

Insular biogeography theory in serpentine grasslands

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ABSTRACT

Insular biogeography investigates the characteristics influencing the biodiversity of isolated or patchy habitats. In California, the distribution of serpentine soil creates patchy insular serpentine grasslands (ISGs) that serve as important habitats for several endemic plant species and therefore merits consideration for conservation. In this study, we tested the effects of area and isolation on plant richness in 15 Northern California ISGs. Plant richness positively correlated with ISG area, but not isolation, contrary to the theory of insular biogeography. Additionally, 68% of plant morphospecies occurred on one or two islands. Of the rare plants that occurred only on one island, 73% were on smaller than average ISGs. This suggests that ISG protections should be placed around several smaller patches to preserve the greatest number of morphospecies. Our results may help advance the theory of insular biogeography and aid in making productive, evidence-based land management decisions to protect species richness in landscapes around the world.

Keywords: insular biogeography, serpentine grassland, morphological species, endemic

INTRODUCTION

Insular biogeography investigates the biotic and abiotic characteristics that influence the biodiversity in various habitats. While most insular biogeography research has studied the effects of geologic events—such as volcanic activity or island emergence—on species richness (Harrison 2006), MacArthur and Wilson’s study focused on the effects of an island’s area and isolation on its species diversity (1967). In addition to applying this theory to oceanic islands, it can be used to predict patterns on insular mainland areas such as desert oases, mountaintops, and

patches of differing habitat. For example, serpentine soil creates island-like mosaics of habitat types, including serpentine grasslands and serpentine chaparral.

Serpentine grasslands are harsh environments that are stressful to plants due to their low calcium to magnesium ratios, high levels of heavy metals, and low levels of important nutrients such as nitrogen, potassium, and phosphorus (Brady 2005). Because of the unique chemical characteristics of serpentine soils, the plants that do occur on these soil types have evolved to adapt to these conditions (Brady 2005). Even though serpentine grasslands provide difficult

growing conditions, they host 12.5% of all California endemic plant species despite occupying just 1% of California's soil composition (Harrison 2006). Therefore, because serpentine grasslands host a disproportionately high level of endemic species relative to their land area, these biodiversity hotspots are of particular concern when it comes to the preservation of species. Studying serpentine flora is crucial to understanding and putting forth conservation plans in California.

In this study, we tested the effects of area and isolation on plant species richness in insular serpentine grasslands (ISGs). We hypothesized that larger, less isolated ISGs will have a greater plant species richness since this has already been observed in oceanic islands. By examining the effects of island area and isolation on species richness, we aim to better understand how to protect these important habitats and the disproportionate variety of unique species they hold.

METHODS

Our study was conducted from February 22 to February 28, 2021 at Donald and Sylvia McLaughlin Natural Reserve, a 7,050-acre reserve located in Northern California in Lake County. This Mediterranean climate hosts chaparral, oak woodland, and grassland environments on both serpentine and nonserpentine soils. Our study focused on ISGs located throughout the reserve.

We selected 15 ISGs based on accessibility (Fig. 1) using vegetation maps. Each ISG was evaluated for area and distance to nearest ISG studied using

Google Maps and ImageJ v1.53. Nine of the ISGs were burned in the 2020 LNU Lightning Complex Fires, while six were not burned (Fig. 1). Burned or unburned status was determined with the Google Earth Time Machine. We determined the longest straight path from one end of the plot to the other using GPS (Avenza Maps v3.13 and Google Maps).

At each ISG site, we surveyed all species present in a belt transect along the longest path from one end of the plot to the other. This method was used to evenly sample plant communities at continuous distances from the edge of the plot (Andrade 2019). As we surveyed, we identified plants into morphological species (morphospecies) groups based on phenotypic differences. We took pictures of each plant to correct for duplicates *ex post facto*.

We analyzed data using JMP Pro Statistical Software v15. Due to the large variation of ISG size, we \log_{10} transformed area. We used a linear regression to test the effect of area, isolation, and the interaction between area and isolation on morphospecies richness in ISGs. We also used an ANOVA to test the effect of burning on morphospecies richness. To visualize the distribution of morphospecies on ISGs, we ranked them from most to least abundant, based on the number of islands each species occurred on, and plotted each species' rank against this abundance. Then for the morphospecies that occurred only on one island, we ranked these species by the absolute island size each species occurred and plotted this rank against each morphospecies' absolute island size.

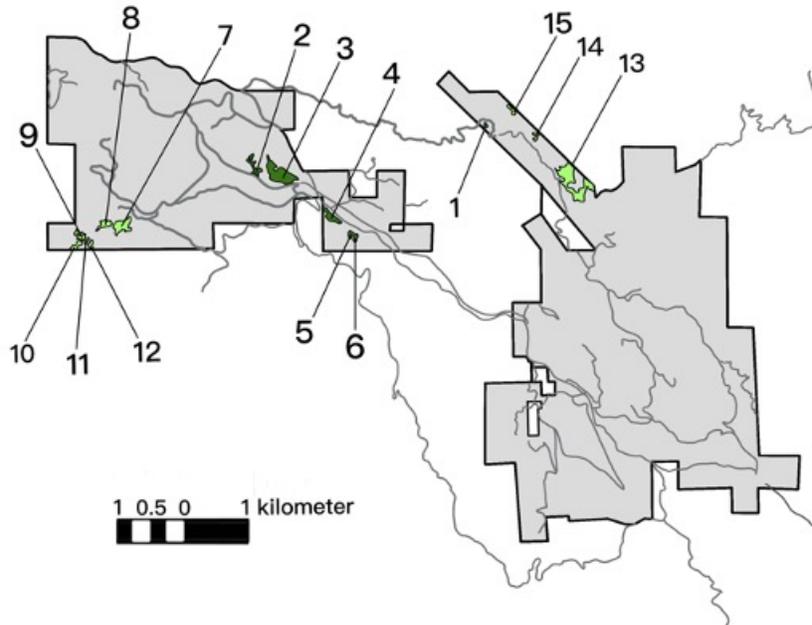


Figure 1: Insular serpentine grassland locations. Each green plot represents an insular serpentine grassland studied. Dark green represents plots that were not burned in the 2020 LNU Lightning Complex Fire. Light green represents plots that were burned. Each plot is labeled with its corresponding site number (1-15). The black outlines represent the borders of Mclaughlin Natural Reserve. The dark grey lines represent local roads both on and off the reserve. The map scale in kilometers is present in the bottom left-hand corner.

RESULTS

In total, we surveyed 15 ISG sites and found 132 morphospecies. There was a positive correlation between ISG area and morphospecies richness (Fig. 2, Table 1). There was no effect of isolation, the interaction between area and isolation, or burning on morphospecies richness (Table 1). Additionally, 76 plant morphospecies (68%) only occurred on one or two islands, while eight species (6%) occurred on 10 or more islands (Fig. 3). Only one species, *Lasthenia californica*, occurred on all 15 ISGs. Lastly, 73% of the species found on one island occurred on smaller than average ISGs (Fig. 4).

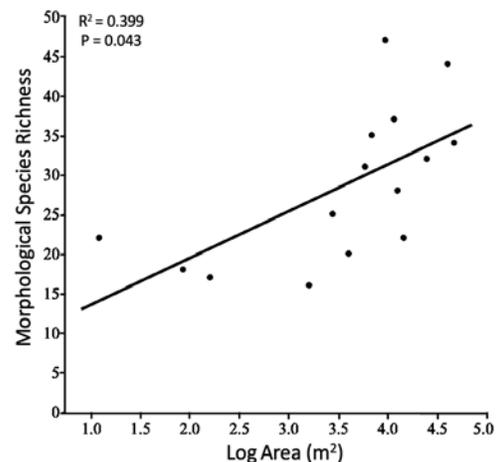


Figure 2: Insular serpentine grassland (isg) patch area versus morphospecies richness. 15 ISGs were sampled, and morphospecies were recorded based on phenotypic differences. Area of each plot was determined using Google Maps and ImageJ v1.53. Due to the large variation in plot size, area was Log_{10} transformed. A positive correlation was found between ISG area and morphospecies richness ($N=15$, $R^2=0.399$, $P=0.043$).

Table 1: Summary statistics testing effects of area, isolation, and fire on morphospecies richness. Depicts the effects of area, isolation and burning on morphospecies richness. Area was Log_{10} transformed to meet linear regression and ANOVA standards of normality and homoscedasticity. Asterisks represents * $P < 0.05$.

Effect	Sample Size	Test Statistic
Area	15	$R^2 = 5.25^*$
Isolation	15	$R^2 = 2.00$
Area x Isolation	15	$R^2 = 1.56$
Burning	15	$X^2 = 1.20$

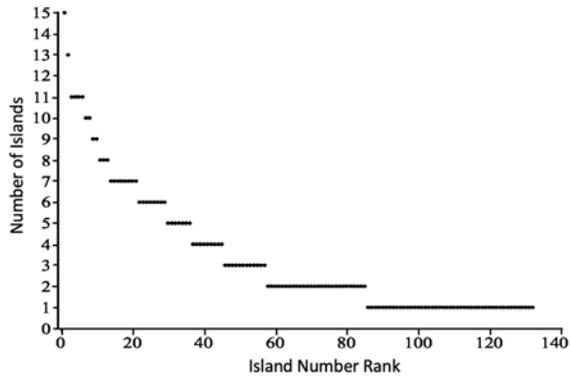


Figure 3: Species occurrence throughout insular serpentine grasslands (isg) patches. Each point represents one morphospecies found across the 15 ISG sites. Rank was based on the number of islands on which each species occurred. Of the 132 species found, 76 species (68%) were found on only one to two islands, while eight species (6%) were found on 10 or more islands. One species, *Lasthenia californica*, was found on all ISG patches.

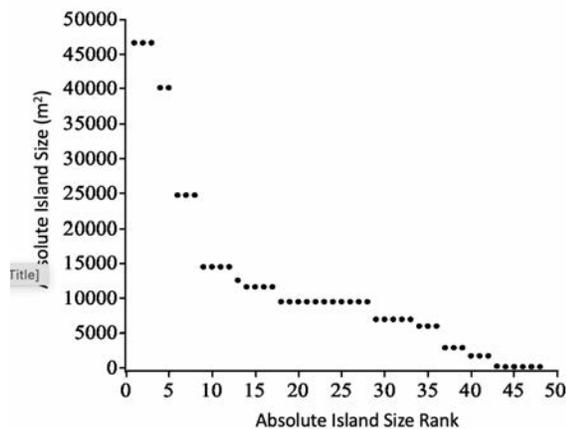


Figure 4: Rare species occurrence on absolute insular serpentine grassland (isg) patches. Each point represents a morphospecies found only on one island. Rank was based on absolute area of the ISG on which the species occurred. Of these species, 73% were found on smaller-than-average ISGs, (average=12109 m²).

DISCUSSION

We found a positive correlation between morphospecies richness and ISG area, consistent with the insular biogeography theory (Fig. 2). These relationships may be due to greater available niches and less competition in larger islands (Chisholm *et al.* 2016), or that larger islands have more variation in soil properties such as moisture and bacterial diversity (Shao-peng Li *et al.* 2020). Despite the harsh abiotic conditions on serpentine soils, these studies could explain how larger ISGs allow for greater morphospecies richness.

In contrast to the insular biogeography theory, we found no effect of isolation on species richness. Due to the lack of a geographic barrier, seed dispersal across ISGs could continue through mammalian, wind, or avian dispersal. In the case of ISGs, which are connected by terrestrial habitats, being within seed dispersal range may drive ecological community diversity (Harrison 2017). An insular biogeography study researching vernal pools located hundreds of miles apart detected that greater isolation causes a significant reduction of species richness (Holland and Jain 1981). In contrast to their study, the lack of elevation differences combined with the close proximity of our ISGs may prevent ISGs from showing the same isolation effects. It also may be necessary to alter the theory of insular biogeography when studying plant ecology in specific landscapes. For instance,

when studying islands located in smaller regions, area could be the only predictor for species richness. Our study has similar findings to Brown's (1978) research on the distribution of boreal birds and mammals which determined that the mountain ranges with larger areas in the Great Basin had significantly greater bird and mammal species. However, consistent with our findings, he found that isolation had no effect on the species richness.

Understanding the impact of habitat patch size on species richness has important conservation implications (Lindenmayer 2019). When determining what habitats conservationists should protect, the tradeoffs of small and large habitats must be analyzed because conservation resources are limited. Although larger islands may harbor a greater number of species, small islands may protect rare species endemic to a particular island (MacArthur and Wilson 1967). Since a majority of the plant morphospecies that occurred on one ISG had smaller than average areas (Fig. 4), ISG protections should be placed around several smaller patches to preserve the greatest number of morphospecies. Serpentine endemics are known to increase biodiversity and provide safety and essential nutrients to the local fauna (Harrison 2002). In order to make land management decisions easier, future research can identify the species located on the ISGs to determine how endemic species numbers change based on island size and isolation. Similar to other global conservations strategies employed to boost species richness, the endemic serpentine grassland species merit protection. With more data collected to advance the theory of insular biogeography, researchers can continue to make

productive, evidence-based land management decisions to improve species richness in landscapes around the world.

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