Predicting invasive potential of smooth crotalaria (*Crotalaria pallida*) in Brazilian national parks based on African records

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Alien weed species rank among the most important threats to conservation of biodiversity, making understanding the extent to which protected natural areas are vulnerable to invasion by weeds pivotal in long-term maintenance and conservation of biodiversity. We investigated the potential geographic range of the invasive paleotropical weed, smooth crotalaria, in protected natural areas across Brazil. The ecological niche dimensions of smooth crotalaria in Africa (its putative original distribution) were modeled using a genetic algorithm. Models for the native range and their projections to South America showed good predictive ability when challenged with independent occurrence data. All Brazilian protected natural areas were predicted as highly vulnerable to invasion by this species. However, smooth crotalaria appears more likely to occur in open (savanna-like vegetation, such as cerrado and pantanal) and highly fragmented (Atlantic forest) areas than in extensive closed forests (Amazon). Management suggestions and research priorities are outlined based on these results.

Nomenclature: smooth crotalaria, *Crotalaria pallida* Ait. CVTMU.

Key words: Alien species, conservation policies, conservation units, ecological niche models, geographic distribution.

Several processes threaten biodiversity in protected natural areas, including hunting, fire, human intrusion, and invasion by alien species (Bhatt et al. 1994; Fensham 1996; Graaff 1986; Kumar and Rohatgi 1999; Mauchamp et al. 1998; Muniappan et al. 1996; Russel and Roberts 1996). Weed invasion in particular can alter the composition, structure, and organization of natural communities (Janzen 1983) by interfering with succession (Rouw 1991), by excluding other plants through competition (D'Antonio and Vitousek 1992; Lodge 1993), or by interfering with population dynamics of other species through indirect and often unpredictable effects (Leslie and Spotila 2001, Rand and Louda 2004). In addition to impacts on natural habitats, alien species also cause severe economic losses (Pimentel et al. 2000; USOTA 1993).

In Brazil, several alien weeds, mostly paleotropical in origin, have spread over large areas, particularly at forest edges and in gaps (Lorenzi 2000). Protection of natural areas from such weed invasions is pivotal to biodiversity conservation. This role is particularly true given that Brazilian wild lands have been destroyed at high rates for more than 3 centuries: some ecosystems (e.g., Atlantic Forest) are now reduced to small forest fragments, largely lacking legal protection (Fonseca 1985; Viana et al. 1997), whereas others (e.g., Amazon forest, savannah-like cerrado), are now being destroyed at elevated rates by the increasing demands of human populations. This elevated rate of conversion to human uses suggests that, within a few decades, protected natural areas in Brazil will constitute the great majority of remaining pristine natural habitats. Hence, the integrity of reserves with respect to the potential for weed invasion is central in biodiversity conservation in Brazil.

Smooth crotalaria is a perennial shrub native to the paleotropics, most likely Africa. This species has invaded several regions around the world (Polhill 1982) and is now considered to rank among the worst weeds, occurring in pastures, roadsides, old fields, and forest edges (Lorenzi 2000). The plant has been recorded in some federal nature reserves in Brazil (Vieira and Pessoa 2001). Although no studies have focused on its effects on natural systems, smooth crotalaria and related species may affect the ecology of invaded areas in several ways: attracting ants to its extrafloral nectaries (Guimarães et al. 2006), intoxicating animals (Diaz et al. 2003), hosting fungi (USDA 2004), enhancing the nitrogen levels in soil (Ohdan and Daimon 1998), allelopathy (Ohdan et al. 1995), and changing nematode communities (Wang et al. 2004).

We used ecological niche modeling (ENM), in which models were developed with a genetic algorithm (Stockwell 1999; Stockwell and Noble 1992; Stockwell and Peters 1999), to assess vulnerability of Brazilian landscapes and protected natural areas, in particular, to invasion by smooth crotalaria. We used the records of smooth crotalaria in Africa (probable natural occurrence) to model its ecological niche
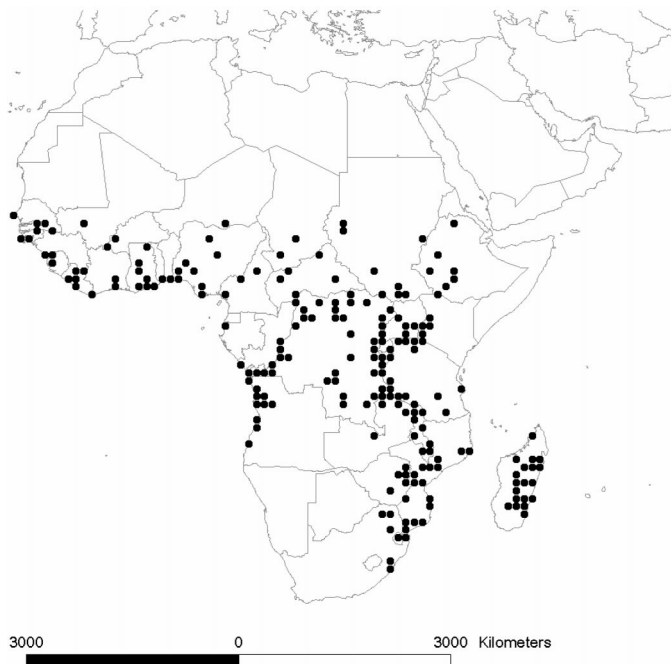
FIGURE 1. Occurrence points for smooth crotalaria in Africa used to develop models.

and projected those data to South America. Previous work has focused on the success of ENM in predicting the geographic potential of species' invasions (Higgins et al. 1999; Holt and Boose 2002; Peterson and Vieglais 2001; Zalba et al. 2000). Beyond invasive species applications, the predictive abilities of ENM have been tested under diverse circumstances (Anderson et al. 2002a, 2002b; Peterson 2001; Peterson and Cohoon 1999; Peterson et al. 2000, 2002, 2003a; Stockwell and Peterson 2002). Specifically, we sought to determine how many protected natural areas in Brazil are susceptible to smooth crotalaria invasion and whether this invasive potential varies among ecosystems.

Materials and Methods

The data used as input to the African niche model were obtained from online, free-access data sets (1° resolution) compiled by the Centre for Ecology, Law and Policy (CELP) Mapping Plant Species Diversity project.[1] WORLDMAP[2] was used for data management. Data regarding the species' South American distribution were obtained from the herbarium of the Universidade Estadual de Campinas (UEC-UNICAMP)[3] and the W[3]TROPICOS database at the Missouri Botanical Garden.[4] Additional records for the species' South American distribution were drawn from the literature, personal communications with ecologists and plant taxonomists, and queries to other Brazilian herbaria. The complete data set used in this study (Figure 1) is available from the corresponding author upon request.

Ecological niches were modeled using the Genetic Algorithm for Rule Set Production[5] (GARP; Stockwell 1999; Stockwell and Noble 1992; Stockwell and Peters 1999). In general, the procedure focuses on modeling ecological niches (the conjunction of ecological conditions within which a species is able to maintain populations without immigration (Grinnell 1917). Specifically, GARP relates ecological char-

acteristics of known occurrence points to those of points sampled randomly from the rest of the study region, seeking to develop decision rules that best summarize factors associated with the species' presence. Occurrence points are divided into training and test data sets—50% of the data points are set aside for a completely independent test of model quality (extrinsic test data), 25% are for developing models (training data), and 25% are used for tests of model quality internal to GARP (intrinsic test data). Because these subsamples are made independently and randomly for each model run, GARP models take advantage of much of the information in the input data set. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection: a method is chosen from a set of possibilities (logistic regression, bioclimatic rules), applied to the training data, and a rule is developed or evolved. Predictive accuracy is then evaluated based on 1,250 points resampled from the test data and 1,250 points sampled randomly from the study region as a whole. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, crossing over, etc. The change in predictive accuracy for one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model and the algorithm, either to 1,000 iterations or until convergence.

We used 15 digital raster data (hereafter "coverages") summarizing elevation, slope, aspect, flow accumulation (upstream area contributing to water flow), flow direction (modeled direction of water flow), topographic index (tendency to pool water; all from the U.S. Geological Survey Hydro-1K data set; USGS 2001), and aspects of climate including mean annual diurnal temperature range, mean annual number of frost days, mean annual precipitation, mean annual solar radiation, mean annual maximum temperature, mean annual minimum annual temperature, mean annual temperature, mean annual water vapor pressure, and mean annual number of wet days (1961 to 1990; from the Intergovernmental Panel on Climate Change; IPCC 2001). Although soil characteristics are important to understanding occurrences of these plants, we choose not to use then because the categorical nature of the soils data available can cause problems in ENM development. We used the resolution of biological data to set the resolution for environmental layers used in modeling at 10 km (Chapman et al. 2005). We used data from Africa (native range) to model the potential distribution of smooth crotalaria and projected it onto South American landscapes where we validated the prediction using independent occurrence data.

We used a jackknife manipulation, in which each coverage was omitted sequentially, as a preliminary exploration of positive and negative effects of inclusion of particular coverages on model quality (Peterson and Cohoon 1999). We calculated the Pearson product-moment correlation coefficients between binary variables describing inclusion and exclusion of each coverage and omission error. Although this coefficient assumes normality of variables, we used it as a preliminary exploratory tool; improved approaches are under investigation. Those coverages for which correlations were high (i.e., inclusion of the coverage in analyses associated with increased omission error), on the order 0.05, of were omitted from further analysis. The overall jackknife procedure was repeated until all remaining coverages were

TABLE 1. Invasive potential by the alien weed, smooth crotalaria, in Brazilian national parks. Percentage of conservation units for each class of threat from smooth crotalaria is shown. Conservation units are divided by ecoregions, and the number of units that were evaluated are in parentheses.

Ecoregions	Class of threat				
	Critically	High	Medium	Low	None
	%				
Coastal parks (9)	33.3	22.2	44.5	0.0	0.0
Amazon forest (32)	40.6	15.6	43.8	0.0	0.0
Campos sulinos (3)	66.7	0.0	33.3	0.0	0.0
Atlantic forest (47)	85.1	12.8	2.1	0.0	0.0
Caatinga (16)	87.4	6.3	6.3	0.0	0.0
Cerrado (26)	96.2	3.8	0.0	0.0	0.0
Pantanal (2)	100	0.0	0.0	0.0	0.0
Total (136)	73.3	11.1	15.6	0.0	0.0

either unassociated or negatively associated with omission error ($r < 0.05$).

Finally, to consider the model-to-model variation that GARP's random-walk nature creates, we filtered numerous replicate models based on error components (omission and commission; Anderson et al. 2003). Using the 'best subsets' function of DesktopGARP, we identified the best 50 models out of 2,000 initial models. These 50 models were summed to produce a final picture of model agreement in predicting potential for presence in each pixel across Africa. We found that using this greater number of models offered a better view of model concordance. In this map, pixels had values ranging from zero (no model predicted potential presence) to 50 (all models predict potential presence). These 50 models were projected to other regions to assess potential suitability in nonnative areas.

Model quality was tested using the extrinsic testing data—the 50% of the occurrence data set aside before modeling and with the invaded range occurrence data. A chi-square test was used to compare observed success in predicting distributions of test points with that expected under a random model of no association between prediction and test points (the proportional area predicted to be present provided an estimate of the occurrence points that would be correctly predicted if the prediction were random with respect to the distribution of the test points; Peterson et al. 2003a).

We restricted our analysis of vulnerability to federal-level protected natural areas—those classified as national parks, biological reserves, ecological stations, and areas of environmental protection. We compiled data for 124 federal conservations units representing a total of 308,146 km[2] (3.6% of the Brazilian land area). Protected areas were classified by ecoregions in accordance with IBAMA[6]: Atlantic forest, cerrado (savanna-like vegetation), caatinga (thorn forest), Amazonian forest, pantanal (flooded open land), seacoast, and "campos sulinos" (natural open lands). Five classes of levels-of-model-agreement in predicting presence (0 to 20, 20 to 40, 40 to 60, 60 to 80, and 80 to 100% of best-subsets models) were created to simplify measures of the invasive potential to national parks by smooth crotalaria, which we designate as presenting no, low, medium, high, and critical invasion risk, respectively. Numbers of parks in each class were tallied by ecoregion, and significance of differences
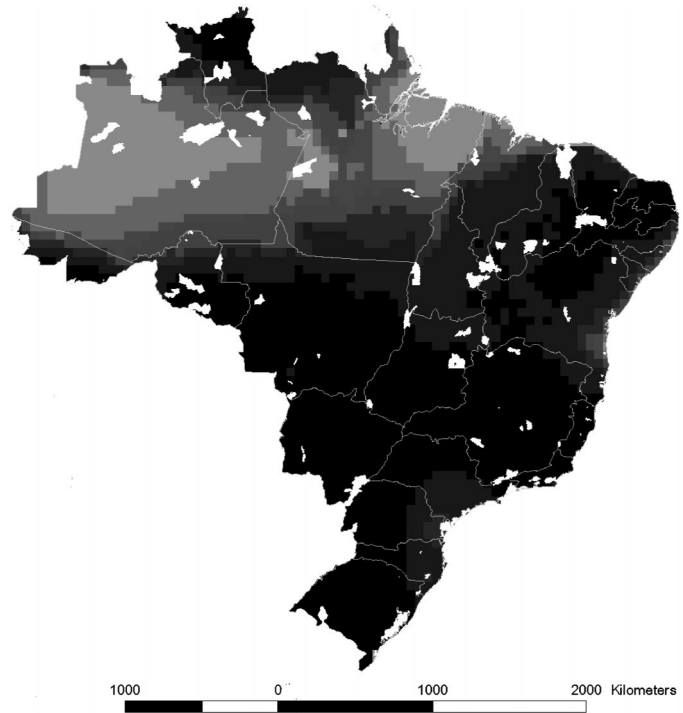

FIGURE 2. Map of Brazilian federal protected natural areas (in white) overlaid on the South American projection of the native-range ecological niche model for smooth crotalaria (black).

among ecoregions was tested using a Kruskal-Wallis test (a posteriori comparisons done using a Tukey-Kramer HSD test). Probability values of $P < 0.05$ were interpreted throughout as statistically significant.

Results and Discussion

All Brazilian protected natural areas showed substantial potential invasion risk by smooth crotalaria (Table 1; Figure 2). Although all protected natural areas were predicted to be vulnerable to some degree to invasion by smooth crotalaria, the potential for invasion was not uniform and vulnerability to invasion in protected areas varied significantly among ecoregions ($\chi^2 = 40.07$, df = 5, $P < 0.001$). The Tukey-Kramer HSD test identified two distinct groups of ecoregions, based on potential invasion risk for smooth crotalaria: open land areas (Pantanal, Cerrado, and Caatinga) vs. Atlantic Forest, Amazon forest, and the coastal parks (Figure 3). The former group of protected natural areas was quite vulnerable to invasion: 100% of area protected in the Pantanal was threatened; Cerrado, 96.15%; and Caatinga 87.50%.

These results likely reflect similarities between the Brazilian ecoregions and African savannas; both are dominated by open lands, and both show at least one dry period in the year. McNaughton et al. (1993) provide comparisons between vegetation structures of arid and semiarid regions of South America and Africa, concluding that great similarities can be observed, including the response of open and dense savannas and woodland to fire.

Caatinga is a semiarid ecosystem of northeastern Brazil, characterized by dry, spiny forest vegetation. Annual mean rainfall in Caatinga ranges 500 to 750 mm, reaching as low as 300 mm in drier years (Sampaio 1995). The Cerrado
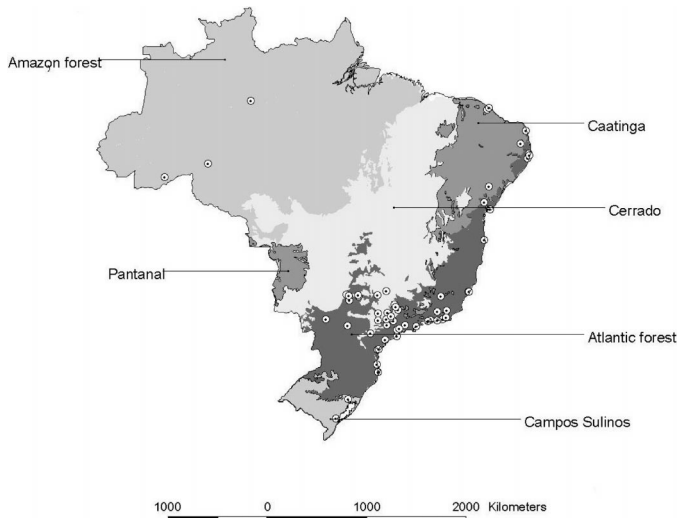
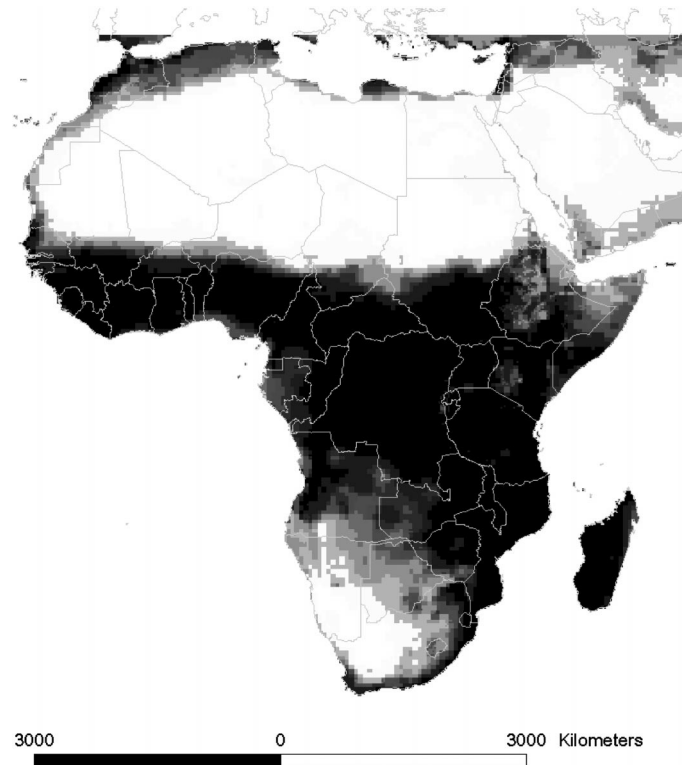FIGURE 3. Ecoregions of Brazil and occurrence points for smooth crotalaria.

FIGURE 4. Prediction of native range of smooth crotalaria across Africa. Increasingly dark shading indicates greater confidence in prediction of smooth crotalaria.

covers approximately 22% of the country's surface area (Oliveira and Marquis 2002) and is very similar to the African savannas. Cerrado climate is typical of moister savanna regions of the world, with an average precipitation for 90% of the area of 800 to 2,000 mm and a pronounced dry season during the southern winter (April to September) and with average annual temperatures of 18 to 28 C (Dias 1992). The Cerrado flora, like that of all savannas, is resistant to fire, showing all of the usual adaptations, such as thick corky bark, xylopodia (lignotubers), tunicate leaf-bases in grasses, etc. Nevertheless, frequent burning causes destruction, particularly of trees and shrubs, and thus favors herbaceous elements at the expense of woody plants (Ratter and Dargie 1997). The Pantanal is an immense alluvial plain, spanning 140,000 km^2 in the states of Mato Grosso and Mato Grosso do Sul. Its landscape encompasses a variety of ecological subregions, including river corridors, riparian forest, perennial wetlands and lakes, seasonally flooded grasslands, and terrestrial forests (The Nature Conservancy and Ecotrópica Foundation 1999).

The second group of biomes in our analysis had lower invasive potential. The Amazon forest, Atlantic forest, and coastal parks, are all wet and represent closed forest systems, except for the highly disturbed portions of the Atlantic forest, where human activities have been changing the landscape for centuries. Some smooth crotalaria populations have been documented in this ecoregion (Guimarães et al. unpublished data).

Campos Sulinos (the biome dominating southern Brazil) had protected areas with intermediate levels of vulnerability, not significantly different from the other two broad groups. Crotalaria usually grows in warm, open areas, which likely explains the variation in its ability to invade different ecoregions. This plant may represent less of a risk to parks in southern Brazil, where it is colder, and less risk as well to the more continuous, closed forest of the central Amazon.

The jackknife procedure identified layers that contributed negatively to model performance, leaving the following set of layers for analysis: diurnal temperature range, compound topographic index, vapor pressure, solar radiation, and maximum, minimum, and mean temperatures. All best-subsets models were significantly more predictive on the native dis-

tributional area than random models ($P \leq 10^{-5}$). Because the models appeared reliable for predicting the native distribution in Africa (Figure 4), we next examined their projections to invaded regions in South America (Figure 5). Once again, coincidence between model predictions and the independent invaded-range test occurrence data set was significantly better than random ($P < 3 \times 10^{-4}$).

Although the occurrence data available had only 1° resolution, and this value did not allow detailed regional analyses, the data probably represent the best information available about the distribution of smooth crotalaria in Africa. Another consideration regarding spatial scale is the availability of sufficient computing power. If modeling is to be done continentally or on broad regional scales, it may not be practical to use environmental layers at very fine resolution because they may prove very large and cumbersome for computing (Chapman et al. 2005).

Invasion of natural areas by alien species is considered among the most important processes threatening biodiversity in the next century (Sala et al. 2000). In the past, management of invasive species was largely reactive in nature, and the only predictive efforts centered on identifying classes of species that had high probability of successful invasion and ecosystems especially vulnerable to invasion (Baker 2004; Sakai et al. 2001). Our results identified a set of biomes that must be considered especially vulnerable to invasion by smooth crotalaria.

Recently, however, development of ecological niche modeling tools and approaches has made it possible to anticipate the geographic potential of future invasions (Peterson et al. 2003b). With respect to smooth crotalaria, our model results clearly indicate broad vulnerability of Brazilian protected ar-
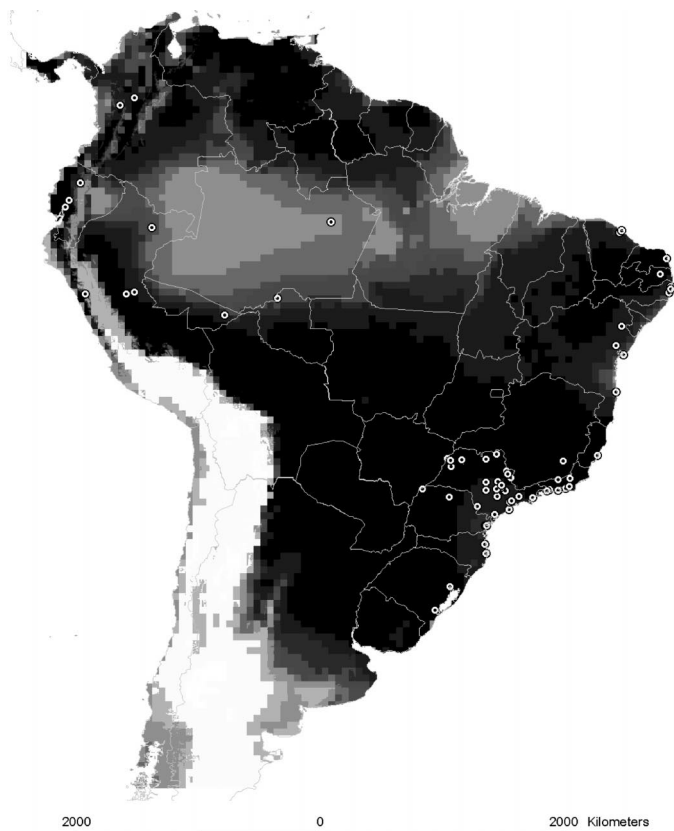
FIGURE 5. Projection of native-range ecological niche model for smooth crotalaria into South America, with independent test occurrence data overlaid. Increasingly dark shading indicates greater confidence in prediction of smooth crotalaria.

eas to invasion by this species but also suggest that some ecosystems, such as Atlantic forest, are more likely to be invaded than others. Similar analyses of other weeds may create a more complete scenario of the vulnerability of the Brazilian protected areas network to invasion of weeds. These results make it possible to develop management policies focused on preventing weed invasions in the most vulnerable protected areas.

Modelling of invasions of protected areas by alien weeds may provide additional help to management policies by identifying areas that are likely to be already invaded. This information is particularly useful to conservation efforts in developing countries, where biodiversity assessments are few, and actual distributions of exotic species are often unknown. Nevertheless, such predictions are only as good as the models on which they are based. In the present case, the models employed were highly predictive of the species' current extent of invasion of protected natural areas in Brazil. We suggest that future work should investigate the extent to which smooth crotalaria already occurs in South America and its impact, if any, on the dynamics of native ecological communities.

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