Invasive Plants in U.S. National Wildlife Refuges: A Coordinated Research Project with Undergraduate Ecology Students

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ABSTRACT

Answering large-scale questions in ecology can involve time-consuming extraction and compilation of data. We show how networks of undergraduate classes can make these projects more manageable and provide an authentic research experience for students. With this approach we examined the factors associated with plant species richness in U.S. National Wildlife Refuges. We found that the richness of harmful invasive plants and native plants were positively associated in mainland refuges but negatively associated in island refuges. Non-native and invasive richness were also positively associated with colonization pressure as indicated by non-native richness around each refuge. Associations between refuge characteristics and invasive plants varied substantially among regions, with refuge area and habitat diversity important predictors of invasion in some regions but not in others. Our results serve to identify the refuges that are most susceptible to plant invasion and demonstrate the potential value of a new model for education and research integration.

Key-Words: invasive species, exotic plants, protected areas, conservation, education

INTRODUCTION

Existing data may offer the best insight into many important questions in ecology and conservation biology, but there are a variety of challenges to using existing data effectively. For one, although the use of large data repositories is increasing, many ecological data sets are never made publicly available. In addition, ecological data sets are rarely uniform, and getting data sets from different sources, sites, and time periods into a consistent format can be tedious. These difficulties may be particularly pronounced when data sets address ecological questions over large spatial or temporal scales.

Our study describes a novel framework for addressing these challenges using networks of undergraduate ecology and conservation biology courses. We used this framework to investigate the geographic patterns of non-native and invasive plants in U.S. National Wildlife Refuges. Tasks were delegated among the students (with instructor supervision) so that students collected and compiled the data for refuges in their own region. From the data that students compiled, we asked: 1) how non-native and invasive plant species richness is related to native species richness, 2) how the pool of non-native species from the surrounding area (i.e. colonization pressure) contributes to non-native and invasive species richness in the refuges, 3) how refuge characteristics such as habitat diversity, refuge area, and elevational range contribute to species richness patterns for native, non-native, and invasive plants, 4) whether invasion patterns differ between mainland and island refuges, and 5) whether invasion patterns vary among Fish and Wildlife Service regions. Below, we outline the scientific background for this project, as well as the specific rationale for each of the questions examined.

Plant Invasion of Protected Areas

Human activity is rearranging ecological communities in an unprecedented way (McKinney and Lockwood 1999, Hobbs et al. 2006, Ricciardi 2007). The novel species interactions resulting from this re-arrangement can threaten existing communities but can also offer valuable insight into a range of evolutionary and ecological questions. The emerging science of invasion ecology focuses on how non-native species enter established communities, how they spread through these systems, and how they affect native species, communities, and ecosystems (Lockwood et al. 2007).

One of the most basic questions in invasion ecology is why some areas have more invasive species than others. Traditionally, ecologists believed that human disturbances were critical to invasion success (e.g., Hobbs and Huenneke 1992). Increasingly, ecologists realize that protected areas are not immune to invasion and the strongest impacts on rare species may occur within these protected areas (Hughes and Convey 2010, Hayward 2012). National Wildlife Refuges may be particularly important in this regard because they are often tasked with managing a specific set of species or habitats.

Most previous studies of invasion patterns have addressed non-native species in general rather than species that are specifically designated as invasive (e.g., Knops et al. 1999, Stohlgren et al. 1999, Fridley et al. 2007). A focus on non-natives in general emphasizes the establishment phase of the invasion process – that is, which species colonize and what makes a site invasible. However, focusing on harmful invasives may be more appropriate for questions of spread, impact, and management. A major challenge in studying harmful invasives is that it can be difficult to designate a species as invasive rather than simply non-native. Some ecologists define an invasive species as one that is both non-native and has impacts on native species (e.g., Lockwood et al. 2007); others define an invasive as a non-native that can establish a self-sustaining population and spread independently to new areas (e.g., Blackburn et al. 2011). Nevertheless, the management of protected areas requires attention to a specific set of species that are spreading and altering native habitats; that is, species that are harmful invaders. Because

National Wildlife Refuges often compile lists of harmful invasive species, these lists present a unique opportunity to compare invasion patterns between non-natives in general and invasives in particular.

Relationship between richness of native, non-native, and invasive species

A common observation from studies of plant invasion is a negative relationship between native and non-native richness at local scales and a positive relationship at regional scales (Herben et al. 2004, Fridley et al. 2007). The negative relationship at small spatial scales is attributed to “biotic resistance,” that is, increased competition for niche space with higher native species richness in the resident community (Elton 1958, Simberloff 1986). The positive relationship between native and non-native species at larger spatial scales is often referred to as “biotic acceptance” (Stohlgren et al. 2006). Biotic acceptance is typically observed because environmental factors may affect native and non-native species richness similarly, so that favorable conditions lead to higher species richness for all groups (Stohlgren et al. 2006).

Importance of colonization pressure

Relationships among native and non-native species richness can be complicated by colonization pressure, the number of species introduced to a site (Lockwood et al. 2009). With more species introduced, the richness of invasive species should increase independently of any species interactions (Lonsdale 1999, Lockwood et al. 2009). We treated the non-native species from the counties surrounding each wildlife refuge, or the regional species pool, as a surrogate for colonization pressure. We then used these data to examine the relationship between colonization pressure and non-native and invasive species richness in wildlife refuges.

Refuge characteristics and native, non-native, and invasive species richness

Native and non-native plants may influence each other's richness, but both groups may also be influenced by environmental characteristics. We focused on three characteristics of refuges that could influence plant species richness – refuge area, habitat diversity, and elevational range. All things being equal, larger refuges should contain more plant species (Gotelli and Colwell 2001, Whittaker and Triantis 2012). That said, area may affect non-native and invasive plants differently from native plants. If non-native plants recruit from adjacent areas, species richness would be more influenced by refuge perimeter than refuge area. Habitat diversity should influence richness of all types of plants, and in previous studies habitat diversity has been suggested as the causal factor behind biotic acceptance. Elevational range was included as an additional measure of habitat heterogeneity as plants may have distinct elevational ranges even when the broader habitat type (e.g. forest, grassland) is similar.

Mainlands versus islands

Patterns of biodiversity often differ between mainlands and islands, and patterns of invasion may differ, as well (Elton 1968, Bolger and Case 1991,Poessel et al. in press). Because islands may be depauperate in native species relative to mainlands, island communities may offer reduced biotic resistance to invasion. In addition, islands may have small populations of naive species that can be vulnerable to extinction (Simberloff 1981). Finally, island refuges may contain an unusual number of rare species, so that island refuges may show impacts of invasion not seen elsewhere. For these reasons, we compared patterns of invasion between mainlands and islands.

Variation among regions

Although continental-scale analyses can provide general insight on geographical patterns of invasion, from a management perspective region-specific patterns may be more useful than continental-scale generalizations. Therefore, we examined the extent to which patterns of plant invasion varied across regions.

METHODS

Project structure

One or two classes were responsible for compiling data from each of the seven U.S. Fish and Wildlife Service regions (as of 2002): Northeast, Southeast, Midwest, Mountain-Prairie, Southwest, Pacific, and Alaska. The Alaskan region contained only 12 refuges with available data, so these were combined with the Pacific region. Both the Pacific and Southeast regions contained many refuges, so refuges in these regions were divided between two classes each. Courses incorporated the group project in a variety of different ways (Panel 1) though student teams all followed research protocols described at the project's website (https://groups.nceas.ucsb.edu/sun). In most cases, refuges were assigned independently to two different students as a means of quality control. Students met to resolve discrepancies between their data entries; instructors for each class then reviewed and collated the class data; and the summarized class data were uploaded to the project website. One of us (DMM) provided a final layer of quality control by checking a subset of each student's data against the original data sources (see below).

Data sources and quality control

We used the National Wildlife Refuge Invasive Species Survey (hereafter "ISS", http://www.nwrinvasives.com) as a starting point for data compilation. This websurvey was administered by the USGS in 2002 and refuge personnel were asked to input information about refuge characteristics and the extent of monitoring for non-native and invasive plants (Tempel et al. 2004). In addition, the survey allowed managers to upload a list of problem non-native plant species (which we refer to as invasives).

ISS data were usually available for area, elevational range, and habitat distribution (Table 1), the latter of which we used to calculate Simpson's index for habitat diversity. However, lists of invasive plants were often missing or obviously incomplete. To supplement the plant lists, we used information from the Comprehensive Conservation Plan (CCP) for each refuge. CCP data are drawn from refuge monitoring programs, from the academic literature, and from consulting services. Most CCPs are recent (last 5-10 years), so they represent current information on refuge biota. In some cases, species lists were also posted on refuge websites. When CCP or refuge website data were not available, students contacted refuge personnel for species lists. Available lists from any of these sources (CCPs, websites, refuge personnel) were given precedence over ISS lists.

We compiled three sets of plant lists for each refuge: natives, non-natives, and problem invasives. Where native and non-native species were not separated, we used the Biota of North America database ("BONAP, Kartesz 2011) to delineate these. To make non-native and invasive lists independent (i.e. non-overlapping), we separated out problem invasive plants from the general list of non-natives for each refuge. For CCPs, we considered Class I non-natives ("currently invading and disrupting natural plant communities") to reflect invasives. Most ISS plant lists echoed these criteria, as did invasive species listed on refuge websites. Invasive lists from different sources (e.g. CCP and ISS) were generally consistent with one another, suggesting that varied definitions tended to yield a similar set of species.

To obtain lists of non-native plants in the vicinity of each refuge (i.e. the non-native species pool), we used county-specific lists from BONAP. These lists were merged for all counties in which a refuge was located. To classify refuges as mainland versus island, we defined islands broadly to include oceanic islands (e.g. Guam, Hawaii), coastal islands (e.g. Nantucket, Florida Keys), and islands within large lakes.

Plant data varied in quality – some lists were based on anecdotal observation whereas others were based on extensive surveys. Thus, for each refuge we calculated a quality score ranging from 1 to 25 that took into account the source of the data (e.g. CCP, ISS) and the kinds of surveys that generated them. Although these scores were subjective, they succeeded in differentiating high quality data from low quality data. For example, refuges having only ISS invasive species data from anecdotal observations typically had quality scores of 5 or less, whereas refuges with CCP data-based on systematic plant surveys usually had quality scores between 15 and 20. We used these scores to weight the data in our analyses as described below.

Data analysis

We analyzed patterns of non-native and invasive richness among USFWS regions using general linear models. We modeled plant richness as Poisson when a goodness of fit test failed to detect overdispersion, and as negative binomial when overdispersion was present.

To quantify the relationships between refuge characteristics, regional species pools, and native, non-native, and invasive species richness, we used structural equation modeling (SEM; Bollen 1989, Grace 2006). Structural equation modeling allows one to simultaneously analyze relationships among multiple variables within a system – in this case, species richness of natives, non-natives, and invasives. Our model (Figure 1) was chosen *a priori* to represent the expected relationships among the variables based on previous large-scale analyses of patterns of plant invasion (Stohlgren et al. 2003, Harrison et al. 2006). Refuge area, habitat diversity, and elevational range were expected to influence each of the three classes of plants. The regional pool of non-natives was expected to influence both non-natives and problem invasives. The relationship between non-natives/invasives and natives was included to represent biotic resistance (a negative relationship) or biotic acceptance (a positive relationship). Islands and mainlands were analyzed separately to permit comparisons between these with respect to patterns of biotic acceptance and colonization pressure.

Structural equation models were fit by maximum likelihood using the “sem” function in the lavaan package for R (Rosseel 2012). The overall model (Figure 1) had one degree of freedom, which allowed a chi-squared test for overall model fit (Grace 2006). All models shown in the results had adequate fit ($p>0.05$) except where specifically noted. To incorporate quality scores for each refuge, models were fit using a covariance matrix calculated by weighting observations by the quality score for the refuge. We used multi-group analyses to test for significant differences in model coefficients between mainland and island refuges and among FWS regions. For these analyses, model fit was compared between a model that fixed parameters to be identical across groups and a model that allowed group parameters to vary.

RESULTS

Data availability and regional patterns

For most refuges, we had data on area (n=392), elevational range (n=369) and habitat diversity (n=295). We located a total of 126 lists of native species, 122 lists of non-native species, and 278 lists of invasive species. Plant data varied in availability across regions (Table 1), with the greatest data availability in the Northeast and Southwest regions and the lowest availability in the Southeast and Mountain-Prairie regions (Table 1). The apparent low data availability in the Mountain Prairie region was due to the inclusion of a large number of easement refuges to which USFWS has no access. When these refuges were removed, the Mountain-Prairie region had data availability similar to the other regions ($\chi^2 = 7.4$, p

= 0.19). Data quality scores tended to track data availability. Quality scores were significantly lower in the Southeast region (GLM, b = -2.65; p = 0.02) and also in the Mountain-Prairie region when easement refuges were included (b = -2.67, p = 0.02).

Overall, non-native and invasive richness varied significantly across regions (likelihood ratio = 34.6, df = 5, $p < 0.001$, likelihood ratio = 15.8, df = 5, $p < 0.01$ respectively). Non-native richness per refuge was highest in the Pacific region (excluding Alaska, $\mathbf{x} = 81.23 \pm 13.5$ SE) and lowest in the Southwest region ($\mathbf{x} = 29.5 \pm 6.4$ SE). Invasive richness was highest in the Northeast ($\mathbf{x} = 11.83 \pm 1.56$ SE) and Pacific ($\mathbf{x} = 11.19 \pm 1.10$ SE) regions and lowest in the Southwest ($\mathbf{x} = 5.81 \pm 0.76$ SE) and Mountain-Prairie regions ($\mathbf{x} = 6.78 \pm 0.88$ SE).

Associations between native, non-native, invasive richness, and the regional non-native pool

For mainland refuges (Fig 3a), the proportion of variation in plant richness explained by the SEM was moderate for natives (R^2= 0.30) and invasives (R^2= 0.23) but low for non-natives (R^2= 0.11). Native richness and non-native richness in mainland refuges were positively associated (r = 0.33). Non-native and invasive richness were both positively associated with the richness of the non-native species pool in areas surrounding each refuge, though these coefficients were low (r = 0.15 and 0.27, respectively). In addition, invasive richness was associated with non-native richness (r = 0.26).

Refuge characteristics

Refuge characteristics influenced all three classes of plants (Figure 3). Native richness was positively associated with refuge area (r = 0.33) and elevational range (r = 0.27). Non-native richness was positively associated with habitat diversity (r = 0.12) and negatively associated with refuge area (r = -0.15). Invasive plants were also positively associated with habitat diversity (r = 0.17) and negatively associated with elevational range (r = -0.14).

Mainland versus island refuges

Patterns of plant invasion on island refuges differed substantially from patterns on mainland refuges ($\chi 2 = 35.4$, df=14, p = 0.002, Figure 3b). Most notably, the associations between non-natives and natives and between invasives and natives were negative (r = -0.61 and -0.27). In addition, the size of the non-native species pools were not significant predictors of non-native and invasive richness within refuges on islands (they were significant for mainlands; Figure 3a). Finally, non-native richness was much more closely associated with refuge area (r = 0.63) on islands as compared to mainlands (r = -0.15).

Regional variation in patterns of invasion

For most individual regions, it was only possible to fit a simplified SEM without the non-native plant class (i.e. only natives and invasives). Using this simplified model, regions differed significantly in patterns of invasion in mainland refuges ($\chi 2 = 14.2$, df=5, p= 0.014). Region-specific parameters should be interpreted with caution; the model was a poor fit for the Midwest region ($\chi 2 = 12.8$, df=1, $p< 0.001$), and regional sample sizes were low. Nevertheless, pronounced variation in regional results was apparent (Figures 4 A-F). Area effects were strongest in the Midwest region. Habitat diversity was most predictive of invasive richness in the Southeast, Southwest, and Pacific regions. And the regional species pool was most the most important predictor of invasive species in refuges located in the Northeast. Associations between native richness and invasive richness were positive in all regions, though the strength of this association was variable.

Student experience and assessment

Student responses to the project were generally positive (Panel 2). Most students agreed or strongly agreed that the project improved their understanding of invasion biology, conservation policy, and data analysis. Students strongly agreed that the project increased their appreciation for the value of good data. Most students also said they felt like they were contributing to an important research project and that the activity was an interesting course experience. The most common positive comment was that students enjoyed working on a real research project rather than a scripted assignment. The most common negative comment concerned the frustration of finding (or not finding) data for the refuges. In particular, many students felt considerable frustration that they could work quite hard in searching for plant data but not have anything to show for it (Panel 2).

DISCUSSION

Our framework for collaboration between undergraduate classes and federal agencies can be compared to citizen-science projects that similarly involve hundreds of participants in coordinated research endeavors (Dickinson et al. 2010, Crall et al. 2011), but networks of undergraduates have additional advantages (Bowne et al. 2011). One advantage of our approach is that course instructors provide a level of highly qualified supervision for coordinated research projects. For any major ecological issue (e.g. climate change, habitat loss, pollution) tens if not hundreds of instructors will have extensive background on the topic and may be interested in course-based collaboration. A second advantage of our approach is that course grades provide a level of incentive and accountability that is typically absent from other kinds of citizen science initiatives. Although it can be difficult to develop approaches to grading students on research projects, it was clear from student self-evaluations that a desire to get a good grade was very important to most participants. A final advantage to enlisting undergraduate courses in research projects is that this approach can be applied to projects that involve some tedium. Whereas enlisting non-scientists to survey birds or frogs might be easy, we expect that it would be considerably harder to find qualified volunteers for data compilation projects. Students, on the other hand, are often willing to accept this type of work if they understand that the project will expand their skill set and provide them with valuable research experience. We believe a wide range of projects involving large-scale data compilation could be carried out through these sorts of collaborations, thereby benefiting students, federal and state agencies, and the scientific community.

With respect to the project results, we found a positive relationship between natives and non-native plant species richness on mainland refuges, consistent with patterns observed in previous studies in non-protected areas (Stohlgren et al. 2003, Fridley et al. 2007). Invasive plants showed a similar relationship with native species richness, suggesting that biotic acceptance at large scales (Stohlgren et al. 2006) is also seen for problem invasive species.

We found that the non-native species pool was associated with the richness of both non-native and invasive species in mainland refuges. Though this result is intuitive, it is novel and offers support for the role of colonization pressure in invasion patterns. Interestingly, there was no detectable association between the non-native species pool and non-native or invasive richness on islands. This may occur because non-native/invasive plants on islands have different modes of transport, such that the regional species pool does not reflect the plants that are likely to arrive or successfully establish.

Another difference between mainland and island refuges was in the relationship between native and non-native or invasive richness. This relationship was positive for mainland refuges, but negative for island refuges. This difference may be due to depauperate island fauna being more susceptible to extinction in the presence of invasive species. Although other studies of plant invasion on islands (e.g. Sax et al. 2002, Sax and Gaines 2008, Long 2009) did not find evidence of such extinctions, a recent review found that invasive plants were far more likely to have negative impacts on native species on islands than on mainlands (Pysek et al. 2012).

Regions differed considerably in the factors that were associated with invasive species richness. Invasive species richness was closely associated with native species richness for refuges in the Northeast and the Pacific regions, but these factors were less associated with native richness in other regions. Refuge area was an important predictor of native and invasive species richness in the Midwest, but refuge area was not associated with species richness in the Northeast. Similarly, habitat diversity was an important predictor in some regions (e.g. Southeast, Northeast), but not in others (e.g. Mountain-Prairie, Midwest). Because of the small sample sizes within regions, any specific regional difference should be treated cautiously. Nevertheless, regional differences do suggest that patterns of invasion may be best understood on a scale smaller than that of the entire United States.

Our model allowed us to quantify the influence of three refuge characteristics that may affect natives and non-native/invasive richness: refuge area, habitat diversity, and elevational range. We found some differences in the way that different types of plants responded to these factors. For example, there was a positive relationship between native species richness and refuge area in five of the six regions. In contrast, relationships between invasive species richness and refuge area were variable across regions and were sometimes negative. One possible explanation for this result is that edge effects, and consequently colonization pressure by invasives, will decrease with refuge area. Another potential explanation is that areas with high invasive richness (e.g. California and Florida) tend to be coastal areas where land is valuable and wildlife refuges are small.

We expected that habitat diversity would be associated with species richness for all three classes of plants (Davies et al. 2005). In fact, we found that non-native and invasive species richness had a positive response to habitat diversity, whereas native species richness had no overall relationship with habitat diversity. One explanation for this difference is that disturbed or man-made habitats may increase non-native and invasive richness but have little effect on native richness (Didham et al. 2005, MacDougall and Turkington 2005). In addition, the lack of a native response to habitat diversity appears to be due in part to differences among regions. In the Northeast and Southeast regions, the relationship between habitat diversity and natives is strongly positive, but in the Pacific region, this relationship is negative. Interestingly, elevational diversity was positively associated with native diversity but negatively associated with both non-native and invasive species richness. This difference may reflect the lack of time for evolutionary diversification in newly arrived species (i.e., non-native and invasive species). It also may reflect colonization pressure – i.e. introduced species may not include non-natives and invasives that can survive at all elevational ranges. In any case, this finding suggests that aspects of habitat diversity maybe be exploited differently by native versus non-native species.

There were several important limitations to our study. First, data were incomplete for a large number of refuges, and, in many cases, lists of invasives were based on anecdotal observations. Although we used weighting to deal with data quality issues, our weighting scheme was somewhat subjective. Second, we relied on managers' opinions as to which non-native species should be considered invasive within each refuge. On the one hand, people working in these refuges should be in the best position to know which species are invasive. However, relying on expert opinion means that different criteria were probably used by different managers in designating which species were problem invaders. Third, our methodology – spreading data compilation among nearly 200 students in 7 different classes – almost certainly resulted in some errors of data compilation and entry. Although an instructor reviewed each data point, some errors in highly collaborative data-compilation projects are probably unavoidable. Fourth, we did not account for land use history and incorporate it into our analysis. Some refuges contained multiple crop species and others contained substantial numbers of non-invasive ornamentals, likely reflecting prior land use in these refuges. The absence of data on prior land use may account for the relatively poorer performance (i.e. the low R^2 value) of the model for non-native plants as compared to invasive plants.

Conclusion

Despite the challenges of compiling invasive plant data, our project yielded several clear patterns with implications for invasive species planning in protected areas. For one, we found that mainland refuges with higher native diversity are more likely to be invaded by non-native and invasive species. This is particularly the case for refuges with high habitat diversity in the Northeast, Southeast, and Pacific regions. In addition, we found that the number of non-natives in the county/counties surrounding a refuge is moderately informative regarding how many non-native and invasive species are likely to colonize these refuges. While these two results have been observed previously for non-native plants, ours is the first study to illustrate that problem invasive plants follow a similar pattern. In terms of regional differences, our results suggest that predictors of invasion may vary considerably from one region to the next. At the extreme, opposing patterns in different regions can cancel each other out when patterns are viewed at the continental scale. Although we cannot easily disentangle the factors that contribute to regional variation, it is clear that when planning for invasive species, data from nearby refuges should be prioritized over information from continental-scale analyses. Similarly, our results suggest that refuges on islands may not behave like their mainland counterparts when it comes to broad-scale patterns of invasion. Finally, our results highlight the significant gaps remaining in invasive species data in protected areas. Filling these gaps will require increased monitoring of non-native establishment and spread in areas that are important for habitat and species conservation.

Acknowledgments

We thank the National Center for Ecological Analysis and Synthesis for facilitating all aspects of this project. Students from Ecology and Conservation Biology courses at Jacksonville University, Mount Holyoke College, San Francisco State University, Stanford University, University of Wisconsin – Stout, Utah St. University, and Western Carolina University contributed data to this project. Gretchen LuBuhn, Beverly Collins, and Joseph Pechmann helped coordinate student efforts. Thomas Stohlgren (USGS) provided helpful suggestions for the methods and Jenny Ericson (FWS) helped steer us to data sources for the project. John Kartesz gave assistance with using Biota of North America software and Jarrett Byrnes gave advice on data analysis. Julie Lockwood and John Knox provided comments on earlier drafts of this manuscript. This project was funded by NSF grant 1118353 to DM Marsh and SE Hampton.

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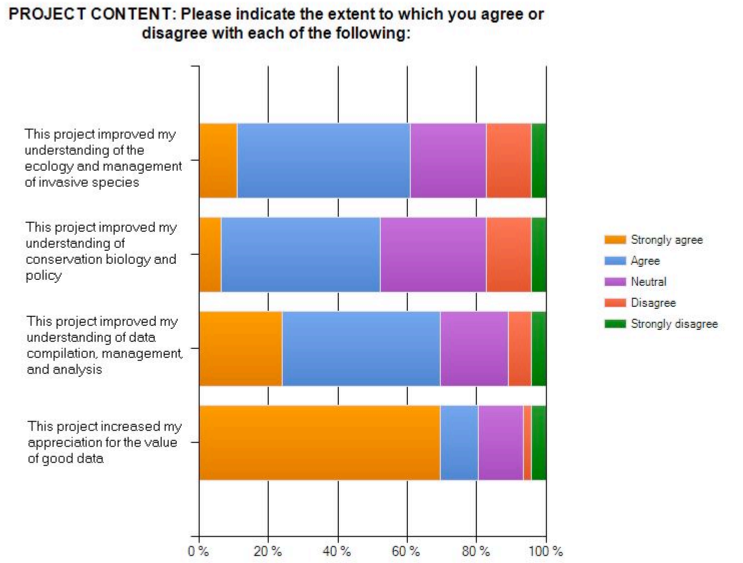
Box 1. Participating courses incorporated the data compilation in a variety of different ways. The Northeast region was compiled by the Invasion Biology class at Mount Holyoke College, which worked on the project as a homework assignment with stepwise due dates and 3 separate weeks of dedicated class periods. The Southeast was handled by the Ecology class at Western Carolina University and the Conservation Ecology class at Jacksonville University. Western Carolina completed the project as part of a multi-week lab assignment spread across three sections. Jacksonville University carried out the project using course time, lab time, and take-home assignments. The Great Lakes region was managed by a two-section Ecology course at University of Wisconsin-Stout which primarily worked on the project during lab periods. The Mountain-Prairie region was compiled by the Ecology course at Massachusetts College of Liberal Arts; their data were compiled during a dedicated four-week course block. The Southwest region was compiled by Utah State University during a five-week course block in Conservation Biology. Finally, the Pacific region was divided between Ecology at San Francisco State University and Conservation Biology at Stanford. SFSU carried out the project primarily as a take-home assignment for two sections whereas, for the Stanford class, students worked on the project as an additional course unit appended to the regular three-credit course.

Box 2. Summary of student responses to project evaluation. Response rate was low (~38%), though we did get respondents from all eight classes. Student responses to major project objectives are shown below. The open response comments from students were also highly informative. Positive comments tended to reflect the real-world nature of the project and the collaborative experience:



"I loved working on a real science project. Sometimes in my bio classes I feel like were "pretending" because we already know the outcome that we are looking for in our labs."

"I had never heard of employing several classes of students to assist with a large data collection and organization effort before taking part in this project, and I was glad to be a part of it."

"I thought that it was fun and interesting to look at data being compiled from actual wildlife areas and refuges across the nation."

"I loved that I was working on something that was going to have an actual real world impact."

"Being able to communicate with (some of the) refuges directly made the practice of conservation feel less nebulous and distant."

Negative comments tended to focus on the frustrations of not being able to find data for assigned refuges. Some negative comments also focused on the website or the project materials – in retrospect, "field-testing" the protocols with students before starting the project would have been beneficial.

"Gathering information from wildlife refuges was very difficult."

"It is very boring and hard to find information on a site that has no information. Neither of my refuges had plant lists."

"My group only had one complete data point out of our eight, so that was rather discouraging."

"Data-collection was hard to standardize. There were problems with the BONAP exotic lists and with identifying what data from websites could be used in the project and what could not."

"Doing this as a group was difficult, because if one person cared and the other didn't it made the entire project seem like a waste of time for the one who cared."

Table 1. Data availability for refuges in the six regions. Total number of refuges providing data are shown, along with the number and percentage of refuges for which lists of native species, non-native species, and problem invasive species were available.

Region	Refuges	Native Lists	Non-native lists	Invasive lists
Northeast	59	26 (44%)	27 (46%)	54 (92%)
Southeast	87	23 (26%)	19 (22%)	57 (66%)
Great Lakes	44	19 (43%)	17 (39%)	36 (82%)
Mountain-Prairie	74	17 (23%)	15 (20%)	41 (55%)
Southwest	36	14 (39%)	18 (50%)	32 (89%)
Pacific (+ Alaska)	95	27 (28%)	26 (27%)	55 (58%)

Table 2. Summary of variables incorporated into the analysis and their sources.

Variable	Type	Source
Refuge area	Continuous	Invasive Species Survey
Elevational range	Continuous	Invasive Species Survey
Habitat diversity (Simpson's D)	Continuous	Invasive Species Survey
Native Species Richness	Discrete	CCPs, refuge websites, refuge personnel
Non-native species richness	Discrete	CCPs, refuge websites, refuge personnel
Invasive species richness	Discrete	CCPs, refuge websites, refuge personnel, ISS
Non-native species pool	Discrete	Biota of North America
Mainland/Island	Categorical	Refuge websites, investigator judgment
Region	Categorical	U.S. Fish and Wildlife Service classifications

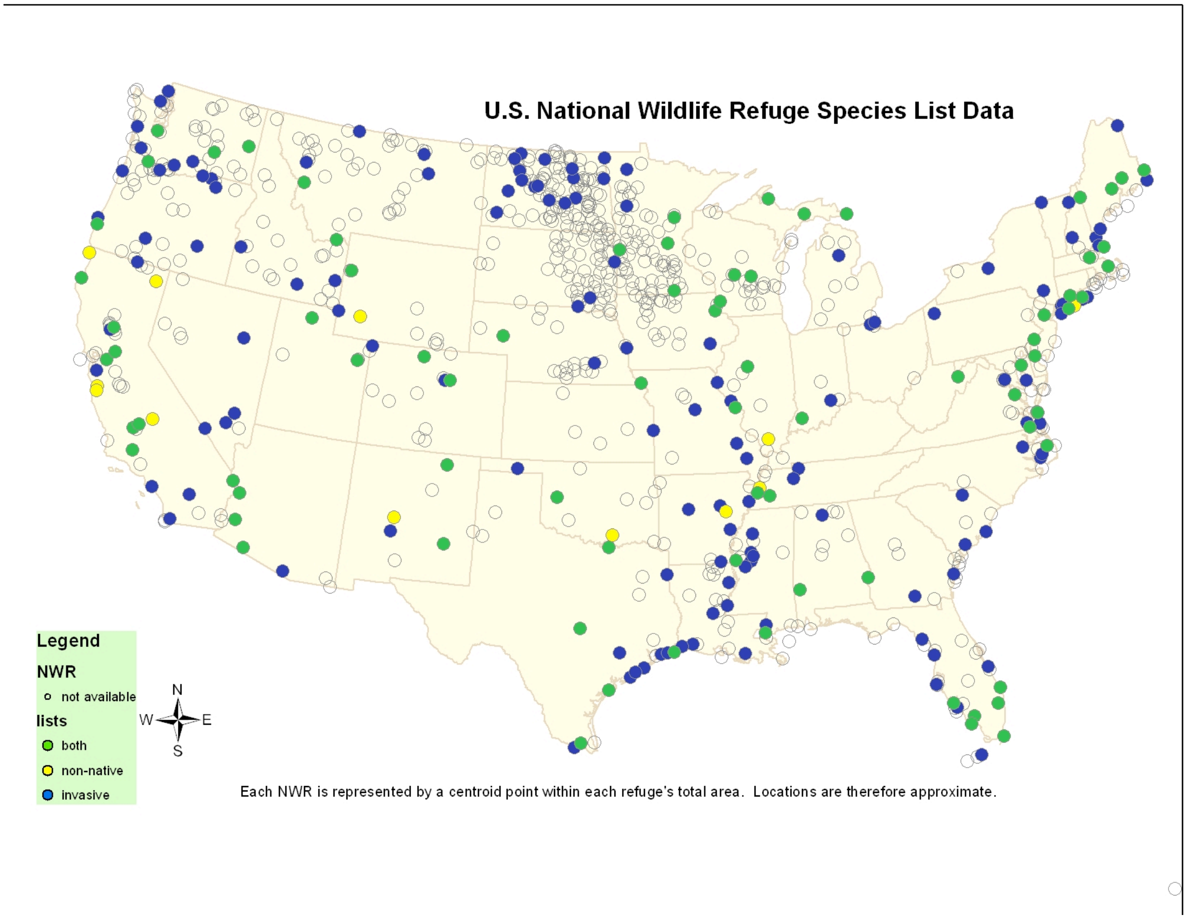
Figure Legends

Figure 1. Map showing locations of National Wildlife refuges and data availability for each refuge in terms of lists of invasive species (blue circles), lists of non-native species (yellow circles), and lists of both invasives and non-natives (green circles).

Figure 2. Structural equation model used to analyze relationships among plant communities and refuge characteristics in wildlife refuges. Native, non-native, and invasive plant communities potentially influence each other and each is in turn influenced by similar sets of refuge characteristics.

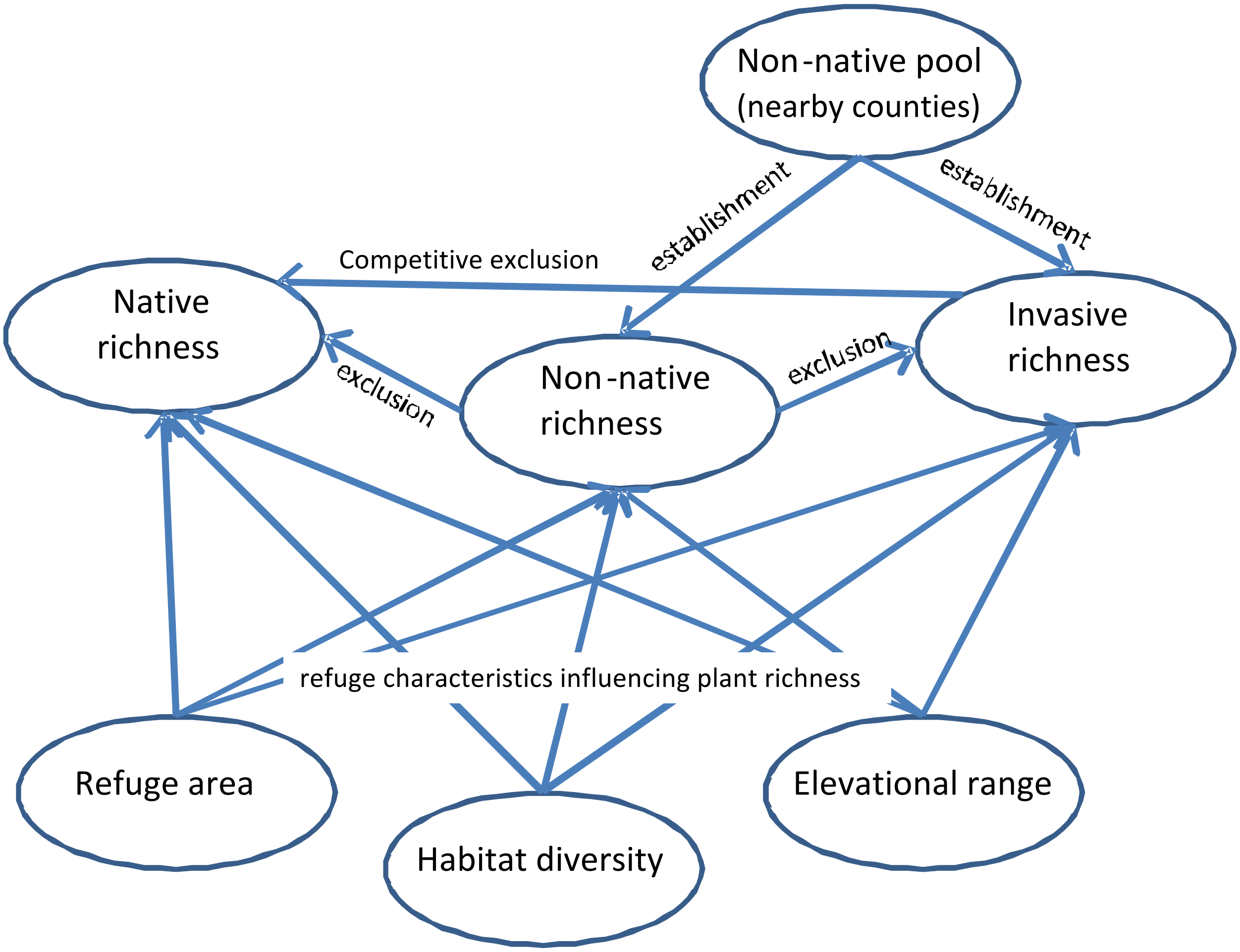
Figure 3. Results from structural equation models for mainland refuges (A) and island refuges (B). Arrows indicate the hypothesized cause-effect relationships between variables. Thicker lines correspond to statistically significant relationships ($p < 0.05$) and coefficients are shown for these parameters.

Figure 4. Results from structural equation models for each Fish and Wildlife Service region. Because sample sizes were small within each region, models included native and harmful invasive species but did not include non-native species. Arrows indicate the hypothesized cause-effect relationships between variables. Thicker lines correspond to statistically significant relationships ($p < 0.05$) and coefficients are shown for these parameters.

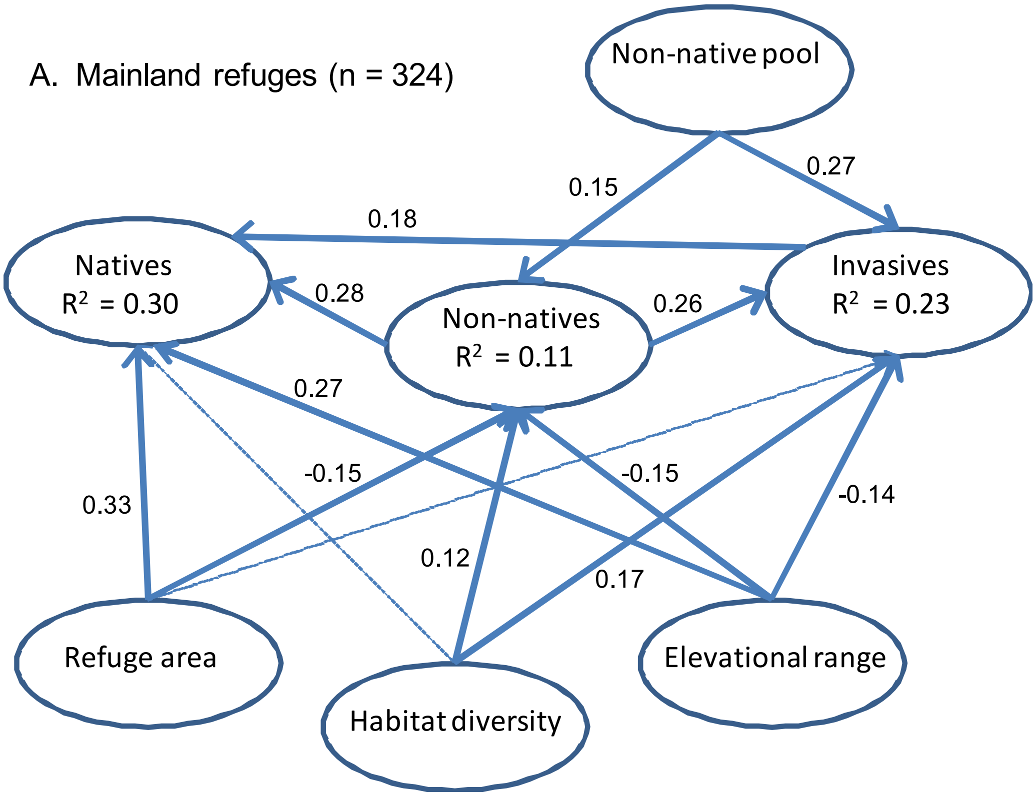


U.S. National Wildlife Refuge Species List Data

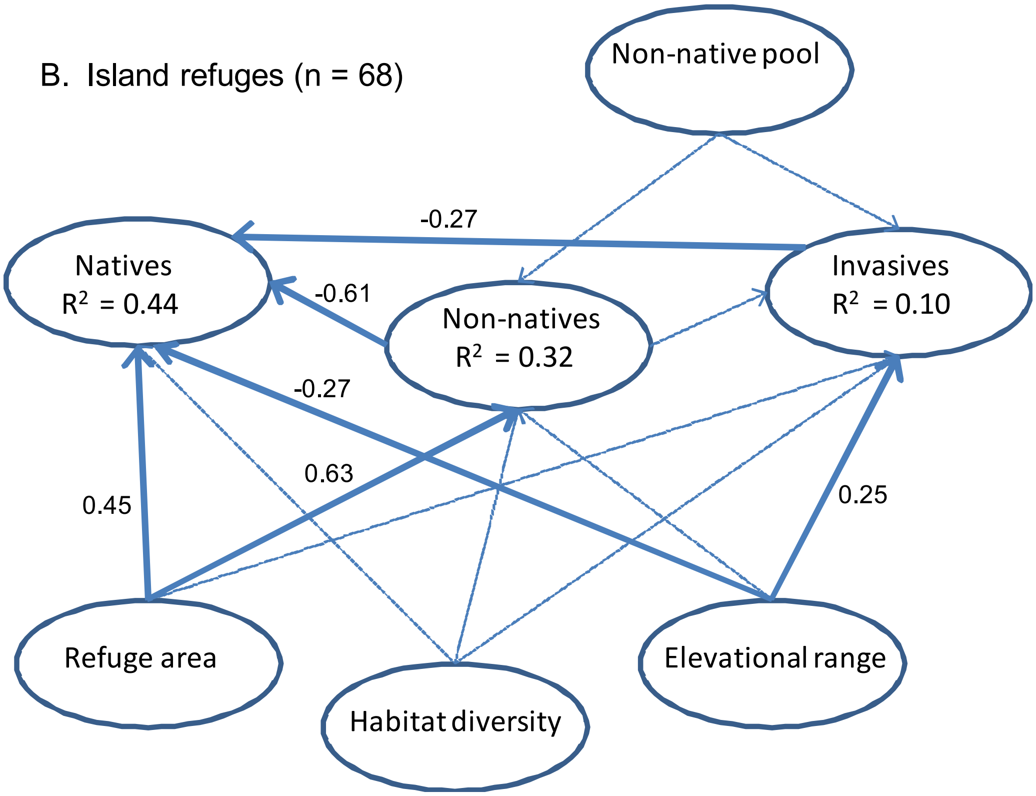
Each NWR is represented by a centroid point within each refuge's total area. Locations are therefore approximate.

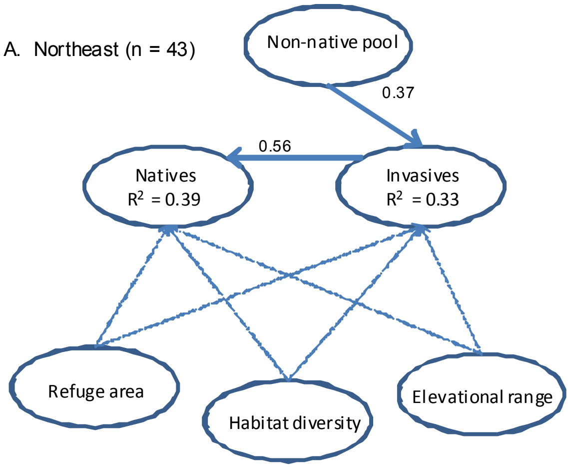

Non-native pool
(nearby counties)
establishment
establishment
Competitive exclusion
Native richness
Invasive richness
exclusion
Non-native richness
exclusion
refuge characteristics influencing plant richness
Refuge area
Elevational range
Habitat diversity

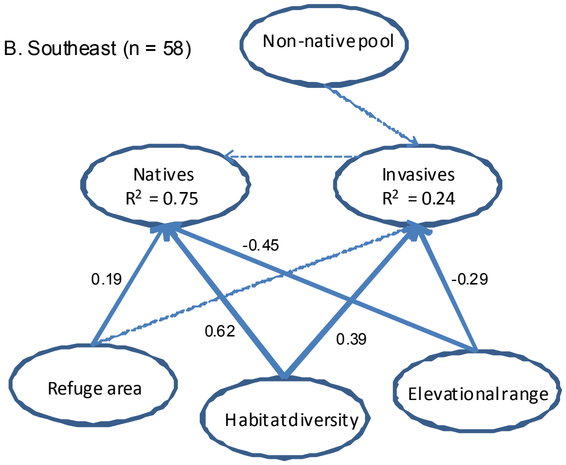
A. Mainland refuges (n = 324)

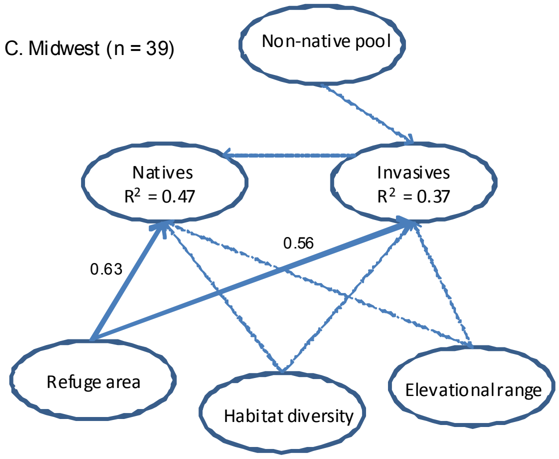


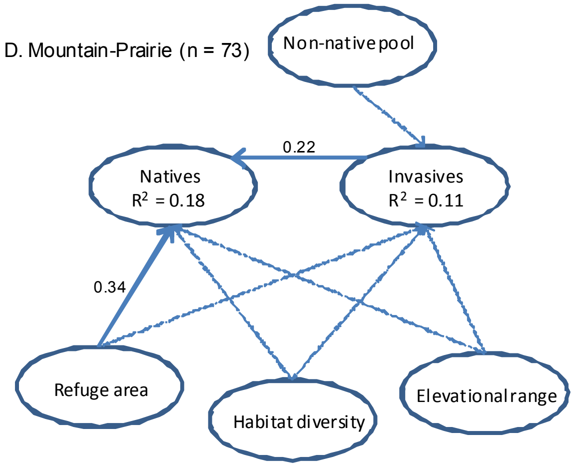
B. Island refuges (n = 68)

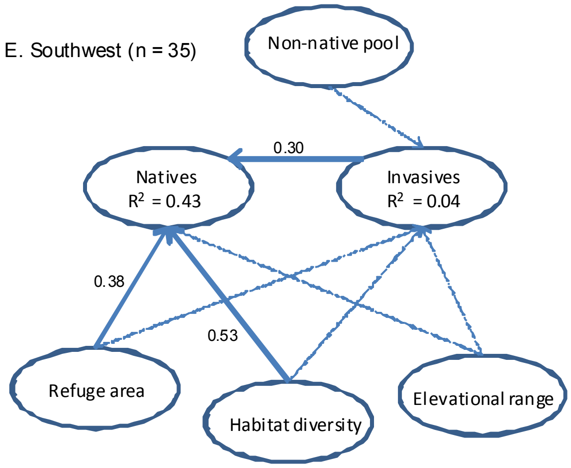


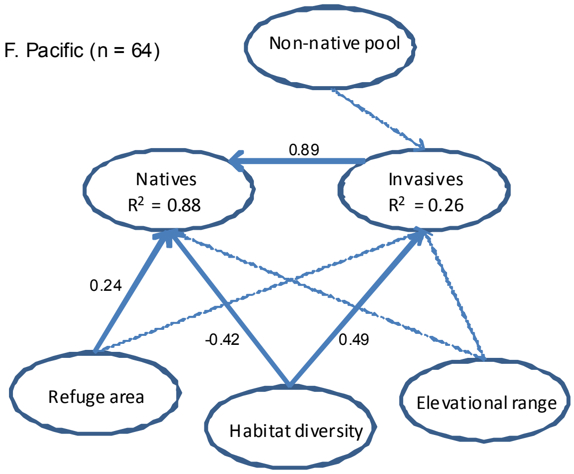

A. Northeast (n = 43)


B. Southeast (n = 58)


C. Midwest (n = 39)


D. Mountain-Prairie (n = 73)


E. Southwest (n = 35)


F. Pacific (n = 64)