our method from chapter 4.

In chapter 2, I provide a first look at how management costs relate to PA features and covary with invasive plant cover. More resolved aspects of how invasive plant funding is allocated remains to be examined. I suggest that a logical next step would be to estimate the implications of aggregating costs across species by using the operations database in chapter 3 to quantify the variation in how funding is allocated across species.

In addition, there has been almost no work on the temporal variation in management costs and most studies assume that costs are constant over time. It would be interesting to investigate how management investment at a PA varies over time and whether actual funding levels ever display the constant levels that suggest maintenance treatment levels have been attained. The invasive plant management cost dataset could provide a first look at this question with its 10 years of detailed funding information across hundreds of PAs.

Our work on measuring the benefit of conservation spending is important and a good first step, but there is much more work that can be done to improve this aspect of conservation practice. The remote sensing data benefit models provide estimates of changes over time in forest structure and composition on a PA. The obvious next step is to examine the out of sample predictive capacity of the model so that it can be used to compare changes on PAs versus off PAs to see if there are differences in forest attributes that relate to being protected.

Meanwhile, the multiplayer model is used in this dissertation to examine the outcomes of spending from the funder's perspective. However, it also is just a first pass at the many questions that can be asked of this system. An important next step would be to examine the implications of asymmetrical distribution of budgets and priorities across the players. We studied the dependence of funder outcomes on priority overlap, but the expansion where overlap can differ across players needs to be examined.

There are still many unanswered questions regarding how to incorporate the costs of preserves into the conservation planning process. However, this dissertation is a step in the direction of understanding allocation of invasive plant management funding and begins to develop tools to help determine the outcomes of funding. These contributions are useful to practitioners and will improve our understanding of protected area management and impact.

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Vita

Gwen's interest in conservation decision making is based on a lifetime of appreciating the joys of visiting public protected areas. As a homeschooled child growing up in central Florida, she spent most of her time riding horseback through the woods admiring plants and animals in their natural habitat. After completing a B.S. degree in biology at Florida Tech, she joined the department of Wildlife Ecology and Conservation at the University of Florida where she studied the drivers of species richness in the beautiful and imperiled longleaf pine savanna. M.S. in hand, Gwen next spent two years working as a field botanist for the Florida Natural Areas Inventory where she visited more than 300 protected areas and had entirely too much fun talking to land managers and mapping the distribution of invasive plants. She came to the University of Tennessee because Paul Armsworth was her ideal advisor, allowing her to examine applied conservation questions at the interface of economics and ecology. After graduation, she will start a post-doc with Hugh Possingham and Kerrie Wilson at the Center for Excellence in Environmental Decisions at the University of Queensland, Brisbane, Australia.