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RELATIONSHIPS OF THE INVASIVE PLANT, *Sisymbrium altissimum* L., WITH
THE PLANTS AND BUTTERFLIES OF CRATERS OF THE MOON NATIONAL
MONUMENT AND PRESERVE

by

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To the Graduate Faculty:

The members of the committee appointed to examine the thesis of SARA E. KAISER find it satisfactory and recommend that it be accepted.

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RELATIONSHIPS OF THE INVASIVE PLANT, *Sisymbrium altissimum* L., WITH THE PLANTS AND BUTTERFLIES OF CRATERS OF THE MOON NATIONAL MONUMENT AND PRESERVE

Thesis abstract—Idaho State University 2009

Invasive plant species can disrupt the pre-invasion food web. Sagebrush steppe is a widespread semi-arid ecosystem that has been degraded by changes in land use and is being invaded by exotic plants. *Sisymbrium altissimum* (Brassicaceae), an abundant invasive mustard species in the western US, is common in sagebrush steppe. Some herbivores, such as pierid butterflies, use native mustards as host plants and may use invasive *S. altissimum* preferentially. However, the trophic interactions between *S. altissimum* and native plants and butterflies are not known. We studied the distribution of plants and butterflies at Craters of the Moon National Monument and Preserve (CRMO) and examined whether the diversity or abundance of native and non-native plants or the abundance of pierid butterflies were related to *S. altissimum* distribution or abundance. We found evidence of lower total native richness at a local scale, and similar trends at a kipuka-wide scale. Native plant cover was also lower where *S. altissimum* was more abundant. Pierid abundance was higher where *S. altissimum* was more abundant. Pierids likely use *S. altissimum* in addition to native mustards as hosts, increasing their abundance, but the relationship between *S. altissimum* and native plants is still unclear.

INTRODUCTION

The invasion of exotic species is second only to habitat destruction as a threat to global biodiversity (Wilcove et al. 1998). An invasive species is one that establishes, increases in abundance, and spreads in an area where it previously was not present (Alpert et al. 2000, Mack et al. 2000, Radosевич et al. 2007). Often, invasives are introduced to an area by people or their activities, but subsequently are able to establish and spread without aid (D'Antonio and Vitousek 1992, Hierro et al. 2005, Coulatti 2005). As a consequence of the significant increase in global transportation and changes in land use over the last few decades, the number of documented invasions is accelerating (Mack et al. 2000, Mooney and Cleland 2001, Pimentel et al. 2005).

Such invasions have resulted in substantial economic and ecological costs in the US and internationally (Pimentel et al. 2005), including the loss of ecosystem services to humans (Ehrlich and Mooney 1983, Chapin et al. 2000). Ecosystem services such as conservation of clean air and water, crop pollination, soil erosion control, regulation of the climate, or production of economically important goods are often lost due to reductions of native biodiversity (Chapin et al. 2000). Moreover, extinction of a species is permanent, and the opportunity to study its ecological role is gone, along with any economic or cultural benefits (option value) to society it may have provided (Naylor 2000). Thus, continuing efforts to minimize or eliminate negative impacts on biodiversity and preserve natural ecosystems are valuable if not critical, and endeavors to conserve ecosystem services are both economically as well as culturally worthwhile.

Invasive species and trophic interactions

The escalating changes in biodiversity that have been caused by invasive species have prompted studies of their impacts on community structure. The introduction of an invasive species to a community can result in disruption of the pre-invasion food web, with positive or negative outcomes depending on the characteristics of the invasive and its interactions with other plants and herbivores. An invasive plant species may outcompete native species for certain resources, causing population decline or local extinction of the inferior competitor (Fig. 1A). Invasive plant species are often associated with lower native species richness. For example, the exotic species *Lonicera*

japonica and *Rosa multiflora* were more abundant in abandoned agricultural fields that had fewer native species (Meiners et al. 2002, Meiners and Cadenasso 2005), and garlic mustard (*Alliaria petiolata*), an abundant invasive species in the Midwest (Anderson et al. 1996), displaces native plant species by reducing seedling growth of native species through disruption of its mycorrhizal associations (Vaughn and Berhow 1999, Prati and Bossdorf 2004, Stinson et al. 2006). However, though these examples imply that in lower species richness is caused by the invasive species, in many cases it is unclear whether lower species richness is a result and/or if non-native species invade areas with fewer other plant species (see below).

In addition to their direct impacts on other plants, invasive plant species may affect species in other trophic levels, such as herbivores. For example, an invasive plant could be an additional food source for an herbivore and so could increase its abundance (Fig. 1B). Alternatively, an unpalatable invasive species (e.g. one with defensive secondary chemistry or morphological characteristics such as spines or barbs) that reduces the abundance of palatable native plant species could also reduce the abundance of herbivores that eat the palatable species (Fig. 1C).

The effects of invasive plants on herbivores can result in indirect effects on native plant species. A positive indirect effect known as “enemy release” or “associational resistance” (Tahavainen and Root 1972, Keane and Crawley 2002) results if the invasive plant causes reduced herbivory on a native species (Fig. 1D). Conversely, “apparent competition” (Holt 1977, Orrock et al. 2008) occurs if the invasive plant causes herbivores to increase in abundance, resulting in greater herbivory to a native plant species. Apparent competition also could occur if the invasive species causes the native species to be more easily located and eaten by herbivores, such as through a cumulative effect of sensory cues that attract herbivores (i.e., plant apparency or associational susceptibility; Feeny 1976, White and Whitham 2000, Lau and Strauss 2005) (Fig. 1E). Though such indirect effects can be difficult to predict, they can be important determinants of community structure and dynamics (e.g. Brown et al. 1986, Lau and Strauss 2005, White et al. 2006).

Sagebrush steppe

Sagebrush steppe is a semi-arid ecosystem that covers 44.8 million hectares of land in the western U.S. (West 1983, West and Young 2000). It has been severely degraded by the activities of humans, such as agriculture, grazing, and recreation (Noss et al. 1995), making it susceptible to invasion by exotic species (Hobbs and Huenneke 1992). Large areas of sagebrush steppe have been converted to non-native agricultural crop species that must be irrigated and fertilized. Grazing by livestock and off-highway vehicle use can destroy native biological soil crusts, which are composed of important microorganisms within this ecosystem (Belnap 1995). Additionally, grazing and the recreational use of off-highway vehicles can assist in the spread of invasives by reducing the abundance of native plants, creating open space for non-native plants to establish, as well as through transportation of their seeds (Olf and Ritchie 1998, Gelbard and Belnap 2003).

The majority of studies of exotics in sagebrush steppe have focused on cheatgrass (*Bromus tectorum*), a highly aggressive invader that has a large impact on ecosystem processes. Cheatgrass is thought to decrease plant species diversity by increasing fire frequency and altering nutrient cycling (Mack 1981, D'Antonio and Vitousek 1992, Knapp 1996, Belnap et al. 2006, Rimer and Evans 2006, Adair et al. 2008). Additionally, cheatgrass can cause changes in the abundance and diversity of soil biota (Belnap et al. 2005). However, few studies have examined the impacts of other exotic plants in sagebrush steppe.

Sisymbrium altissimum L.

Sisymbrium altissimum L., a mustard (Brassicaceae) species that was originally introduced from Eurasia and has since become naturalized within the U.S. and Canada (USDA, NRCS 2006), is one of the most abundant invasive plant species in the Great Basin (Holmgren et al. 2005). The biology and ecology of *S. altissimum* lend to its success as an invasive species. *S. altissimum* is an annual that germinates in either late fall or spring; thus, it becomes established and uses resources before most other plant species have germinated (Piemeisel 1951, Young et al. 1970). One *S. altissimum* plant can produce up to 1.5 million seeds (Howard 2003), which can be dispersed long

distances when the plant breaks off at the base and tumbles along the ground, driven by wind. Additionally, its seeds can accumulate in the soil and germinate several years after dispersal (Howard 2003). *S. altissimum* is most commonly found along roadsides and other disturbed areas, but it is also able to colonize plant communities that have little to no disturbance (Rollins 1993).

Little is known about the relationships of *S. altissimum* with native plants or herbivores. Within the plant community, *S. altissimum* could fill a niche not occupied by native or other exotic plants, increasing plant species richness. Alternatively, it may be a superior competitor for resources, resulting in a decrease in native plant diversity. In addition, *S. altissimum* may alter the relationships between herbivores and native plants. For instance, both the larvae and adults of butterflies feed on plants and many have specific host-plant preferences for oviposition and larval growth and development (Verschaffelt 1910, Ehrlich and Raven 1965, Scott 1986). One example of such specificity is the preference of white butterflies (Lepidoptera: family Pieridae, subfamily Pierinae) to oviposit on plant species in the mustard family (Brassicaceae), which the larvae then consume (Chew 1977, Scott 1986). Mustard species produce glucosinolates, which are toxic secondary compounds that act as a chemical defense to most herbivores (e.g. Feeny 1977, Hopkins et al. 2009). However, glucosinolates are not toxic to pierid butterflies and may be used by adult pierids to locate host plants (Renwick 1994, 2001; Hopkins et al. 2009).

Sisymbrium altissimum is a potential larval host for pierids, so it may affect the abundance of pierids and/or alter the interactions between pierid butterflies and their other host plants. Pierids use native mustard species as host plants, resulting in a direct negative effect on these plants (Ehrlich and Raven 1965, Scott 1986). Pierids can use *S. altissimum* as a food resource (Shapiro 1975, Garth and Tilden 1986); thus, *S. altissimum* could benefit pierids by supporting a higher abundance than would otherwise be present. If *S. altissimum* supports a higher abundance of pierids, then native mustards could experience more herbivory as a result of apparent competition. However, if pierids preferentially use *S. altissimum*, a native mustard could have reduced herbivory from pierids through associational resistance.

Craters of the Moon National Monument and Preserve

Here we examine the relationships between *S. altissimum* and the native plants and butterflies of kipukas at Craters of the Moon National Monument and Preserve (CRMO). CRMO is a federally protected tract of land that covers over 186,000 ha within the Snake River Plain of SE Idaho (Huntly 2009) and contains islands of vegetation known as kipukas. A kipuka, Hawaiian for “window,” is a patch of native sagebrush steppe which was surrounded and isolated by lava flows 15,000 to 2,000 years ago (Tisdale et al. 1965, Huntly 2009). The kipukas are good sites for studying invasion by exotic plants because they comprise a set of replicate natural communities that vary in plant species composition, including non-native plant abundances.

Study goals

We asked: What is the distribution and abundance of *S. altissimum* in the kipukas of CRMO? Is there evidence that the abundance of *S. altissimum* may have affected the diversity and/or abundance of native plants, particularly native mustards, in kipukas? What is the diversity of butterfly species at CRMO and what are their distributions? Is the distribution and/or abundance of pierid butterflies related to *S. altissimum*?

Based on the biology of *S. altissimum*, we predicted that native plant species diversity would be lower where *S. altissimum* was more abundant. We also predicted that native mustard abundance and diversity would be lower where *S. altissimum* was more abundant, since *S. altissimum* could outcompete natives. Additionally, we expected to see more pierid butterflies in kipukas where the abundance of both *S. altissimum* and native mustards was higher, since pierids use *S. altissimum* as a host plant (Fig. 2).

METHODS

Study area. We studied the plant communities of the Wapi flow and the relationships of *S. altissimum* with the native plants and butterflies of the sagebrush steppe communities that characterize kipukas at Craters of the Moon National Monument and Preserve (CRMO). CRMO (park headquarters: 43°27'44.35"N, 113°33'40.85"W) is located in the northern Snake River Plain, which stretches across most of southern Idaho. CRMO is

comprised of two separate flows, which cover a total of 460,000 acres of land (NPS 2007): the larger Craters of the Moon flow, which is composed of both a'a (crunchy) and pahoehoe (ropy) lava types, and the smaller Wapi flow, which is mostly pahoehoe lava. The kipukas within the flows vary in size (0.02 to 2200 acres), as well as distance from the edge of the flow (< 1 to 7000 m), and their soil types vary, but most contain fine-grained silty clay or clay loams (Tisdale et al. 1965, Huntly and Kaiser 2009).

The climate of CRMO is typical of a semi-arid region. Yearly temperatures can range from -20°F in the winter to $\geq 100^{\circ}\text{F}$ in the summer, though the average range is $10-85^{\circ}\text{F}$ (WRCC 2009). The surface temperatures of lava can exceed 170°F in the summer (NPS 2007), providing a thermal challenge to both plants and animals. CRMO is dry and receives an average of only 390.9mm precipitation per year (WRCC 2009), mostly in the form of recharge from winter snow accumulation (West 1983). Additionally, winds are frequent and strong, causing substantial evapotranspirational losses from soil and vegetation (West 1983) and promoting soil erosion (West and Young 2000).

The majority of kipukas and the lava surrounding them are generally not accessed by humans. Entering the kipukas on foot across the lava is challenging and can be dangerous in rainy conditions. The kipukas are scattered throughout the lava flows and are spatially separated from the surrounding sagebrush steppe and agricultural areas. Additionally, much of CRMO is surrounded by public lands that have only a few, poorly maintained roads. Most of the eastern edge of the Wapi flow is bordered by privately owned agricultural fields or grazing allotments, and some routes to enter the park require crossing private land (Kaiser pers. obs.). Thus, much of CRMO is rarely visited by people.

Sample design. We surveyed the plant communities of kipukas in 2007 and 2008, recording species' presence, percent cover, and abundance. We used two survey methods, one quantitative method to record percent cover of all species (point-frame method; Floyd and Anderson 1987) and one qualitative method to rank abundances of all species present (observational survey method; rank abundance categories modified from Palmer 1995, Whiteaker et al. 1998).

In 2007, we visited and surveyed the plant communities of 99 kipukas in the Wapi flow of CRMO. The Wapi was recently added to the park by proclamation of President Clinton (Clinton 2000), and the plant communities of the Wapi kipukas had not been surveyed. In 2008, an additional 104 kipukas were surveyed, 57 in the Wapi flow and 47 in a southern portion of the Craters of the Moon flow that also had not been surveyed. Upon visit, three kipukas in 2007 and eight in 2008 did not fit the criteria for designation as kipukas; these kipukas either did not have a distinct border or had only extremely shallow soil. These 11 kipukas were defined as false and were not further surveyed. Thus, our study was of 153 kipukas in the Wapi flow and 39 in the southern CRMO flow.

In both years, we also surveyed the plant communities of twelve kipukas. We divided the park into four regions (North, West, South, and Wapi; Fig. 3) for purposes of drawing a geographically representative sample, and we selected three kipukas from each region to survey. These twelve kipukas provide baseline data on annual variation in the plant community (Huntly 2009; Fig. 4). We refer to these 12 kipukas below as “long-term survey” kipukas.

Measurement of rank abundance. We recorded rank abundance of species for all 192 kipukas that we sampled in 2007 and 2008. We compiled lists of all plant species observed for each of these kipukas and estimated the rank abundance of each species on a scale of 1 to 4 (1 = rare, 2 = common, 3 = abundant, and 4 = dominant; Huntly and Kaiser 2009). Voucher plants were collected and unidentified plants were taken to the lab for later identification (Hitchcock and Cronquist 1973, Popovich and Atwood 2006).

Measurement of species' cover. We surveyed vegetation in the 12 long-term survey kipukas and an additional nine kipukas selected from the Wapi flow (see below) using the point-frame method (Floyd and Anderson 1987). We placed a 25m transect in each of the four cardinal directions from a point near the center of each kipuka (Fig. 5). Each transect was located halfway between the center point and the edge of the kipuka. We measured the plant community using a 1m x 0.5m point frame structure that contained a 9 x 4 grid of sample points. The point frame was placed on alternate sides of the transect every 2m along each transect beginning at 1m (Fig. 5). Plant species intersected by the 36 sample points within the grid were recorded. This survey gave percent cover species present on a local (1m x 0.5m area) level.

Butterfly census. In 2008, we also surveyed the butterflies of CRMO. In order to have quantitative information on the plant community for a large number of kipukas for which the abundance of *S. altissimum* varied from absent to highly abundant, we chose nine additional kipukas from those surveyed in 2007 in the Wapi region (Fig. 6). The abundances of *S. altissimum* within these kipukas were estimated during observational surveys in 2007 and were ranked using a scale of 0 to 4 (0 = absent, 1 = rare, 2 = common, 3 = abundant, and 4 = dominant; see above), and we chose two kipukas randomly from each group with rank abundance 4, 3, and 2 of *S. altissimum* (Kipukas 465 and 538, 493 and 537, and 543 and 585, respectively). We also chose one kipuka randomly from rank abundance 1 (K587) and one from a kipuka where *S. altissimum* was not present (K436). We only chose one kipuka each from rank abundances 1 and 0 because many of the twelve long-term survey kipukas had little to no *S. altissimum*, so we chose a larger number from groups with higher rank abundances of *S. altissimum*. A ninth kipuka was surveyed due to an error in locating kipuka 520 for sampling. Thus, we sampled 21 kipukas (the 12 long-term survey kipukas, plus the additional 9 Wapi kipukas) representing a broadly geographically distributed sample of kipukas with a broad range of *S. altissimum* abundance (Fig. 7).

We surveyed butterflies in 17 of these 21 kipukas. Three of the 17 kipukas were located in the North, two were in the South, and the remaining twelve were in the Wapi region (Fig. 8). The three long-term survey kipukas in the West, as well as one in the South, were not sampled for butterflies due to time constraints and difficulty in accessing them. Each kipuka was surveyed for butterflies twice within the late spring to early summer. Two kipukas (K520 and K520A) were surveyed a third time, and for these 2, we chose two of the three surveys to obtain a balanced, equal-effort data set that includes 2 surveys for each kipuka over the sampling period. Survey 1 from 520 (6/14) and survey 1 from 520A (5/19) were not included in the analyses that used this quantitative data set.

We surveyed butterflies using the Pollard walk (Pollard 1977). A single observer walked at a slow, steady pace along a 50m transect located across the center of each kipuka and recorded any butterfly species seen within a moving window of up to 5m above the ground and from 2.5m in front of or on either side of the observer. We used a

sweep net to pursue and capture butterflies for identification, and those that escaped capture were identified to family only (e.g. Pieridae sp.). We attempted to survey in conditions in which butterflies are most active: between mid-morning and late afternoon on clear days with ambient to warm temperatures and minimal wind (Pollard and Yates 1993). However, due to time constraints, 1 survey was performed in unfavorable weather conditions.

Data analysis. We mapped the distribution and rank abundances of *S. altissimum*, based on the rank abundance survey, using ArcGIS software (ESRI ArcMap 9.2). We used data from the 12 long-term survey kipukas to examine whether *S. altissimum* appeared to be increasing in abundance or occurrence on kipukas. Both frequency of occurrence (number of times present in kipukas) and abundance (percent cover) of *S. altissimum* were calculated.

Species richness and abundance. The numbers of native and non-native plant species (species richness) for all kipukas surveyed in 2007 and 2008 were calculated. Plants identified to genus only, such as a perennial grass species which had no inflorescences, were not included in species richness counts unless there were no other species of that same genus within a kipuka. Unique unidentified forb and grass species were treated as independent taxa and included in species counts.

We measured species richness on two scales: kipuka-wide and local. Kipuka-wide species richness is all species we observed within a kipuka during observational surveys. Local species richness is the number of species we observed in each point frame. We examined species richness from two different spatial scales to examine plant-plant relationships at both a small scale, where individuals interact, and a larger scale, where patterns of plant diversity often correspond with environmental heterogeneity (Shea and Chesson 2002, Davies et al. 2005).

We compared the median native and non-native species richnesses among kipukas in the South and Wapi regions, where *S. altissimum* abundance was ranked from 0 to 4, using Kruskal-Wallis tests (PROC NPAR1WAY; SAS 9.1). We used a non-parametric

analysis of variance due to unequal sample sizes for the 5 rank abundances of *S. altissimum*.

We also compared native and non-native species richnesses with *S. altissimum* percent cover for the 21 kipukas that were point-frame sampled in 2008 and for the Wapi kipukas alone using Spearman rank correlation (PROC CORR SPEARMAN; SAS 9.1). We used a non-parametric test because the data were non-homogeneous and could not be corrected by data transformation.

We calculated native species' abundance for each of the long-term survey kipukas (12), as well as for those we added in 2008 (9). We compared native species' abundance to percent cover of *S. altissimum* in all 21 kipukas, as well as Wapi kipukas only, using Spearman rank correlation (PROC CORR SPEARMAN; SAS 9.1).

Local species richness. We calculated local native and non-native species richnesses for each 0.5 x 1.0m point-frame in each of the long-term survey kipukas (12), as well as for those we added in 2008 (9). For each point frame, native or non-native richness was calculated as the total number of native or non-native species intersected by the point frame, which was always between 0 and 36.

For each kipuka where *S. altissimum* was present, we evaluated the relationship between local native and non-native species richnesses and the abundance (percent cover) of *S. altissimum* using Spearman correlations (PROC CORR SPEARMAN; SAS 9.1).

Mustard species richness and abundance. Native and non-native species richnesses of mustards were calculated for all kipukas surveyed in 2007 and 2008. Native mustards included *Descurainia pinnata*, *D. richardsonii*, *Erysimum asperum*, *Lepidium densiflorum*, *Phoenicaulis cheiranthoides*, and *Schoenocrambe linifolia*, and several species of *Arabis*. Non-native mustards included *Alyssum desertorum*, *Camelina microcarpa*, *Chorispora tenella*, *Descurainia sophia*, *Draba verna*, *Isatis tinctoria*, *Lepidium perfoliatum*, and *Sisymbrium altissimum*. Species identified only to genus were not included in species richness counts unless they were known to be distinct from identified mustard species.

We compared the mean ranks of total native and non-native mustard species richnesses among kipukas with different abundances of *S. altissimum* in the South and Wapi regions using Kruskal-Wallis tests (PROC NPAR1WAY; SAS 9.1). We used non-parametric analyses of variance due to unequal sample sizes for the 5 different rank abundances of *S. altissimum*.

We also compared native and non-native mustard species richnesses and the total abundance of native mustards with *S. altissimum* abundance for all kipukas point-frame sampled in 2008, as well as separately for those in the Wapi only, using Spearman rank correlation (PROC CORR SPEARMAN; SAS 9.1).

Butterfly diversity and abundance. We grouped butterflies by family for analyses. We calculated butterfly diversity and abundance, as well as abundance of pierids. Butterfly diversity was calculated as the number of unique families seen during surveys. Butterfly and pierid abundances were calculated as the total number of butterflies or pierids seen during surveys. We did not calculate the diversity of pierid butterflies, since many individuals could not be identified to species. We mapped the distributions and proportional abundances of butterfly families using ArcGIS software (ESRI ArcMap 9.2).

We examined the relationships between butterfly diversity, butterfly abundance, and pierid abundance and the percent cover of *S. altissimum* using linear regression in SAS (PROC GLM; SAS 9.1). We made these comparisons using data from all kipukas surveyed for butterflies (n = 17) as well as those from the Wapi alone (n = 12). We also compared the relative abundance of pierids (as a proportion of all butterflies observed) with the percent cover of *S. altissimum* in the butterfly census kipukas (n = 17) as well as those in the Wapi alone (n = 12) using linear regression in SAS (PROC GLM; SAS 9.1).

RESULTS

Distribution and abundance of plant species

We observed many different species of shrubs, grasses, and annual and perennial forbs in the kipukas we surveyed in 2007-2008 (Fig. 9, Table 1). Two species, *Artemisia tridentata*, a shrub, and *Bromus tectorum*, a non-native grass, were observed in all kipukas we surveyed (n = 192). In the majority of kipukas, *A. tridentata* was the

dominant species (rank 4, 175 of 192, 91%). *Bromus tectorum* was also dominant in several kipukas (44 of 192 kipukas, 23%), but most often was abundant (rank 3, 116 of 192 kipukas, 60%). The most commonly observed forb in the Wapi was *Lappula occidentalis* (147 of 153 kipukas, 90%), but it was generally rare (rank 1). *Crepis acuminata* was the most common forb observed in the South and was common in most kipukas there (rank 2, 37 of 39 kipukas, 95%); it was the second most common species in the Wapi, but tended to be rare (rank 1, 144 of 153 kipukas, 94%).

We also saw slight differences in the plant species composition between kipukas in the South versus the Wapi region (Fig. 9). Twenty-two of the 30 most common species were the same in both regions, though their frequency of occurrence differed. For example, *Phlox longifolia* was one of the 30 most common species in both the Wapi and the South (ranked 10th and 21st most common, respectively), but it occurred in different proportions in each region (81% vs. 64% of kipukas, respectively). Additionally, *Descurainia sophia* was the 30th most frequently observed species in the Wapi (57% of kipukas), but occurred at a much lower frequency in the South (13% of kipukas).

A total of 15 non-native species were observed in kipukas in 2007-2008 (Fig. 10, Table 2). Eight of these, *B. tectorum*, *S. altissimum*, *Tragopogon dubius*, *Lactuca serriola*, *Draba verna*, *Alyssum desertorum*, *Descurainia sophia*, and *Ranunculus testiculata*, were the most commonly observed non-natives and occurred in both the South and Wapi regions. Six other non-natives, *Taraxacum officinale*, *Poa bulbosa*, *Chorispora tenella*, *Camelina microcarpa*, *Isatis tinctoria*, and *Medicago sativa*, were found only in the Wapi, and one (*Poa pratensis*) occurred only in the South. *Bromus tectorum* had the highest average rank abundance (3 = abundant), followed by *S. altissimum*, which was common (rank 2). The other 13 non-natives were rare or absent (average ranks 1 or 0).

Sisymbrium altissimum distribution and abundance

Sisymbrium altissimum was present in a large proportion of the kipukas we surveyed in both the Wapi and South regions. *S. altissimum* was present in 140 of 153 kipukas (91.5%) and was the second most frequent non-native species in the Wapi (Fig. 11). In the South, *S. altissimum* was observed in 32 of 39 kipukas (82.1%) and was the

fourth most frequent non-native species (Fig. 12). *Bromus tectorum*, *T. dubius*, and *L. serriola* were the first, second, and third most frequent non-native species in the South (100%, 89.7%, and 87.2% of kipukas, respectively).

The abundance of *S. altissimum* varied regionally (Fig. 13), as well as within the South and Wapi regions, where our sampling effort was focused. *S. altissimum* was absent from the North and West regions, and ranged from absent (rank 0, 7 of 39 kipukas, 18%) to dominant (rank 4, 1 of 39 kipukas, 3%) in the South. In the Wapi, *S. altissimum* was generally common (rank 2, 61 of 153 kipukas, 40%) but ranged from absent (rank 0, 13 of 153 kipukas, 8%) to dominant (rank 4, 2 of 153 kipukas, 1%).

Sisymbrium altissimum occurred on an increasing number of the long-term survey kipukas, present in one, two, four, and four of 12 kipukas in 2004, 2005, 2007, and 2008, respectively (Fig. 14). *S. altissimum* also increased in total percent cover from 2% in 2004 to 66% in 2008 in these 12 kipukas (Fig. 14). Additionally, there was an average increase in percent cover of *S. altissimum* (mean $\pm$ SD = 16.05% $\pm$ 11.3) in kipukas where it was present in 2008 (K79, 81, 520, and 582). Kipuka 582 had the largest increase in percent cover of *S. altissimum* (32.87% from 2005 to 2007).

Native species richness and abundance

Native plant diversity ranged from 7 to 56 species per kipuka (mean 29), and the range and average were similar in the Wapi (13 to 53, mean 29) and the South (7 to 56; mean 27). In the South, median native plant species richness was significantly different among kipukas with different rank abundances of *S. altissimum* (K-W ANOVA, $H = 11.285$, d.f. = 3, $p = 0.010$; Fig. 15), but the difference was not significant in the Wapi ($H = 5.113$, d.f. = 3, $p = 0.164$; Fig. 15). Similarly, native species richness decreased significantly with increasing percent cover of *S. altissimum* for all kipukas point-framed sampled in 2008 ($\rho = -0.455$, $n = 20$, $p = 0.044$), but the relationship was not statistically significant for the Wapi alone ($\rho = -0.360$, $n = 11$, $p = 0.277$; Fig. 16).

At a local level, native species richness and percent cover *S. altissimum* were significantly negatively correlated in 10 of the 13 kipukas where *S. altissimum* was present (Table 3).

Native plant abundance ranged from 10.2 to 87.2% per kipuka (mean 45.7%) in those point-frame sampled in 2008. Native plant cover was significantly negatively related to cover of *S. altissimum* in all kipukas ($\rho = -0.853$, $n = 21$, $p < 0.0001$) and in the Wapi kipukas only ($\rho = -0.790$, $n = 12$, $p = 0.002$; Fig. 17).

Non-native species richness

Non-native plant species richness ranged from 0 to 10 per kipuka (mean 5). The range and average was similar in the Wapi (2 to 10, mean 6) and the South (2 to 8, mean 5). Additionally, the median number of non-native plant species was significantly different among kipukas where the rank abundance of *S. altissimum* differed in the Wapi (K-W ANOVA, $H = 12.042$, d.f. = 3, $p = 0.007$; Fig. 15) and in the South ($H = 12.996$, d.f. = 3, $p = 0.005$; Fig. 15). Non-native species richness increased with increasing percent cover of *S. altissimum* in all kipukas point-frame sampled in 2008 ($\rho = 0.666$, $n = 20$, $p = 0.001$), but there was not a significant relationship in the Wapi region alone ($\rho = 0.146$, $n = 11$, $p = 0.669$; Fig. 16).

At a local scale, there were no significant correlations between non-native species richness and percent cover of *S. altissimum* (Table 3). Two kipukas (K81 and 538) had marginally significant negative relationships ($p = 0.091$ and $p = 0.08$, respectively), and one (K493) had a marginally significant positive relationship ($p = 0.061$).

Mustard species richness and abundance

Sisymbrium altissimum was the most frequent mustard species observed in the kipukas in both the Wapi and South regions (92% vs. 82% of kipukas, respectively), but we observed many other native and non-native mustards (Fig. 18, Table 4). The most commonly observed native mustard in the Wapi was *Descurainia pinnata* (121 of 153 kipukas, 79%), while *Arabis holboellii* was most common in the South (32 of 39 kipukas, 82%). Other natives were much less frequent in both regions (Fig. 18). Additionally, non-native mustard species other than *S. altissimum* were observed at fairly high frequencies. *Draba verna*, *Descurainia sophia*, and *Alyssum desertorum* were common in both regions (71%, 55%, and 48% of kipukas, respectively), but non-native mustards were rare.

At the kipuka-wide level, species richness of native mustards ranged from 0 to 3, with an overall average of only 2 species. There were more non-native species, which ranged from 0 to 5 species, but the average diversity was the same, 2 species. The species richness of native mustards was lower in the North and West regions (1) compared to the South and Wapi (2), as was the richness of non-native mustards, though it was more variable among regions (0 and 1 vs. 2 and 3, respectively). Five of the 15 non-native species at CRMO were mustard species, and of the seven that were observed in $\geq 50\%$ of kipukas, 4 were mustard species.

Native mustard richness was not significantly higher among kipukas where the abundance of *S. altissimum* differed in the South or Wapi regions (K-W ANOVA, $H = 4.207$, d.f. = 3, $p = 0.240$ and $H = 2.868$, d.f. = 3, $p = 0.413$, respectively; Fig. 19). In contrast, there was a significant difference in non-native mustard richness in the Wapi ($H = 16.073$, d.f. = 3, $p = 0.001$) and the South ($H = 8.219$, d.f. = 3, $p = 0.042$; Fig. 19).

Additionally, no relationship was found between native mustard species richness and percent cover of *S. altissimum* in all kipukas point-frame sampled in 2008 ($\rho = 0.280$, $n = 21$, $p = 0.218$), nor in those in the Wapi ($\rho = -0.148$, $n = 12$, $p = 0.647$; Fig. 20). However, there was a positive significant relationship between non-native mustard species richness and percent cover of *S. altissimum* in all kipukas point-frame sampled in 2008 ($\rho = 0.839$, $n = 21$, $p < 0.0001$; Fig. 20). This relationship was marginally significant among kipukas in the Wapi alone ($\rho = 0.536$, $n = 12$, $p = 0.072$; Fig. 20). There was not a significant relationship between percent cover of native mustard species and percent cover of *S. altissimum* for all kipukas ($\rho = -0.157$, $n = 21$, $p = 0.497$) or for those in the Wapi alone ($\rho = -0.368$, $n = 12$, $p = 0.239$; Fig. 21).

Butterfly species richness and abundance

We observed a total of 186 butterflies from 10 subfamilies during surveys over the sampling period (Fig. 22, Tables 5, 6). The number of butterflies seen during a survey ranged from zero to 15 (mean 9.8). The range in number of butterflies observed was similar for the Wapi (0 to 15) and the other regions (0 to 14), but the average was slightly lower in the Wapi (8.9 butterflies per kipuka) than other regions (13.2). The most frequently observed butterflies belonged to the subfamily Pierinae, or the white

family (86 of 186 observations, 46%); the least frequently observed subfamily was the Papilioninae (1 of 186 observations, 0.5%).

The abundance and diversity of butterflies differed among regions (Fig. 23, Table 7). More butterflies were seen in the Wapi than in either the North or South regions (107 compared to 62 and 17, respectively), but more kipukas were surveyed in the Wapi than in other regions (12 compared to 3 and 2, respectively). In the North, the most commonly observed butterflies were members of the Satyrinae (average 14 per kipuka), whereas Pierinae were most common in the South (8) and Wapi (6). We only observed one papilionid in all 36 surveys.

Additionally, the number of butterfly families differed among regions. Butterflies from 9 subfamilies were observed during surveys in the Wapi, compared to 7 in the North and 2 in the South regions (Table 7). We did not observe any swallowtails (Papilioninae) or skippers (Hesperiinae) in the North or South, but butterflies from these families were seen in the Wapi. The species of butterflies that were observed varied considerably over the course of the sampling period (Fig. 24). Some subfamilies were seen only in early (i.e., Hesperiinae) or late surveys (i.e., Lycaeninae), while others were consistently present over the sampling period (i.e., Pierinae and Nymphalinae).

We also observed many butterflies outside of the surveys. In the North and the West, we saw numerous small wood nymphs (Subfamily Satyrinae: *Cercyonis oetus*), as well as a few whites (Subfamily Pierinae), blues (Subfamily Polyommatainae), and fritillaries (Subfamily Nymphalinae: *Speyeria* spp.) In the South, we saw several whites in nearly every kipuka we surveyed, and fritillaries were also abundant. Additionally, we observed a few blues, small wood nymphs, ringlets (Subfamily Satyrinae: *Coenonympha tullia*), hairstreaks (Subfamily Theclinae), and painted ladies (Subfamily Nymphalinae: *Vanessa cardui*), as well as one sulphur (Subfamily Coliadinae). In contrast, we saw proportionately more species of butterflies in the Wapi, including some species that were not seen in any other region, such as grass skippers (Subfamily Hesperiinae) and swallowtails (Subfamily Papilioninae). We also observed a few sulphurs, ringlets, blues, and many more painted ladies than seen in other regions. Though small wood nymphs were observed in all other regions, we did not see any in the Wapi.

Butterfly abundance was not linearly associated with percent cover of *S. altissimum* ($R^2 = 0.103$, d.f. = 16, $p = 0.210$), but butterfly diversity was weakly associated with *S. altissimum* ($R^2 = 0.163$, d.f. = 16, $p = 0.108$; Fig. 25). Pierid abundance also was not significantly related to percent cover of *S. altissimum* ($R^2 = 0.048$, d.f. = 16, $p = 0.399$; Fig. 25). In the Wapi, butterfly abundance ($R^2 = 0.036$, d.f. = 11, $p = 0.554$) and pierid abundance ($R^2 = 0.0001$, d.f. = 11, $p = 0.972$) were not significantly related with percent cover of *S. altissimum*, though butterfly diversity tended to be lower where *S. altissimum* was more abundant ($R^2 = 0.205$, d.f. = 11, $p = 0.140$; Fig. 25). However, there was a significantly higher proportion of pierids in kipukas with more *S. altissimum* ($R^2 = 0.327$, d.f. = 16, $p = 0.016$); this pattern was similar, though not significant, in the Wapi kipukas alone ($R^2 = 0.197$, d.f. = 11, $p = 0.148$; Fig. 26).

DISCUSSION

We examined the relationships of plants and butterflies with *S. altissimum* abundance. We found some evidence to support the hypothesis that native plant species richness would be lower in areas where *S. altissimum* was present. At a local scale, native plant richness and *S. altissimum* abundance were significantly negatively related. At a kipuka-wide level, this relationship was also significant overall but not among Wapi kipukas alone. We also found a significant difference among native richness where rank abundance of *S. altissimum* differed in the South, but not the Wapi. In contrast, we did not find any support for the hypothesis that *S. altissimum* would decrease native or non-native mustard species richness or abundance.

We also found some evidence to support the prediction that more pierids would be observed where *S. altissimum* was more abundant. We found no significant relationship between pierid abundance and percent cover of *S. altissimum*, though the trend suggests that there are more pierids where *S. altissimum* is more abundant. The pierids comprised a significantly greater proportion of the butterflies observed in kipukas with higher percent cover of *S. altissimum*, and the Wapi kipukas alone show the same trend, though not significant.

Distribution and abundance of S. altissimum

The pattern of *S. altissimum* distribution illustrates both N-S and E-W gradients. In the kipukas we surveyed, *S. altissimum* is more abundant in the Wapi, the southernmost part of the Park, than in the North, where it is absent. Additionally, there was also a distinct pattern of abundance among kipukas in the South and Wapi regions. Northern kipukas in the South region had less *S. altissimum* than those in the southern. The Wapi had many kipukas with high abundances of *S. altissimum*, but those on the western side of the flow tended to have more than those on the eastern side. This pattern could be explained by the direction of the local winds, which move from west to east (pers. obs.). Thus, kipukas on the west side of the flow may have higher propagule pressure, since *S. altissimum* likely tumbles more easily across sagebrush steppe than across lava, where it could be lodged in the crevices or blocked by the peaks in the flow. Propagule pressure is necessary for invasive plants to be introduced to new environments (Davis et al. 2000), and kipukas on the western side of the Wapi may experience a higher propagule pressure than those on the eastern side.

Native species richness

We examined the relationship between native species richness and *S. altissimum* on two scales: kipuka-wide and local. For entire kipukas, native species richness differed significantly among kipukas with different rank abundances of *S. altissimum* in the South, and it was lowest where SIAL was most abundant (rank 3 or 4), which agrees with our predictions. Native species richness did not differ significantly among Wapi kipukas where *S. altissimum* rank abundance differed.

We also examined the relationship between native plant richness and percent cover of *S. altissimum* and found some support for our hypothesis. Native species richness was significantly higher overall where *S. altissimum* was rare or absent. We did this comparison using only kipukas in the Wapi and found no significant relationship. In sum, these results show some evidence that *S. altissimum* is affecting native species richness at a kipuka-wide level.

At a local level, we found strong evidence to support the hypothesis that *S. altissimum* would decrease native plant diversity. *S. altissimum* was present in 13 of 21

kipukas, and in 10 of these 13, local native species richness decreased significantly with increasing percent cover of *S. altissimum*. Other studies comparing native species richness of invaded local plots found results similar to ours. Species richness decreased with increasing cover of the exotic species *Lonicera japonica* and *Rosa multiflora* within 0.5 x 2m plots (Meiners et al. 2002, Meiners and Cadenasso 2005). In a study of plant diversity in sagebrush steppe, 1m² quadrats that contained introduced species, including *S. altissimum*, had lower species richness compared to uninvaded controls (Allen and Knight 1984).

These results imply that invasive *S. altissimum* may be outcompeting native species locally, but the relationship between native species richness and *S. altissimum* abundance at a larger scale is difficult to determine. Our results agree with the assertions of Shea and Chesson (2002) and Davies et al. (2005) that native species richness and non-native abundance are negatively related at small scales, where direct competitive interactions take place, but that this relationship is positive at larger scales, reflecting environmental differences among sampled areas. Plants compete locally for limiting resources such as water or nutrients; within the whole kipuka, however, this is less likely.

Non-native species richness

Non-native species richness increased significantly with increasing rank abundance of *S. altissimum* in both regions, and regions where *S. altissimum* was absent (North and West) had the fewest non-native species. Additionally, non-native species richness increased significantly with increasing percent cover of *S. altissimum* in the kipukas we point-frame sampled. This same trend, though not significant, was present in the Wapi kipukas alone. These results show that there are more non-native species where the abundance of *S. altissimum* is high.

S. altissimum may be invading areas that are more invisable because of the availability of resources or because the presence of other non-natives facilitates its establishment. The presence of unused resources could allow other non-native species to also colonize these same areas, resulting in an overall increase in species richness. Davis et al. (2000) suggest that fluctuations in resource availability could increase the

invasibility of an area, facilitating the establishment and spread of exotic species and increasing species diversity.

Native and non-native mustard richness and abundance

We also examined the relationship between native mustard species richness and the abundance of *S. altissimum*. On a kipuka-wide level, native mustard richness did not differ significantly among kipukas with different rank abundances of *S. altissimum* in either the South or Wapi. However, in the South, native mustard richness was zero where *S. altissimum* was dominant. *S. altissimum* was dominant (rank abundance 4) in only 1 South kipuka and 2 Wapi kipukas.

Native mustard species richness was not significantly related to percent cover of *S. altissimum*, but there tended to be more mustard species where *S. altissimum* was more abundant. Unexpectedly, these relationships were both slightly positive, implying that native richness increased with increasing cover of *S. altissimum*. This trend could indicate indirect effects, since we would predict a decrease in native mustard richness with increasing *S. altissimum*. One possible scenario that could explain these results is that the high abundance of *S. altissimum* relative to native mustard species results in less herbivory on native mustard species. This release from herbivore pressure, or associational resistance, has been shown to occur in communities of mustard species (Tahvanainen and Root 1973). More often, though, studies indicate that associational susceptibility occurs (e.g., Thomas 1986, White and Whitham 2000, Lau and Strauss 2005), so it is not likely that it is occurring in our study, especially since our results were not significant. Again, native mustard species did not seem to be affected by *S. altissimum*.

Additionally, we also compared the percent covers of native mustard species and *S. altissimum* and found no significant relationship, though the trend showed a decrease in cover of native mustards with increasing *S. altissimum*, which contrasts that of the previous comparison. However, there were few native mustard species in these samples: the highest percent cover of native mustards in a kipuka was only 2.4%, and the median percent cover was 0.06%, so it is likely that this negative trend is driven by the three kipukas (K335, 436, and 587) that had near zero abundance of *S. altissimum* and high

percent cover of native mustards (1.9%, 2.3%, and 2.4%, respectively). A larger range of all species would make these relationships clearer.

From our results, there is little evidence to suggest that *S. altissimum* affects native mustard species on either a kipuka-wide or local level. The most commonly observed native mustards were *Arabis* species, which flowered and began fruiting earlier in the season than *S. altissimum* (pers. obs.). Thus, native mustards may not be directly competing with *S. altissimum* for resources at all due to differences in their phenology. On the other hand, *S. altissimum* is an early germinant, often beginning rosette growth in either late fall or early spring and continuing until flowering in mid- to late summer, so perhaps it does compete with native mustards for resources. The rarity of native mustard species at CRMO makes it difficult to assess relationships with *S. altissimum* in a sample survey.

Alternatively, it may simply be that these comparisons do not reflect the complicated relationship of mustard species with native herbivores, such as pierid butterflies. Because *S. altissimum* is a food source for pierids in addition to native mustard species such as *Arabis* (Scott 1986, Robinson et al. 2009), any potential indirect effects on native mustard species are difficult to tease apart from direct effects. Because we did not manipulate the presence of pierids or the abundances of *S. altissimum* and native mustards, we cannot determine whether *S. altissimum* is directly affecting natives through competitive effects, or if there are indirect effects due to the presence of herbivores. We also do not know the feeding preferences of pierids or if what relationships exist between pierids and other mustards, especially other non-native mustards, or if other herbivores on mustard species have strong impacts on the presence or abundance of these species. More studies should be conducted to elucidate these relationships.

We also found that non-native mustard richness was significantly higher with increased *S. altissimum* abundance. This pattern mirrors those we detected with the comparisons between *S. altissimum* and total non-native species richness. Non-native mustards were highly prevalent and make up a large proportion of non-native species that we saw, so they influenced the comparisons that we made that included all non-native species.

Butterfly diversity and abundance

Butterfly diversity and abundance in kipukas was relatively high and similar to results of surveys conducted in nearby areas. During surveys, we saw 186 butterflies from a total of 5 families and 10 subfamilies, though most individuals seen were pierids. In 2008, a North American Butterfly Association (NABA) 4th of July count conducted in Laidlaw Park, a very large kipuka located in the West region of CRMO, found 244 individuals from five butterfly families. Of those observed, 198 individuals (80%) were pierids, and the few remaining individuals observed were from other taxa (M. Austin, pers. comm.). Horning (1966) collected individuals from 7 butterfly families and 14 subfamilies at CRMO and nearby areas, but the majority of these (including many species not seen during our surveys) were collected at a riparian site in the Pioneer Mountains north of CRMO. Additionally, surveys conducted in similar vegetation sites on BLM lands near Twin Falls, Idaho (42°34'14.69"N 114°18'55.12"W), in 2006 found similar diversity (Fothergill, unpub. data), though ringlets (*Coenonympha tullia*) and Mylitta crescents (*Phyciodes mylitta*) were more commonly observed than pierids (40% and 28% vs. 16%, respectively). These surveys were conducted every 10 days from April to November, so they likely include far more individuals than our sample.

Butterfly diversity and abundance tended to decline with increasing abundance of *S. altissimum*. This could indicate that *S. altissimum* is reducing native plant species and thus negatively indirectly affecting butterfly diversity and abundance, but we did not examine this relationship in this study.

In addition, a thorough seasonal survey of butterflies at CRMO would be of value and would no doubt reveal more species than we found in this brief survey. Many butterfly species respond to environmental cues such as the availability of food resources, and others are migratory and are present during specific times of the year (Scott 1986), so our brief survey likely underestimates both density and diversity of butterflies at CRMO. A survey that included repeat visits to a set of kipukas over the full growing season, including late summer and early fall, also would improve our ability to determine the relationships between butterflies and plants present within the Park and to ascertain

whether or not the abundance of invasive *S. altissimum* is affecting butterfly diversity and/or abundance.

Additionally, pierid abundance tended to increase with percent cover of *S. altissimum*, as predicted. Adult pierids are known to use *S. altissimum* as a host plant (Scott 1986, Robinson et al. 2009), so we expected to see more pierids where the abundance of *S. altissimum* was higher. We did not see any pierids in one kipuka (K493) where *S. altissimum* cover was relatively high (9%), but this may be because surveys in this kipuka were conducted in less favorable conditions than other surveys. Otherwise, we saw pierids in all other kipukas where *S. altissimum* was present. We also found a positive significant relationship when we compared the relative abundance of pierids (as a proportion of the total number of butterflies seen) with the percent cover of *S. altissimum* in kipukas. This relationship showed the same trend in the Wapi kipukas alone and was marginally significant. Thus, we might conclude that the abundance of *S. altissimum* has a positive direct effect on pierids by increasing their abundance.

Conversely, it appears that herbivory by pierids is not strong enough to deter the spread of *S. altissimum*, given its wide distribution and abundance. We saw many pierids in kipukas other than those we surveyed for butterflies (data not shown), including those throughout the South and Wapi regions. Thus, even though the abundance of pierids appears to be high in the park, they are probably not reducing the abundance of *S. altissimum*. This is in accordance with that of Maron and Vila (2001), who review the evidence for the biotic resistance hypothesis and find little support for the idea that herbivory actually diminishes the spread of invasive plants. Additionally, we did see a small beetle on *S. altissimum* (Kaiser pers. obs.) that looked like *Phyllotreta cruciferae*, the crucifer flea beetle. *P. cruciferae* is a common pest species of cultivated mustard crops such as cabbage, broccoli, cauliflower, and canola (Root 1973), but we do not know its feeding preferences for native or non-native mustard species, nor do we know its effects (if any) on the fitness of the plants. However, given the high abundance of *S. altissimum* within the Park, it is not likely that herbivory from any one herbivore or combination of herbivores is limiting the spread of *S. altissimum*.

It is possible that pierids may become dependent upon *S. altissimum*, since it is the most abundant mustard species at CRMO. Many butterfly species have become

dependent on exotic plant species in California, including several pierid species on *S. altissimum* (Shapiro 2002, Graves and Shapiro 2003). Similarly, exotic *Eucalyptus* trees in California now are used by many bird and salamander species, as well as by monarch butterflies (*Danaus plexippus*) for overwintering (Westman 1990). Such relationships of native species with exotic plants complicate decisions about the eradication of invasive plants.

CONCLUSION

Our study provides baseline information on *S. altissimum*, the plant community, and butterflies of CRMO that may help managers determine the best course of action for controlling *S. altissimum*. *S. altissimum* was the second most frequent non-native species observed within the kipukas at CRMO and was increasing in abundance within the long-term survey kipukas. *S. altissimum* was widespread across the Wapi and occurred less frequently in the South; however, neither the North nor West kipukas that we surveyed had been invaded. Both this regional pattern and the long-term survey data suggest that *S. altissimum* is actively expanding within the park.

We also observed numerous butterfly taxa and recorded their distributions within the Park. We saw many species of butterflies during surveys that were not previously documented at CRMO. A large proportion of the butterflies we observed in surveys were pierids, and there tended to be more pierids where *S. altissimum* was more abundant, suggesting that a strong plant-insect interaction exists between them.

S. altissimum appears to be changing the diversity of native species, especially at a local level, and may ultimately change the community composition over time. Our study provides valuable baseline data for future examination of the specific relationships between *S. altissimum* and native plant diversity, as well as potential trophic interactions among native mustards, *S. altissimum*, and pierid butterflies. These data will allow more informed management decisions for the control and eradication of *S. altissimum*. More extensive surveys and direct experimentation could clarify the roles of *S. altissimum* in native sagebrush steppe.

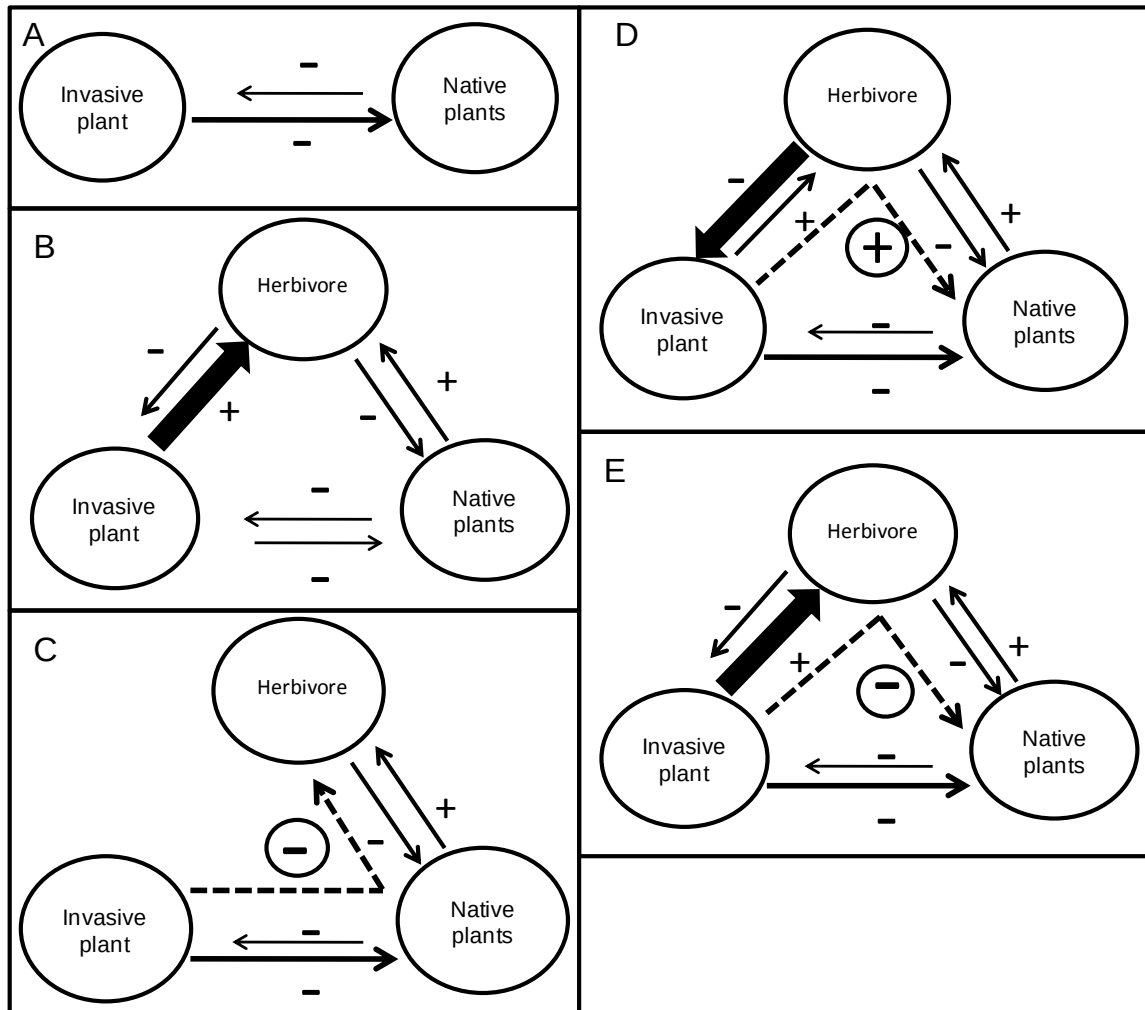


Fig. 1. Direct (A, B) and indirect (C - E) interactions between an invasive plant, native plants, and an herbivore. A. Competition between primary producers. B. Direct positive effect of an invasive plant that is an additional food source on an herbivore. C. When it is not consumed by the herbivore, the invasive plant species indirectly negatively affects the herbivore by reducing the abundance of its native host species. D. Enemy release. The invasive plant species "releases" the native plants from herbivore pressure by functioning as an additional food source. E. Associational susceptibility or plant apparency. The invasive plant species has a negative indirect effect on the native plant species by attracting herbivores which consume the native species. Solid arrows represent direct interactions and dashed arrows represent indirect effects. Arrow size indicates the strength of the interaction.

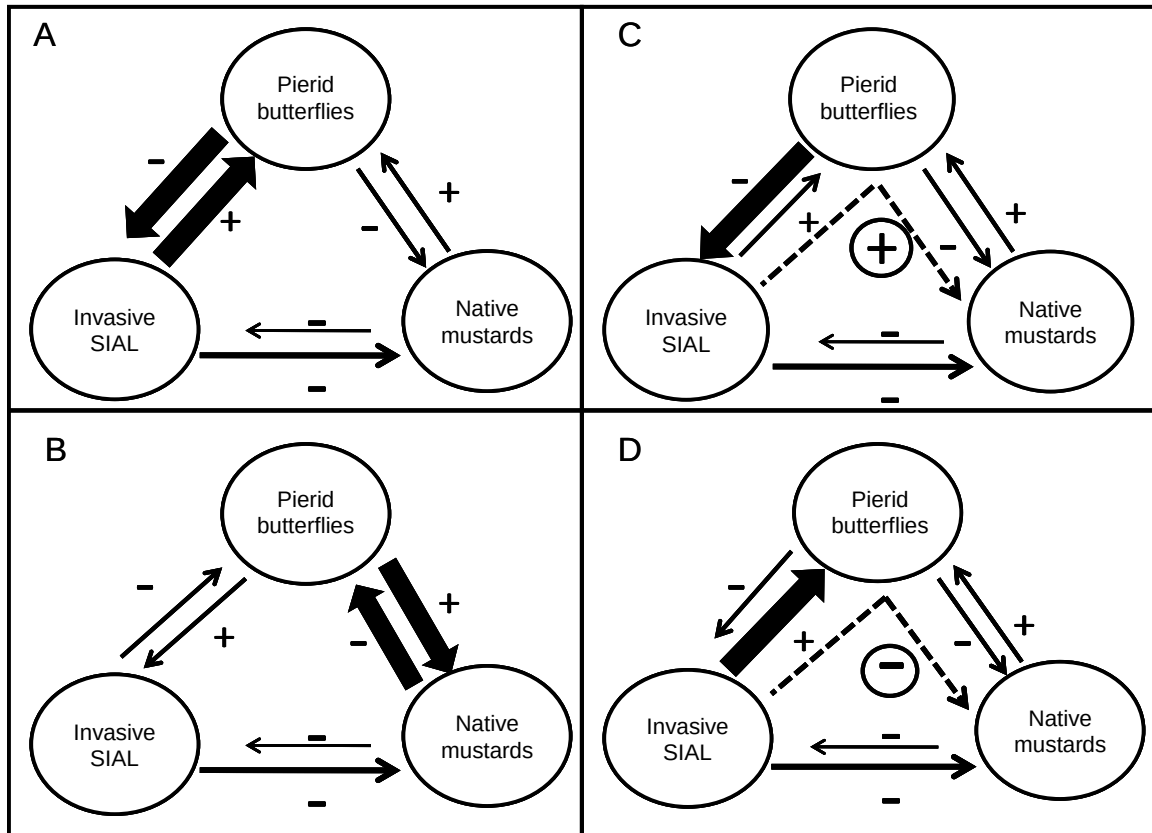


Fig. 2. Potential direct (A, B) and indirect (C, D) interactions between invasive *S. altissimum*, native mustard species, and pierid butterflies. Pierids may prefer *S. altissimum* for food (A), resulting in less herbivory on native mustards (C). Conversely, pierids prefer native mustards for food (B). Additionally, if no food preference exists, the presence of *S. altissimum* could increase pierid abundance or attract more pierids to an area, causing increased herbivory on native mustards (D).

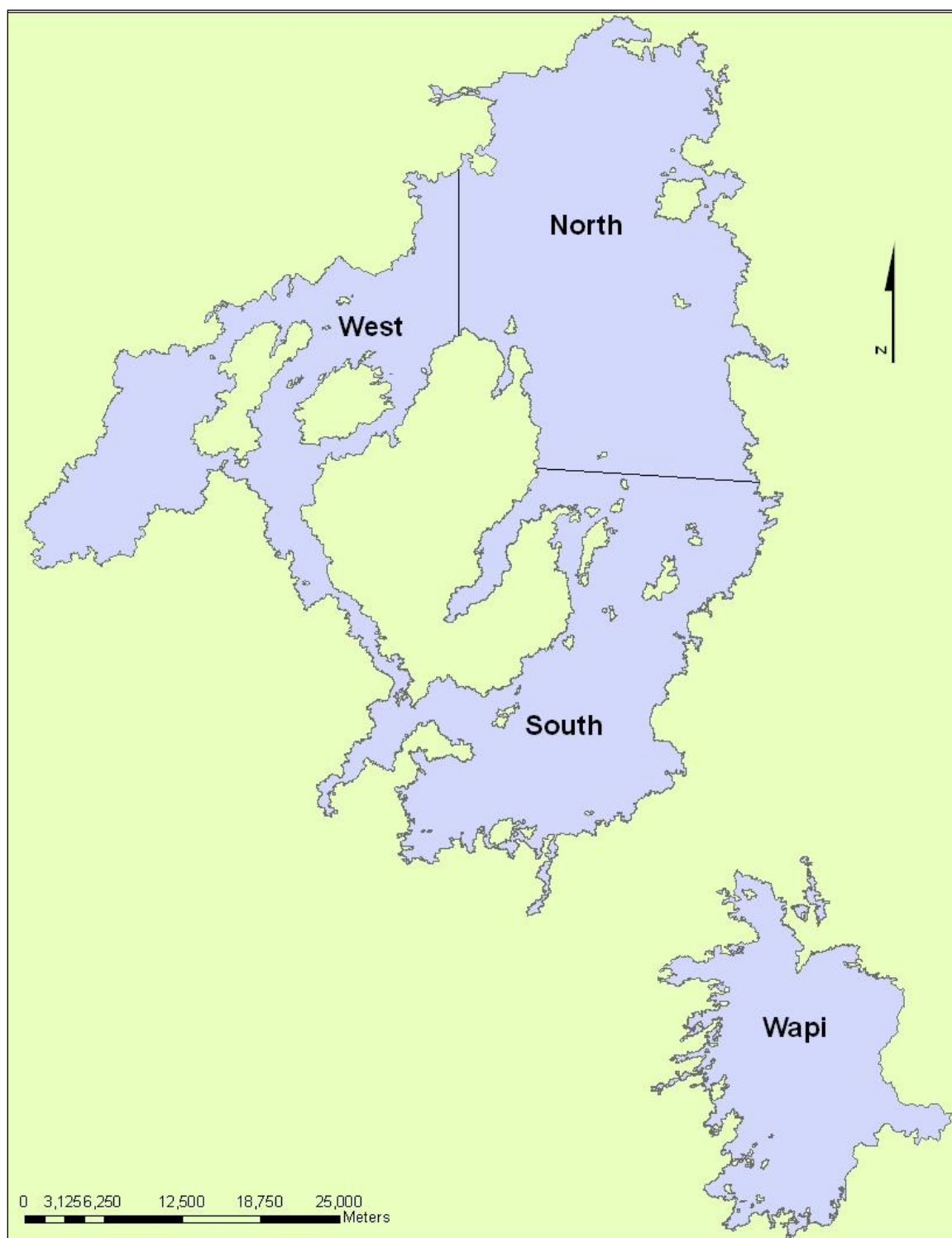


Fig. 3. The four sampling regions (North, West, South, and Wapi) of CRMO, Idaho, USA.

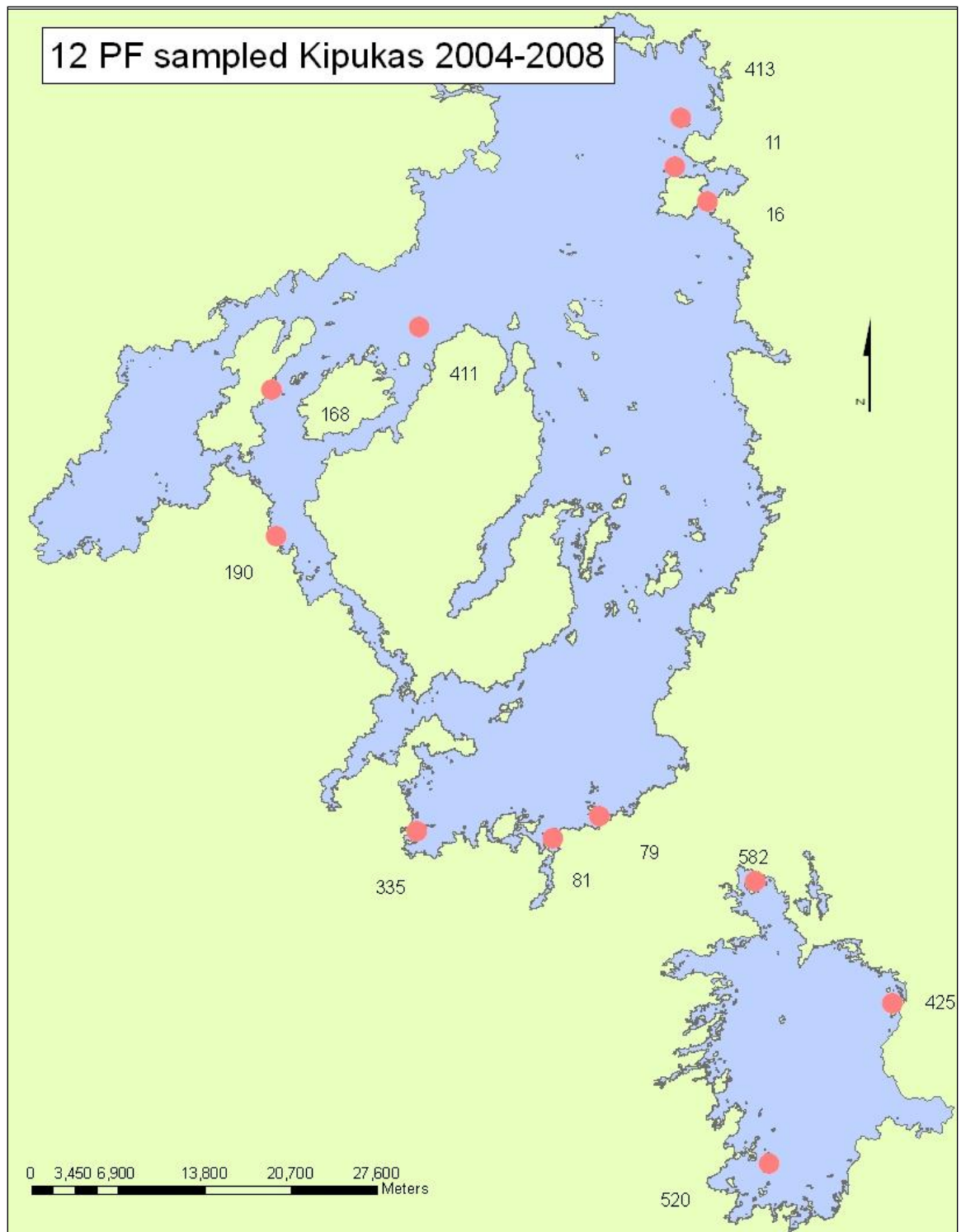


Fig. 4. Locations of the 12 long-term survey kipukas at CRMO, Idaho, USA. Numbers are the kipuka number in the CRMO GIS database.

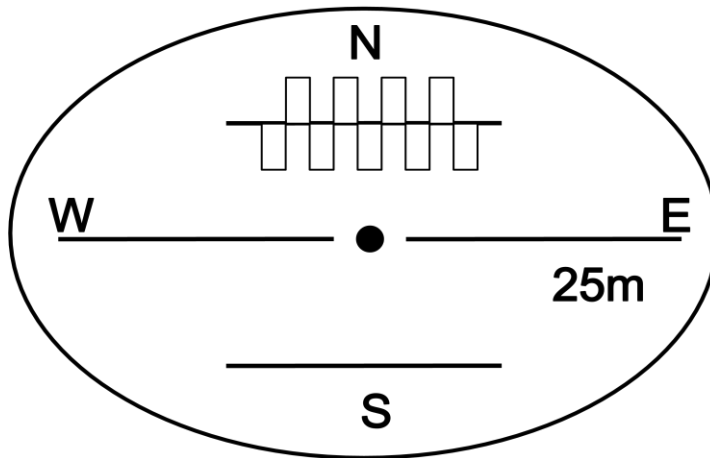


Fig. 5. Arrangement of transects within a kipuka for point frame sampling. The lines and oval represent transects within the kipuka perimeter, respectively. Small rectangles represent the point frame placement alternating along each side of each transect.

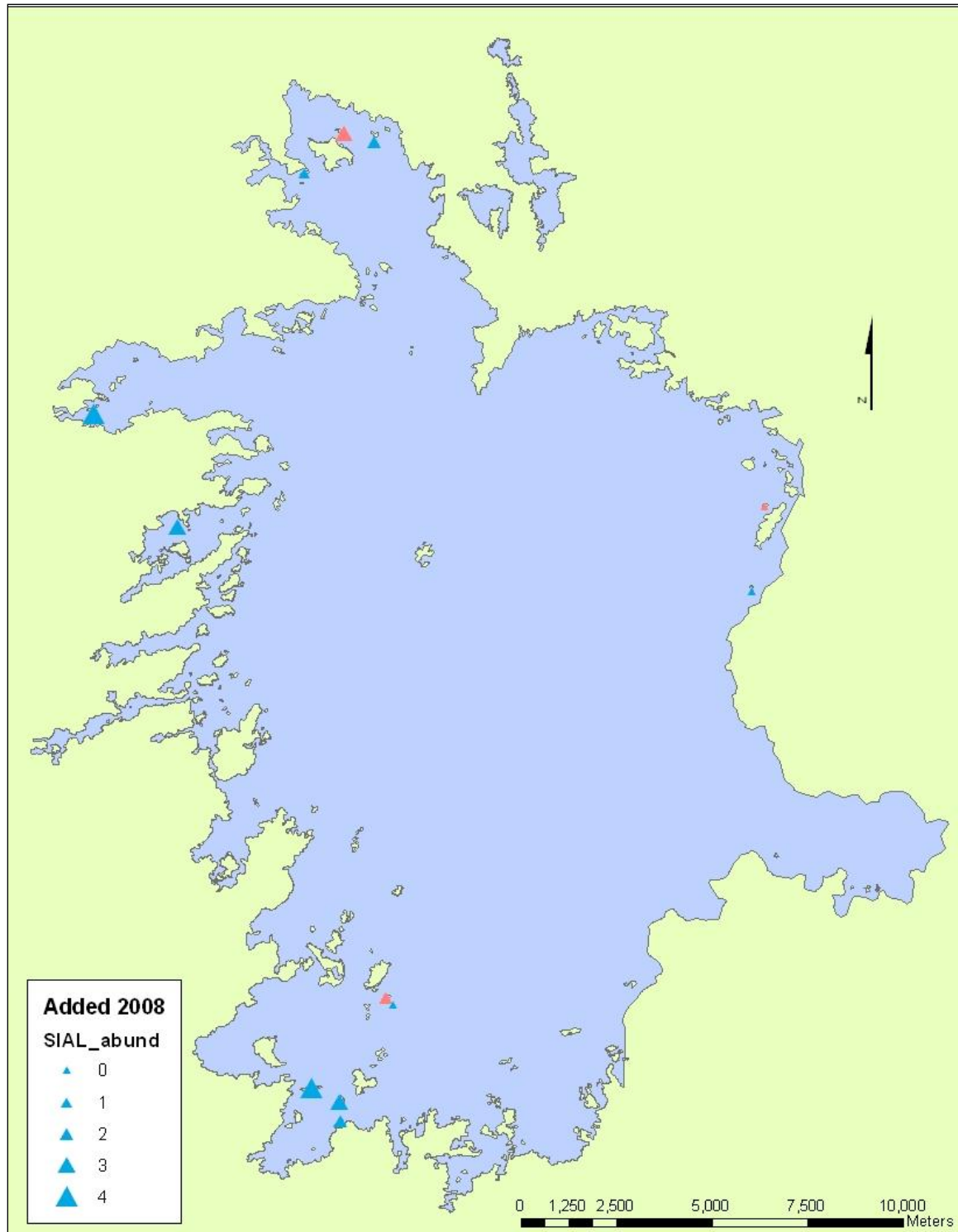


Fig. 6. Kipukas in Wapi point-framed sampled in 2008. Pink triangles indicate long-term survey kipukas, and blue triangles indicate kipukas added in 2008. Triangle size represents rank abundance of SIAL in kipuka (estimated in 2007 from observational surveys).

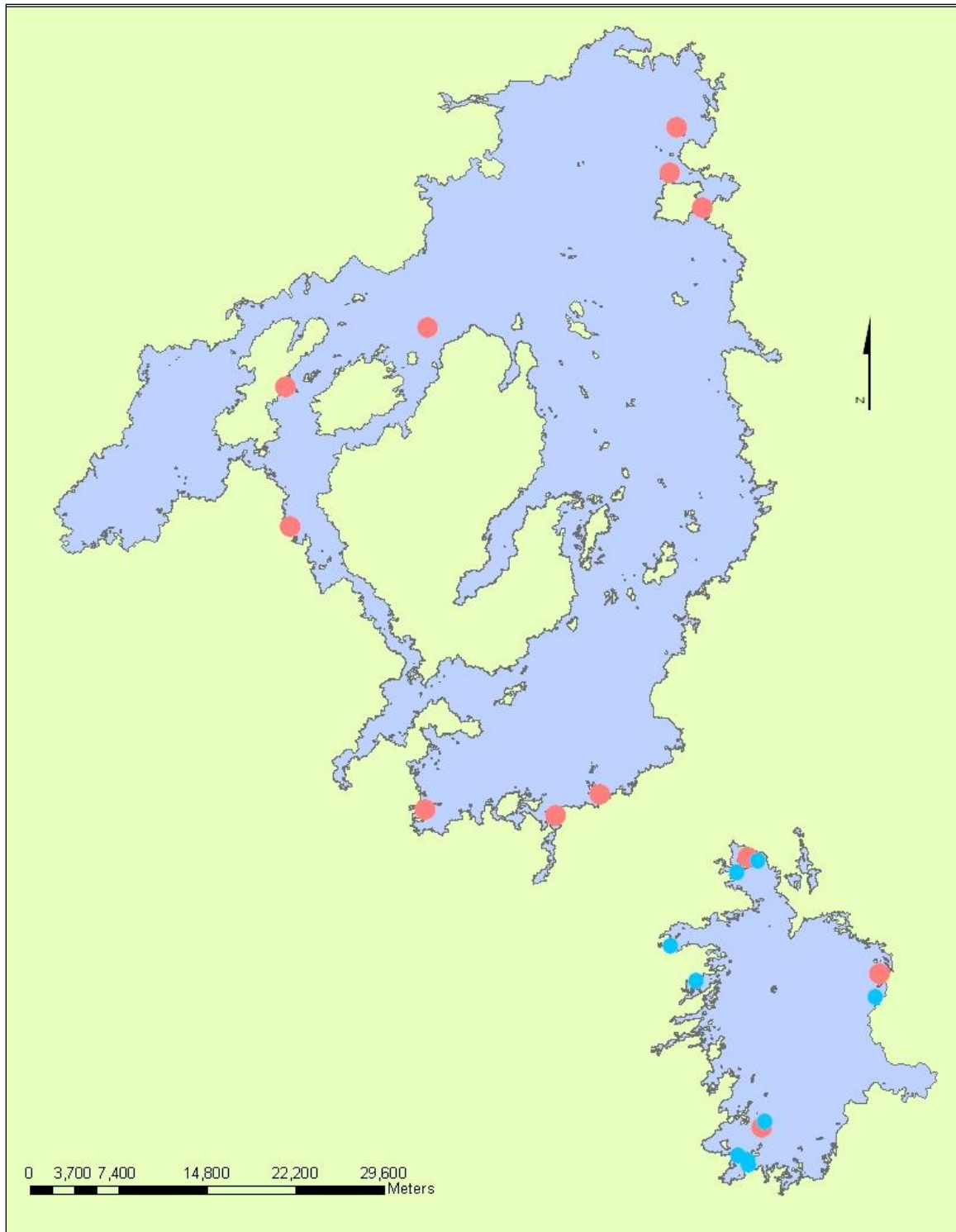


Fig. 7. Location of 21 kipukas point-frame sampled in 2008 at CRMO, Idaho, USA. Pink dots indicate the locations of the 12 long-term survey kipukas, and blue dots indicate kipukas added in 2008.

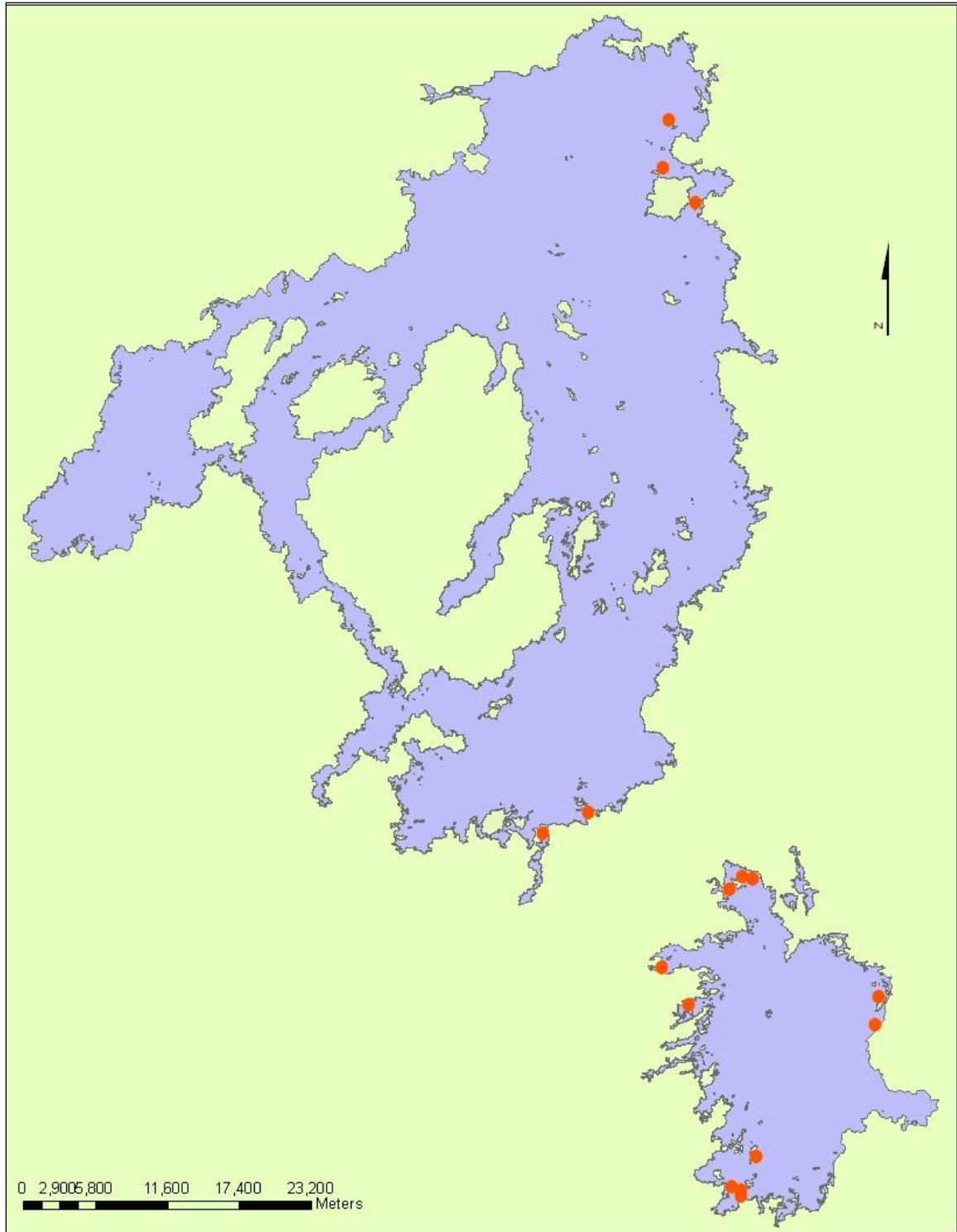


Fig. 8. Butterfly census locations in 2008 at CRMO, Idaho, USA.

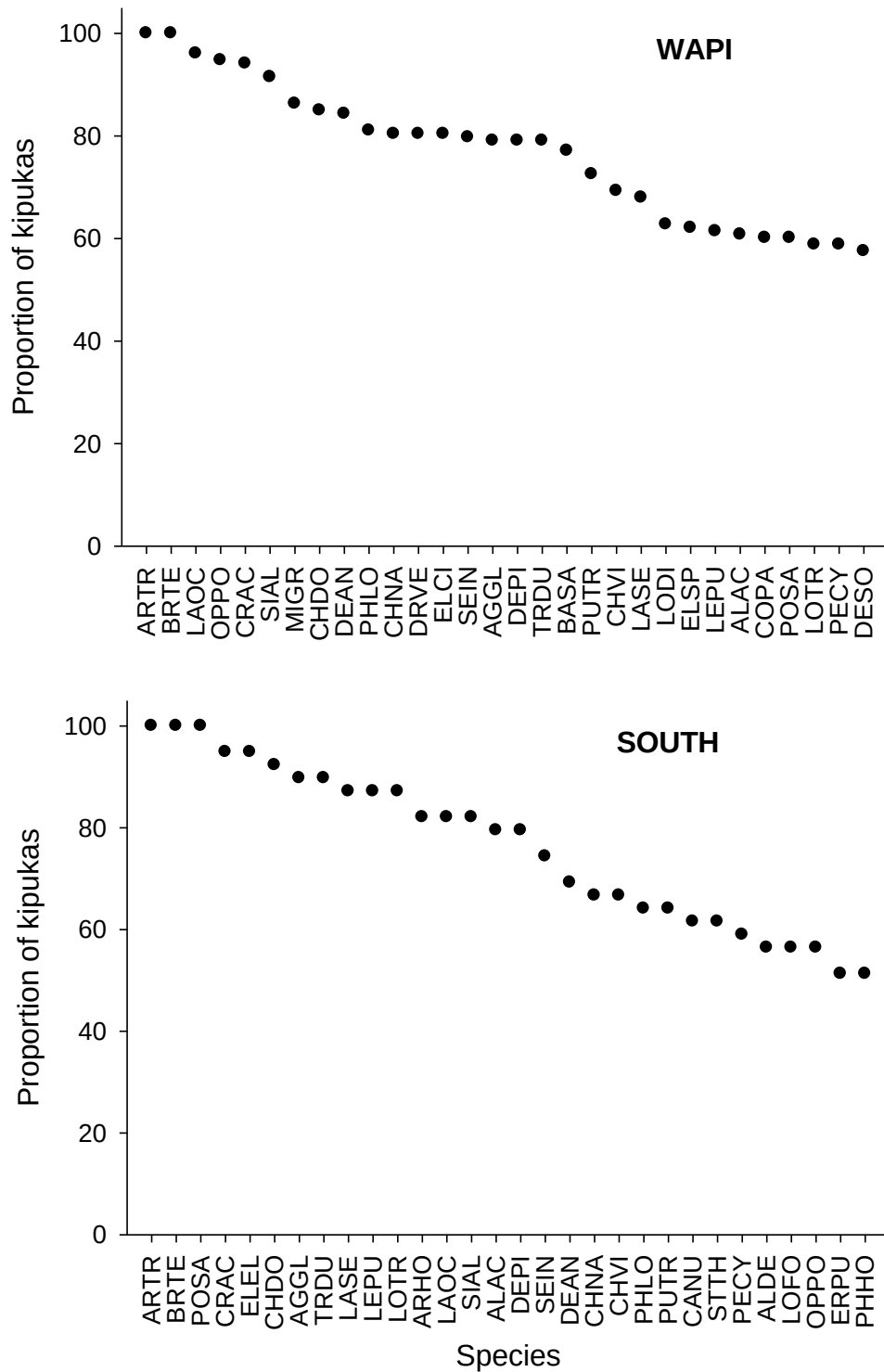


Fig. 9. Frequency of occurrence of the 30 species most commonly observed in the kipukas in the Wapi (n = 153; top) and the South (n = 39; bottom) in 2007-2008 at CRMO.

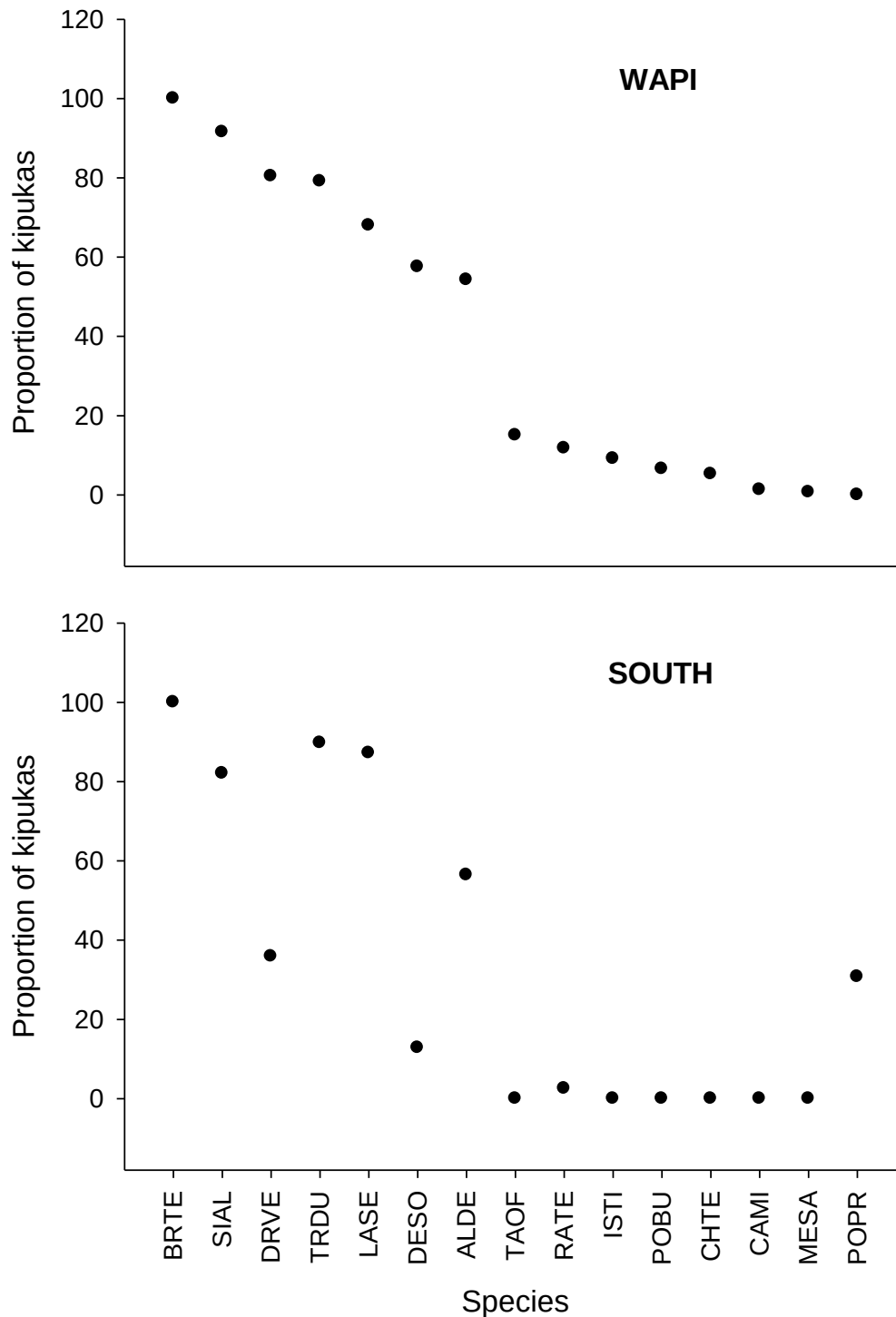


Fig. 10. Frequency of occurrence of all non-native species observed in the kipukas in the Wapi (top) and South (bottom) regions in 2007-2008 at CRMO (n = 153 and n = 39, respectively). The order of species is the same in both plots.

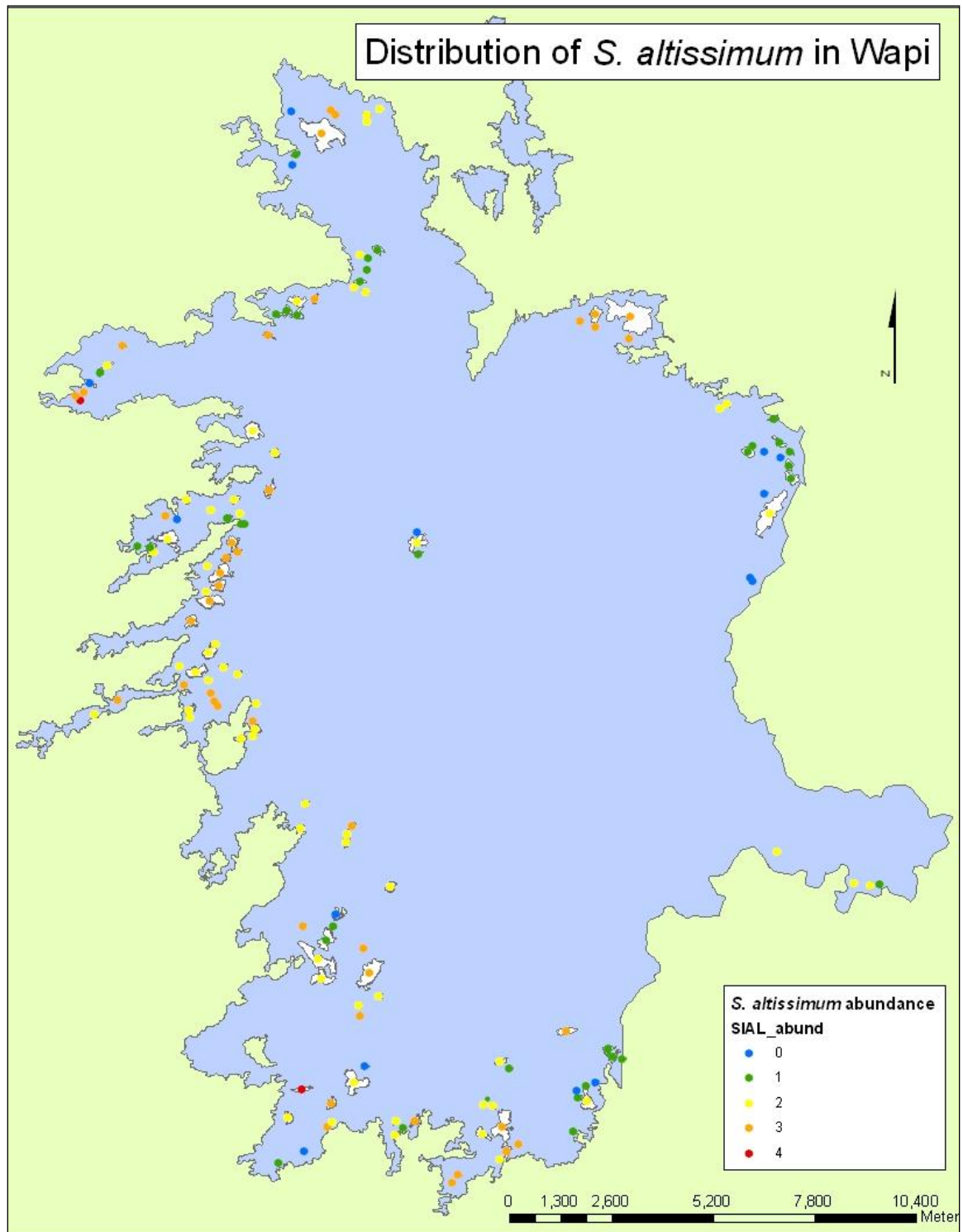


Fig. 11. Distribution and rank abundance of *S. altissimum* within kipukas in the Wapi flow (42°50'17.15"N, 113°13'42.79"W) at CRMO, Idaho, USA, in 2007-2008.

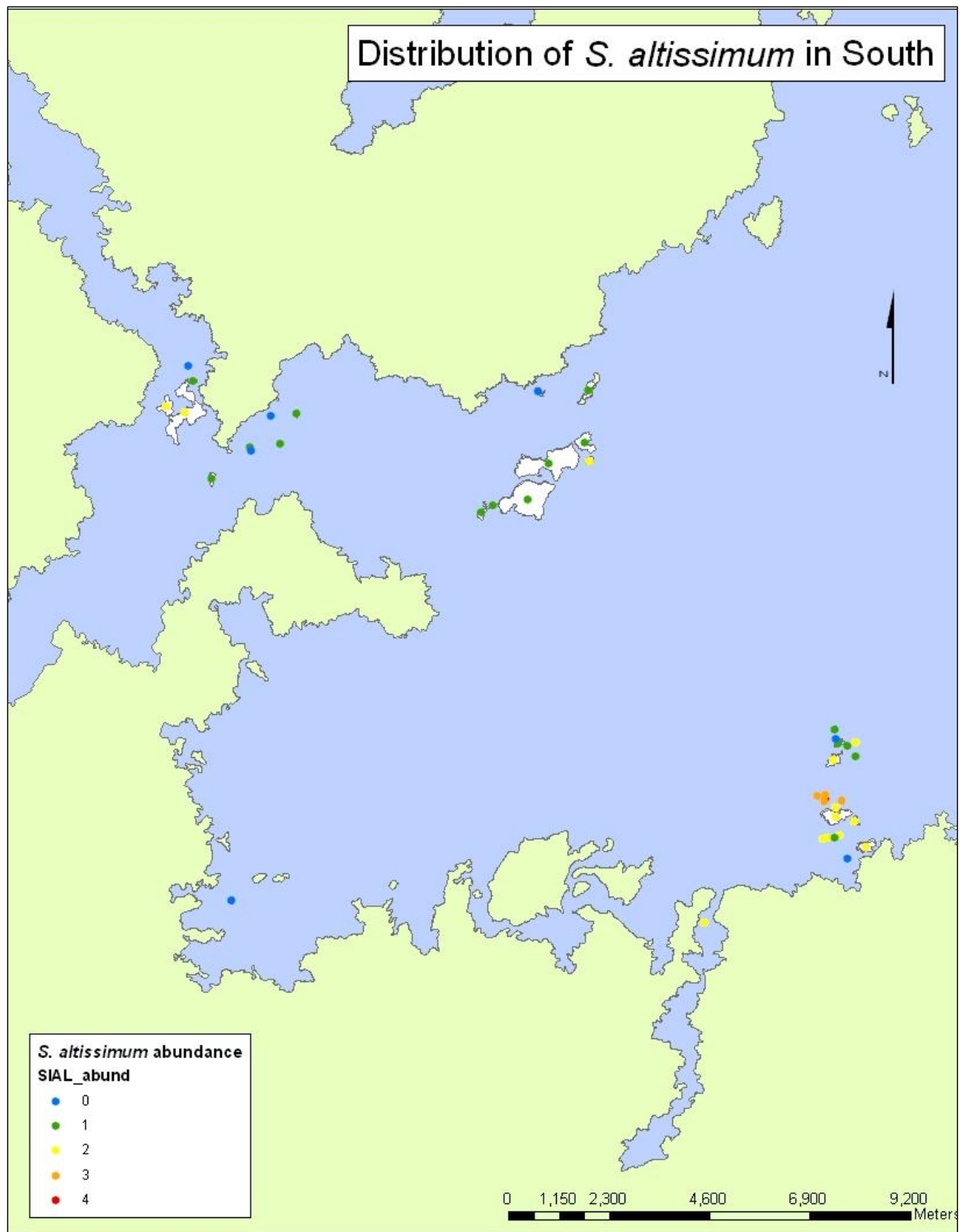


Fig. 12. Distribution and rank abundance of *S. altissimum* within kipukas in the South region of the CRMO flow (43°01'50.57"N, 113°31'47.94"W) in Idaho, USA, in 2007-2008.

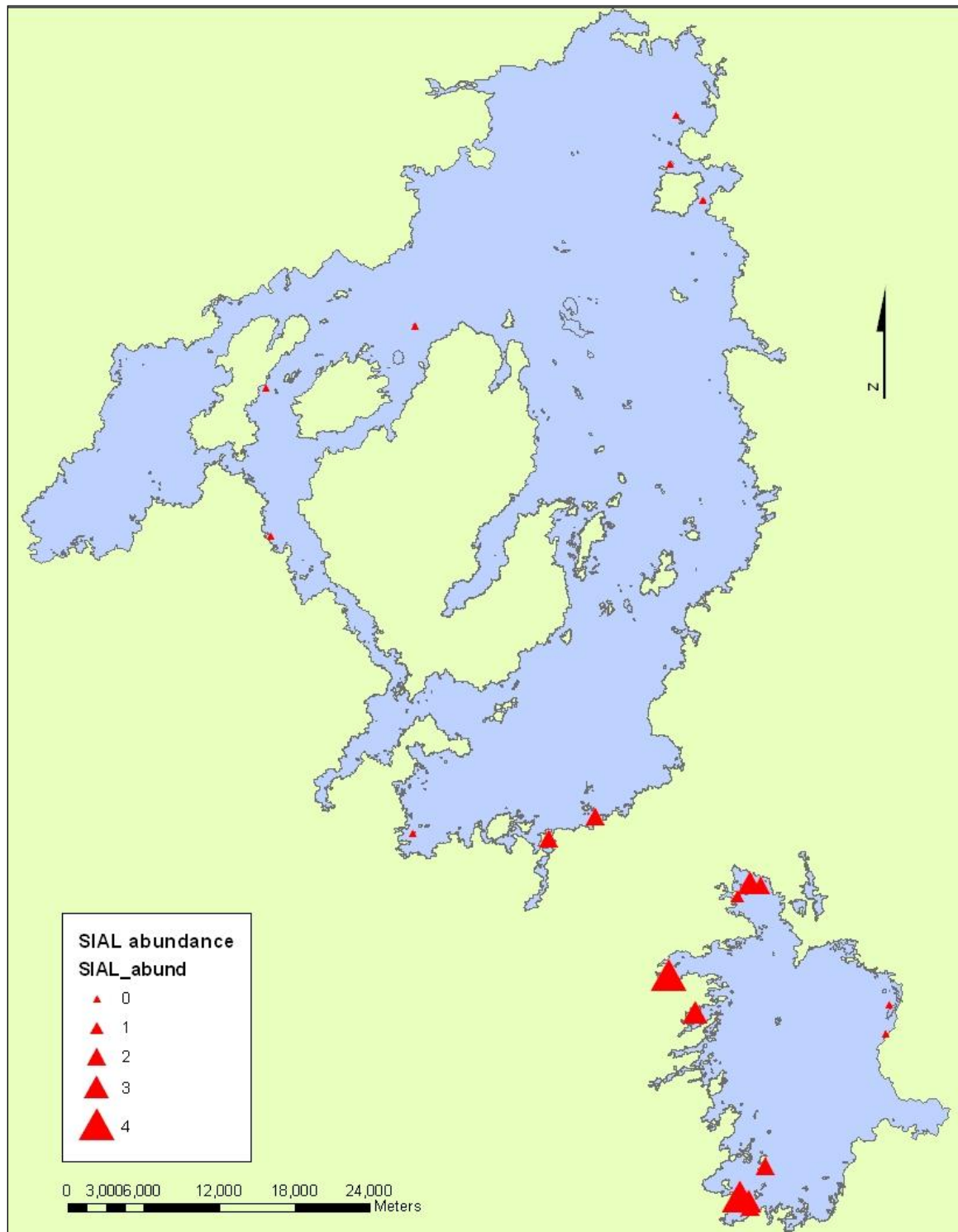


Fig. 13. *S. altissimum* abundance in kipukas point-frame sampled in 2008 at CRMO, Idaho, USA. Triangle size represents abundance.

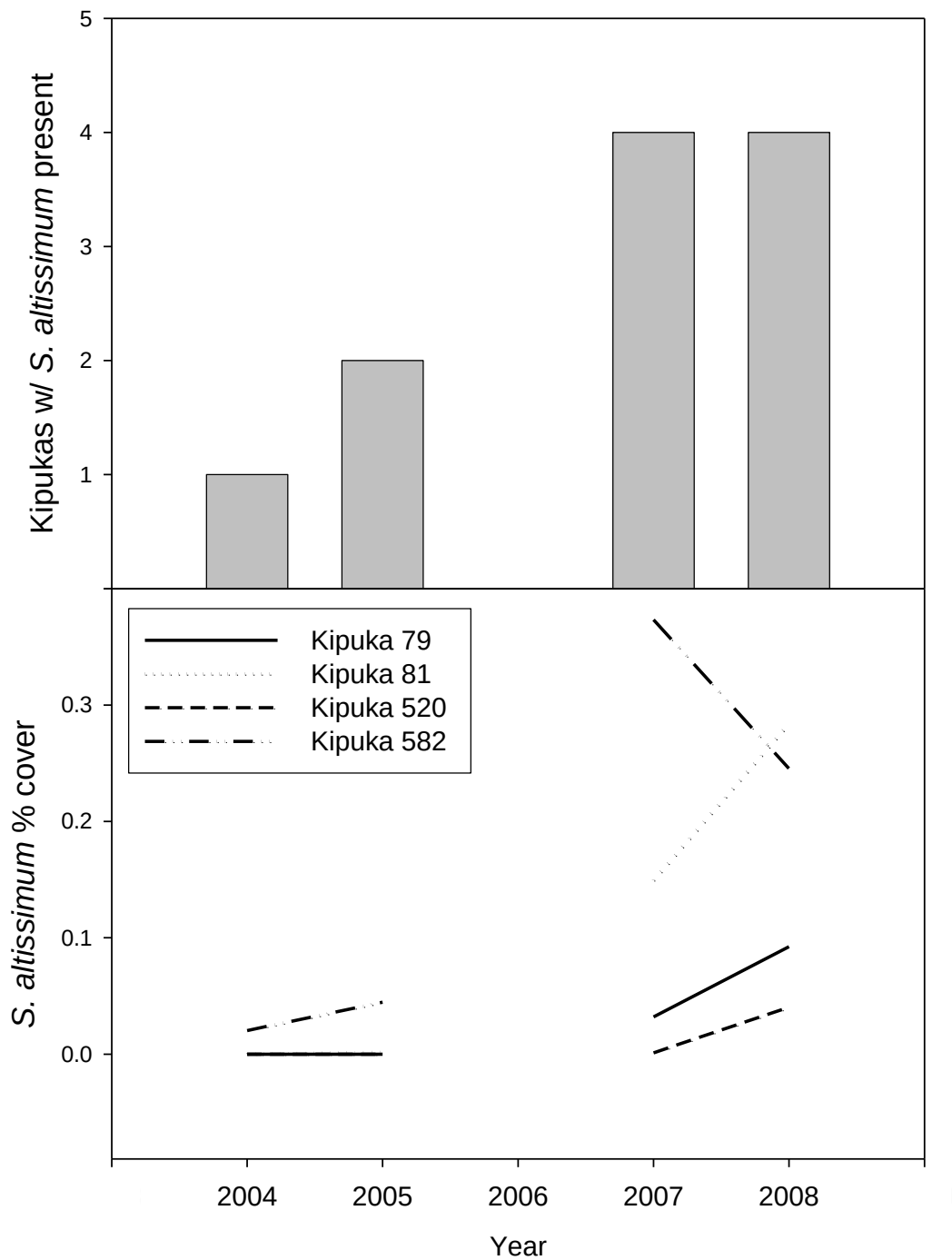


Fig. 14. Number of long-term survey kipukas ($n = 12$; top) with *S. altissimum* present and changes in percent cover of *S. altissimum* in four kipukas (K79, 81, 520, and 582) over a four year sampling period (2004-2008; no sample was taken in 2006).

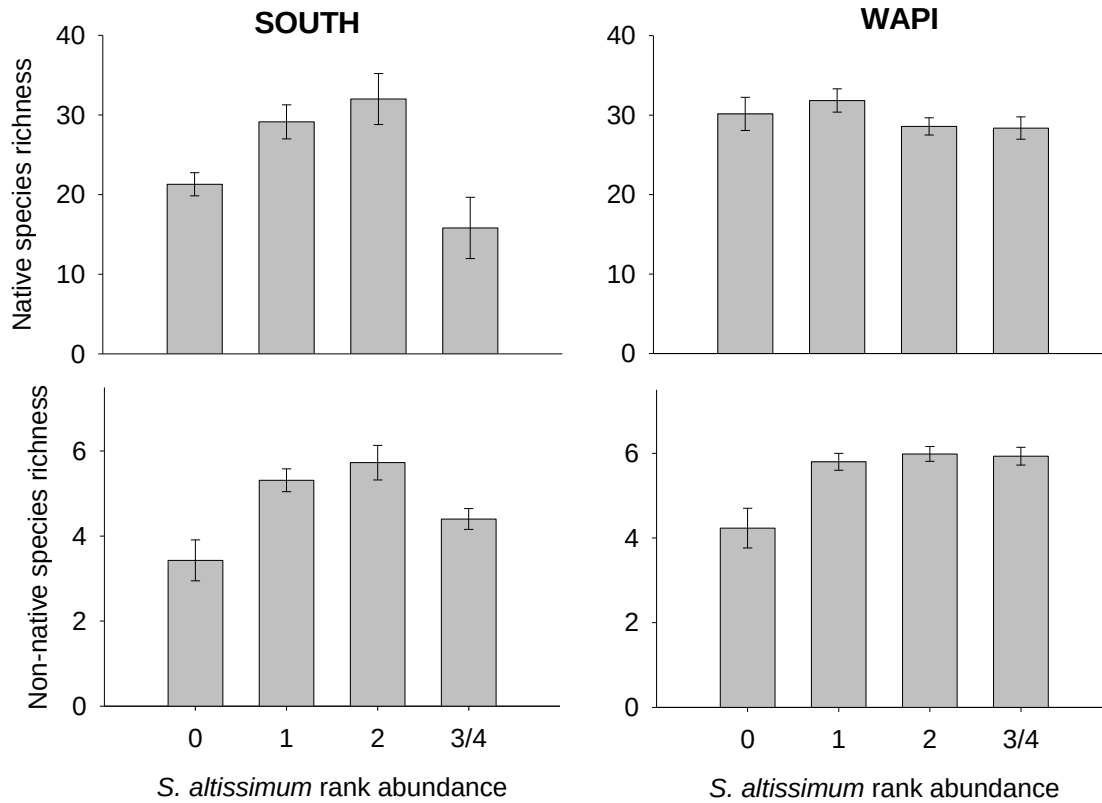


Fig. 15. Native and non-native species richnesses (± 1 SEM; top and bottom panels, respectively) in kipukas where the abundance of *S. altissimum* was ranked 0, 1, 2, or 3 - 4 in the South CRMO ($n = 7, 16, 11$, and 5 , respectively; left panels) and Wapi ($n = 13, 35, 61$, and 44 , respectively; right panels) flows. Abundance categories 3 and 4 were combined. There was a significant difference in native species richness among kipukas with different rank abundances of *S. altissimum* in the South ($H = 11.285$, d.f. = 3 , $p = 0.010$) but not in the Wapi ($H = 5.113$, d.f. = 3 , $p = 0.164$). There was a significant difference in non-native species richness among kipukas where the abundance of *S. altissimum* differed in the South ($H = 12.996$, d.f. = 3 , $p = 0.005$) and the Wapi ($H = 12.042$, d.f. = 3 , $p = 0.007$).

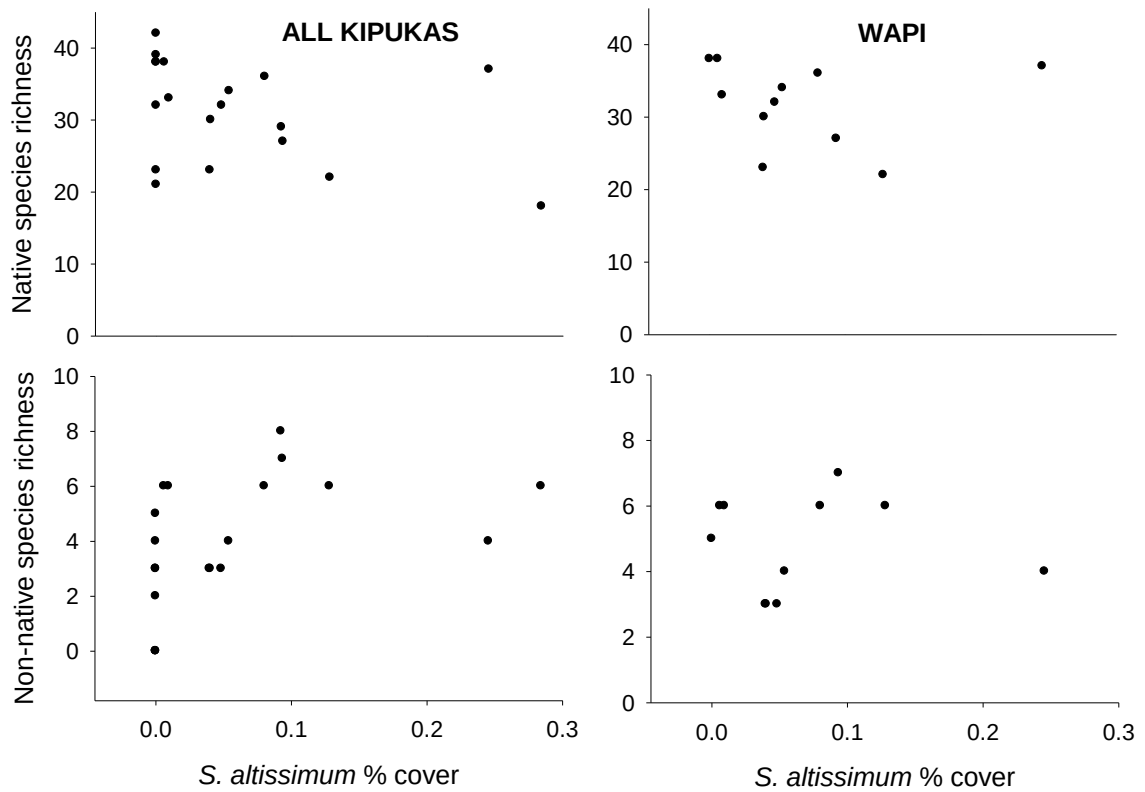


Fig. 16. Native and non-native species richness (top and bottom panels, respectively) versus percent cover of *S. altissimum* in all kipukas point-frame sampled ($n = 20$; right panels) and kipukas in the Wapi alone ($n = 11$; left panels). Native species richness decreased significantly with percent cover of *S. altissimum* in all kipukas point-frame sampled in 2008 ($\rho = -0.455$, $p = 0.044$), but not in the Wapi alone ($\rho = -0.360$, $p = 0.277$). Non-native species richness increased significantly with percent cover of *S. altissimum* in kipukas point-frame sampled in 2008 ($\rho = 0.666$, $p = 0.001$), but not in the Wapi region alone ($\rho = 0.146$, $p = 0.669$).

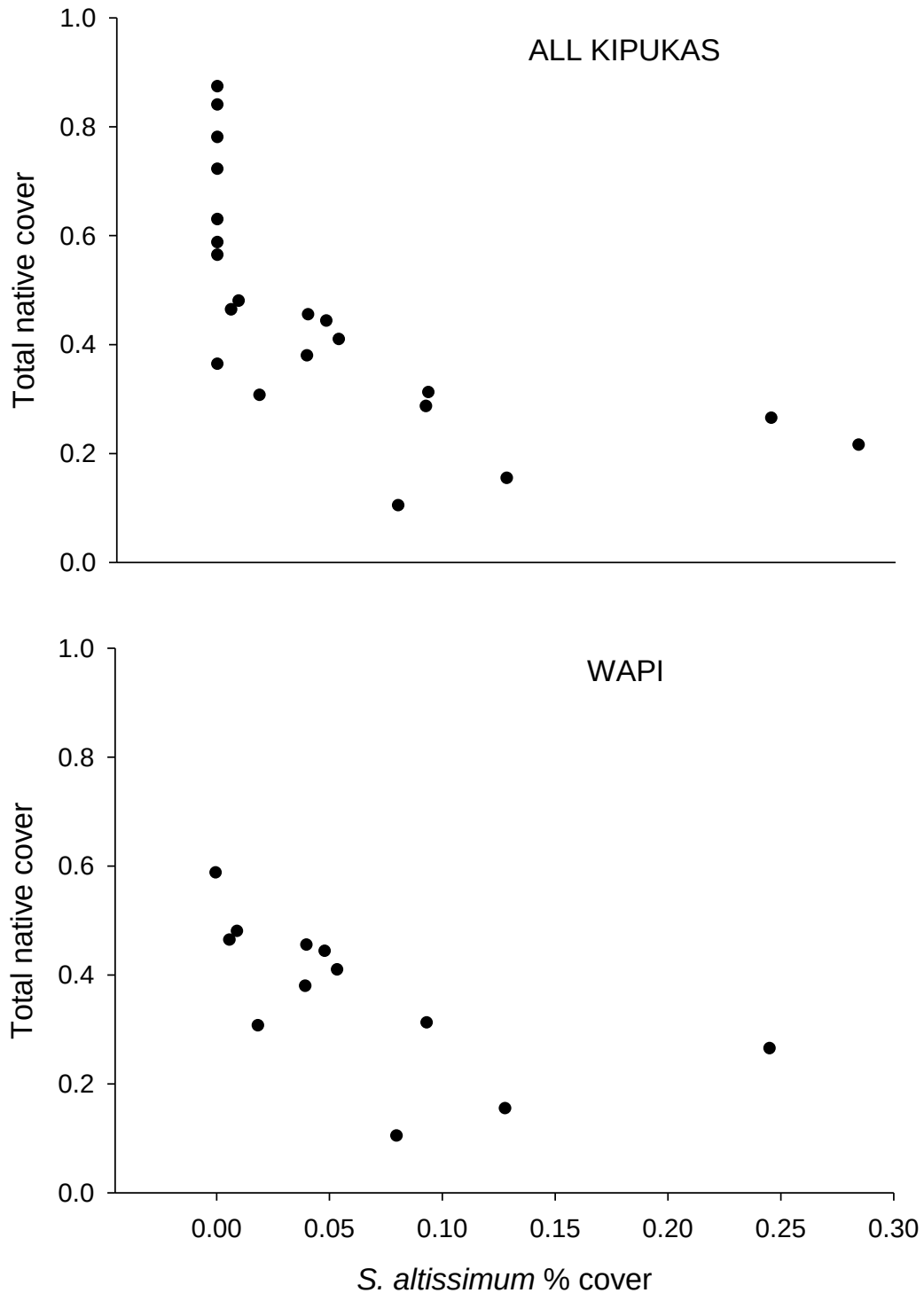


Fig. 17. Native plant cover versus *S. altissimum*. There was a significant negative correlation between native plant cover and cover of *S. altissimum* in all kipukas ($\rho = -0.853$, $n = 21$, $p < 0.0001$; top) and in the Wapi kipukas only ($\rho = -0.790$, $n = 12$, $p = 0.002$; bottom).

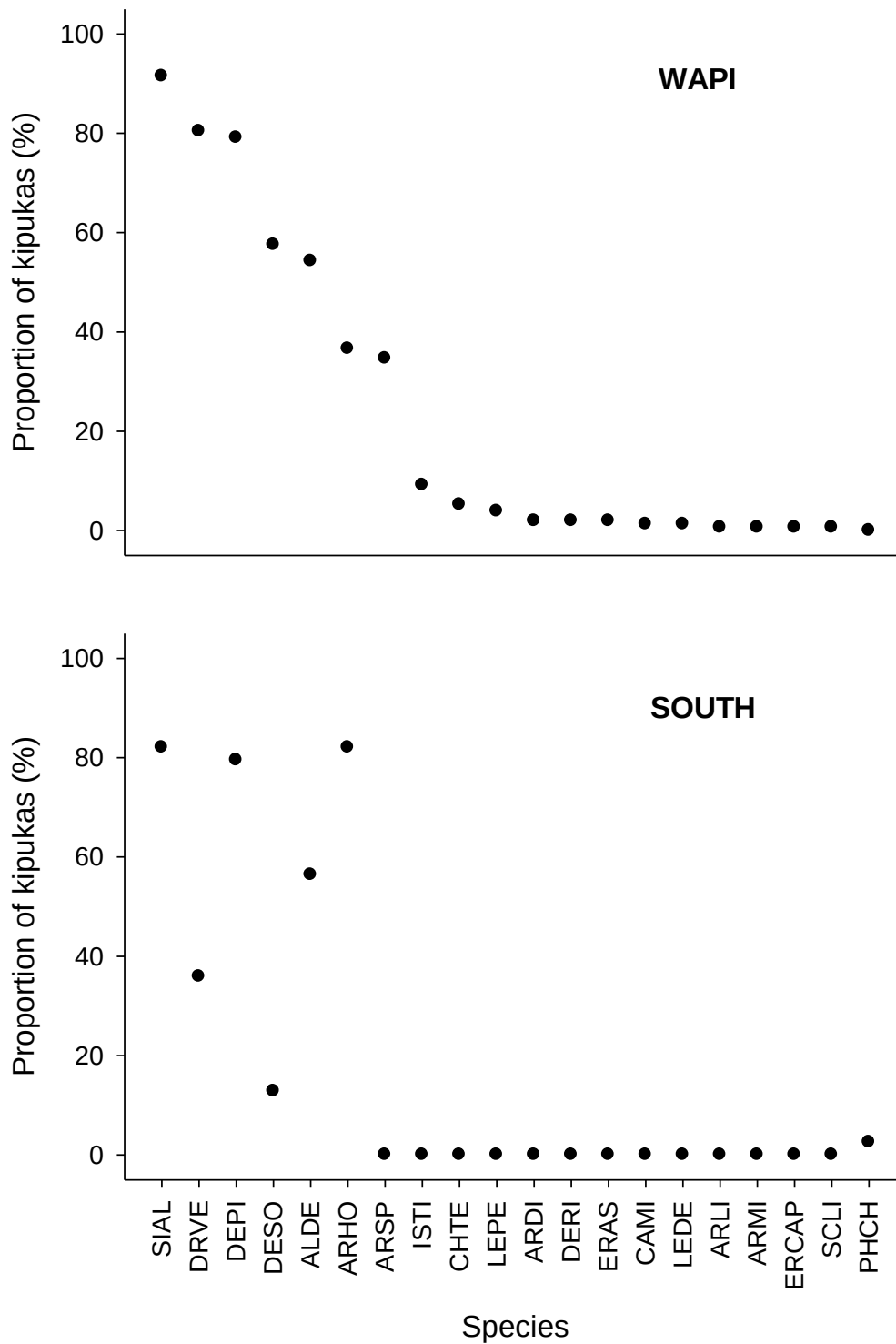


Fig. 18. Frequency of occurrence of mustard species in the Wapi (top) and South (bottom) regions of CRMO in 2007-2008 ($n = 153$ and $n = 39$, respectively). The order of species is the same in both plots.

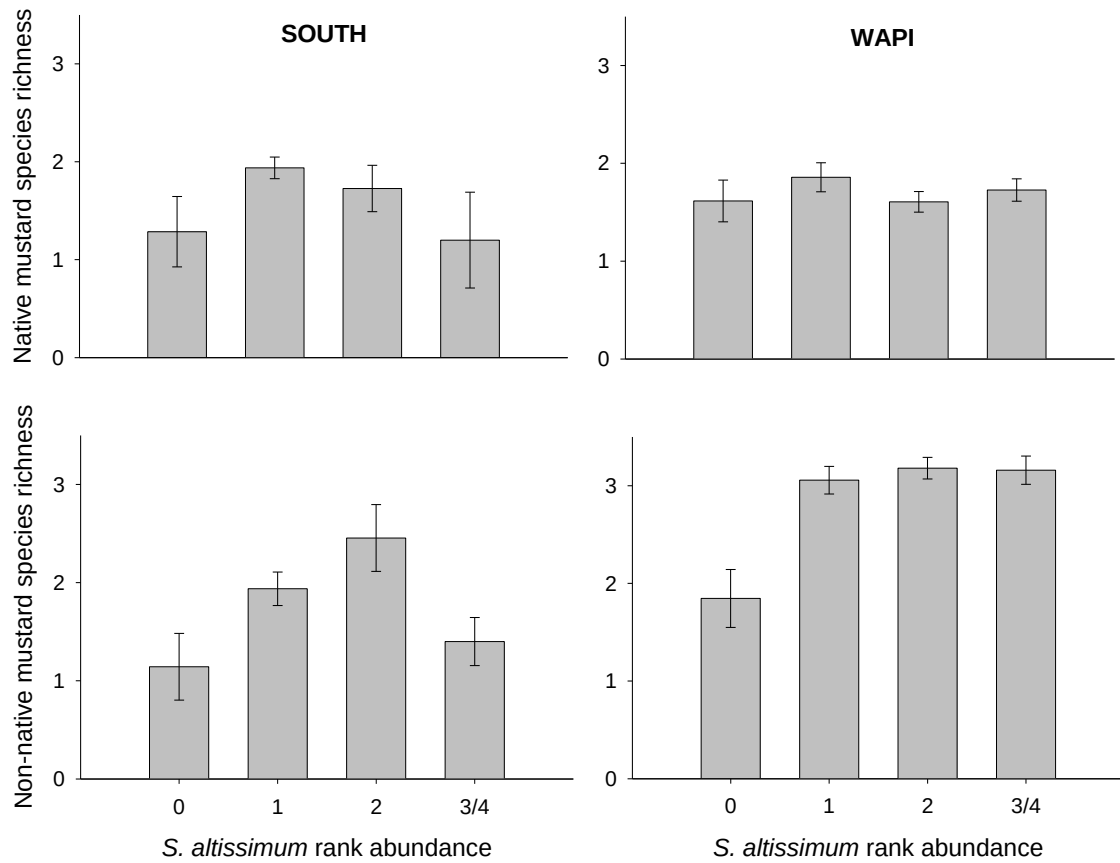


Fig. 19. Native and non-native mustard species richness (± 1 SEM; top and bottom panels, respectively) in kipukas where the abundance of *S. altissimum* was ranked 0, 1, 2, or 3 or 4 in the South CRMO ($n = 7, 16, 11,$ and $5,$ respectively; left panels) and Wapi ($n = 13, 35, 61,$ and $44,$ respectively; right panels) regions. There was not a significant difference in native mustard species richness among kipukas where the abundance of *S. altissimum* differed in the South ($H = 4.207, d.f. = 3, p = 0.240$) or the Wapi ($H = 2.868, d.f. = 3, p = 0.413$), but there was a significant difference in non-native mustard species richness in the Wapi ($H = 16.073, d.f. = 3, p = 0.001$) and the South ($H = 8.219, d.f. = 3, p = 0.042$).

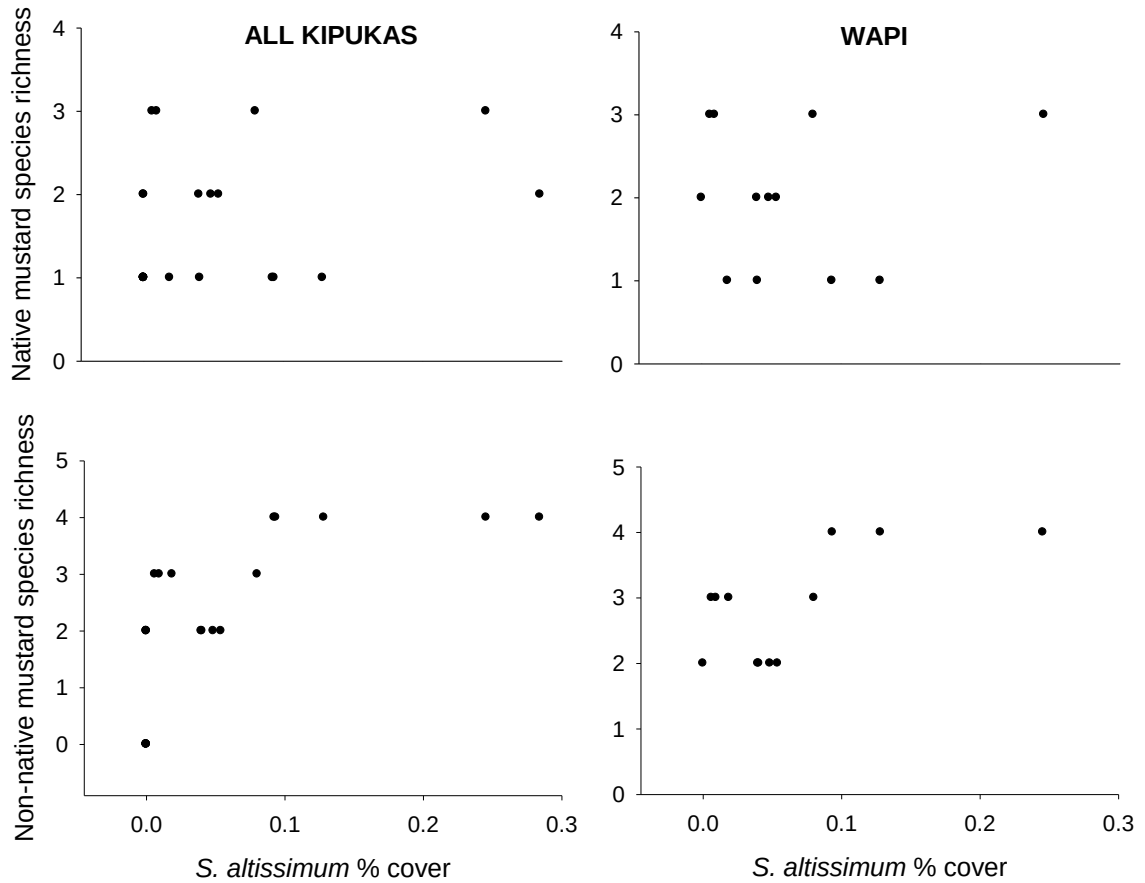


Fig. 20. Native and non-native mustard species richness (top and bottom panels, respectively) versus percent cover of *S. altissimum* in all kipukas point-frame sampled ($n = 21$; left panels) and kipukas in the Wapi alone ($n = 11$; right panels). Native mustard richness and percent cover of *S. altissimum* were not significantly related in all kipukas ($\rho = 0.280$, $p = 0.218$), nor in the Wapi kipukas alone ($\rho = -0.148$, $p = 0.647$). Non-native mustard species richness is significantly positively related to percent cover of *S. altissimum* in all kipukas point-frame sampled ($\rho = 0.839$, $p < 0.0001$), and marginally significantly positive in the Wapi kipukas alone ($\rho = 0.536$, $p = 0.072$).

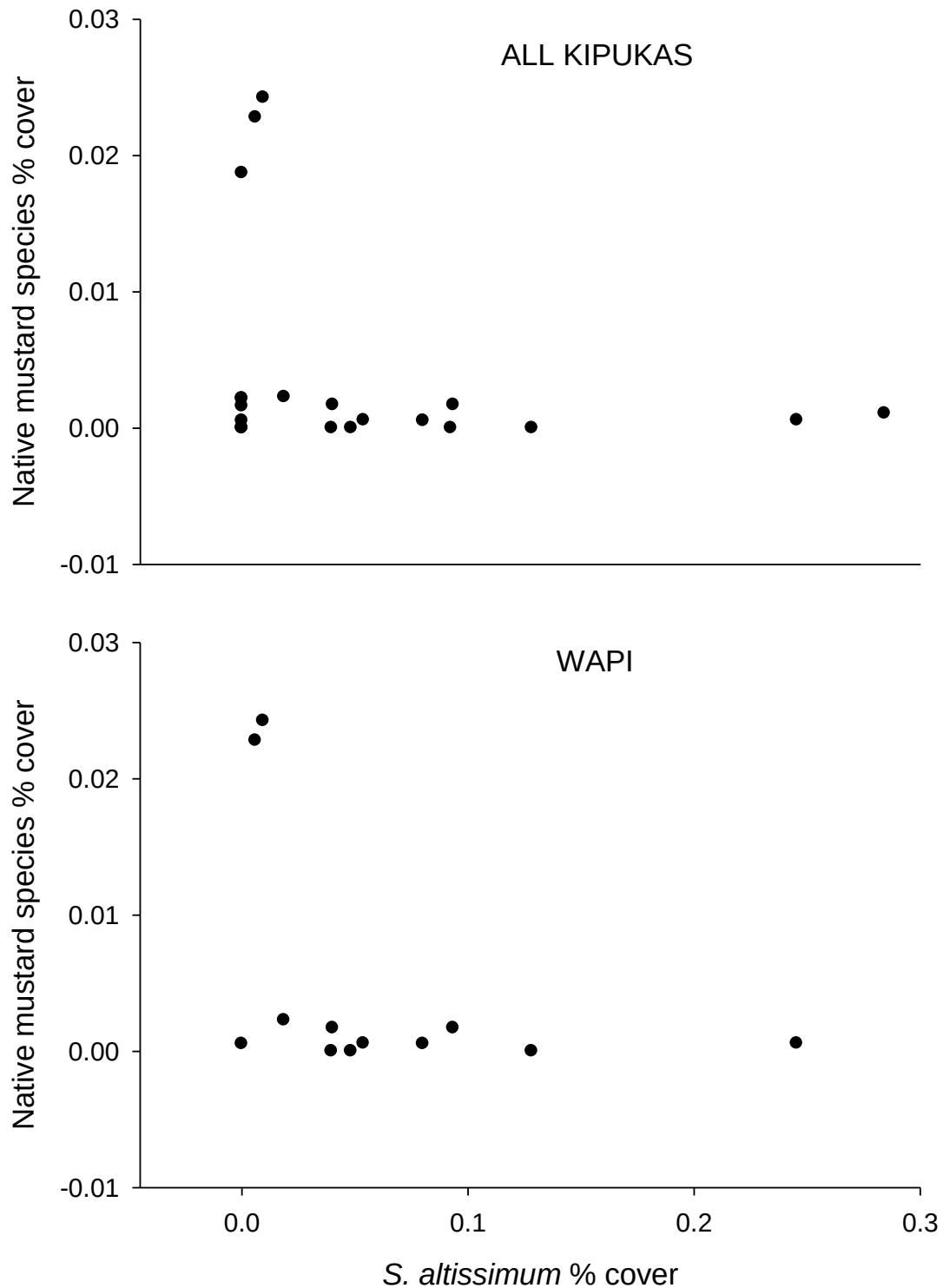


Fig. 21. There was not a significant relationship between percent covers of native mustard species and *S. altissimum* in all kipukas point-frame sampled ($\rho = -0.157$, $n = 21$, $p = 0.497$), nor in those in the Wapi region only ($\rho = -0.368$, $n = 12$, $p = 0.239$).

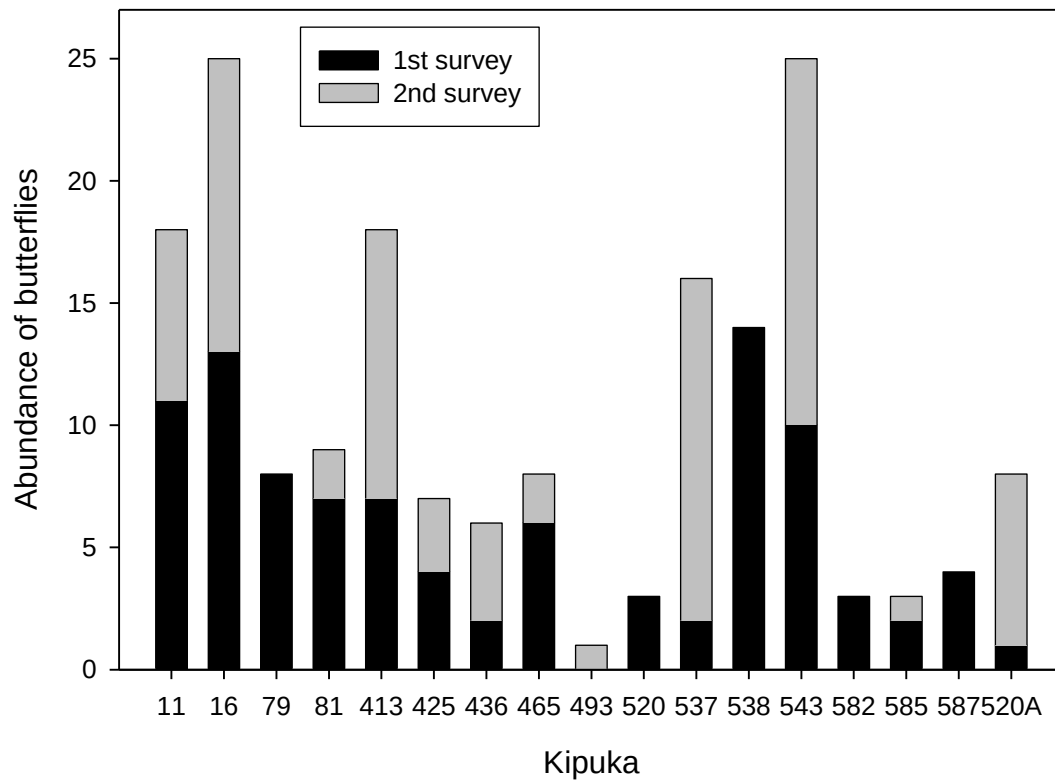


Fig. 22. Abundance of butterflies observed in two surveys of 17 kipukas at CRMO, Idaho, USA, in 2008. Kipukas are identified with numbers from the CRMO kipuka GIS database.

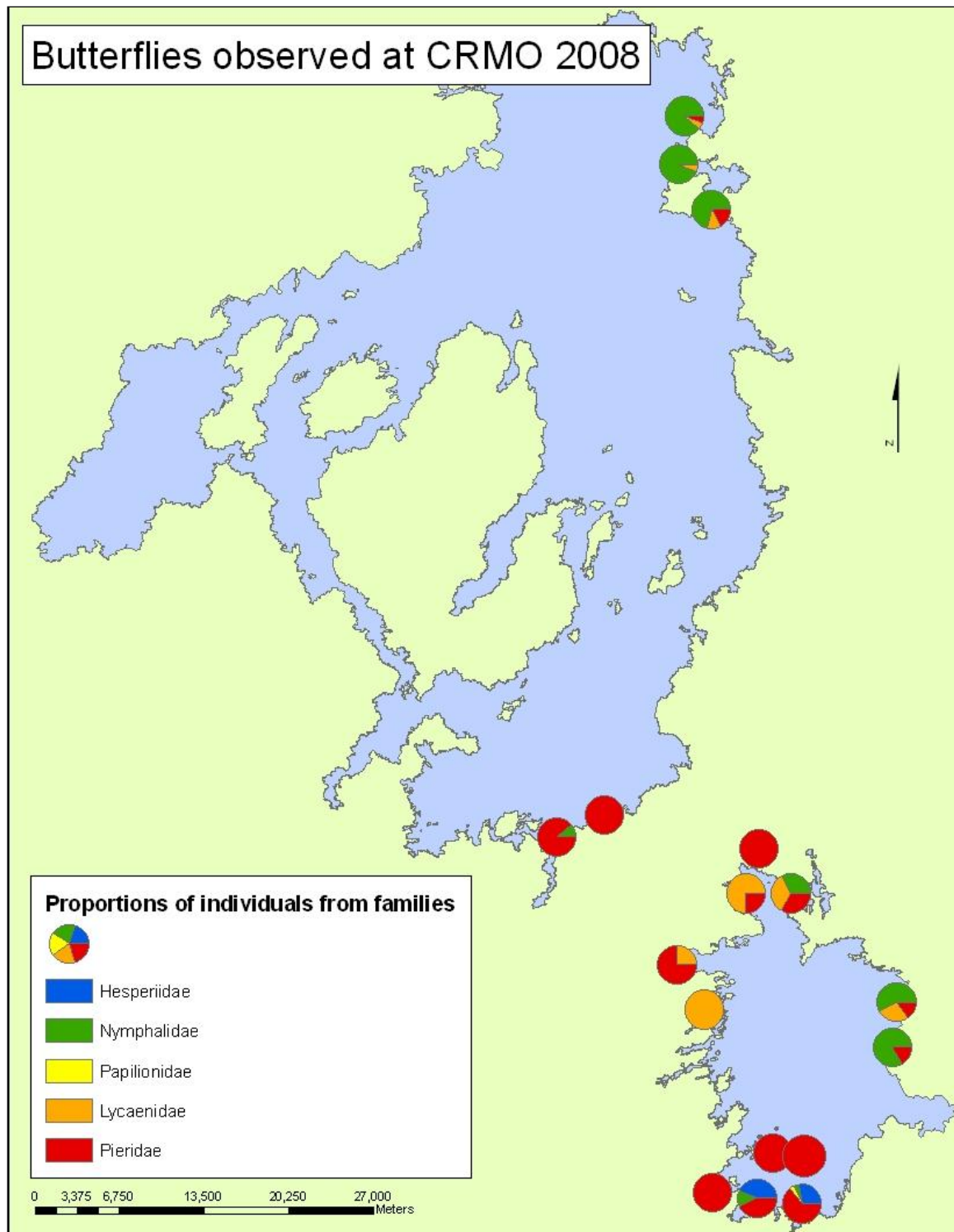


Fig. 23. Proportions of butterflies from five families observed during surveys in 2008 at CRMO, Idaho, USA.

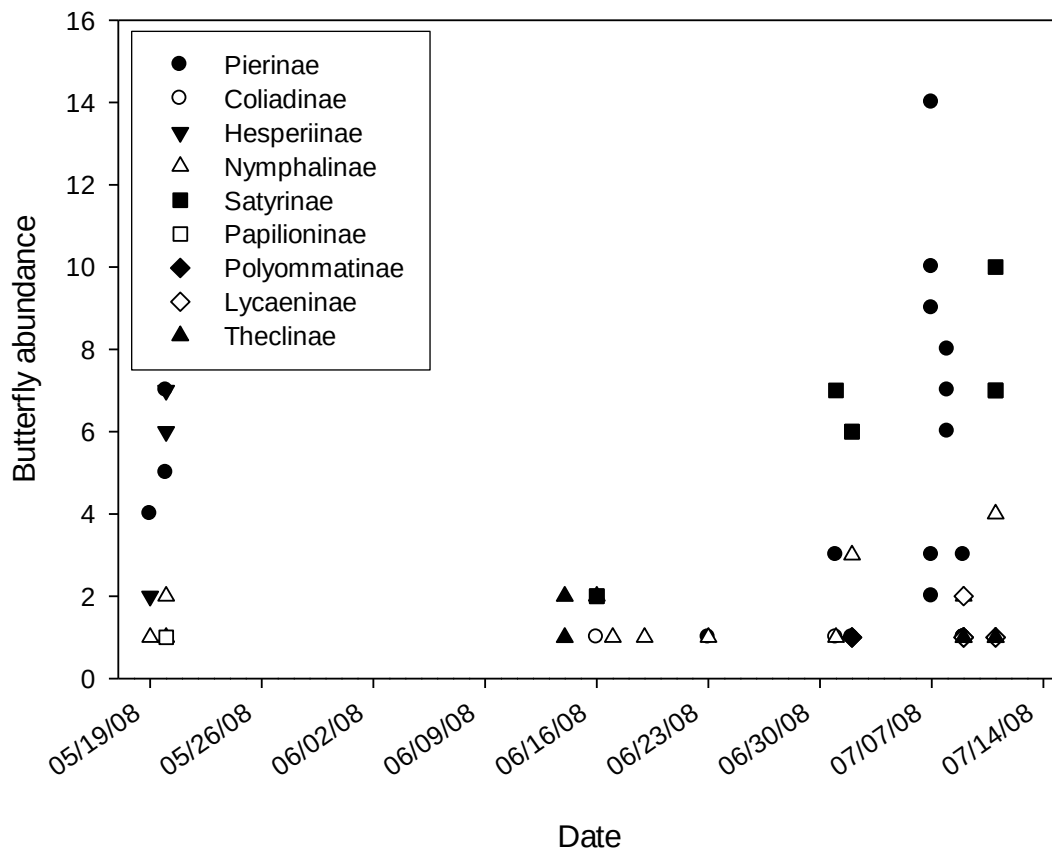


Fig. 24. The temporal distribution of butterflies observed during surveys at CRMO, Idaho, USA, in 2008. Symbols indicate butterfly subfamily.

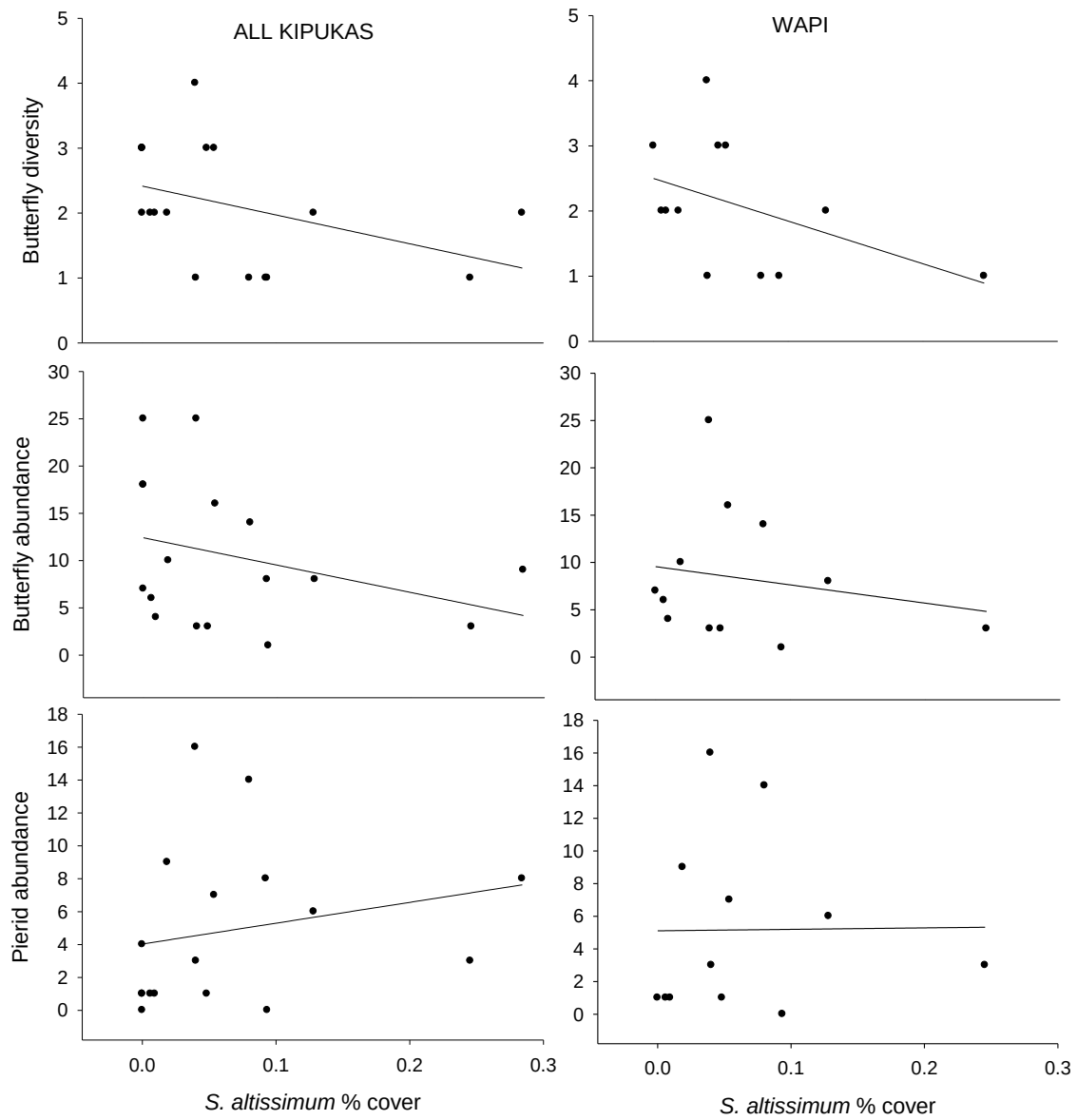


Fig. 25. The relationship between butterfly diversity (by family; top), butterfly abundance (center), and pierid abundance (bottom) and percent cover of *S. altissimum* in kipukas point-frame sampled (left) and those in the Wapi alone (right) in 2008. There are no significant relationships between percent cover of *S. altissimum* and butterfly diversity ($R^2 = 0.163$, $df = 16$, $p = 0.108$ and $R^2 = 0.205$, $df = 11$, $p = 0.140$, respectively), butterfly abundance ($R^2 = 0.103$, $df = 16$, $p = 0.210$ and $R^2 = 0.036$, $df = 11$, $p = 0.554$, respectively), or pierid abundance ($R^2 = 0.048$, $df = 16$, $p = 0.399$ and $R^2 = 0.0001$, $df = 11$, $p = 0.972$, respectively).

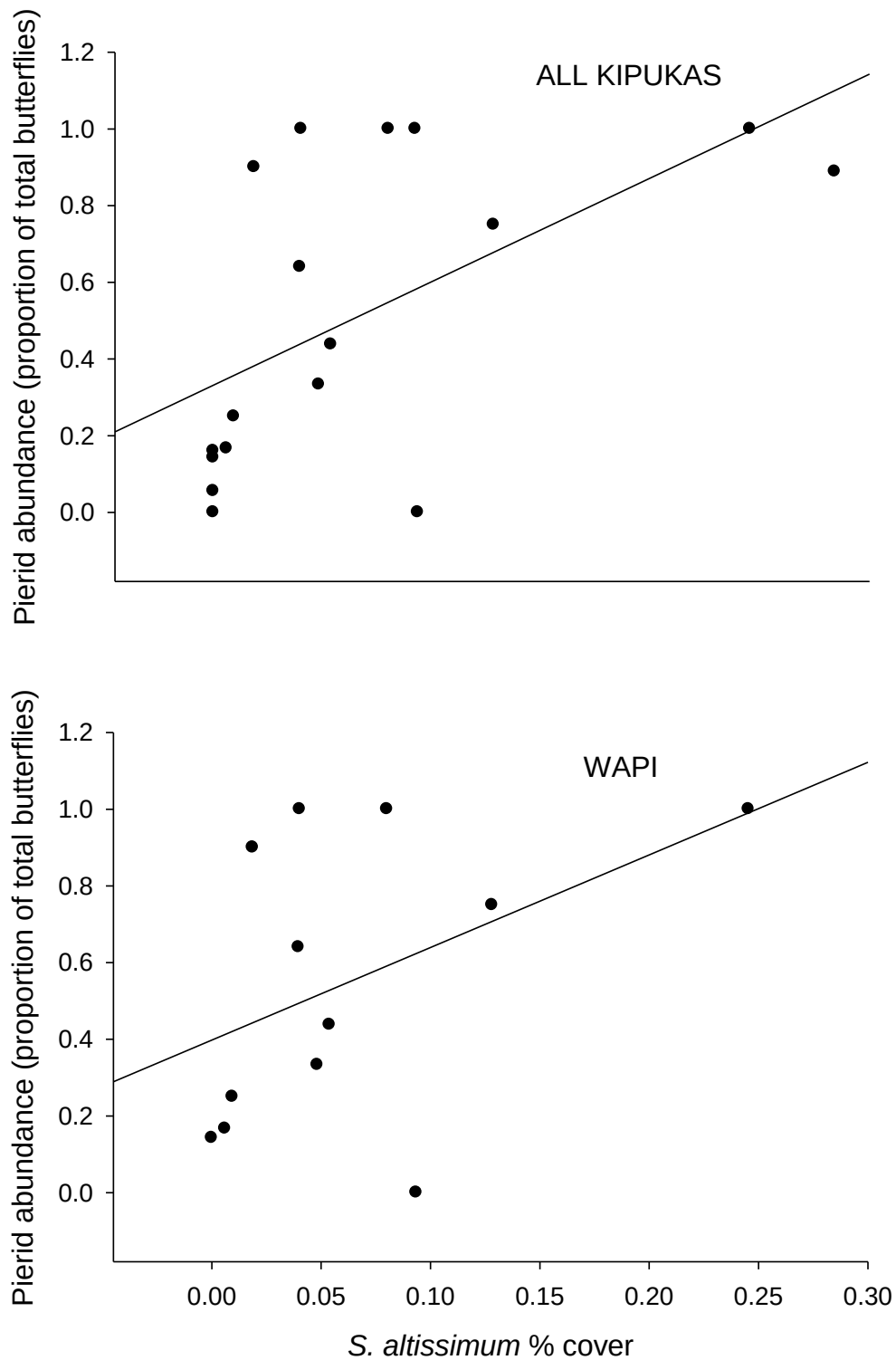


Fig. 26. There was a significantly higher pierid abundance in kipukas with more *S. altissimum* in all kipukas censused ($R^2 = 0.327$, d.f. = 16, $p = 0.016$; top), but this relationship was not significant among the Wapi kipukas only ($R^2 = 0.197$, d.f. = 11, $p = 0.148$; bottom).

Table 1. Frequency of occurrence (%) and average rank abundance (0 – 4) of the plant species (categorized by life form) most commonly observed in kipukas in the Wapi and South regions at CRMO in 2007-2008. Asterisks (*) indicate non-native species.

	Species	Code	Frequency of occurrence		Average rank abundance	
			Wapi	South	Wapi	South
Shrubs	<i>Artemisia tridentata</i>	ARTR	100%	100%	3.60	3.72
	<i>Chrysothamnus nauseosus</i>	CHNA	80%	67%	1.26	0.81
	<i>Purshia tridentata</i>	PUTR	73%	64%	0.99	0.67
	<i>Chrysothamnus viscidiflorus</i>	CHVI	69%	67%	1.04	1.03
	<i>Artemisia tripartita</i>	ARTP	22%	5%	0.39	0.06
	<i>Grayia spinosa</i>	GRSP	1%	10%	0.01	0.11
Grasses	<i>Bromus tectorum*</i>	BRTE	100%	100%	3.04	3.06
	<i>Elymus cinereus</i>	ELCI	80%	38%	1.14	0.42
	<i>Elymus spicatus</i>	ELSP	62%	39%	0.96	0.28
	<i>Poa secunda</i>	POSA	60%	100%	1.65	2.36
	<i>Elymus elymoides</i>	ELEL	52%	95%	0.67	1.64
	<i>Stipa thurberiana</i>	STTH	2%	62%	0.02	0.94
Forbs	<i>Lappula occidentalis</i>	LAOC	96%	82%	1.27	0.83
	<i>Crepis acuminata</i>	CRAC	94%	95%	1.42	1.89
	<i>Sisymbrium altissimum*</i>	SIAL	92%	82%	1.90	1.39
	<i>Microsteris gracilis</i>	MIGR	86%	41%	1.37	0.36
	<i>Chaenactis douglasii</i>	CHDO	85%	92%	0.89	0.94
	<i>Agoseris glauca</i>	AGGL	79%	90%	0.97	0.92
	<i>Tragopogon dubius*</i>	TRDU	79%	90%	0.89	0.97
	<i>Lactuca serriola*</i>	LASE	68%	87%	0.82	1.08
Other	<i>Opuntia polyacantha</i>	OPPO	95%	56%	1.18	0.61
	<i>Leptodactylon pungens</i>	LEPU	61%	87%	0.69	1.14
	<i>Gutierrezia sarothrae</i>	GUSA	58%	23%	0.69	0.22
	<i>Juniper scopulorum</i>	JUSC	33%	0	0.40	0

Table 2. Frequency of occurrence (%) and average rank abundance of non-native species observed in kipukas at CRMO in 2007-2008.

Species	Abbreviation	Frequency of occurrence		Average rank Abundance	
		Wapi	South	Wapi	South
<i>Bromus tectorum</i>	BRTE	100%	100%	3.04	3.06
<i>Sisymbrium altissimum</i>	SIAL	92%	82%	1.90	1.39
<i>Tragopogon dubius</i>	TRDU	79%	90%	0.89	0.97
<i>Lactuca serriola</i>	LASE	68%	87%	0.82	1.08
<i>Draba verna</i>	DRVE	80%	36%	1.34	0.31
<i>Alyssum desertorum</i>	ALDE	54%	56%	0.75	0.58
<i>Descurainia sophia</i>	DESO	58%	13%	0.67	0.06
<i>Taraxacum officinale</i>	TAOF	15%	0	0.17	0
<i>Ranunculus testiculatus</i>	RATE	12%	3%	0.24	0
<i>Isatis tinctoria</i>	ISTI	9%	0	0.16	0
<i>Poa praetensis</i>	POPR	0	31%	0	0.36
<i>Poa bulbosa</i>	POBU	7%	0	0.07	0
<i>Chorispora tenella</i>	CHTE	5%	0	0.06	0
<i>Camelina microcarpa</i>	CAMI	1%	0	0.02	0
<i>Medicago sativa</i>	MESA	1%	0	0.04	0

Table 3. Spearman correlation coefficients (ρ) and p-values for the relationships between local native and non-native species richnesses and percent cover of *S. altissimum*.

Kipuka	<i>S. altissimum</i> present	Local native species richness		Local non-native species richness	
		ρ	p	ρ	p
11	N				
16	N				
79	Y	-0.651	<0.0001	-0.067	0.638
81	Y	-0.676	<0.0001	-0.237	0.091
168	N				
190	N				
335	N				
411	N				
413	N				
425	N				
436	Y	-0.226	0.115	-0.093	0.52
465	Y	-0.280	0.044	0.161	0.253
493	Y	-0.493	0.0003	0.27	0.061
520	Y	-0.306	0.032	0	1
520A	Y	-0.310	0.030	-0.089	0.545
537	Y	-0.579	<0.0001	?	?
538	Y	-0.344	0.013	-0.245	0.08
543	Y	-0.257	0.075	-0.119	0.415
582	Y	-0.578	<0.0001	0.08	0.583
585	Y	-0.113	0.435	0.017	0.91
587	Y	-0.214	0.148	-0.028	0.853

Table 4. Frequency of occurrence (%) and average rank abundance of native and non-native mustard species observed in Wapi and South kipukas at CRMO, Idaho, USA, in 2007-2008.

Species	Code	Status	Frequency of occurrence		Average rank abundance	
			Wapi	South	Wapi	South
<i>Descurainia pinnata</i>	DEPI	Native	79%	83%	1.06	0.86
<i>Arabis holboellii</i>	ARHO	Native	37%	89%	0.59	1
<i>Arabis sparsiflora</i>	ARSP	Native	35%	0%	0.65	0
<i>Arabis divaricarpa</i>	ARDI	Native	2%	0%	0.04	0
<i>Descurainia richardsonii</i>	DERI	Native	2%	0%	0.03	0
<i>Erysimum asperum</i>	ERAS	Native	2%	0%	0.05	0
<i>Lepidium densiflorum</i>	LEDE	Native	1%	0%	0.03	0
<i>Arabis lignifera</i>	ARLI	Native	1%	0%	0.01	0
<i>Arabis microphylla</i>	ARMI	Native	1%	0%	0.01	0
<i>Erysimum capitatum</i>	ERCAP	Native	1%	0%	0.01	0
<i>Schoenocrambe linifolia</i>	SCLI	Native	1%	0%	0.01	0
<i>Phoenicaulis cheiranthoides</i>	PHCH	Native	0%	3%	0	0.03
<i>Sisymbrium altissimum</i>	SIAL	Non-native	92%	83%	1.9	1.39
<i>Draba verna</i>	DRVE	Non-native	81%	31%	1.34	0.31
<i>Descurainia sophia</i>	DESO	Non-native	58%	6%	0.67	0.06
<i>Alyssum desertorum</i>	ALDE	Non-native	54%	56%	0.75	0.58
<i>Isatis tinctoria</i>	ISTI	Non-native	9%	0%	0.16	0
<i>Chorispora tenella</i>	CHTE	Non-native	5%	0%	0.06	0
<i>Lepidium perfoliatum</i>	LEPE	Non-native	4%	0%	0.11	0
<i>Camelina microcarpa</i>	CAMI	Non-native	1%	0%	0.02	0

Table 5. Butterfly survey dates and total numbers of butterflies observed in 2008 at CRMO, Idaho, USA.

Kipuka	Region	Survey 1 Date	Survey 2 Date	Total # butterflies
11	North	2-July	11-July	18
16	North	1-July	11-July	25
79	South	19-June	8-July	8
81	South	23-June	8-July	9
413	North	2-July	11-July	18
425	Wapi	16-June	9-July	7
436	Wapi	16-June	9-July	6
465	Wapi	14-June	8-July	8
493	Wapi	14-June	8-July	1
520	Wapi	19-June	7-July	3
520A	Wapi	19-May	7-July	10
537	Wapi	20-May	7-July	16
538	Wapi	14-June	7-July	14
543	Wapi	20-May	7-July	25
582	Wapi	17-June	9-July	3
585	Wapi	17-June	9-July	3
587	Wapi	17-June	9-July	4

Table 6. Butterfly species observed in 2008 at CRMO, Idaho, USA. An asterisk (*) indicates a species that was not previously documented in the park.

Family	Subfamily	Tribe	Species	Common name
Pieridae	Pierinae		<i>Pontia beckerii</i>	Becker's white
			<i>Pontia sisymbrii</i>	Spring white*
			<i>Pontia protodice</i>	Checkered white
			<i>Euchloe lotta</i>	Desert marble*
	Coliadinae		<i>Colias philodice</i>	Clouded sulphur
Hesperiidae	Hesperiinae		<i>Hesperia juba</i>	Juba skipper*
	Pyrginae		<i>Pyrgus communis</i>	Common checkered skipper
Nymphalidae	Nymphalinae	Melitaeini	<i>Vanessa cardui</i>	Painted lady
			<i>Euphydryas chalcedona</i>	Chalcedon variable checkerspot
	Heliconiinae	Argynnnini	<i>Speyeria cybele</i>	Great Spangled Fritillary
	Satyrinae		<i>Coenonympha tullia</i>	Common ringlet
			<i>Cercyonis oetus</i>	Small wood nymph
Papilionidae	Papilioninae		<i>Papilio zelicaon</i>	Anise swallowtail*
Lycaenidae	Polyommatainae	Polyommataini	<i>Plebejus melissa</i>	Melissa blue
			<i>Glaucopsyche piasus</i>	Arrowhead blue
	Theclinae	Theclini	<i>Satyrrium behrii</i>	Behr's hairstreak
			<i>Satyrrium californica</i>	California hairstreak
			<i>Callophrys gryneus</i>	Juniper hairstreak*

Table 7. Average and total number of butterflies (by subfamily) observed in two Pollard walk surveys in each of 17 kipukas in 2008 at CRMO, Idaho, USA.

Family	Subfamily	Region			TOTAL
		North (n = 3)	South (n = 2)	Wapi (n = 12)	
Pieridae	Pierinae	1.3	8.0	5.5	86
	Coliadinae	0.3	0.0	0.1	2
Hesperiidae	Hesperiinae	0.0	0.0	1.3	15
Nymphalidae	Nymphalinae	3.0	0.5	0.9	21
	Satyrinae	14.3	0.0	0.3	47
Papilionidae	Papilioninae	0.0	0.0	0.1	1
Lycaenidae	Polyommatainae	1.0	0.0	0.1	4
	Lycaeninae	0.3	0.0	0.3	5
	Theclinae	0.3	0.0	0.3	5
TOTAL abundance		62	17	107	186
TOTAL richness (by subfamily)		7	2	9	9

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