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Eastern Fox Squirrels and Western Gray Squirrels in Southern California

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ABSTRACT: Eastern fox squirrels have been introduced to many regions within the western United States including areas within California, Idaho, Montana, Oregon, and Washington. In California, fox squirrels have been introduced to San Francisco, Fresno, Los Angeles, San Diego, Berkeley, Mount Diablo in Clayton, Bakersfield, and Santa Barbara. The geographic range of the eastern fox squirrel has expanded greatly both through natural dispersal and additional intentional introductions by humans. The fox squirrel has replaced the native western gray squirrel in certain habitats while the two species coexist in other habitats. Western gray squirrels exist by themselves in a third type of habitat even though eastern fox squirrels have occupied adjacent habitat for about 30 years. Habitat Suitability Models (HSMs) have been used to predict the presence and/or abundance of a particular species within a habitat. Analysis of 9 habitat variables using Discriminant Analysis produced a HSM where replacement, coexistence, and exclusion habitats can be identified using only 3 of the 9 habitat variables: average height of ground cover, percent canopy cover, and percent of total trees that are deciduous. A field study underway for over two years at Rancho Santa Ana Botanic Garden in Claremont, CA is testing the validity of the HSM with the study site predicted to be a long-term coexistence habitat. The ratio of western gray squirrels to eastern fox squirrels has gone from 3:1 shortly after the fox squirrel entered the habitat to 1:1, but after 2.5 years of coexistence both species are commonly observed in the study site. The HSM is also being tested through the analysis of additional habitats. Although coexistence of the two species is possible for many decades, the number of western gray squirrels in coexistence habitats is often small, coexistence habitats are geographically isolated from each other, and the probability of extinction of western gray squirrels from these habitats could be high. We are also looking for new habitats which could support western gray squirrels if individuals were moved to these habitats.

KEY WORDS: coexistence, eastern fox squirrel, habitat suitability model, invasive species, replacement, *Sciurus griseus*, *Sciurus niger*, tree squirrels, western gray squirrel

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INTRODUCTION

An invasive species is defined by U.S. Department of Agriculture Executive Order 13112 as a species of animal, plant, or other organism that is not native to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm, or harm to human health. Human actions are the primary means of the introduction of invasive species and over 1,700 invasive species have been identified that reside in or are a threat to enter California (ISCC 2011).

Three examples of how a native species of tree squirrel can be threatened by an invasive species of tree squirrel include the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) with Abert's squirrel (*Sciurus aberti*), the Eurasian red squirrel (*Sciurus vulgaris*) with the eastern gray squirrel (*Sciurus carolinensis*), and Abert's squirrel (*Sciurus aberti*) with the eastern fox squirrel (*Sciurus niger*). The Mount Graham red squirrel is native to the Pinaleno Mountains of southeastern Arizona in the U.S., while Abert's squirrel was introduced to the Pinaleno Mountains in the 1940s (Davis and Brown 1988). Abert's squirrels raid middens established by Mount Graham red squirrels, affecting the viability and persistence of this endangered subspecies of red squirrel (Hutton et al. 2003, Rushton et al. 2006). The Eurasian red squirrel has been replaced throughout most of Britain, Ireland, and northern Italy by the eastern gray squirrel, which was introduced to the United Kingdom in the late 19th or early 20th century

(Gurnell 1987, Wauters et al. 1997). A reduction in body mass of juvenile and sub-adult red squirrels caused by exploitative competition for food and space, as well as the eastern gray squirrel being a carrier of a pox virus which is deadly to the Eurasian red squirrel, may lead to eventual population extinction (Gurnell et al. 2004, Rushton et al. 2000). The eastern gray squirrel also damages trees through de-barking, causing both environmental and economic damage to forests and timber crops (Bertolino and Genovesi 2002). Abert's squirrel, living in the Black Forest of Colorado, has experienced a population decline attributed to competition with the invasive eastern fox squirrel (Fitzgerald et al. 1994).

In the greater Los Angeles, CA area, native western gray squirrels (*Sciurus griseus*) are declining in number. The decrease in population size coincides with the introduction of the eastern fox squirrel from the eastern United States (King et al. 2010). The eastern fox squirrel was first introduced to Los Angeles County in 1904 (Becker and Kimball 1947). Additional introductions have occurred at many locations in California (King 2004).

The western gray squirrel includes Southern California as part of its native distribution and lives predominantly near, or in, local mountain ranges. However, these squirrels can still be found in less disturbed open areas in the Los Angeles metropolitan area (King 2004). Over the 100+ years since introduction, *S. niger* has flourished in urban and suburban areas within Los Angeles, Orange, and

Ventura Counties, expanding their distribution by 0.44-3.44 km/yr (King et al. 2010). As the eastern fox squirrel continues to expand its distributional range, it is moving into many habitats occupied by the native western gray squirrel (King 2004). Western gray squirrels disappear from some habitats soon after the arrival of the eastern fox squirrel (Muchlinski et al. 2009).

An ecological niche has been traditionally defined by where an organism lives and the role that organism plays in its environment. Hutchinson (1959) expanded the ecological niche concept by distinguishing the fundamental niche, the combination of conditions and resources which allow a species to maintain a viable population in the absence of interspecific competition or predation, and the realized niche, a narrower range of conditions and resources in which a viable population is maintained in the presence of competitors and predators.

A method for quantifying an ecological niche is a Habitat Suitability Model (HSM). Habitat Suitability Models are operational applications of the ecological niche, which use environmental variables to predict the presence, absence, or abundance of a species within a habitat (Hirzel and Le Lay 2008). A HSM is a tool for protecting habitats for endangered or threatened species, and they have been used in a wide variety of cases by conservation biologists. Because of the complex nature of natural systems, HSMs simplify and present a method of understanding the spatial distribution of species based on a range of biotic and abiotic factors. In this study, a HSM was developed to determine 1) variables that exclude *Sciurus niger* from habitats occupied by *Sciurus griseus*, 2) variables that allow *S. griseus* to coexist with *S. niger* in certain habitats, and 3) variables which lead to replacement of *S. griseus* by *S. niger*.

METHODS

Three different types of habitats were analyzed to develop the Habitat Suitability Model. The first habitat type included locations where only *S. griseus* exist, even though *S. niger* have been located in adjacent habitat for one or more decades. The second habitat type included locations where both *S. griseus* and *S. niger* have coexisted for a minimum of 10 years up to over 40 years (Lewis 2009). It was important that coexistence occurred for many years to conclude that the two species are actually coexisting, rather than being in a temporary state of coexistence after habitat invasion by *S. niger*. The third habitat type included locations with a historical record of supporting a population of *S. griseus*, but now support only a population of *S. niger* without a significant change to the structure of the habitat over time.

The 8 locations where *S. niger* replaced *S. griseus* include: 1) Lacy Park in San Marino; 2) the residential area of Lanterman Developmental Center in Pomona; 3) a campground/park located on the western edge of Lanterman Developmental Center in Pomona; 4) the main quad at California State Polytechnic University, Pomona; 5) a semi-natural area near Kellogg Center West at California State Polytechnic University, Pomona; 6) a residential area in eastern Altadena; 7) a residential area in northwestern Altadena; and 8) an area adjacent to Walnut Creek Elementary School in Walnut. Study sites ranged

in size from 2.0 to 8.8 hectares and each study site had a resident population of western gray squirrels for many decades. For example, western gray squirrels were present on the campus of California State Polytechnic University, Pomona for more than 40 years.

The 8 locations where both species of tree squirrels are known to coexist and their period of coexistence are: 1) the Bird Sanctuary within Griffith Park, Los Angeles (~30 yrs); 2) Pacific Palms Golf Course in City of Industry (~25 yrs); 3) the main quad area at Pomona College in Claremont (~10 yrs); 4) a residential area in Calabasas (~40 yrs); 5) San Dimas Canyon Park in San Dimas (~20 yrs); 6) Schabarum Park in City of Industry (~20 yrs); 7) a semi-natural area at Pomona College in Claremont (~10 yrs); and 8) Walnut Creek Park in San Dimas (~15 yrs). Representative study sites within these habitats ranged in size from 0.9 to 7.1 ha, depending on accessibility to areas within the larger habitat.

The 8 locations that were identified to support the continued existence of *S. griseus* even though *S. niger* are in an adjacent habitat include: 1) Monrovia Canyon Park, Monrovia; 2) Big Santa Anita Canyon, Sierra Madre; 3) Little Santa Anita Canyon, Sierra Madre; 4) woodlands surrounding the San Gabriel Canyon Environmental Education Center, Azusa; 5) Topanga Canyon State Park, Topanga; 6) Big Dalton Canyon Wilderness Park, Glendora; 7) Millard Canyon, Altadena; and 8) Fish Canyon, Azusa. The sizes of the exclusion study sites varied from 1.0 - 2.6 ha. The size of each study site was based on accessibility and was an adequate representation of the entire habitat type.

Data for the following 9 habitat variables were collected from each of the 24 study sites:

1. density of trees
2. percent of study area covered by tree canopy
3. number of closed canopy areas
4. number of tree species
5. mean number of trees per closed canopy area
6. oak trees as a percent of total trees
7. percent of total trees that are deciduous
8. average ground cover height
9. distance to closest residential area.

Data were analyzed using the classification technique of Discriminant Analysis (SPSS Version 18, IBM Corp., Armonk, NY). Discriminant Analysis created mathematical rules for classifying and separating the habitat types using the habitat variables. A model was created to determine which habitat variables best predict habitats that support *S. griseus* while excluding *S. niger*. The model is also useful in the identification of potential coexistence and replacement locations.

Discriminant Analysis was first used to determine whether or not the 3 habitat types can be distinguished by using the 9 habitat variables from the study. An ANOVA tested the null hypothesis that the means of each variable were equal across the 3 habitat types. Since the overall test was significant ($P < 0.05$), results were used to determine variables that differed significantly between the 3 habitat types. Also, a stepwise regression analysis was used to review and evaluate each variable for its contribution to

Table 1. Mean ± S.E. values and results of ANOVA tests for the 9 independent variables measured for replacement, coexistence, and exclusion type habitats.

Independent Variable	Replacement Habitat	Coexistence Habitat	Exclusion Habitat	F Value	P Value
Trees per Hectare	46.7 ± 11.7	129.6 ± 24.4	102.7 ± 9.2	6.57	.006
Percent Tree Canopy Coverage	40.7 ± 6.4	78.3 ± 6.1	92.2 ± 2.6	25.05	.000
Number of Tree Species	13.6 ± 1.2	9.5 ± 1.9	3.8 ± 0.5	13.80	.000
Closed Canopies per Hectare	1.5 ± 0.6	4.1 ± 1.6	1.8 ± 0.6	1.83	.186
Trees per Closed Canopy	7.7 ± 0.7	46.3 ± 25.2	109.1 ± 26.8	5.81	.010
Percent Oak Trees	9.5 ± 2.5	26.6 ± 9.8	58.4 ± 11.2	8.10	.002
Percent Deciduous Trees	46.0 ± 7.6	9.2 ± 2.6	20.9 ± 6.8	9.67	.001
Ground Cover Height (cm)	5.7 ± 0.8	6.2 ± 1.3	59.4 ± 5.3	93.56	.000
Closest Residential Area (km)	0.4 ± 0.2	0.4 ± 0.2	1.7 ± 0.4	6.42	.007

discrimination between habitat types.

The number of discriminant functions generated is the number of habitat types minus 1. Both discriminant functions yielded an eigenvalue that reflects the percent of variance explained in the dependent variable cumulating to 100% total variance for all discriminant functions (Garson 2008). High eigenvalues indicate high discriminating power of the discriminant functions. The canonical correlation for each discriminant function is a measure of the association between the groups where 1.0 represents all variability (Garson 2008). Canonical correlation values close to 1.0 indicate that the function accounts for a large proportion of total variation.

A fast way to distinguish between habitat types is by using the minimum number of variables needed for a useful mathematical model. Three mathematical equations, generated using 3 independent variables identified in the stepwise regression analysis, were then used to separate replacement, coexistence, and exclusion type habitats from one another.

The model was tested statistically using the cross validation technique. Cross validation removes one habitat site at a time and creates a model based on all remaining habitats. The habitat site that was removed was then treated as a new habitat and was classified by the discriminant functions derived from all other 23 habitats. Results generated by the cross validation technique assess the validity and predictive value of the model. A field study at Rancho Santa Ana Botanic Garden (RSABG) in Claremont, CA is also being used to test the predictive value of the model. A monthly census using transect lines has been conducted since October 2009. Based upon the variables used in the HSM, RSABG should be a long-term coexistence site for the native and introduced species of tree squirrels.

RESULTS

The overall test of significance for the two discriminant functions with all 9 variables entered at the same time was significant (Function 1: 0.014 ; $\chi^2 = 72.345$; $df = 18$, $P < 0.001$ and Function 2: 0.189 ; $\chi^2 = 28.301$; $df = 8$; $P < 0.001$). The two eigenvalues (Function 1 = 12.341 and Function 2 =

4.284) indicate a strong association between the groups formed by the habitat variables and the two discriminant functions. The two canonical correlation values from the overall analysis show a high level of correlation (Function 1 = 0.962 and Function 2 = 0.900). Therefore, it is possible to discriminate between the replacement, coexistence, and exclusion type habitats using the 9 independent variables included in the study.

The mean and standard error values with results of the individual ANOVA tests on the hypothesis that $\mu_1 = \mu_2 = \mu_3$ for the 9 independent variables are shown in Table 1. Significant differences ($P < 0.05$) among μ_1 , μ_2 , μ_3 were found for 8 of the 9 independent variables. The only variable in which the mean value did not differ significantly across habitat types was the number of closed canopies per ha.

Results from the stepwise regression analysis indicate that only 3 variables (average height of ground cover, percent of area covered by tree canopy, and percent of trees that are deciduous) need to be included in the model for separation of the 3 types of habitats. The result of the stepwise regression analysis remained highly significant (Function 1: 0.023 ; $\chi^2 = 75.688$; $df = 6$, $P < 0.001$ and Function 2: 0.227 ; $\chi^2 = 29.656$; $df = 2$; $P < 0.001$). The two eigenvalues (Function 1 = 8.990 and Function 2 = 3.405) still indicate a strong association between the groups formed by the 3 habitat variables and the two discriminant functions. The canonical correlation values for each discriminant function (Function 1 = 0.949 and Function 2 = 0.879) still indicate high correlation between the discriminant functions and the 3 types of habitat. The Structure Matrix obtained through stepwise analysis is shown in Table 2.

The canonical discriminant functions created by the stepwise analysis are shown in Figure 1. Discriminant Function 1, along the x-axis, separates exclusion habitats from coexistence and replacement habitats using

Table 2. The Discriminant Structure Matrix showing pooled within-group correlations between the 3 independent variables and the discriminant functions from the stepwise regression analysis.

Independent Variable	Discriminant Function 1	Discriminant Function 2
Mean Height of Ground Cover	+ 0.995	+ 0.051
Percent Tree Canopy Coverage	+ 0.379	- 0.567
Percent Deciduous Trees	- 0.078	+ 0.504

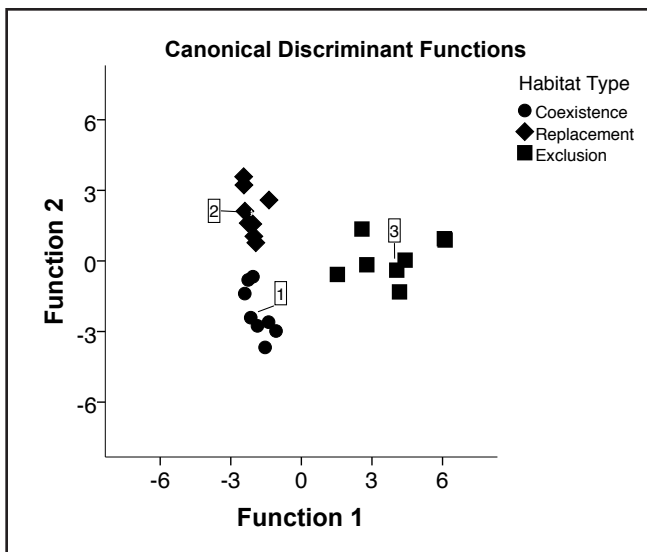


Figure 1. Canonical discriminant functions from the stepwise regression analysis showing separation of the 24 habitat sites into 3 distinct habitat groups. Group centroids would be located at the end of the line projecting from each numbered box.

the variable “average height of ground cover”. For Discriminant Function 2, the Structure Matrix contains the variables “percent of site covered by tree canopy” and “percent of total trees that are deciduous,” which represent the largest absolute correlation (-0.567 and 0.504 respectively) to Discriminant Function 2. Discriminant Function 2, along the y-axis, can be used to distinguish coexistence habitats from replacement habitats.

Assuming that a sufficient number of trees are present to support a population of tree squirrels, the variable “average height of the ground cover” can be used to separate exclusion habitats from coexistence and replacement habitats. A location with a high average ground cover height, a high percentage of canopy cover, and a low percentage of the total trees that are deciduous would correlate with a higher probability that the habitat will continue to support only *S. griseus*, while excluding *S. niger*. A low average ground cover height, even if the site had a large percentage of tree canopy and low percentage of trees that are deciduous, would correlate with a higher probability that the habitat would be a coexistence or replacement type habitat.

Values in the Structure Matrix show that Discriminant Function 2 is needed to separate coexistence from replacement type habitats. As seen in Figure 1, coexistence and replacement habitats have approximately the same value for Discriminant Function 1 (average height of ground cover). Discriminant Function 2, along the y-axis, uses the variables “percent of study site covered by tree canopy” and “percent of total trees that are deciduous” to separate replacement from coexistence habitats. A study site with a high percentage of canopy cover would correlate with a

coexistence habitat as long as a low percentage of the trees forming the canopy were deciduous.

To predict what habitat type a particular site will identify with, data for the 3 variables are put into the equations shown below. The equation that yields the highest value represents the predicted habitat type.

$$\text{Coexistence Habitats} = -15.948 + .400 (\% \text{ tree canopy}) - .088 (\% \text{ of total trees deciduous}) - .135 (\text{average height of the ground cover})$$

$$\text{Replacement Habitats} = -6.682 + .129 (\% \text{ tree canopy}) + .124 (\% \text{ of total trees deciduous}) + .038 (\text{average height of the ground cover})$$

$$\text{Exclusion Habitats} = -32.682 + .294 (\% \text{ tree canopy}) + .030 (\% \text{ of total trees deciduous}) + .597 (\text{average height of the ground cover})$$

The HSM shows excellent predictive value, as 100.0% of the groups were correctly classified using the cross-validation statistical technique (Table 3). Also, census data from RSABG (Figure 2) indicate the two species may coexist for a long time in this predicted coexistence habitat. More detailed data documentation and analysis is provided in Gatza (2011).

DISCUSSION

Habitats in southern California that have historically supported *S. griseus* but now only support *S. niger* have low percentages of tree canopy coverage correlating with a smaller number of trees, high percentages of deciduous trees that make up the canopy, and low average ground cover heights. Vander Haegan et al. (2007) reported that

Table 3. Original classification and cross-validation results of the stepwise regression analysis. In cross-validation one of the original habitats is held out of analysis at a time and the analysis is conducted using the 23 remaining habitats. The one habitat held out of the analysis is then treated as a new habitat and is classified by the functions derived from the 23 remaining habitats. The model has excellent predictive value with 100% of original grouped cases correctly classified.

Habitat Type	Predicted	Predicted	Predicted	Total
	Habitat Group	Habitat Group	Habitat Group	
	Replacement	Coexistence	Exclusion	
Original Habitats				
Count: Replacement	8	0	0	8
Count: Coexistence	0	8	0	8
Count: Exclusion	0	0	8	8
% Replacement	100	0	0	100
% Coexistence	0	100	0	100
% Exclusion	0	0	100	100
Cross Validated Habitats				
Count: Replacement	8	0	0	8
Count: Coexistence	0	8	0	8
Count: Exclusion	0	0	8	8
% Replacement	100	0	0	100
% Coexistence	0	100	0	100
% Exclusion	0	0	100	100

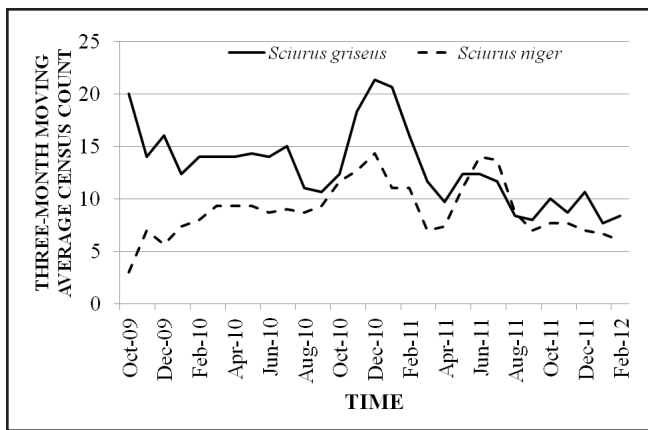


Figure 2. Census data for western gray squirrels (*Sciurus griseus*) and eastern fox squirrels (*Sciurus niger*) at a study site within Rancho Santa Ana Botanic Garden in Claremont, CA. The first two data points on each line represent absolute counts for the specific month while all other data points are 3-month moving averages.

an important characteristic of habitat for *S. griseus* is continuous tree canopy, as individuals use the canopy to travel between trees. While *S. griseus* do utilize habitats with low tree canopy coverage, a high percentage of deciduous trees, and low height of ground cover as part of their fundamental niche, habitats with this structure are not part of the realized niche in the presence of *S. niger*. Habitat loss and fragmentation cannot be the sole underlying causes for replacement of *S. griseus* by *S. niger*. Replacement habitats are located in a variety of areas such as city parks, college campuses, recreational areas, and residential neighborhoods which have not had drastic changes to the structure of the landscape during the time of replacement. Muchlinski et al. (2009) reported replacement of *S. griseus* by *S. niger* in only 1 year at the main quad at California State Polytechnic University, Pomona and within 4 years on a more heavily wooded section of the campus. No drastic changes were made to the landscape of the campus during the time of replacement.

While continuous tree canopy is important for the presence of *S. griseus* in a habitat that also contains *S. niger*, coexistence of the two species will only occur when the continuous tree canopy is composed of a very low percentage of deciduous trees. While live oak and California bay trees (*Umbellularia californica*) are the main native non-deciduous trees in southern California, non-native, non-deciduous trees such as eucalyptus, coastal redwood (*Sequoia sempervirens*), pine, and cedar trees are often associated with coexistence of the two species of tree squirrels in southern California. Also, while the variable “percent of oak trees” was not included in the model produced through stepwise analysis, exclusion habitats have a higher percentage of oak trees than coexistence habitats, which have a higher percentage of oak trees than replacement habitats. Certainly, the model needs to be refined to take into account issues like sources of food, and the model should be tested within other regions of California. Further refinement may be necessary once the model is tested in regions outside those tested in this study.

While *S. niger* do not include the foothill canyons, which have high ground cover as part of their habitat in southern California, it is probably only a matter of time before this species reaches the mixed oak-conifer and conifer forests located in the San Gabriel, San Bernardino, and San Jacinto mountain ranges that line the northern and eastern boundaries of the Los Angeles basin and associated valleys. As documented by King (2004), many residents, frustrated by the damage that *S. niger* inflict on their citrus and nut-bearing trees, trap and relocate animals to habitats some distance from their homes. If someone does transport *S. niger* to a habitat that is contiguous with or part of the mixed oak-conifer and conifer forests of California, large numbers of western gray squirrels could be put at risk of replacement. The low average ground cover height found in oak-conifer and pine forests in the local mountains could provide a new habitat in which the eastern fox squirrel impacts the native western gray squirrel.

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