An Application of the Species Area Relationship to Coastal Californian Grasses

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Abstract The species area relationship (SAR) is an ecological method for measuring species distribution within plant communities. What does it reveal about the differences in species distribution when comparing mirco-site plant communities composed of bothe native perennial and exotic annual grasses? This study analyzed 2 fixed plots, each 4 m^2, located within the Golden Gate Recreational Area, in California. The organization of the plots followed a complete nested design and was divided into a total of 256 cells, the smallest unit of area at $1/64m^2$. The numbers of species present were recorded at the smallest unit of area, which were then aggregated into 8 different units of area and the mean species richness was calculated for each size. This study finds a higher number of species in the native plot at the largest scale along with greater slope value of the native SAR curve. It also finds that a greater rate of species increase with plot size in the native plot, but a lower average absolute number at the smallest scale. The resulting SAR curves reveal that the structure of an established native plant micro site community follows the SAR relationship closer than an exotic annual plant micro site community.

Introduction

The conversion of Californian grasslands from native perennial bunchgrass to Eurasian annual grassland is a radical large-scale community change which has occurred in North America's biota over the last three centuries (Mack, 1989). Many factors, such as resource availability and species diversity are determinants for community-wide patterns and are considered during management and restoration of native dominated habitats (Peart & Foin, 1985, Crawley, 1987, Levine & D'Antonio, 1999, Seabloom, 2003). In particular, it has been hypothesized that species-rich sites are more resistant to invasion (Elton, 1958, Tilman, 1997) and investigation of species richness for areas where invasion has already occurred might indicate whether this hypothesis holds true.

In light of prior research, this project poses the question, what are the differences in species distribution between native- and exotic- dominated grassland? In this project, I applied the species area relationship (SAR) to mixed native perennial and exotic annual Californian coastal grassland to examine and evaluate the differences in distribution of native and exotic grassland species.

The species area curve is a frequently applied model in ecology to examine species richness and predict the number of species occurring within an area (Connor & McCoy, 1979). The model predicts that, as the size of area increases, so does the number of species present. The standard way to plot species-area curves for analysis is to convert both area and number of species into logarithms; the log-log plot aligns the data linearly (Rosenzweig, 1995). The fundamental equation, first suggested by Olof Arrhenius (Arrhenius, 1921) (see Figure 1), predicts the number of species that will be present in a given area. This power-law form has become widely accepted ecological model. (Preston, 1962; May, 1975; Rosenzweig, 1995).

$$\mathbf{S=cA^z}$$
$$\log S = \log c + z \log A$$

Figure 1. S= # of species in an area c= constant, A= area, & z= characteristic of the environment

Only recently has the species area curve been applied to invasive plant species. Crawley compares the number of native and invasive plant species occurring in Britain, Australia and the United States. On the continental scale, native plants increase in number with area more steeply than do the exotic species (Crawley, 1987). Pysek examines the occurrence of exotic species in Central European cities and finds that the exotic species area curves showed a significantly steeper species-area slope than do natives. There is significant debate over species distribution patterns when both native and exotic species are present within a communitry, and my study contributes to analysis about native and exotic plant dominance.

I hypothesize a different species area relationship for a native-dominated area compared to an exotic-dominated area based on observation of the study site. At my research site, the dominant native grass at the site, *Festuca rubra,* is a bunchgrass morphologically different than the exotic annuals; the native grass has a deeper root system that competes for resources in the soil differently than exotics. Peart & Foin (1985) compared the competitive ability of different native perennial bunch grasses in coastal Californian grassland (about 200km north of San Francisco) and found that patchiness in species distributions and localized disturbances strongly affected the outcomes of species interactions. I assume that the bunchgrass structure limits resources for competing species and therefore, hypothesize a native-dominated plot will have lower species richness. Similarly, I hypothesize the exotic-dominated grass plots will display a steeper slope in an species-area plot, indicating more species as the unit of area increases, along with a greater species richness.

Methods

The research site is coastal grassland, located within the Golden Gate Recreational Area in Marin County, California (37°51000 N, 122°31000 W). The research plots are located on terrain that ranges from flat to 3% slopes, has a northeast aspect, and has soils composed of well-drained, sandy loam on bedrock derived from sandstone and shale (USDA, 1985). The climate of the region is influenced its close proximity to coastal weather patterns; summers are warm, dry, and moderated by the coastal fog; winters are cool with annual precipitation averaged between 60 and 90 cm, which falls between the months of November to April (Koteen, 2005).

I am conducting my study with two conditions, a native dominated and an exotic dominated grassland plot. There are no large patches of pure native or exotic grasses at my research site, although I have purposively selected for native or exotic dominance in each of two plots. Each plot size is 2 meter x 2 meter, an area large enough to contain many small units of area for variety, but feasible to the scale for identifying and counting of grass species. The organization of the plots follows a complete, nested design (see Figure 2). A total of 256 (1/64 m^2) cells were aggregated into 128 (1/32 m^2), which in turn were aggregated into 64 (1/16 m^2) and so on, until the last aggregation included the entire 4 m^2 plot. If there were two ways to join cells (in rows or in columns) both were used during data analysis. The mean species number for all cells of both aggregation schemes was calculated and then the number of species for the two schemes was averaged.

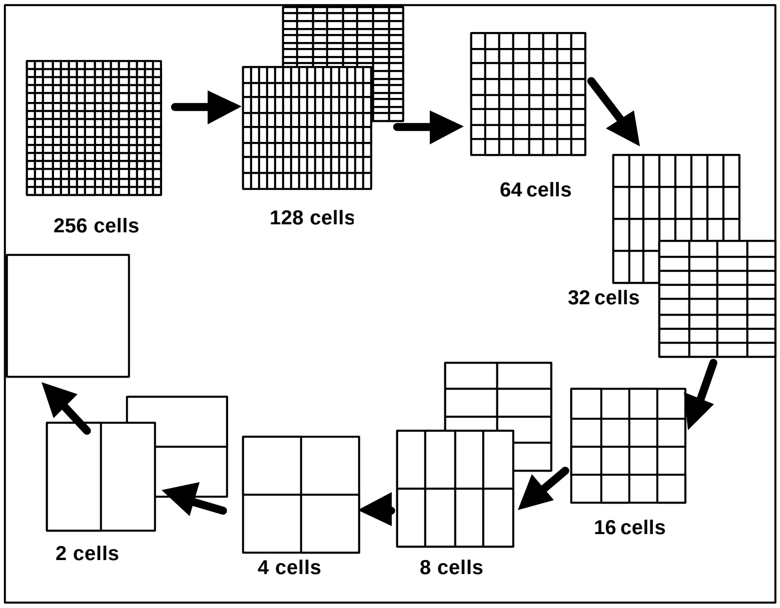


Figure 2. Complete Nested Design. All squares represent 4 meter^2 Species richness data was collected at the scale of 256 cells, and then was determined for the other 8 possible areas shown in the diagram. (Smith, unpublished).

Data collection occurred at the beginning of the flowering season of the grasses which, depending on the length of the winter season, is sometime near the end of March. A quadrat, made of PVC pipe (0.5 x 0.5 meter in dimension with string that has been strung across the square) was gently placed on top of the subplot area. Within each of the smallest units of area, the number of species of grass present were identified and recorded. For unknown genus and species, I applied designations consistently throughout the plot and took a sample (not from the plot, but the surrounding area) so that they could be later compared to species in a library, such as the University and Jepson Herbarium. To analyze the data, the log of the mean number of species at each scale was regressed against the log of the area of each cell for which the mean was calculated.

Results

In my study I developed values for the SAR based on the empirical species richness data collected as described in the methods. The resulting graphs and tables provide data that can be used to compare the species area relationships for native and exotic grassland species? I find that there is indeed a difference in species richness at different sizes of area (see Table 1). It is expected of a SAR curve that as area increases, so does the number of species occurring, and both the native and exotic plot follow this trend. A close look at Table 1 reveals that at the smallest unit of area there are more species occurring (higher species richness) in the exotic plot, and this trend continues up until the two largest size areas (at 128 and 256 cells). At the two largest areas there are more species occurring in the native plot.

To comprehensively analyze the data presented in Table 1, other methods of data analysis will be applied. For example, the rate of the species richness increasing or decreasing is displayed in the SAR curves (see Figure 3). The statistical analysis of the species richness means listed will be discussed in Table 4. A look at the type of species occurring in the plots will be presented in Table 2. Finally, a look at how an individual species is distributed between the plots will be presented in Figures 4-7 with a description of the range area relationship.

Table 1. Species Richness of Native and Exotic Plot.

Area	**1/64m^2**	**1/32 m^2**	**1/16m^2**	**1/8m^2**	**1/4m^2**	**1/2m^2**	**1 m^2**	**2 m^2**	**4 m^2**
Scale (#of cells)	1	2	4	8	16	32	64	128	256
Native Species Richness	4.5	6.3	8.5	11.9	14.2	18.1	23.5	30.1	39
Exotic Species Richness	8.1	10.4	12.1	16.5	17.8	20.2	24.3	26.3	29

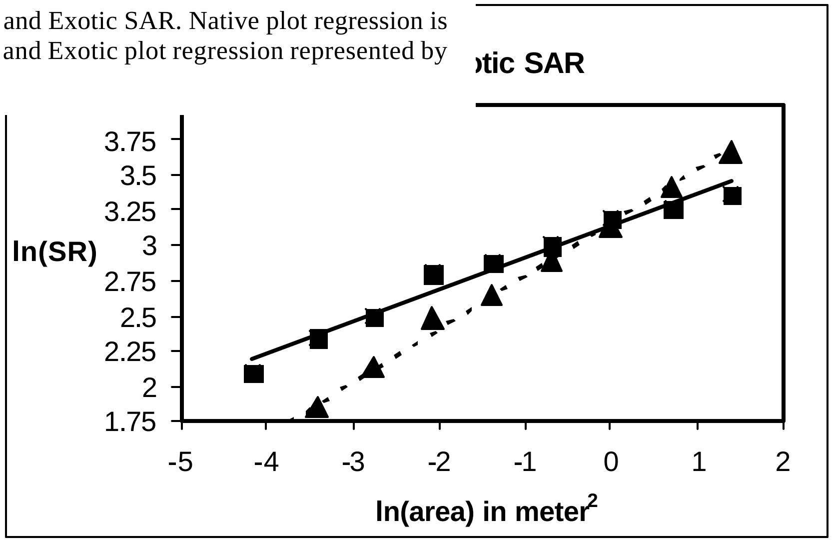
Species list In order to asses the differences in the species richness of the two plots, it is important to analyze what type of species are occurring in each of the plots and how they might be different. The list of identified species (see Table 2) displays the heterogeneity of both plots. Poaceae is considered the grass family and it is accompanied by 13 other plant families. Grasslands are diverse communities that are not only composed of grass species. Usually grasses account for only twenty percent of the species composition and forbs compose the majority of species, although the grasses are responsible for the bulk of community productivity (Barbour & Billings, 2000). In my study, I identified only 24 species and 11 of which occurred in both the native and exotic plot. There are a total of 10 unknown species in the exotic plot and 23 unknown species in the native plot. The number of unknown species limits a quantitative conclusion about how 'native' and how 'exotic' each plot is. Since it is difficult to make any further conclusions about the species composition, a closer look at visual observations of the plot will assist in accounting for the difference between the plots. At the study site, an observer can see that the native plot consists of close-to-the ground bunch grasses and the exotic plot consists of tall individuals. There are potentially more open spaces for new individuals to come into the plot due to the gaps between the bunch grasses. Each plot's physiognomy, bunchgrasses versus tall individuals, accounts for the difference in species composition and will be further analyzed for accounting for the difference in the SAR curves in the discussion.

Table 2. List of identified species occurring at the study site.

Species	Family	Native or Exotic	Plot Presence
Achillea millefolium	Asteraceae	native	Native Plot
Hypochaenis glabra	Asteraceae	exotic	Exotic Plot
Cerastium glomeratum	Caryophyllaceae	exotic	Exotic Plot
Dichondra repens	Convolvulaceae	exotic	Native Plot
Lupinus nanus	Fabaceae	native	Both
Trifolium dubrium	Fabaceae	native	Native Plot
Vicia Americana	Fabaceae	native	Native Plot
Geranium dissectum	Geraniaceae	exotic	Both
Erodium cicuturiu	Geraniaceae	exotic	Both
Chlorogalum pomeridianum	Lilaceae	exotic	Exotic Plot
Sidalcea malvaeflora	Malvaceae	native	Both
Oxalsis albicans ssp. pilosa	Oxalidaceae	native	Both
Eschscholzia californica	Papaveraceae	native	Both
Plantago lanceolata	Plantaginaceae	exotic	Both
Aira caryophyllea	Poaceae	exotic	Both
Avena barbata	Poaceae	exotic	Exotic Plot
Bromus carinatus	Poaceae	native	Exotic Plot
Lolium multiforum	Poaceae	exotic	Exotic Plot
Elymus glaucus	Poaceae	native	Exotic Plot
Festuca rubra	Poaceae	native	Native Plot
Vulpia microstachys	Poaceae	native	Exotic Plot
Rumex acetosella	Polygonaceae	exotic	Both
Claytonia perfoliata	Portulacaceae	native	Both
Anagallis arvensis	Primulaceae	exotic	Both

Comparison of slopes & intercepts According to the power law form of the species area relationship described in the introduction (see Figure 1), the natural log of the species richness is plotted against the natural log of area to create the SAR data points. Then, a linear regression analysis on these data points, produces the SAR curve. Linear regression of the native plot produces a curve fit with an equation $y = 0.38x + 3.16$ and an R^2 value of 0.995. The R^2 value indicates that the least square line accounts for over 99% of the variation in the data.

Figure 3. Native and Exotic SAR. Native plot regression is a dashed ? line and Exotic plot regression represented by solid ¦ line.



The exotic plot linear regression follows the equation y = 0.22x + 3.14. The R^2 value 0.97 indicates the least square line accounts for over 97% of the variation in the data. The slope of the regression line is steeper for the native plot as compared to the exotic plot. Overlaying the two regressions (see Figure 3) the graph shows this steeper slope, as a greater rate of increase of species occurring in the native plot as size increases. The graph also allows for a visual display of the lower average number of species occurring in the native plot (the y values in the regression line are lesser than the exotic plot, up until the two greatest sizes of area). The intercept of the two lines indicates the area at which both graphs contained the same number of species; at area size of $1m^2$, containing 64 cells, the native plot has 23.5 species and the exotic plot has 24.3 species.

Range area relationship The species area relationship analyzed the difference in total number of species occurring in each plot. But, what is the distribution for an individual species within both plots? Is there a difference in how one species is distributed in either a native or exotic dominated plot? The range area relationship can be used to measure the occupancy of an individual species. It is similar to the SAR in that it is a species specific fractal area of range and assesses how much of each plot is occupied by that species. This data analysis follows the same units of area as the SAR, but instead of an average number of species the y-axis will be the average of one species occurring. The RAR is not an abundance analysis; rather it measures where the species are present, and as area increases, what proportion of the area (the range) it occupies. Thereby quantitatively revealing if a single species occupies more area and the rate at which it increases its presence in a native- dominated as compared to an exotic dominated plot.

Table 3. Characteristics of the most dominant grass and forbs species occurring in both plots (Jepson Manual).

	Exotic Grass *Aira caryophyllea*	**Native Forbs** *Eschscholzia californica*	**Exotic Forbs** *Anagallis arvensis*
Structure	Annual to bamboo-like; roots generally fibrous	Annual, perennial herb; taproot sap colorless or clear orange	Annual, perennial herb, glabrous to glandular-hairy
Habitat	Sandy soils, open or disturbed sites	Grassy open areas.	Common. Disturbed places, ocean beaches.

The RAR attempts to take a closer look at the individual species occurring in each plot. Table 3 summarizes the characteristics of the individual species chosen for the RAR. The number of species chosen for the RAR was limited by the incomplete species list (Table 2) because the number of known native grasses or exotic grasses didn't occur in *both* plots. Therefore, I chose one exotic grass species, one exotic forbs, and one native forbs which had a frequent presence in both plots, but not a homogenous distribution as the most dominant species. It would not be significant to choose a species that occurred in every cell, because it wouldn't indicate anything more about its distribution than that it is present everywhere.

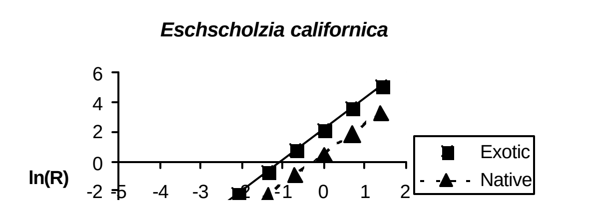
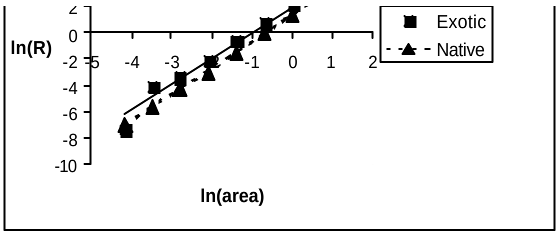


Figure 4. *Eschscholzia californica*. Native plot regression line y=2x + 0.41 with a R^2 =1 and Exotic plot regression line y = 2.09x + 2.19 *and a* $R^2 = 0.9872$.

The results for the range area relationships indicate that although the native plot had a higher total number of species, of those species present, the individual species occupy more area and increase at a greater rate with area in the exotic plot. The results from the RAR are different than the SAR in terms of the individual species are occurring at a greater richness in the exotic plot with a steeper regression line as compared to the native plot. Figure 4 displays the range area relationship for a native forbs, *Eschscholzia californica.* The native plot regression line has a higher R^2 value, but there are more species in the exotic plot. Figure 5, the result for an exotic forbs, *Anagallis arvensis*, displays a remarkably similar species distribution for both native and exotic plots, with an only slightly greater species richness and R^2 value in the exotic plot. In Figure 6, the result for the exotic grass *Aira caryophyllea*, displays a slightly greater slope in the exotic plot and a greater R^2 in the native plot.

Figure 5. Anagallis arvensis. Exotic plot regression line y = 2.01x + 1.3 with an R^2=0.9997 and the Native plot regression line y = 1.96x + 1.85 with an R^2= 0.9746.



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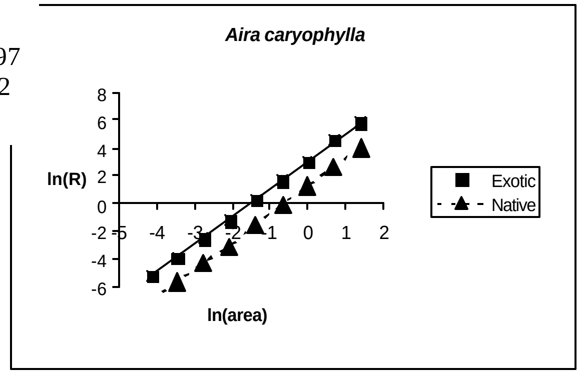

Comparing species richness means To calculate the SAR, the mean number of species to the cell's areas yields the relationship, and a statistical comparison of those means will indicate whether or not those means are significantly different from each other. It would be common for a statistical test to be applied to the SAR regression lines, but since the SAR follows a complete nested design, the species number at each scale depends on the species number of other scales; the points along each line are not independent of one another. Therefore, a direct statistical comparison of the two regression lines is not significant. Instead, a t-test (not paired, unequal variance) was used to compare means for a data set with more than thirty numbers. Table 4 shows that all of these means (1/64 m^2 through 1/8 m^2) showed statistical significance. A Wilcoxon rank sum test was used for all the means for a data set with less than thirty numbers. Of those tests, only ¼ m^2 has statistical significance. The remaining species richness means are for the larger areas and the test shows greater p values, larger confidence intervals and therefore, less statistically significant results. In conclusion, the statistical analysis confirms that the species richness means for each plot are statistically significant from one another up until the largest areas and the number of cells included into that area have decreased; the species richness means for the entire native plot is not statistically significant from the entire exotic plot.

Table 4. Statistical significance.

Area	***Native*** Mean	***Native*** Standard Deviation	***Exotic*** Mean	***Exotic*** Standard Deviation	? mean	P value	95% Confidence Interval
1/64 m^2	4.5	1.9	8.1	1.9	3.6	0.001	3.3 - 3.9
1/32 m^2	6.3	2.4	10.4	2.0	4.1	0.001	3.7 - 4.5
1/16 m^2	8.5	2.8	11.8	2.2	3.3	0.001	2.4 - 4.2
1/8 m^2	11.9	3.0	16.5	2.9	4.6	0.001	3.6 - 5.6
¼ m^2	14.1	3.1	17.8	2.2	-3.7	0.0005	1.8 - 5.6
½ m^2	18.0	3.4	20.2	1.8	-2.1	0.029	-0.24 -4.2
1 m^2	23.3	3.2	24.3	1.5	-1.0	0.59	-3.3 - 5.2
2 m^2	30.5	4.0	26.3	1.7	4.2	0.10	-1.1 - 9.5

Discussion

The intention of this study was to investigate what the SAR could reveal about species distribution for two separate micro-site plant communities, which indeed it does indicate a greater rate of increase of species occurring in the native plot as size increases. The results demonstrate three characteristics of the native bunchgrass-dominated plot that differ from the plot dominated by exotic annual grasses. In the native plot, 1) the data more closely follow a classical SAR curve because it had 2) a higher total number of species occurring at the largest unit of area and 3) a steeper regression line slope.

The methods supporting this result contain two types of bias and a limitation for this scope of research. One, the location of the plots was not randomly assigned, but was purposively chosen to represent dominantly native or dominantly exotic species composition. Two, the study lacks replication of sampling for a variety of native-and exotic- dominated areas and varieties of plot sizes. The sample sizes chosen were primarily a result of my time constraints. Were it feasible, I would test a larger number of samples and different sizes to determine if the relationship holds at various areas. Not determining a quantification of how dominantly native or exotic each plot was, limited the progress of my research. Percent cover was not collected nor was a complete species list determining the native or exotic characteristic of the species occurring within each plot.

There are properties of a plant community which determine the species richness, but which were not addressed, but may include belowground biomass, litter mass, light penetration, resource availability (Tilman, 1993). A quantitative estimation for a pattern of species for a plant community largely depends on the interpretation of these characteristics.

One qualitative explanation and observation for the differences in the graphs includes the difference in plant morphology between the native and exotic grasses. The native plot consists of a few species of large bunch grasses with locally rare small species in the open areas between the bunches. On a small scale, lack of open spaces would result in low species richness, but as the area increases, the rare individuals added up for high species richness. Since an individual perennial bunch grass covers a larger area than an individual annual grass, there will be more individuals, or open areas, for individuals in an annual system, hence, the greater species richness at the smallest scale. The results from the range area relationship support this observation; the individual species tested had a greater occurrence and rate of distribution in the exotic plot with locally more open spaces, as compared to the native plot.

The values in the SAR demonstrate how species richness varies with the addition of exotic species and the extinction of natives (assuming the exotic plot once looked like the native plot). The change in species composition suggests a loss in species richness at the largest spatial scale, with the complete conversion to exotics. Within the broader context of grassland ecology and biological invasions, this study supports the SAR as a measurement to be used in quantifying the dynamic relationship between native and exotic grasses. Proposed ideas regarding properties of plant communities such as the concept of “ecological resistance” suggest that greater community diversity caused greater invasion resistance (Elton, 1958). Another property of the study site relating to invasion resistance includes its history of grazing. Some ecologists hypothesize that exotic annuals are not superior competitors, and have attributed prior disturbance and current rarity of native perennials toward the competitive dominance of exotic annuals (Seabloom, 2003, D’Antonio, 1992).

The results in this study can not be directed to a noticeably similar study, but can contribute to vegetation field applications of SAR. The higher species richness in the native plot may support future research and adds onto the compilation of SAR research such as Crawley (1987) and Pysek (1998) which were mentioned in the introduction. Species richness of plant communities can help to investigate and understand other properties of ecosystem functions. Does diversity of native plants perennials or exotic annuals differently affect the stability of the community? In the future, applications of the SAR with plant community invasions should be supplemented with analysis of other ecological determinants in order to distinguish the properties contributing or deterring invasability of plant species.

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