Survey of Plant Communities of Kipukas
within
Craters of the Moon National Monument and Preserve

Final Report

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EXECUTIVE SUMMARY

We visited and sampled kipukas at Craters of the Moon National Monument and Preserve (CRMO) during 2004 and 2005, focusing in particular on their plant communities, but also recording other attributes, including cultural and natural resources. Some putative kipukas proved either to be misclassified from aerial images or were false kipukas (apparently areas of lower lying lava over which some soil had drifted), and we updated the CRMO GIS kipuka database to reflect this. For the true kipukas, we sampled the plant community by visual survey, by using a point-frame to estimate percent cover of each species present, or both. We also recorded kipuka attributes and evidence of cultural and natural resources, using a checklist (Resource Observation Form) that was developed by CRMO personnel.

We sampled 88 distinct kipukas during the 2-year survey using one or both methods. Additionally, percent cover of all species was sampled for a set of 12 randomly selected kipukas both in both years to provide a baseline of annual variation and longer term trends in abundances of plant species.

We identified 174 total species from the 88 kipukas that were surveyed in 2004 and 2005. This species list is not exhaustive, as some plants could not be identified because they did not have diagnostic characters at the time a kipuka was visited. A list of species identified in this survey is included as Appendix A, and lists of species recorded from each sampled kipuka are included as Appendix B.

No state-listed noxious species were found on any of the surveyed kipukas, but 17 non-native species were recorded. The invasive annual grass, *Bromus tectorum* (cheatgrass) was the most abundant and widespread of the non-natives and was on most of the kipukas that were surveyed, excepting those of the North region of CRMO, where it was neither common nor abundant. *B. tectorum* was present on 84% of the sampled kipukas, was present on 78% of the kipukas that were sampled by point-frame in 2005, and was often the most abundant or one of the most abundant species on a kipuka. Additionally, there were fewer total species of plants on kipukas where *B. tectorum* was more abundant. The most abundant and frequent of the non-native forbs were *Sisymbrium altissimum* (tall tumblemustard), *Draba verna* (spring whitlow grass), *Lactuca serriola* (prickly lettuce), *Tragopogon dubius* (dandelion), and *Alyssum desertorum* (desert madwort).

Because kipukas are insular patches of sagebrush steppe vegetation surrounded by lava, one might expect that measures of insularity, particularly kipuka size and isolation, would predict the diversity of plant species present in the flora of a kipuka. We examined this possibility, but found that neither area nor isolation was a strong predictor of plant species diversity. Larger kipukas had a weak tendency to have more species, but some small kipukas had as many plant species as the larger kipukas.

Isolation explained somewhat more of the variation in plant diversity of kipukas, but the relationship was not as expected. Kipukas that were more distant from the edge of the lava flows, so more isolated from the surrounding historic sagebrush steppe landscape, had more plant species, contrary to the expectation that habitat isolation results in lower diversity.

Another measure of isolation, distance to the nearest other kipuka, explained somewhat more of the variation in plant diversity of kipukas. Kipukas that were nearer other kipukas had higher numbers of plant species than kipukas that were farther from other kipuka.

Collectively, these results suggest that isolation from the landscape surrounding the lava flows of CRMO has helped preserve the diversity of the sagebrush steppe flora of the kipukas, perhaps by protecting kipukas from intensive use by people, reducing the likelihood of fire, or reducing likelihood of establishment of non-native plants. However, kipukas also may benefit from proximity to other kipukas, perhaps because these patches of sagebrush steppe harbor plant species typical of historic sagebrush steppe that help maintain the populations on nearby kipukas.

Levels of both soil carbon (C, %) and soil nitrogen (N, %) were relatively low, as is typical of sagebrush steppe. Both carbon and nitrogen contents varied considerably within and among kipukas and tended to be highest in the North and lowest in the Wapi. There were more C and N in surficial soils (0-10 cm depth) than in deeper (10-20 cm) soils and there were more of both elements below the canopies of shrubs (primarily *Artemisia tridentata*, big sagebrush) than in open locations between shrubs. The higher soil C and soil N under *Artemisia* indicates a fertile island effect, as also was reported by Bechtold and Inouye (2007) for soils associated with *A. tridentata.* Additionally, plant species richness was higher for kipukas that had more heterogeneous soils (more within-kipuka variation in soil N or C).

Kipukas tended to be individually distinct in plant species composition: the plant communities of kipukas had only relatively low similarity to each other. This pattern suggests that the kipukas harbor unique local communities. Additionally, the native vegetation changes predictably along a roughly north-south gradient at CRMO (see Bangert and Huntly 2009) and also is associated with soil properties. The diversity of plant communities found in the kipukas of CRMO may represent a range of the community types that can occur within sagebrush steppe in the absence of intensive land use. The high uniqueness of kipukas indicates the value of protecting many kipukas, as they appear to preserve different sub-sets of the flora of sagebrush steppe.

There was substantial geographic variation in plant diversity of kipukas. The kipukas from the more northern parts of CRMO, especially the North and West regions, had significantly higher numbers of plant species. The diversity gradient among regions, roughly from south to north, corresponds to gradients in many factors, including soil fertility (indexed in this study by soil nitrogen and carbon contents), climate (the north is wetter and cooler), number of non-native plant species, and frequency and abundance of the invasive non-native grass, *Bromus tectorum* (cheatgrass). A further analysis of these data by Bangert and Huntly (2009), which used structural equation models to test which of several a priori models for the relationships underlying the diversity of native plants on the kipukas best fit the inter-correlated data, drew some additional conclusions. Based on comparison of a biogeographic model, an environmental model, and a model that included biological interactions among non-native and native plants, Bangert and Huntly concluded that the evidence best supported a model in which (1) species composition of native plants on kipukas at CRMO is associated with environmental factors, especially the temperature-moisture gradient from the southern to northern parts of CRMO, (2) the diversity and abundance of non-native plants decreases with distance from the railroad that runs along the southern edge of CRMO, and (3) the species richness of native plants decreases as exotic increase.

The analysis by Bangert and Huntly supports the general conclusions that area and isolation are not the most important factors controlling plant diversity of kipukas at CRMO. Their analysis suggests that non-native species, which appear to be expanding into CRMO from the southern boundary region, near the railroad, are causing loss of native species from kipukas, particularly in the southern parts of the park. Thus, although the kipukas are in some sense isolated and retain many native species characteristic of sagebrush steppe, they appear not to be immune to the threats to biodiversity that have affected sagebrush steppe over most of its historic range.

INTRODUCTION

Kipukas, from the Hawaiian word for window, are isolated islands of soil and vegetation that were formed when they were surrounded by lava flows. Craters of the Moon National Monument and Preserve (CRMO) includes over 500 kipukas, or areas that have been tentatively identified as kipukas, based on aerial imagery of the area. The proclamation that expanded the former 53,440-acre Craters of the Moon National Monument to the current more than 460,000-acre National Monument and Preserve added an estimated 570 kipukas to the previous 14 that had been within the Monument's boundaries. The expansion proclamation stated that:

> "*The kipukas provide a window on vegetative communities of the past that have been erased from most of the Snake River Plain. ….. These tracts of relict vegetation are remarkable benchmarks that aid in the scientific study of changes to vegetative communities from recent human activity as well as the role of natural fire in the sagebrush steppe ecosystem*."

Several kipukas at CRMO have been designated as ecological benchmarks that represent virtually pristine habitat, some have been the sites of previous research, and more have been visited, but most have not been studied. For most kipukas, there are no records of vegetation, evidence of disturbance, or other attributes of the ecological community and its condition. Further, sagebrush steppe vegetation is increasingly invaded by exotic plants, including cheatgrass (*Bromus tectorum*) and such state-listed noxious species as rush skeletonweed (*Chondrilla juncea*), dyer's woad (*Isatis tinctoria*), spotted knapweed (*Centaurea maculosa*), and leafy spurge (*Euphorbia esula*), but the distribution and abundance of such exotic species on kipukas at CRMO are not well known.

Kipukas at CRMO are patches of sagebrush steppe that were surrounded by lava during eruptions from the Great Rift from 15,000 to 2,000 years ago and now are surrounded by the more sparsely vegetated basalt lava substrate of the Craters of the Moon and Wapi lava fields (Tisdale et al. 1965, Kuntz et al. 1988). Historically, several of the edge and some of the internal kipukas have been grazed and a few have been farmed (P. Wolken, pers. comm.). However, the majority of these areas have not been farmed or grazed by livestock, and what grazing did occur was of limited duration. Thus, the kipukas are believed to retain native sagebrush-steppe habitat that has been minimally influenced by contemporary land uses. It is also generally believed that isolation by lava flows has protected kipukas from people, exotic plants, and fire. Thus, the kipukas are believed to provide a baseline for the condition of relatively pristine sagebrush steppe.

Since kipukas are inherently insular, by virtue of being patches of sagebrush steppe on native soils surrounded by recently formed lava beds, principles of island biogeography could apply. If so, then knowledge of the size and isolation of kipukas, which are easily measured, would allow coarse-scale prediction of their biological diversity, susceptibility to invasion by non-native species, and vulnerability to extinction of native populations. The MacArthur-Wilson (MW) model of island biogeography (MacArthur and Wilson 1967) provides a mechanistic framework for understanding and predicting the species diversity of many insular habitats. The MW model assumes that smaller islands or insular patches have higher rates of local population extinction than larger ones. Thus, the MW model predicts that larger kipukas will harbor more species of plants than smaller kipukas. The MW model also assumes that islands that are more distant from sources of dispersing individuals, such as the seeds of plants, have lower rates of colonization and establishment of populations. Thus, the more isolated kipukas would harbor fewer plant species than kipukas that are nearer other sagebrush steppe habitat. Additionally, since kipukas are remnant patches of what once was extensive sagebrush steppe, the MW model predicts they would be expected to have lost species in conformity with their post-lava-flow smaller sizes.

Study of the populations of habitat fragments has increasingly relevance for conservation, as the landscape of North America is increasingly fragmented by land use (Saunders et al. 1991). In agricultural regions, including ever more of the historic range of sagebrush-steppe, native vegetation is found only in discrete patches within a matrix of agricultural lands (McIntyre and Hobbs 1999; Knick and Rotenberry 1995, 1997; Welch 2005). Of the 10.3 million ha of sagebrush-steppe that historically were found in Idaho (West 1983), approximately 3.5 million have been cleared for agriculture (Lipske 2000). Agricultural land use also has led to the spread of non-native plants, including some state-designated noxious weed species and the non-native grass, *Bromus tectorum* (cheatgrass) (D'Antonio and Vitousek 1992), through much of the historic sagebrush steppe ecosystem. Cheatgrass has increased the frequency of fire and so has exacerbated fragmentation of sagebrush steppe (Melgoza et al. 1990, Knick and Rotenberry 1997). The flora of kipukas may provide a reference point against which to evaluate the effects of the more recent fragmentation of sagebrush steppe by changing land use.

The general goal of this project was to survey the plant communities of kipukas within Craters of the Moon National Monument and Preserve in order to improve knowledge of their vegetative characteristics, including the distributions of exotic plant species. A second and more specific goal was to test how well the plant community of a kipuka could be predicted from its geographic features, particularly its size or its apparent degree of isolation from more extensive sagebrush steppe habitat. Because of their insular status, we hypothesized that the species diversity of kipukas (1) would decline with increasing isolation (distance from more extensive sage habitat beyond the edges of the lava flows) and (2) would increase with kipuka size, consistent with the theory of island biogeography of MacArthur and Wilson (1967).

We also examined the soils of kipukas. Soil characteristics, particularly texture and nutrient contents, often are good predictors of plant species composition and plant diversity (e.g., Lovejoy 1980, Tilman 1988). Total soil N is frequently a good predictor of nitrogen availability to plants. Total soil C is generally an indicator of soil organic matter content, so typically is an indicator of both the N content and the water holding capacity of soil. Additionally, fertile islands, patches of higher nutrient content and higher fertility, are associated with shrubs in many arid landscapes and can be unique sites of biodiversity (Schlesinger et al. 1996, Schlesinger and Pilmanis 1998, Bechtold and Inouye 2007). Thus, we documented the nitrogen and carbon content of soils of kipukas, both under the canopies of the dominant shrub species (*Artemisia* spp., mostly *A. tridentata*, big sagebrush) and in openings between shrubs. We tested whether areas associated with shrubs had more nitrogen- or carbon-rich soils and whether plant diversity was related to soil nutrient content.

Additionally, we searched for and recorded evidence of natural and cultural resources for each kipuka in the survey. Information gained by this project is intended to serve as a foundation for interagency management plans designed to protect the natural values of these unique insular ecosystems and their increasingly rare native plant communities.

METHODS

Design of the Kipuka Survey

A GIS database of kipukas (referred to hereafter as the CRMO GIS database), which was constructed using ArcView (ESRI, Redlands, CA), was used to measure the size and isolation of kipukas and to select a stratified random sample for the survey. Steve Hanser made the database for the Craters of the Moon Lava Flow as part of an earlier study (Hanser and Huntly 2006) and CRMO Resource personnel added the Wapi Lava Flow to the database. In each case, apparent kipukas were identified on United States Geological Survey digital orthophoto quarter-quadrangles (DOQQ) and digital raster graphs (DRG) obtained from the Idaho State University GIS Training and Research Center and these were digitized into the GIS.

At the beginning of this study, we identified 533 potential kipukas in the database, with mean isolation of 142 m (range 9 to 8627 m) and mean area of 3.99 ha (range 0.05 to 85.82) (Table 1). We did not include very large kipukas (e.g., Huddle's Hole) or areas that had imaged as potential kipukas but had since been determined to be false kipukas or areas of lava with differing surface characteristics that imaged as distinct. We calculated each kipuka's area (m^2, ha) and isolation (m, km) using ArcGIS and the CRMO GIS database. We estimated a kipuka's isolation as the shortest straight-line distance from the edge of a kipuka to the nearest tract of continuous historic sagebrush steppe outside of the lava flow (i.e., the sagebrush-steppe 'mainland'). For each kipuka, we also located the nearest other kipuka (the nearest neighbor, NN) and calculated the distance to it as a second measure of isolation.

We obtained a geographically representative sample of kipukas by stratifying the Monument into four geographic regions consisting of the northern, western, and southern portions of the main Craters of the Moon lava flow, plus the Wapi flow (North, West, South, and Wapi, Figure 1). Far more kipukas are small than large, and far more are located near the edges of the lava beds than are nearer their centers. Thus, to ensure sampling of kipukas from a range of sizes and distances to the mainland, we divided kipukas into size and isolation classes and selected kipukas for sampling by randomly drawing a sample from these classes (all combinations of size and isolation) from each region. We sampled a subset of the kipukas for species cover in both years so that differences in plant presence or abundance due to weather conditions of a year could be assessed.

Methods for Plant Survey

The datum of all geographic data collected in this study is NAD83, UTM Zone 12, and kipuka coordinates represent the center of each kipuka polygon in the CRMO GIS database.

Kipukas Sampled in 2004

We divided kipukas into 5 size classes (0.25-0.5 ha, 0.5-1.0 ha, 1.0-2.5 ha, 2.5-5.0 ha, and >5 ha) and 2 (<1 km and $\geq$1 km) isolation classes and selected kipukas for sampling by randomly drawing kipukas from the size-isolation classes, distributed evenly among the 4 geographic regions. Within each geographic area, we randomly selected 1 kipuka from each of the 10 combinations of size and isolation classes, resulting in a total of 10 kipukas from each geographic region (N, S, W, Wapi). We added 16 additional kipukas (4 per region) that we had previously sampled in 2003 and had designated to resample in each year to provide a baseline for assessing the influence of annual weather conditions on the abundances of plant species. This gave a target list of 56 kipukas to be sampled in the summer of 2004.

Our actual sample was somewhat altered from this initial selection. Most plants could be identified effectively beginning in mid-May, so we began our samples then. Advancing seasonal phenology resulted in most forbs being too dried to be identified by mid-July, putting a firm end to the sample period. Some kipukas in the original sample proved to be false kipukas, and a few were simply patches of smooth lava within rougher lava. We replaced these non-kipukas in our sample with kipukas of similar size and location as possible. Approximately 7 kipukas in our final sample were visited because of their proximities to selected kipukas. Consequently, the final sample matches closely but not exactly the original criteria for selecting kipukas.

We were able to visit 60 kipukas from May through July, 2004 (Table 2, Figure 2). Eleven of these had little soil or vegetation, were judged to be false kipukas that had formed in low-lying areas of lava over which some soil had drifted, and were not further surveyed. We surveyed the other 49 by foot and, for each, listed all plant species observed. For each kipuka, we also recorded cultural and natural resources, using a Resource Observation Form developed by CRMO resource personnel. For a subset of 19 kipukas, we quantified plant cover of each plant species using a point-frame, as described below.

Kipukas Sampled in 2005

Again, we selected a target set of kipukas (48) for sampling by randomly drawing kipukas from a combination of size classes and isolation classes. We used a sixth size class in 2005 to get more information about the largest kipukas within our sample frame. Since large kipukas are relatively rare, defining a larger size class was necessary to be sure some of the largest kipukas were represented in the sample. Thus, we drew the year's sample from size classes of 0.25-0.5, 0.5-1, 1-2.5, 2.5-5, 5-10, and 10-20 ha and isolation classes of <1 km or ≥1 km from the nearest edge of the lava flow. This sample was incremented by 12 of the original set of 16 kipukas that had been designated to be sampled in each year. The number was reduced to 12 to allow more time to survey new kipukas, in keeping with the primary project objective.

We were able to visit and sample 58 kipukas (Table 2, Figure 3). As in 2004, we filled out Resource Observation forms and generated species lists for each kipuka. We quantified plant cover by species using the point-frame method on 50 of these, including 38 new kipukas and the 12 kipukas that were sampled in both years, using the same design as in 2004. For the other 8 kipukas, species lists were the only source of information.

Plant Survey

We sampled the plant communities of the kipukas (Figure 4) using 2 methods. First, 2 observers surveyed each kipuka on foot and generated a list of all plant species they observed. Second, we estimated percent cover of plant species using the point-frame method (Floyd and Anderson 1982). At each kipuka, percent cover was sampled, using a 1m x 0.5m point-frame with a 9 x 4 grid of sample points, along 4 transects. We placed the 4 transects evenly over each kipuka, using the CRMO GIS map to calculate the distance from the center point of the kipuka to the edge of the kipuka in each of four cardinal directions, then locating a 25m transect, running north-south, midway between the center and the edge of the kipuka in each cardinal direction (Figure 5). For some of the smallest kipukas, this placement of transects was not feasible and we spaced transects as evenly as possible over the kipuka in as close to a north-south orientation as possible. At each kipuka, we recorded plant cover, by species, below a point-frame at every other meter along each transect, resulting in a sample of 13 frames/transect and 52 frames/kipuka or 1872 sample points from each kipuka.

Our final sample was of 88 distinct kipukas (Figure 4), many of which were visited more than once (noted in Appendix B), 57 of which were sampled quantitatively using the point-frame method. Twelve kipukas were sampled quantitatively in both years.

Voucher specimens were collected during surveys of kipukas to verify plant identification and to identify plants that were unknown at the time of a census. Field identifications were primarily by C. Pedersen and J. Frank, who used the CRMO Herbarium for reference. Pressed and dried plants were identified by C. Pedersen, N. Huntly, K. Holte (Emeritus Curator of the Ray J. Davis Herbarium), C. Davis (Bannock Ecological, Inc.), and H. Albano. Specimens were examined in the lab using a dissecting microscope and were identified using primarily Flora of the Pacific Northwest (Hitchcock and Cronquist 1973) and the Intermountain Flora and Vascular Plants of the Pacific Northwest volume sets. However, all floras listed as “References for Plant Identification” at the end of this report were used at some point during plant identification. Uncommon species, such as *Nama densum* var. *densum, Cistanthe rosea*, and *Cryptantha ambigua*, were also verified by comparison with the identified specimen(s) of the Ray J. Davis Herbarium. Some specimens could not be identified with certainty due to limited material, e.g., senesced and fragmentary specimens, immature specimens, or lack of flowers or fruits. These collections were marked with “?” or have only been identified to the family or genus level. Nomenclature in this report and the associated data files follows NPSpecies, as given for Craters of the Moon by Popovich and Atwood (October 2006).

Soils

We collected 2 20cm soil cores from each end of each transect of each kipuka to describe the total soil carbon and nitrogen contents of the kipukas, to relate vegetation to these often-important soil characteristics, and to evaluate whether ‘fertile islands’ were associated with the dominant shrubs, *Artemisia* spp. One core was taken from underneath the canopy of the sagebrush (*Artemisia tridentata* or *A. tripartita*) nearest to the end of each transect, while the other was taken from the nearest intercanopy space. Each soil sample was sectioned to 0-10 and 10-20 cm depths. Thus, we collected 16 samples, separated into 2 depth-stratified subsamples, from each kipuka. Sectioned samples were placed in labeled whirl-pak bags, returned to the lab, oven-dried at 100^{o}C for 72 hours, sieved, homogenized with a mortar and pestle, and analyzed for total carbon (C) and total nitrogen (N) contents by combustion using a Carlo Erba CHN 2600 in the CERE Lab at Idaho State University. Funds were sufficient to analyze only ½ of the samples, so we analyzed the set of 4 samples from one randomly chosen end of each transect from each kipuka.

Resource Observations and Photographs

Kipukas were photographed along each transect, usually supplemented with 1-2 additional broader angle photos. Additionally, a number of photos were taken of plants or habitats that appeared to characterize kipukas or in some other way were interesting or revealing. These images were delivered to CRMO.

Data Files and Data Analysis

A list of species encountered in censuses of kipukas, along with the codes we used to designate each, is given in Appendix A. Plant species are identified using 4-letter codes (first 2 letter of genus, first 2 letters of species – GGSS) unless there was more than one species that would have the same code, in which case a 3 letter code (GGSSS) was used. Species identified to genus or family only are given 6 letter codes (e.g., DESCUR = *Descurania* sp., BRASSI = Brassicaceae). Plant data from both census methods and both years were summarized to produce lists of all species that were recorded on each kipuka. These are included as Appendix B. The tables in Appendix B state the number and nature (i.e., point-frame, species list) of samples that resulted in each species list. Soil N and C data are presented as Box plots, which show the medians and quartiles, in Appendix C. Resource observations, summarized in Excel, are included as Appendix D.

Analyses of Species Composition and Diversity of Plants of the Kipukas

All statistical analyses of the plant diversity of kipukas that follow are based on the data taken in 2005 using the point-frame method and the associated soil data. We used these data for statistical analyses because a large number of kipukas were sampled with this quantitative and equal-effort method in 2005. Additionally, we were better able to identify plants quickly and accurately in the field in 2005 than in 2004, so had more confidence in the consistent quality of the samples taken in 2005. Comparisons of diversity and distribution generally require equal sample effort, which precludes using all data we gathered for this purpose. Although only the 2005 data were analyzed to describe patterns of variation in plant diversity and test what factors were the best predictors of this variation, all species that were recorded on a kipuka in any census in either year appear in the species lists (Appendix B).

Using the 2005 point-frame data, we summarized percent cover of each plant species on each kipuka. We calculated frequency of occurrence (proportion of sampled kipukas at which a species was observed) for each plant species. We calculated plant diversity as the number of species present, i.e., species richness.

We tested how well kipuka size (area), isolation, geographic location (N, S, W, and Wapi sample regions), and soil characteristics, separately and in combination, predicted plant diversity of kipukas, using simple and multivariate linear models. We also examined variation in soil C and N among the sample regions and tested whether these elements were significantly higher under the canopy of *Artemisia* shrubs, which would indicate a fertile island effect. We also examined the distribution and abundance of the invasive non-native annual grass, *Bromus tectorum* (cheatgrass), and tested whether plant species richness was related to the abundance of *B. tectorum*. All of these analyses were done using SAS 9.1. Additionally, we used PC-Ord vs. 4 to quantify the similarity of vegetation among kipukas by calculating the pair-wise Sorensen's index for each pair of kipukas within a region and for all pairs of kipukas that were sampled.

RESULTS and DISCUSSION

We identified a total of 174 species from the 88 kipukas surveyed in 2004 and 2005 (Appendix A). This is not an exhaustive species list, as there were species that could not be identified because sufficient material was not available. There also may be some misidentification of species, especially from 2004. The 2004 census was not well-vouchered as a consequence of destruction of many of the specimens that were collected that year.

Exotic Plants

We did not record any species from the State of Idaho noxious plant list in the floras of the kipukas we sampled, but we did record 17 non-native species (nativity determined from S. J. Popovich, October 15 2006, *Craters of the Moon Vascular Plant Checklist*, 72 pp). Several of these were widespread (Table 3) or locally abundant. The non-native species were: *Agropyron cristatum* (crested wheatgrass, present on 7 kipukas), *Alyssum desertorum* (desert alyssum, 12 kipukas), *Bromus tectorum* (cheatgrass, 73 kipukas), *Chenopodium album* (lamb's quarters, 2 kipukas), *Chorispora tenella* (purple mustard, 1 kipuka), *Descurainia sophia* (flax tansymustard, recorded in 3 kipukas, but likely in more, as many *Descurainia* could be identified only to genus in the field), *Draba verna* (spring whitlowgrass, 17 kipukas), *Festuca bromoides* (brome fescue, 4 kipukas), *Lactuca serriola* (prickly lettuce, 44 kipukas), *Lepidium perfoliatum* (claspingleaf pepperweed, 1 kipuka), *Poa bulbosa* (bulbous bluegrass, 2 kipukas), *Poa pratensis* (Kentucky bluegrass, 1 kipuka), *Ranunculus testiculatus* (5 kipukas), *Sisymbrium altissimum* (tall tumblemustard, 23 kipukas), *Taraxacum officinale* (dandelion, 8 kipukas), *Thlaspi arvense* (pennycress, 2 kipukas), and *Tragopogon dubius* (salsify, 34 kipukas).

Patterns in the Plant Community

Species richness of kipukas in the standard-effort sample survey ranged from 14 to 38 (average being 25). Twenty-nine species occurred on at least 16 of the 48 kipukas (1/3) that were sampled in 2005 (Figure 6, Table 4). The 2 most frequent species were 2 expected co-dominants of sagebrush steppe in this region, *Artemisia tridentata* and *Poa secunda sensu amplo*. *Bromus tectorum*, however, was the 5th most commonly occurring species, recorded on 38 of the 48 (79%) kipukas. *B. tectorum* was the only non-native species present on more than 1/3 of kipukas and was by far the most widespread non-native.

Six different species were the most abundant (highest % cover) on at least 1 sampled kipuka (Figure 7). The species that was most often the most abundant was *B. tectorum* (cheatgrass), followed closely by the expected dominant of sagebrush steppe, *A. tridentata* (big sagebrush), and 2 common co-dominant or regionally dominant native species, *Poa secunda* (*sensu amplo*, secund bluegrass) and *Artemisia tripartita* (three-tip sagebrush).

Twenty-two species were among the 5 most abundant on at least 2 kipukas (Figure 8). Two other non-native species, *Sisymbrium altissimum* (tall tumblemustard) and *Draba verna* (spring whitlowgrass), appear on this list. Thus, *B. tectorum* was the only non-native that was frequently the most abundant species on a kipuka, and *S. altissimum* (tall tumblemustard) and *D. verna* were the only other non-native forbs to have been among the most abundant species on several kipukas.

How Well Do Insular Attributes Predict Plant Diversity?

We tested whether kipuka size (area) or isolation (distance to similar habitat) was a good predictor of the plant diversity of a kipuka, because these are often significant predictors of diversity and species composition of insular habitat patches. Because CRMO covers a large geographic area over which soils, temperatures, and precipitation vary significantly, we also examined whether the plant community varied systematically with geographic location (region: North, South, West, Wapi) and soils (average and variability of soil C and N contents).

Plant species richness was higher in the North and West and lower in the South and Wapi regions (Mood median test, Chi-square = 7.26, $DF = 3$, $P = 0.064$; Figure 9). Median number of plant species in a sample of 52 point-frames was 27 in the North, 28 in the West, 21 in the Wapi, and 20.5 in the South.

Neither kipuka size nor isolation from the surrounding historic sagebrush steppe by surrounding lava beds were good predictors of the plant species richness of kipukas. Larger kipukas, on average, had more plant species, but the relationship was weak and explained less than 8% of the variation in plant species richness (Figure 10). The largest kipukas were among the most species rich, but the small kipukas (> 5 ha) had a broad range of species richnesses, including some that were as diverse as the largest kipukas. The relationship of plant species richness with area was somewhat improved when examined separately within each region (Figure 11, Table 5), but kipuka size remained a mediocre predictor of plant diversity.

Isolation, measured by the distance of a kipuka to the edge of the lava flows where more extensive sagebrush is or was present (distance to the mainland), also had little effect on the species richness of kipukas. Neither linear distance (R^2 = 0.2%, P = 0.30) nor log distance (R^2 = 1.48%, P = 0.20) of a kipuka to the sagebrush-steppe mainland beyond the lava beds was a significant predictor of the plant species richness of a kipuka. Distance to the mainland predicted about 13% of the variation in plant diversity within each of the 4 regions, but the more isolated kipukas were **more** diverse, particularly those of the least diverse region, the Wapi, and the most diverse region, the North (Figure 12, Table 6). Higher diversity in more isolated kipukas is the opposite pattern than was expected from the MW model. This surprisingly result suggests that plant diversity of kipukas may benefit from isolation from the surrounding area that once was extensive sagebrush steppe but now is largely either converted to agriculture or grazed.

A second index of isolation, distance to the nearest kipuka, was a somewhat better predictor of plant diversity within regions (Figure 13, Table 7). Combined with the minor and negative effect of distance to the edge of the lava flow, this pattern suggests that the most important source of propagules to support the plant diversity of kipukas is other kipukas, not the historic extensive sagebrush steppe. These results also support the belief that kipukas support a residual reservoir of the historic plant diversity of sagebrush steppe.

The best predictive model using any combination of geographic attributes (i.e., size, distance to mainland or nearest other kipuka, region) was a model that used area, distance to the nearest kipuka, and region to predict plant species richness. This model explained close to 22% of the variation in diversity of a kipuka (Table 8). Thus, both kipuka size and proximity to other kipukas appear to play some role in the diversity of the flora of kipuka, but geographic location (region) was a more important predictor. However, these parameters together gave only a loose estimate of the species diversity of vegetation of a kipuka.

Soils and Associations of Plant Diversity with Soils

Levels of soil carbon (C) and nitrogen (N) were relatively low, as is typical of sagebrush steppe (Figure 14, Figure 15). Both soil C and soil N contents were higher under the canopies of sagebrush (Figure 16, Figure 17) than in open areas.

There also were strong geographic gradients in soil C and N contents. The North region of CRMO had significantly higher soil N and C than any other region (Figure 18). Box plots of soil carbon and nitrogen for each kipuka also are included as Appendix C.

Plant species richness of kipukas was correlated with heterogeneity of both soil N and soil C, particularly in the richer surficial (0-10cm depth) soils (Figure 19). Species richness increased with variance in shallow N content (R^2 = 28.32%, P = 0.001), deep N content (R^2 = 14.33%, P = 0.016), shallow C content (R^2 = 19.83%, P = 0.005), and deep C content (R^2 = 19.9%, P = 0.005).

Since both plant species richness and soil N and C differed among the 4 geographic regions we had designated, we also tested the ability of the soil data to predict the species richness of kipukas within each region. These regressions gave the best predictions of plant diversity of any of the simple or multivariate linear models we tested. In fact, soil chemistry alone predicted species diversity better than region did, and region was no longer a significant predictor in these models. The best predictor, using both shallow and deeper soil samples, was variance in soil C, which predicted 35.2% of the variation in plant species richness ($P = 0.001$), Soil C typically is highly correlated with soil organic matter, and soil organic matter affects both water holding capacity and nutrient fertility.

Relationship of *Bromus tectorum* (Cheatgrass) and Plant Species Diversity

Cheatgrass was present on most kipukas in the South, West, and Wapi regions and was often abundant (Figure 20). It was least frequent and least abundant in the North region. There was no significant relationship of cheatgrass abundance to isolation of a kipuka from the lava-edge sagebrush mainland ($P > 0.7$); however, kipukas that were nearer to other kipukas tended to have higher proportions of cheatgrass (Figure 21). Thus, nearness to other kipukas appears to increase the abundance of cheatgrass on a kipuka.

Plant species richness decreased as the abundance of cheatgrass increased (Figure 22). The relationship was strongest in the West and was absent in the North, where cheatgrass was rare (Figure 23).

Using Structural Equation Models to Evaluate Alternative Hypotheses for Diversity of the Kipuka Plant Communities

The results described above make clear that many of the factors that could affect plant diversity of kipukas covary (e.g., kipukas in the North of CRMO have higher species richness, soils with higher C and N contents, fewer exotic species, less cheatgrass, and they tend to be farther from the mainland and from other kipukas). Thus, we recently reanalyzed these data using structural equation models (SEMs) to test how well several different models of species richness were supported by the data. The results of this work are presented in detail elsewhere (Banger and Huntly 2009) and are only briefly reviewed here, as they significantly update interpretation of the analyses that were central to this kipuka survey project.

Bangert and Huntly (2009) used structural equation models to assess the abilities of 3 different models to predict the diversity of sagebrush steppe vegetation and found, in agreement with analyses above, that metrics of insularity were not good predictors of diversity. They found the best model to be one that assumed that (1) the species richness of exotic plants was associated with distance from a transportation corridor, the railroad that runs along the southern boundary of CRMO, and that (2) native plant diversity was associated with environmental factors (proxied as the latitudinal location, a finer scale measure of variation in precipitation, temperature, and soils than the Regions used in this report) and decreased as the species or cover of exotic plants increased. Because this analysis tested among alternative biologically-motivated models for the relationships of native plant diversity with insularity, environmental factors, and interactions with exotic species, and used a method designed to incorporate and assess inter-correlated variables, the results reported in Bangert and Huntly (2009) are the best current mechanistic interpretation of the data in this report.

How Unique Are Individual Kipukas?

The plant diversity of kipukas did not have the geographic patterns that were expected by the MW model for insular habitat patches: area and isolation metrics did not predict plant diversity well. Nevertheless, both the data and the photographs of kipukas show that the plant communities of the kipukas vary substantially. To further examine the uniqueness of the floras of kipukas, we compared the similarities of their plant communities, using Sorensen's Index to assess the proportion of the total flora of each pair of kipukas that is held in common. We calculated Sorenson's Index for all pairs of kipukas within each of the 4 geographic regions of CRMO and for all pairs of kipukas in the entire sample (Figure 24).

Average similarity of the vegetation of kipukas was relatively low, indicating that the floras of kipukas were quite distinct and heterogeneous. Average vegetational similarity of kipukas was lowest, only 40%, in the North, which also had the most species rich kipukas. Average similarity of the plant species composition of kipukas was 51% in the West 52% in the South, and 63% in the Wapi.

The overall similarity of kipukas for CRMO as a whole was only 38%. This lower value reflects the tendency of kipukas from different regions to be less similar in plant species composition than were kipukas from within the same region. The overall similarity of 38% was very like the 40% similarity reported for large plots of sagebrush steppe vegetation on the Idaho National Laboratory (INL, Anderson and Inouye 2001). The INL is largely a protected area and has not been grazed since the mid 20th century. Thus, it is like the kipukas we sampled in being largely without direct impact of the common current land uses of the region.

CONCLUSIONS

Although kipukas are arguably insular habitats, the kipuka floras do not conform well to expectations from the classic theory of island biogeography. There was only a weak tendency for larger kipukas to have more species-rich floras. This is in contrast to an earlier study by Carter-Lovejoy (1982), but that study was of far fewer kipukas (14), twelve of which were relatively near the eastern edge of what is here designated as the North region of CRMO. Thus, his study did not represent the range of kipuka sizes, isolations, geographic locations, or plant communities that we sampled. Additionally, the data shown in Carter-Lovejoy (1982) include one kipuka that is far larger than the others in the sample and may have had large influence on the species/area relationship that he reported.

Plant diversity was better related to the distance of a kipuka from the nearest large tract of sagebrush at the edge of the lava flows, but this correlation was the opposite of what would be predicted from island biogeographic theory: kipukas farther from the lava's edge, so more isolated from the outlying historic sagebrush steppe, were more diverse than those nearer the edges of the flows. This may indicate that the area around CRMO no longer is a significant source of seeds of sagebrush steppe species. In fact, isolation from the area surrounding CRMO, which for the most part has been converted to agriculture or is used as rangeland, may have maintained more of the potential diversity of sagebrush steppe on the more isolated kipukas.

Another measure of isolation, distance to the nearest other kipuka, was better associated with species richness, and this measure of isolation showed the expected relationship with plant diversity: kipukas nearer other kipukas had more plant species. This also supports the interpretation that the main current source of new plant propagules to kipukas, supporting their diversity, is other kipukas and their remnant sagebrush flora.

The soils of kipukas overall had soil N and C contents within the range expected for sagebrush steppe. The much higher N and C in the soils under shrubs suggests that *Artemisia* spp. have associated fertile islands of soil, as has been found for shrubs in desert ecosystems of the southwestern United States (Schlesinger and Pilmanis 1998) and for sagebrush in Idaho (Bechtold and Inouye 2007).

The differences in soil chemistry between regions appear to be responsible for some of the differences in plant species diversity among regions, with the more fertile and more variable northern part of CRMO also having higher plant species richness. Of the potential predictors of plant species diversity that we examined, the best single predictor of species richness of the flora of a kipuka was the heterogeneity of soil N or C content. This suggests that spatial heterogeneity in the soil characteristics of kipukas plays a significant role in setting the plant diversity of a kipuka. Finally, the role of soils in plant diversity appears to be partly a role of *Artemisia* shrubs, since the analysis of soils was based on a comparison of paired shrub and interspace samples. This suggests that *Artemisia* shrubs may play an important role in supporting the plant diversity of the sagebrush steppe flora of the kipukas, as has been argued for sagebrush steppe in general by Welch (2005).

We did not find State-designated noxious weeds in this kipuka survey, but we did find that several non-native species were common and widespread. The known problematic annual grass, *Bromus tectorum* (cheatgrass), was the most abundant and widespread of these and was found on 84% of the sampled kipukas. *B. tectorum* also may be having an impact on diversity of kipukas, as species richness of a kipuka was negatively correlated with the amount of *B. tectorum* in its vegetation. The most abundant and frequent of the non-native forbs were *Sisymbrium altissimum* (tall tumblemustard), *Draba verna* (spring whitlow grass), *Lactuca serriola* (prickly lettuce), *Tragopogon dubius* (dandelion), and *Alyssum desertorum* (desert madwort).

This study was a sample survey, so the relationships we report do not necessarily identify causal relationships. Because many factors that were associated with plant diversity covaried, we have pursued follow-up analyses to more directly test for the most likely causal relationships, taking into account the inter-correlations in the data. We (Bangert and Huntly 2009) analyzed these data separating the native and non-native plant species and using structural equation modeling to test alternative models for diversity of the two groups. This analysis suggested that a major environmental gradient and non-native species are primary causes of the variation in diversity and species composition of the native plant communities of the kipukas at CRMO. Additionally, the analysis suggested that non-native plants may be actively expanding into the kipukas of CRMO from the southern edge, near the railroad. See Bangert and Huntly (2009) for more details of the analyses and results.

The kipukas at CRMO support a rich and highly variable flora. Kipukas overall had not only reasonably high plant diversity, but also high uniqueness. The average pair-wise similarity of the plant communities of the kipukas we sampled was only 38%. The average pair-wise similarity of plots protected from grazing in the big desert on the Idaho National Laboratory based on similar sampling methods to those we used, was 40% in 1995 (Anderson and Inouye 2001). These two studies suggest that sagebrush steppe that is not subject to high intensity land use such as grazing is both locally diverse and spatially variable in species composition. The high uniqueness of the kipukas of CRMO argues that there is value in their general protection, as they appear to represent many local manifestation of the range of plant communities that can occur within sagebrush steppe. However, these communities appear to be threatened by non-native plant species that are particularly common in the more southern areas of CRMO.

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