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Invasive Plants in Wildlife Refuges: Coordinated Research with Undergraduate Ecology Courses

Karen H. Beard, *Utah State University*

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MARTHA F. HOOPES, DAVID M. MARSH, KAREN H. BEARD, NISSE GOLDBERG, ALBERTO APARICIO, ANNIE ARBUTHNOT, BENJAMIN HIXON, DANELLE LAFLOWER, LUCAS LEE, AMANDA LITTLE, EMILY MOONEY, APRIL PALLETTE, ALISON RAVENSCRAFT, STEPHEN SCHEELE, KYLE STOWE, COLIN SYKES, ROBERT WATSON, AND BLIA YANG

Answering large-scale questions in ecology can involve time-consuming data compilation. 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 US national wildlife refuges. We found that the richness of harmful invasive plants and the richness of native plants were positively correlated in mainland refuges but negatively correlated in island refuges. Nonnative richness and invasive richness were also positively correlated with colonization pressure as indicated by nonnative 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.

Keywords: invasive species, exotic plants, protected areas, conservation, education

Existing data may offer the best insight into many important questions in ecology and conservation biology, but there are various challenges to using existing data effectively. First, 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 reformatting data sets from different sources, sites, and time periods in a consistent manner can be tedious. These difficulties may be particularly pronounced when data sets involve ecological questions over large spatial or temporal scales.

In the present study, we organized networks of students in undergraduate courses to address these challenges and to investigate the geographic patterns of nonnative and invasive plants in sites in the US National Wildlife Refuge System. The students collected and compiled the data for refuges in their own region. From the data that the students compiled, we asked (a) how nonnative and invasive plant species richness is related to native species richness; (b) how the pool of nonnative species from the surrounding area (i.e., colonization pressure) contributes to nonnative and invasive species richness in the refuges; (c) how refuge characteristics such as habitat diversity, refuge area, and elevational range contribute to species richness patterns for native, nonnative, and invasive plants; (d) whether invasion patterns differ between mainland and island refuges; and (e) whether invasion patterns vary among US Fish and Wildlife Service (USFWS) 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 rearrangement can threaten existing communities but can also offer valuable insight into a range of evolutionary and ecological questions. The emerging science of invasion ecology is focused on how nonnative species enter established communities; how they spread through these systems; and how they affect native species, communities, and ecosystems (Lockwood et al. 2013).

One of the most basic questions in invasion ecology is why some areas have more invasive species than do others. Traditionally, ecologists believed that human disturbances were critical to invasion success (e.g., Hobbs and Huenneke

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1992). However, ecologists have begun to realize that protected areas are not immune to invasion and that the strongest impacts on rare species may occur within these areas (Hughes and Convey 2010, Hayward 2011). 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 been focused on nonnative species in general (including nonspreading ornamentals) rather than on species that are specifically designated as *invasive* (e.g., Knops et al. 1999, Stohlgren et al. 1999, Fridley et al. 2007). Focusing on harmful invasives may be more appropriate for questions of spread, impact, and management, because different factors may be important in allowing a species to transition from establishment to spread and impact. A major challenge in studying harmful invasives is that it can be difficult to identify a species as *invasive* rather than simply *nonnative*. Some ecologists define an invasive species as one that both is nonnative and has impacts on native species (e.g., Lockwood et al. 2013); others define an invasive as a nonnative that can establish a self-sustaining population and that can spread independently to new areas (e.g., Blackburn et al. 2011). The management of protected areas requires attention to 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 plants (defined in refuge conservation as plant species that are currently invading and disrupting natural plant communities), these lists present a unique opportunity to compare invasion patterns between nonnatives and invasives.

A comparison of richness among native, nonnative, and invasive species

A common observation from studies of plant invasion is a negative correlation between native and nonnative richness at local scales and a positive correlation at regional scales (Herben et al. 2004, Fridley et al. 2007). The negative correlation at small spatial scales is attributed to *biotic resistance*, defined as increased competition for niche space as native species richness increases (Elton 1958, Simberloff 1981). The positive correlation between native and nonnative species at larger spatial scales is often referred to as *biotic acceptance* (Stohlgren et al. 2006). Biotic acceptance is typically observed when environmental factors affect native and nonnative species richness in a similar manner, so that favorable conditions lead to higher species richness for all groups (Stohlgren et al. 2006).

The importance of colonization pressure

Relationships between native and nonnative 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 nonnative 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 nonnative and invasive species richness in wildlife refuges.

Refuge characteristics and native, nonnative, and invasive species richness

Native and nonnative 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), but area may affect nonnative and invasive plants differently from how they affect native plants. If nonnative plants are recruited from adjacent areas, species richness would be influenced more by refuge perimeter than by refuge area. Habitat diversity should influence richness of all types of plants, and previous studies have suggested that habitat diversity influences biotic acceptance. Elevational range was included as an additional measure of habitat heterogeneity, because 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 1958, Case and Bolger 1991, Poessel et al. 2013). Because islands may be depauperate in native species relative to mainlands, island communities may offer reduced biotic resistance to invasion. Islands may also have smaller populations of native species, which may lead to greater extinction vulnerability (Simberloff 1981). Finally, island refuges may contain an unusual number of rare species, which may lead to impacts of invasion not seen elsewhere. For these reasons, we compared the 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.

Project structure

One or two classes were responsible for compiling data (see table 1 for data variables and sources) from each of the seven USFWS 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 those from the Pacific region. Both the Pacific and Southeast regions contained many refuges, so refuges in these regions were divided between two classes each. The courses incorporated the group project in a variety of ways (table 2), although the student teams all followed the same research protocols (described at the project's Web site, *https://groups.nceas.ucsb.edu/sun*). The basic structure in all of the courses was that each refuge was assigned to two different students as a means of quality control. The students compiled refuge background data and species lists independently, then met to resolve discrepancies; the instructors for each class then reviewed and collated the class data, and the summarized class data were uploaded to the project Web site. 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).

Table 1. Summary of variables incorporated into the analysis and their sources.

Variable	Type	Source
Refuge area	Continuous	Invasive Species Survey (ISS)
Elevational range	Continuous	ISS
Habitat diversity (Simpson's *D*)	Continuous	ISS
Native species richness	Discrete	Comprehensive conservation plans (CCPs), refuge Web sites, refuge personnel
Nonnative species richness	Discrete	CCPs, refuge Web sites, refuge personnel
Invasive species richness	Discrete	CCPs, refuge Web sites, refuge personnel, ISS
Nonnative species pool	Discrete	Biota of North America Program
Mainland or island	Categorical	Refuge Web sites, investigator judgment
Region	Categorical	US Fish and Wildlife Service classifications

Data sources and quality control

We used the US National Wildlife Refuge Invasive Species Survey (hereafter, ISS; *www.nwrinvasives.com*) as a starting point for data compilation. This Web survey was administered by the US Geological Survey in 2002, and refuge personnel were asked to include information about refuge characteristics and the extent of monitoring for nonnative and invasive plants (Tempel et al. 2004). In addition, the survey allowed the managers to upload a list of problem nonnative plant species (which we refer to as *invasives*).

ISS data were usually available for the area, elevational range, and habitat distribution (table 3), 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

Table 2. Project description for each institution and student evaluation.

					Time frame (weeks)				
School	Course	Course type	Course level	Setting	Course time	Dedicated class or lab time	Participation	Grades	Presentations
MHC	Invasions	Seminar	Upper	a, c	9	3.5	f, h, i	g, l, m, n	Group discussion
WCU	Ecology	Lab and lecture	Intermediate	a, b	4	4	k	l, o, p, q	In class
JU	Conservation	Lab and lecture	Upper	a, b, c	10	3	f, g	none	In class
UW–S	Ecology	Lab	Intermediate	b	5	3	f, g	g, l, m	Poster session
MCLA	Ecology	Lab and lecture	Upper	a, b, c	4	4			
USU	Conservation	Lecture	Upper	a, b, c	5	5	e, f, g, i, j	o or p	Group discussion
SFSU	Ecology	Lecture	Intermediate	a, b, c	3	0			
SU	Conservation	Lecture	Upper	d	8	8	e, f, g, h, i, j		In class

Note: The Northeast region was compiled at Mount Holyoke College (MHC). The Southeast was handled at Western Carolina University (WCU) and Jacksonville University (JU). The Great Lakes region was managed at the University of Wisconsin–Stout (UW–S). The Mountain–Prairie region was compiled at the Massachusetts College of Liberal Arts (MCLA). The Southwest region was compiled at Utah State University (USU). Finally, the Pacific region was divided between San Francisco State University (SFSU) and Stanford University (SU). *Setting* describes the type of work: (a) in class, (b) in a lab, (c) as homework, and (d) in an additional period for extra credit. *Time frame* describes the number of weeks the course engaged in the project. Participation credit was given for (e) timeliness with contacting refuges, (f) timeliness with data compilation, (g) data accuracy, (h) cooperation with the other student working on a specific refuge, (i) timeliness with revisions, (j) timeliness with data analysis, and (k) participation in the lab. The graded assignments included (g) data accuracy, (l) individual analysis of data, (m) a lab write-up based on group hypotheses, (n) a lab write-up based on individual hypotheses, (o) a research paper on one central hypothesis, (p) a research paper on an original hypothesis, and (q) an oral presentation. MHC had a 3-hour class period with half of each meeting period devoted to lecture and half devoted to student-run discussion. Five halves and one whole period were devoted to this project, starting on the third class meeting and ending on the last day of class. At UW–S, one student presented her analysis at a research symposium for the whole institution. The course at USU did not have a lab associated with it but a lab space was used for 3 weeks of the course for this project.

from consulting services. Most CCPs are recent (i.e., created in the last 5–10 years), so they represent current information on refuge biota. In some cases, species lists were also posted on refuge Web sites. When CCP or refuge Web site data were not available, the students contacted refuge personnel for species lists. We analyzed data only for refuges from which we could obtain reliable plant lists (figure 1), and lists from any of these sources (CCPs, Web sites, refuge personnel) were given precedence over ISS lists.

We compiled three sets of plant lists for each refuge: natives, nonnatives, and problem invasives. Where native and nonnative species were not separated, we used the Biota of North America Program database (BONAP; *www.bonap.org*) to delineate these. To make nonnative and invasive lists independent (i.e., nonoverlapping), we separated out problem invasive plants from the general list of nonnatives for each refuge. For CCPs, we considered category I nonnatives (those that were currently invading and disrupting natural plant communities) to reflect invasives. Most ISS plant lists echoed these criteria, as did those for invasive species on refuge Web sites. Invasive lists from different sources (e.g., CCP and ISS) were generally consistent with one another, which suggests a consistent definition of invasive species.

To obtain lists of nonnative plants in the vicinity of each refuge (i.e., the nonnative species pool), we used county-specific lists

Table 3. Data availability for refuges in the six regions.

Region	Refuges	Number of native lists	Number of nonnative lists	Number of invasive lists
Northeast	59	26	27	54
Southeast	87	23	19	57
Great Lakes	44	19	17	36
Mountain–Prairie	74	17	15	41
Southwest	36	14	18	32
Pacific and Alaska	95	27	26	55

Note: The total number of refuges providing data is shown, along with the number and percentage of refuges for which lists of native species, nonnative species, and problem invasive species were available.

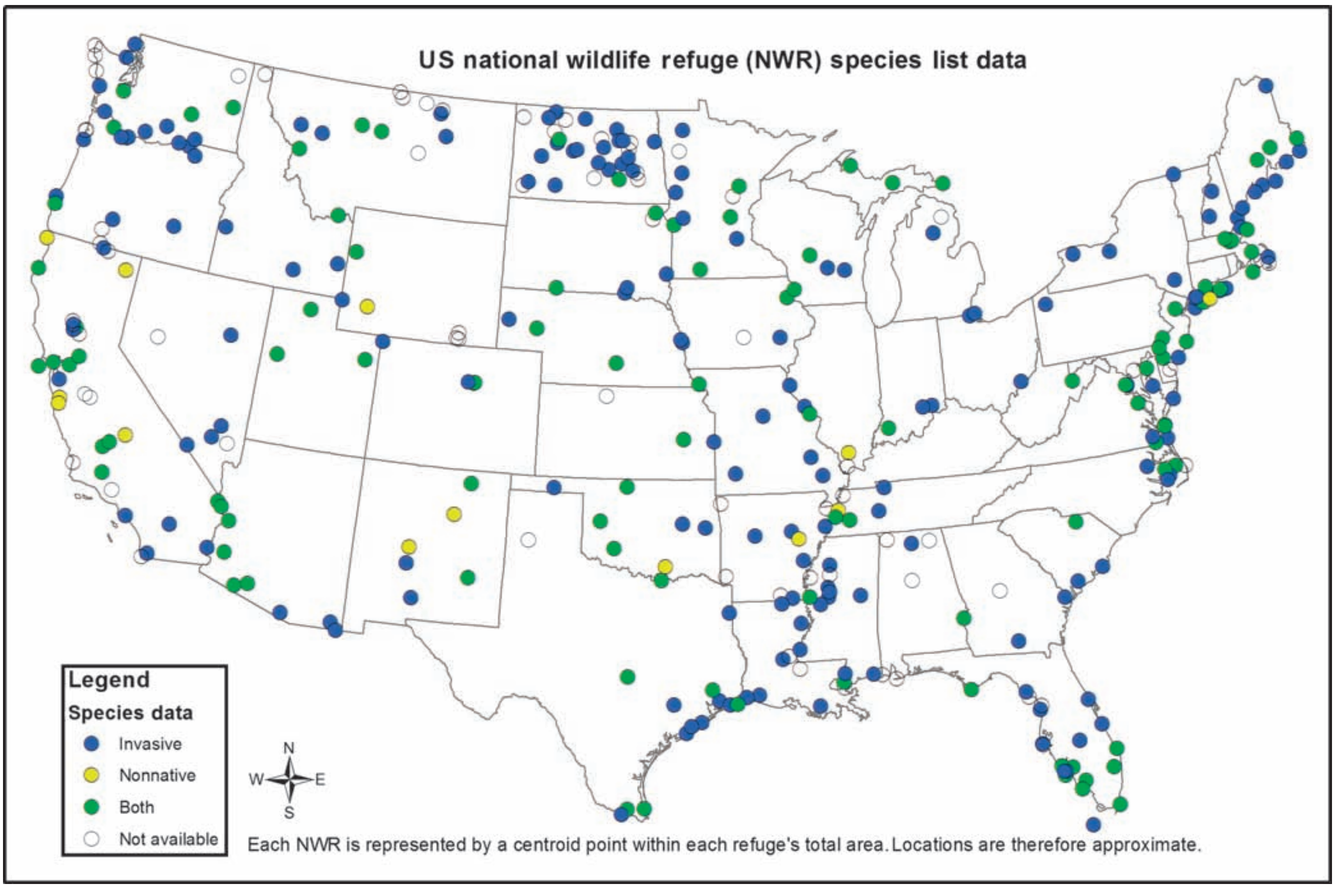

Figure 1. The locations of national wildlife refuges and data availability for each refuge. Those with available lists of invasive species are marked with blue circles, those with lists of nonnative species are marked with yellow circles, and those with lists of both invasives and nonnatives are marked with green circles.

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, the Florida Keys), and islands within large lakes.

The plant data varied in quality. Some lists were based on anecdotal observation, whereas others were based on extensive surveys. Therefore, 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. All of the students used the same protocol to calculate the scores, and all of the classes practiced using the same example refuges. Discrepancies in scores for the two students assigned to a refuge were helpful for indicating that the students had found different data sources. These scores successfully differentiated high-quality data from low-quality data. For example, refuges having only ISS invasive species data and no monitoring programs typically had quality scores of 5 or lower, whereas refuges with CCP data based on systematic plant surveys usually had quality scores between 15 and 20. We used quality scores to weight the data in our analyses in the manner described below.

Data analysis

We analyzed patterns of nonnative and invasive richness among USFWS regions, using general linear models. We modeled plant richness with a Poisson distribution when a goodness-of-fit test failed to detect overdispersion and with a negative binomial distribution when overdispersion was present. To quantify the relationships among refuge characteristics; regional species pools; and native, nonnative, and invasive species richness, we used structural equation modeling (SEM; Bollen 1989, Grace 2006). SEM allows one to simultaneously analyze relationships among multiple variables within a system—in this case, species richness of natives, nonnatives, and invasives. Our model (figure 2) was chosen a priori to represent the expected relationships among the variables on the basis of previous large-scale analyses of patterns of plant invasion (Stohlgren et al. 2003, Harrison et al. 2006). Refuge area, habitat diversity (i.e., the Simpson's index calculated from the habitat distribution data on the ISS), and elevational range were expected to influence each of the three classes of plants. The regional pool of nonnatives was expected to influence both nonnatives and problem invasives. The relationship between nonnatives or invasives and natives was included to represent biotic resistance (a negative correlation) or biotic acceptance (a positive correlation). Islands and mainlands were analyzed separately to permit comparisons between them 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 2) had one degree

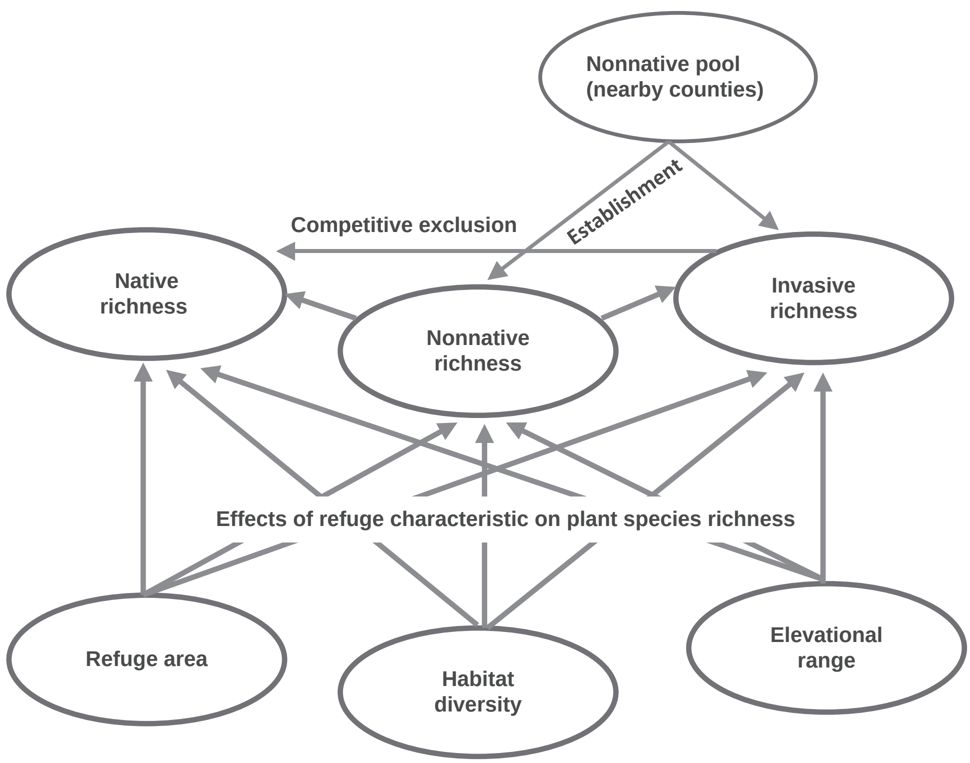

Figure 2. Structural equation model used to analyze the relationships among plant communities and refuge characteristics in wildlife refuges. Native, nonnative, and invasive plant communities potentially influence each other, and each is in turn influenced by similar sets of refuge characteristics.

of freedom, which allowed a chi-squared test for overall model fit (Grace 2006). All models shown in the results had adequate fit ($p > .05$), except where it is specifically noted otherwise. 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 multigroup analyses to test for significant differences between the model coefficients for mainland and island refuges and among those for USFWS regions. For these analyses, the fit of a model that used fixed, identical parameters across groups was compared with that of a model that allowed group parameters to vary.

Student involvement and assessment

Students in all classes were involved in the data collection and compilation aspects of the project. In addition, a subset of students (one or two per institution) participated in a workshop at the National Center for Ecological Analysis and Synthesis (NCEAS) to synthesize the data across classes, to analyze the resulting data set, and to interpret the results. The highly dispersed and collaborative nature of this project made it difficult to allow the students autonomy with respect to research questions and methodology. Nonetheless, each course offered opportunities for the students to explore other aspects of the scientific process, from hypothesis development to data analysis and presentation (table 2). These opportunities varied with the type of course, the course size, and the expertise of the professors involved in the project, but the most common approach was to have students write a formal paper or lab report based on an analysis of the data from their region. Similarly, approaches to presenting the background material for the project, grading student performance, and assessing student learning varied by course (table 2).

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 nonnative species, and 278 lists of invasive species. The plant data varied in availability across regions (table 3), with the greatest data availability in the Northeast and Southwest regions and the lowest availability in the Southeast and Mountain–Prairie regions (table 3). The apparent low data availability in the Mountain–Prairie region was due to a large number of easement refuges to which the USFWS has no access. When these refuges were removed, the Mountain–Prairie region had data availability similar to that of the other regions ($\chi^2(5) = 7.4$, $p = .19$). The data quality scores tended to track data availability. The quality scores were significantly lower in the Southeast region (general linear model, $b = –2.65$, $p = .02$) and also in the Mountain–Prairie region when the easement refuges were included ($b = –2.67$, $p = .02$).

Overall, nonnative and invasive richness varied significantly across regions (likelihood ratio, LR(5) = 34.6, $p < .001$, and LR(5) = 15.8, $p < .01$, respectively). The nonnative richness was highest in the Pacific region (excluding Alaska, $x = 81.23$, standard error (SE) = 13.5) and lowest in the Southwest region ($x = 29.5$, SE = 6.4). Invasive richness was highest in the Northeast ($x = 11.83$, SE = 1.56) and Pacific ($x = 11.19$, SE = 1.10) regions and lowest in the Southwest ($x = 5.81$, SE = 0.76) and Mountain–Prairie ($x = 6.78$, SE = 0.88) regions.

Associations among native, nonnative, invasive richness, and the regional nonnative pool

For mainland refuges (figure 3a), the proportion of variation in plant richness explained by the SEM was moderate for natives ($R^2 = .30$) and invasives ($R^2 = .23$) but low for nonnatives ($R^2 = .11$). Native richness and nonnative richness in mainland refuges were positively correlated (Pearson's correlation coefficient, $r = .33$). Nonnative and invasive richness were both positively correlated with the richness of the nonnative species pool in areas surrounding each refuge, although these coefficients were low ($r = .15$ and $r = .27$, respectively). In addition, invasive richness was correlated with nonnative richness ($r = .26$).

Refuge characteristics

Refuge characteristics influenced all three classes of plants (figure 3). Native richness was positively correlated with refuge area ($r = .33$) and elevational range ($r = .27$). Nonnative richness was positively correlated with habitat diversity ($r = .12$) and negatively correlated with refuge area ($r = –.15$). Invasive plants were also positively correlated with habitat diversity ($r = .17$) and negatively correlated with elevational range ($r = –.14$).

Mainland versus island refuges

The patterns of plant invasion in island refuges differed substantially from those in mainland refuges ($\chi^2(14) = 35.4$, $p = .002$; figure 3b). Most notably, on islands, the correlations between nonnatives and natives and between invasives and natives were negative ($r = –.61$ and $r = –.27$, respectively). In addition, the size of the nonnative species pools were not significant predictors of nonnative and invasive richness within refuges on islands (they were significant for mainlands; figure 3a). Finally, nonnative richness was much more closely correlated with refuge area ($r = .63$) on islands than on mainlands ($r = –.15$).

Regional variation in patterns of invasion

For most individual regions, it was only possible to fit a simplified SEM without the nonnative plant class (i.e., only natives and invasives). Using this simplified model, the regions differed significantly in patterns of invasion in mainland refuges ($\chi^2(5) = 14.2$, $p = .014$). Region-specific parameters should be interpreted with caution; the model was a poor fit for the Midwest region ($\chi^2(1) = 12.8$, $p < .001$), and the regional sample sizes were low. Nevertheless, pronounced variation in the regional results was apparent (figure 4a–4f). Area effects were strongest in the Midwest

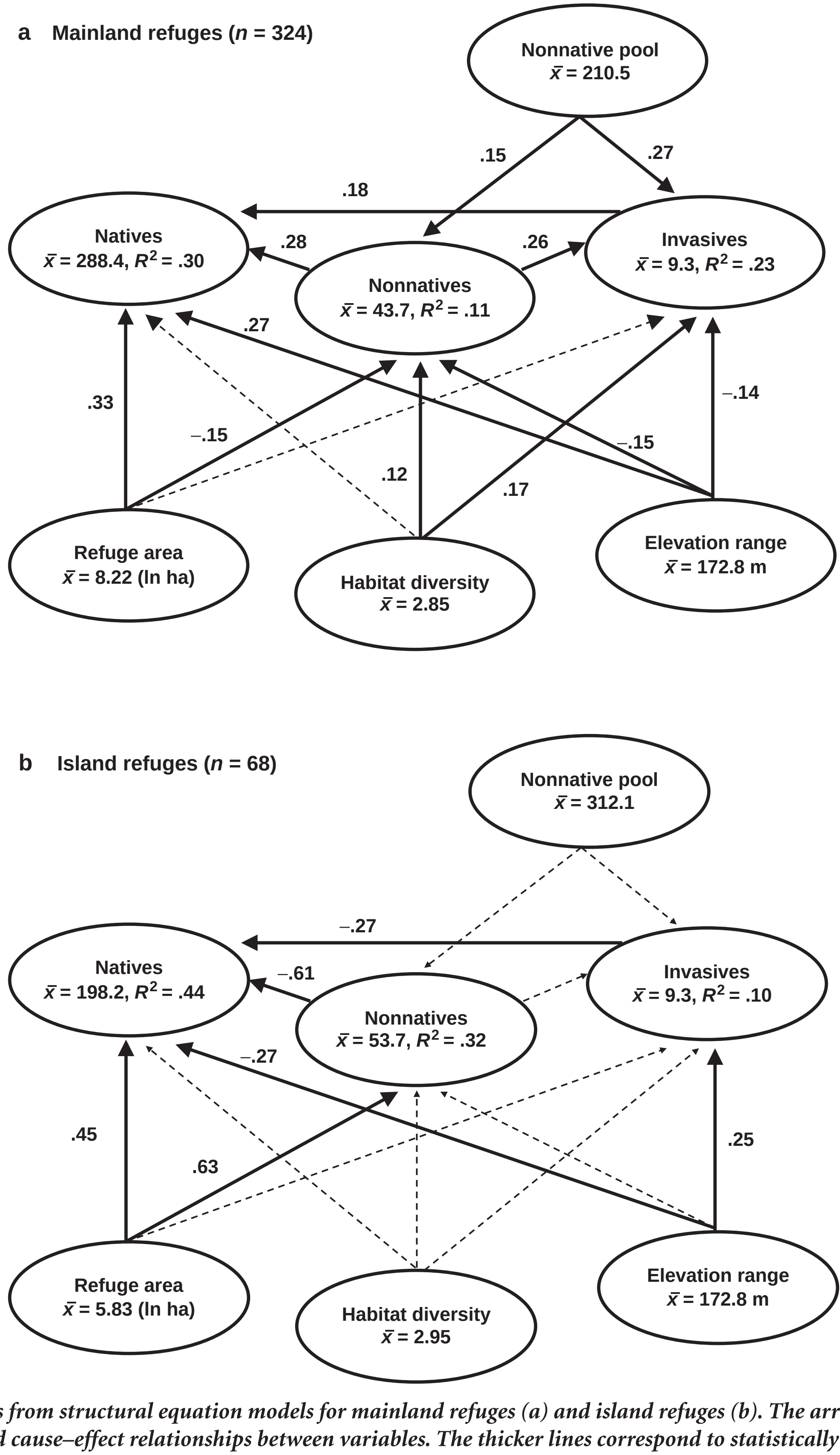

Figure 3. Results from structural equation models for mainland refuges (a) and island refuges (b). The arrows indicate the hypothesized cause–effect relationships between variables. The thicker lines correspond to statistically significant relationships ($p < .05$), and path coefficients from the structural equation model, which are analogous to Pearson correlation coefficients corrected for direct and indirect relationships to other variables, are shown for these parameters. Means are also shown for all variables included in the models. Abbreviations: ln ha, natural log of the value in hectares; m, meters; $\bar{x}$, the mean value.

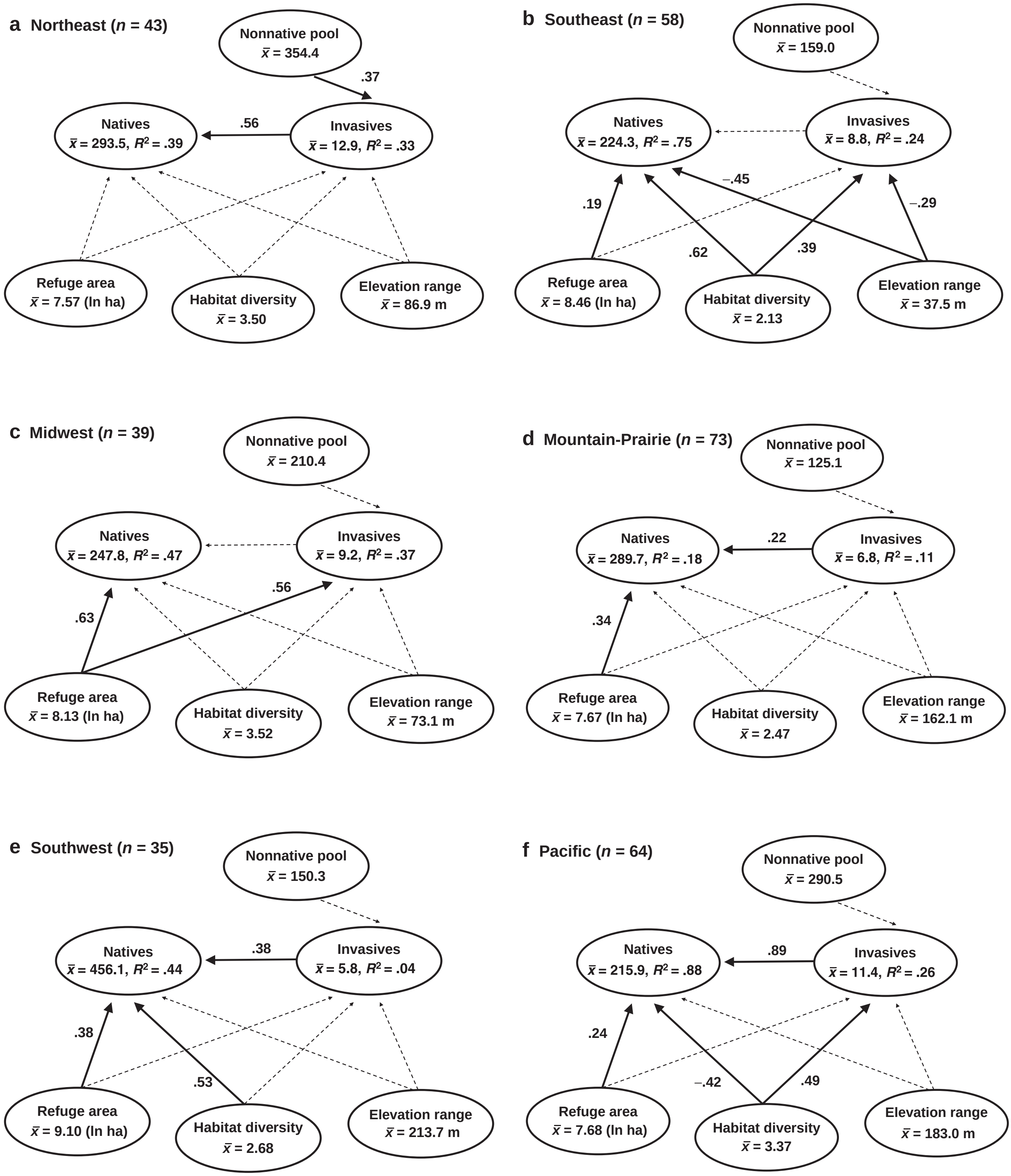

Figure 4. Results from structural equation models for each US Fish and Wildlife Service region. Because the sample sizes were small within each region, the models included native and harmful invasive species but did not include nonnative species. The arrows indicate the hypothesized cause–effect relationships between variables. The thicker lines correspond to statistically significant relationships (at p *< .05; path coefficients [see figure 3] are shown for these parameters). Means are also shown for all variables included in the models. Abbreviations: ln ha, natural log of the value in hectares; m, meters;* x̄, *the mean value.*

region. Habitat diversity was most predictive of invasive richness in the Southeast, Southwest, and Pacific regions. In the refuges located in the Northeast, the regional species pool was the most important predictor of invasive species. The correlations between native richness and invasive richness were positive in all regions, although the strength of this correlation was variable.

Student experience and assessment

The student responses to the project were generally positive (box 1). Most of the students agreed or strongly agreed that the project improved their understanding of invasion biology, conservation policy, and data analysis. The students strongly agreed that the project increased their appreciation of the value of good data. Most of the students also said that they felt that they were contributing to an important research project and that the activity was an interesting course experience. The most common positive comment was that the students enjoyed working on a real research project rather than on a scripted assignment. The most common negative comment concerned frustration with finding (or not finding) data for the refuges. In particular, many of the students felt considerable frustration that they could work quite hard in searching for plant data but not have anything to show for it (box 1). The students who participated in the data synthesis and analysis workshop at NCEAS had consistently more positive responses than did the general pool of participating students (box 2).

Project structure and pedagogical insights

Our framework for collaboration between undergraduate classes and federal agencies can be compared with 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 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. It was clear from the students' self-evaluations that a desire to get a good grade was very important to most of them. This approach can also be applied to projects that involve some tedium. Whereas enlisting

Box 1. Summary of student responses to project evaluation.

The response rate was low (45 respondents, or approximately 38%), although we did get respondents from all eight classes. The student responses to major project objectives are shown below. The open response comments from the students were also highly informative (see the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.8.7*). The 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 we're '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."

The negative comments tended to be focused on the frustrations of not being able to find data for assigned refuges. Some negative comments were also focused on the Web site 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 [Biota of North America Program database] exotic lists and with identifying what data from Web sites 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."

Box 2. Summary of student responses to the workshop meeting.

All of the participating students (11) responded (see table 4 and the supplemental material, available online at *http://dx.doi.org/10.1525/bio.2013.63.8.7*, for the complete evaluations). In terms of educational benefits, positive comments included the following:

> "It was really awesome to see the thought processes of all the people working together. It also motivated me to take a lot of statistics to learn how to create models."

> "I particularly enjoyed being introduced to varying statistical models (i.e., path analysis, SEM [structural equation modeling], regression) and R programming language."

> "I really felt like I was part of something important."

> "The conference enhanced my interest in data-based research. Unfortunately, at the undergraduate level, we have not been exposed to data-based research. I learned more than I can say. Thank you."

> "It opened my eyes to large-scale research and how tricky it is to work with large data sets."

> "I got to collaborate on a large, multiuniversity project. That was cool and it felt really exciting."

> "Doing research is cool. I'm definitely thinking about grad school now."

Negative responses were few, but some of the students felt that they were falling behind at the meeting or had suggestions for improving the meeting structure:

> "I wish we were more in tune with R. I… feel like only professors know the material and we were left in the dark."

> "It would have been nice to do more actual data analysis and less time cleaning up data."

> "Maybe if we had spent more time analyzing the data and less time playing catch-up with the data it would have been a little more valuable."

> "Have a solid agenda for the meeting with extra time allotted for things that come up that are unexpected. Have a goals sheet for the meeting because, for me, the goals of the meeting were a little fuzzy."

Table 4. Percentage of respondents at levels of agreement with descriptions of their educational experience.

Statement	Strongly agree	Agree	Neutral	Disagree	Strongly disagree
The meeting enhanced my understanding of data management.	**63.6**	36.4	0	0	0
The meeting enhanced my understanding of statistical analysis.	27.3	**54.5**	18.2	0	0
The meeting increased my sense of the importance of collaboration in scientific research.	**90.9**	9.1	0	0	0
I consider the meeting to have been a valuable educational experience.	**81.8**	18.2	0	0	0
The meeting made it more likely that I will participate in scientific research in the future.	**45.5**	36.4	18.2	0	0

Note: The majority response is marked in bold.

nonscientists 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.

There were also pedagogical advantages to our project structure. Because the project was centrally planned, the students were able to compile a much larger data set than would otherwise have been available for individual classes to analyze. Having a predefined project that fit neatly within a 4–6 week course unit offered an opportunity for the students to participate in important original research in a traditional course structure. In addition, the courses without a lab component were able to contribute to research that addressed large-scale questions in ecology and conservation biology, thereby enhancing the overlap between the research project and the conceptual material covered in the participating classes. We believe that a wide range of projects involving large-scale data compilation could be carried out through this sort of collaboration, thereby benefiting students, federal and state agencies, and the scientific community.

The highly collaborative and dispersed structure of the project was essential to its successful aspects, but this structure also created substantial challenges. First, because methodology needed to be consistent, it was difficult to offer students a central role in determining the project methodology or the primary research questions. Nevertheless, some courses did require the students to identify or develop an additional research question or hypothesis based on the data set, and some of these student hypotheses informed our final analysis. We believe that formulating and testing new questions while working on an established project is potentially good practice for graduate work in collaborative research labs. Unfortunately, our survey of student responses did not allow us to determine whether these additional pieces improved the student learning experience.

This assessment difficulty highlights a second challenge of the project: assigning grades and assessing learning. Credit for participation may have mitigated student frustration with finding poor-quality data (or no data at all), but it also seemed to create problems with variability in student effort. The students appeared most comfortable with grades based on traditional assignments (e.g., lab reports in lab classes, papers in lecture classes). At Mount Holyoke, for example, which had the only course specifically focused on invasion ecology, surveys of student satisfaction indicated that appreciation for the project improved after data analysis and ended very high (14 of 16 students were extremely satisfied, although the other 2 were extremely dissatisfied). It appeared that more-advanced students in more specific courses experienced less frustration and found the project more rewarding, although this cannot be rigorously demonstrated across the classes. Although we wish that our final survey had allowed a better determination of how course characteristics affected the student experience of the project, our sample size (i.e., eight courses) was too small to allow any statistical insight. Coordinated research projects currently under way are attempting to better gauge the optimal approach for incorporating a collaborative research experience into an undergraduate biology course.

Finally, anyone who has tried to include investigative learning in a course knows that the most challenging aspects are sometimes also the most rewarding. The aspect of this course that frustrated the students the most (i.e., obtaining high-quality data) contributed to the greatest course success (student perception of increased understanding of data quality; box 1). Our quality scores may have contributed to this benefit by encouraging student discussion about data sources and demonstrating the importance of high-quality data for synthetic projects. Nevertheless, one might argue that similar collaborative projects could be made less frustrating for students by basing them on well-defined data sets for which data availability is not a problem.

Invasion insights

Our model allowed us to identify some differences in the way native, nonnative, and invasive species richness responded to three refuge characteristics: refuge area, habitat diversity, and elevational range. For example, there was a positive correlation between native species richness and refuge area and no correlation or a negative correlation between invasive or nonnative species richness and refuge area. One possible explanation for this result is that edge effects and, consequently, colonization pressure by invasives decrease with refuge area. Another potential explanation is that areas with high invasive richness tend to be highly populated with small refuges.

We expected that habitat diversity would be correlated with species richness for all three classes of plants (Davies et al. 2005). Instead, we found that nonnative and invasive species richness was positively correlated with habitat diversity, whereas native species richness had no overall relationship with habitat diversity. One explanation for this difference is that disturbed or humanmade habitats may increase nonnative and invasive richness but have little effect on native richness (Didham et al. 2005, MacDougall and Turkington 2005).

Interestingly, elevational diversity was positively correlated with native diversity but negatively correlated with both nonnative and invasive species richness. This difference may reflect the lack of time for evolutionary diversification in newly arrived species (i.e., nonnative and invasive species). It may also reflect colonization pressure; that is, introduced species may not include nonnatives and invasives that can survive at all elevational ranges. In any case, this finding suggests that aspects of habitat diversity may be exploited differently by native and nonnative species.

We found a positive correlation between native and nonnative plant species richness in mainland refuges, consistent with the results of previous studies in nonprotected 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 nonnative species pool was correlated with the richness of both nonnative and invasive species in mainland refuges. Although it is intuitive, this result is novel and offers support for the role of colonization pressure in invasion patterns. Interestingly, there was no detectable correlation between the nonnative species pool and nonnative or invasive richness on islands. This may be the case because nonnative and 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 the correlation between native and nonnative or invasive richness. This correlation was positive for mainland refuges but negative for island refuges. This difference may be due to depauperate island fauna's being more susceptible to extinction in the presence of invasive species. Although in other studies of plant invasion on islands no evidence was found for such extinctions (e.g., Sax et al. 2002, Sax and Gaines 2008, Long et al. 2009), Pyšek and colleagues (2012) concluded in a recent review that invasive plants were far more likely to have negative impacts on native species on islands than on mainlands.

The regions differed considerably in the factors that were correlated with invasive species richness. Invasive species richness was strongly correlated with native species richness for refuges in the Northeast and the Pacific regions but not in other regions. Refuge area was an important predictor of native and invasive species richness in the Midwest but not in the Northeast. Similarly, habitat diversity was an important predictor in some (e.g., Southeast, Northeast) regions but not in others (e.g., Mountain–Prairie, Midwest). Because of the small sample sizes within the 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.

There were several important limitations to our study. First, the data were incomplete for a large number of refuges, and lists of invasives were occasionally based on anecdotal observations. Although we used weighting to deal with data-quality issues, weighting cannot mitigate missing data if there was a pattern or trend to the gaps. Second, our methodology—spreading data compilation among 120 students in eight 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. Third, we did not account for land-use history. Some refuges contained multiple crop species, and others contained substantial numbers of noninvasive ornamentals, which probably reflects prior human 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 nonnative plants compared with that for invasive plants.

Conclusions

Despite the challenges of compiling invasive plant data across multiple classes and institutions, our project led to an apparent increase in student understanding of ecology, conservation, and invasive species management and a strong increase in student appreciation for high-quality data. The project also yielded several clear patterns with implications for invasive species planning in protected areas. First, we found that mainland refuges with higher native diversity are more likely to be invaded. 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 nonnatives in the county or counties surrounding a refuge is moderately informative regarding how many nonnative and invasive species are likely to colonize these refuges. In terms of regional differences, our results suggest that predictors of invasion may vary considerably from one region to the next, with patterns in different regions potentially canceling each other out when viewed at the continental scale. When planning for invasive species management, data from nearby refuges should therefore be prioritized over information from continental-scale analyses. Similarly, our results suggest that refuges on islands may not behave as their mainland counterparts do when it comes to broadscale patterns of invasion. Finally, our results highlight significant gaps remaining in invasive species data from protected areas. Filling these gaps will require increased monitoring of nonnative establishment and spread in areas that are important for habitat and species conservation.

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Martha F. Hoopes is an associate professor of biology at and Annie Arbuthnot and Danelle Laflower are recent graduates of Mount Holyoke College, in South Hadley, Massachusetts. David M. Marsh (marshd@wlu.edu) is a professor of biology at Washington and Lee University, in Lexington, Virginia. Karen H. Beard is an associate professor of biology at and Robert Watson is a recent graduate of Utah State University, in Logan. Nisse Goldberg is an assistant professor of biology at and Benjamin Hixon is a recent graduate of Jacksonville University, in Jacksonville, Florida. Alberto Aparicio is a recent graduate of San Francisco State University, in San Francisco, California. Lucas Lee and Blia Yang are recent graduates of and Amanda Little is an associate professor of biology at the University of Wisconsin–Stout. Emily Mooney is an assistant professor of biology at Massachusetts College of Liberal Arts, in North Adams, from which Colin Sykes is a recent graduate. April Pallette and Kyle Stowe are graduate students at Western Carolina University, in Cullowhee, North Carolina. Alison Ravenscraft is a graduate student at and Stephen Scheele is a recent graduate of Stanford University, in Stanford, California.