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Habitat fragmentation provides a competitive advantage to an invasive tree squirrel, *Sciurus carolinensis*

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Abstract Changes in the composition of biological communities can be elicited by competitive exclusion, wherein a species is excluded from viable habitat by a superior competitor. Yet less is known about the role of environmental change in facilitating or mitigating exclusion in the context of invasive species. In these situations, decline in a native species can be due to the effects of habitat change, or due to direct effects from invasive species themselves. This is summarized by the "driver-passenger" concept of native species loss. We present a multi-year study of tree squirrels that tested the hypothesis that tree canopy fragmentation, often a result of human development, influenced the replacement of native western gray tree squirrels (*Sciurus griseus*) by non-native eastern gray tree squirrels (*Sciurus carolinensis*). We tested this hypothesis along a continuum of invasion across three study sites in central California. We found that within the developed areas of the University of California at Santa Cruz campus and city of Santa Cruz, *S. carolinensis* excluded *S. griseus* from viable habitat. The competitive advantage of *S. carolinensis* may be due to morphological and/or behavioral adaptation to terrestrial life in fragmented hardwood forests. We classify *S. carolinensis* as a "driver" of the decline of native *S. griseus* in areas with high tree canopy fragmentation. Future habitat fragmentation in western North America may result in similar invasion dynamics between these species. Our study warrants consideration of existing and predicted interactions between potentially invasive species that co-occur with native species where land use change is proposed.

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Introduction

Understanding the effects of human development on the structure of biological communities is critical for the successful management and conservation of species worldwide. Habitat fragmentation, a process

by which continuous habitat is subdivided into smaller parcels surrounded by habitat unlike the original, is one of the primary threats to biodiversity globally (Andren 1994; Fahrig 2000). Anthropogenic habitat fragmentation, including urban development, is known to alter biological assemblages through changes in community dynamics (Saunders et al. 1991; Andren 1994; Fahrig 2000).

A common example of a community response to habitat fragmentation is competitive exclusion via interspecific competition, in which one species excludes another from a shared niche space (Hardin 1961). Competitive exclusion by invasive species is often cited as a primary reason for native species decline (Sakai et al. 2001; Vila and Weiner 2004). However, less is known about the role of landscape change, including habitat fragmentation, in facilitating or mitigating biological invasions (Holway 1999; Mack et al. 2000; Gonzales et al. 2008; Lawes and Grice 2010; Bennet et al. 2011). Part of the difficulty in understanding the cause of native species decline in this context is that landscape change can covary with invasive species impacts (Didham et al. 2005). The "driver-passenger" model of native species loss in the context of invasive species and habitat modification is a theoretical framework that attempts to disentangle these effects (Didham et al. 2005; MacDougall and Turkington 2005). In this model, an invasive species is considered a "driver" of native species decline when they compete directly with, and exclude or eliminate native species. In contrast, an invasive species is considered a "passenger" when landscape change causes a decline in native species, and the invader subsequently occupies areas previously inhabited by natives. While experimental tests of this hypothesis have been performed (e.g. MacDougall and Turkington 2005), there is a lack of quantitative field studies to identify invasive species as "drivers" or "passengers" of native species loss in modified environments (With 2004; Grarock et al. 2013).

The eastern gray squirrel (*Sciurus carolinensis*) is a rodent native to eastern North America that has been introduced by humans to many areas of the world, including England, Italy, South Africa, and western North America (Steele and Koprowski 2001). These introductions have often been followed by a displacement or population decline of native tree squirrels (Reynolds 1985; Gurnell 1987; Skelcher 1997; Bruemmer et al. 2000; Wauters et al. 2002a). For

example, Reynolds (1985) showed that red squirrels (*Sciurus vulgaris*) native to England were displaced in Eastern England following the introduction of *S. carolinensis* around the turn of the 20th century. In Washington State, USA, competition with introduced *S. carolinensis* is thought to play a key role in the recent decline of native western gray tree squirrels (*Sciurus griseus*), which have now been classified as "threatened" in the state (Linders and Stinson 2007). The ecological mechanisms governing the replacement of native tree squirrels by invasive *S. carolinensis* are highly variable, but likely include interference and exploitation competition for shared niche factors such as seed caches and nest sites (Wauters et al. 2000, 2002b).

Sciurus carolinensis was introduced to the San Francisco Bay area in the 1970's and has since spread across central California, including the counties of Santa Clara, San Mateo, and Santa Cruz (Hall 1981; Carraway and Verts 1994). Its exact range is unknown, but it is frequently documented in urban areas such as city parks. For example, Haff et al. (2008) qualitatively reported that *S. carolinensis* is commonly observed in the core University of California at Santa Cruz (UCSC) campus grounds whereas the native western gray squirrels, *S. griseus,* are rarely seen near the center of the campus. The ecological mechanisms underpinning the distributions of non-native *S. carolinensis* and native *S. griseus* in North America are poorly understood, but examining the drivers of tree squirrel community structure in response to landscape change will lead to a better understanding of invasion dynamics and native species loss.

This study tests the hypothesis that tree canopy fragmentation resulting from human development is facilitating the competitive exclusion of *S. griseus* by *S. carolinensis,* and that *S. carolinensis* is therefore a "driver" of native species loss. We defined habitat fragmentation in this study as the loss of tree canopy cover, since canopy cover is an important feature for tree squirrels and forest loss is a known cause of habitat fragmentation (Laurance et al. 2002). We also test the alternative hypothesis that human development is the direct cause of decline in *S. griseus*, and that *S. carolinensis* is therefore a "passenger" of landscape change. Finally, we also test the hypothesis that forest composition has an effect on the distribution and abundance of these species, and that any

observed differences in population metrics between these species are the result of habitat preference.

Using a combination of observational and hair snare surveys, we index the relative abundance of native and non-native tree squirrels and compare estimates of canopy cover, development cover, and forest type along a spectrum of invasion at three study sites: no invasion (Santa Rosa), to partial invasion (UCSC), to full invasion (Santa Cruz). Where these species cohabitate (i.e. UCSC and the city of Santa Cruz), we predict that areas of high development are characterized by low canopy cover and that these areas will be dominated by *S. carolinensis*. We further predict that *S. griseus* can be found in areas with high development cover but only when *S. carolinensis* is not present (i.e. the city of Santa Rosa). Identifying the drivers of tree squirrel community composition in Western North America such as competition and tree canopy fragmentation is necessary for the conservation and management of these species. Field studies such as this can also test whether habitat fragmentation can alter the competitive dynamics of invasive species.

Materials and methods

Ethics statement

Observational and hair snare surveys were conducted in collaboration with the UCSC Campus Natural Reserve under the supervision of Gage Dayton and The Institutional Animal Care and Use Committee (IUCAC) (Permit # DAYTG1108, California Dept. of Fish and Wildlife). No live capture, handling, or tagging of individuals was conducted as a part of this study.

Study areas

This study was carried out in three locations in central California: The University of California at Santa Cruz campus, the city of Santa Cruz, and the City of Santa Rosa (Sites A, B and C respectively; Fig. 1). We selected the UCSC campus because it is known to have populations of both *S. griseus* and *S. carolinensis*. We selected the city of Santa Cruz as a study area because it is one of the first cities that *S. carolinensis* spread to in California. We selected the city of Santa Rosa

because *S. griseus,* but not *S. carolinensis*, has been observed there (possibly due to the geographic barrier of the San Francisco Bay). Each area is considered temperate, with dry, warm summers and mild, wet winters. The UCSC campus is dominated by mixed-evergreen coastal forests, redwood forests, and grasslands, while the cities of Santa Cruz and Santa Rosa are urban areas with populations of approximately 60,000 and 170,000 people respectively (Thomas 1961; Haff et al. 2008). All of these areas are known to support populations of tree squirrels because of the abundance of nut and pine bearing trees such as the coast live oak (*Quercus agrifolia*), tan oak (*Quercus parvula* var. *shrevei*), and knobcone pine (*Pinus attenuata*) (Haff et al. 2008). These trees are used by squirrels for food, movement, and the construction of nests called *dreys*.

Observational Surveys

Observational surveys of squirrels were conducted at all three study areas to estimate the relative abundance of *S. griseus* and *S. carolinensis* as well as estimate proportion of canopy and development cover. We delineated 5.6 km^2 rectangular study areas located in the center of the UCSC campus and the downtown areas of Santa Cruz and Santa Rosa. North-facing transects (500 m) were placed randomly on intersections of a 125 m × 125 m grid pattern at UCSC overlaid using ArcGIS software (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Identical transects of 500 m were randomly placed on city roads in the downtown areas of Santa Cruz and Santa Rosa.

We conducted 108 observational surveys at UCSC, and 82 and 87 surveys in Santa Cruz and Santa Rosa, respectively, from January 2012 through May 2015. Surveys were carried out twice per day on 3 randomly chosen days of a week. Survey times were chosen randomly between 0700 and 1900 h. We did not survey during rain or other poor weather conditions and instead rescheduled for a later date. Tree squirrels were surveyed by walking slowly northward on each transect and counting each individual observed. Squirrels were identified to the species level based on differences in morphology. Coat color was the primary method used to distinguish between species since *S. carolinensis* sports brown hair on the flanks, face, and guard hairs while *S. griseus* has an

Fig. 1 Locations of three 5.6 km² study areas used: the UCSC campus (A) (N36.9994, W122.0672), city of Santa Cruz (B) (N36.5816, W122.0206), and city of Santa Rosa (C) (N38.2648, W122.4246). Coordinates used are latitude and longitude in decimal degrees

exclusively silver and white coat (Carraway and Verts 1994; Koprowski 1994).

We estimated the proportion canopy cover and proportion development cover at 5 m intervals along each transect in all study areas using a binary hit/miss densitometer to generate a total of 100 readings each for canopy and development cover along each transect. Canopy cover was defined as any foliage greater than 3 m in height directly above the observers head. Development was defined as any building, road, or other human-made surface constructed of concrete, plastic, metal, or wood, but not including small dirt paths or trails.

Each transect at UCSC was assigned one of four forest types using an existing vegetation classification from Haff et al. (2008) and the Center for Integrated Spatial Research (CISR) at UCSC. Northern maritime chaparral is dominated by low shrubs and some dwarf trees such as blue blossom (*Ceanothus thyrsiflorus*) and warty-leaved ceanothus (*Ceanothus papillosus* var. *roweanus*), manzanita (*Arctostaphylos* spp.), and oak trees (*Quercus* spp.). Chaparral/evergreen ecotone represents a transition zone between the chaparral and evergreen communities and contains a mixture of plant species present in both vegetation types. Mixed evergreen forest is composed of evergreen, broadleaf trees such as the coast live oak (*Quercus agrifolia*), shreve oak (*Q. parvula* var. *shrevei*), madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*) and tan oak (*Lithocarpus densiflorus*), though conifers can be found as well. Finally, redwood forest is dominated by large stands of coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) as well as other evergreen trees. Surveys were not conducted in land cover types that do not support populations of tree squirrels, such as grasslands or coastal prairies.

Hair snare tube surveys

Hair snare tubes are an inexpensive method of remotely detecting the presence of mammals, and have been previously used to study tree squirrels including *S. griseus* and *S. carolinensis* (Fimbel and Freed 2008). Tubes were constructed from 7.5 cm diameter ABS pipes 40 cm in length. Square blocks with dimensions of 3 cm × 3 cm were covered in 2-sided sticky tape and placed on the inside end of each tube. A whole walnut was placed at the center of each tube as bait. Squirrels entering the tube to retrieve the walnut left guard hairs attached to the tape blocks that could later be identified to the species level based on the color banding patterns of the hair. Hair from each tube was assumed to be collected from a single individual because squirrels avoid snare tubes once the bait is removed.

We used hair tube surveys to detect *S. griseus* and *S. carolinensis* in different locations across the UCSC campus. We established 500 m transects with one hair tube placed every 50 m, for a total of 10 hair tubes per transect. Tubes were left for 72 h before being retrieved and 3 hairs from each tube were removed and examined under a 30X binocular dissecting scope to identify squirrels to the species level based on the color banding patterns of the hairs (Fimbel and Freed 2008) (Table 1). Species were positively identified if at least 2 of 3 hairs showed characteristics of that species. Any tree squirrel hairs that were unable to be identified were labeled as "unidentified" and not counted towards either species' total. Hair tube surveys were also used to measure the proportion canopy cover, proportion development cover, and forest type in a manner identical to the observational studies.

Hair snare tube surveys were carried out from the first week of January 2012 through the last week of June 2013. Studies were carried out once per day on a randomly chosen day of each week for a total of 35 surveys over 18 months. Hair tubes were deployed at times chosen randomly between 0700 and 1900 h. Surveys were not started during rain or other poor weather conditions and were instead rescheduled for a later time in the same week, or the following week.

Statistical analyses

We used a negative binomial distribution to model squirrel count data from observational and hair snare surveys at all study sites because our count data were overdispersed. Negative binomial regression as a generalized linear model was performed using IBM SPSS, version 24 (IBM Corp., Armonk, N.Y., USA) to determine if tree canopy cover and/or development cover were significant predictors of the abundance of *S. griseus* and *S. carolinensis*. We also estimated Kilometric Abundance Indices for each species in each study area, measured as the number of squirrels observed per kilometer of transect (Vincent et al. 1991; Buckland et al. 1993). All proportional data from canopy cover and development cover estimations were logit transformed to account for transects with extremely high or extremely low proportions. If *S. carolinensis* is a "passenger" of decline in *S. griseus,* we would expect that development cover has a significant negative effect on the abundance of *S. griseus* across study sites. Conversely, if *S. carolinensis* is a "driver" of decline, then we would expect that development cover has little effect on the abundance of *S. griseus*, particularly at the Santa Rosa site, where only *S. griseus* occurs. We tested the effects of forest type on squirrel counts for both species using a 1-way ANOVA. If forest type is the primary driver of squirrel abundance, we would expect a significant effect of forest type on the abundance of either species. We used an alpha value of 0.05 for all significance tests ($\alpha = 0.05$).

Table 1 Characteristics of tree squirrel guard hairs used to distinguish between *S. griseus* (n = 19) and *S. carolinensis* (n = 23) (Fimbel and Freed 2008)

Species	Guard hair characteristics for identification
S. griseus	Clear or white bands present
	Absence of cream or yellow bands
	Black bands at tips long (>1.25 mm)
S. carolinensis	Cream or yellow bands present
	Yellow or white distal band long (>1.25 mm)
	Black bands at hair tip short (<1.25 mm)

Results

Within all of our study areas, increasing development cover had a strong, negative effect on tree canopy cover (R = −0.84; $p < 0.01$) (Fig. 2). The cities of Santa Rosa and Santa Cruz are medium-density urban areas with little tree canopy cover. However, the UCSC campus can be considered a mix of urban areas and dense areas of canopy closure, such that there is a gradient of canopy cover ranging from low density in the core of the campus, to high density canopy cover in the wildlands at the outside edges of campus. At UCSC, the mean estimate of proportional canopy cover was 0.53 (SE = 0.25), while the mean estimate of proportional development cover was 0.22 (SD = 0.24). Canopy cover was greatest at the outside edges of UCSC where there is little development and a greater density of trees. There was relatively less canopy cover in the interior where there is a high density of academic buildings and roads. The study areas of Santa Cruz and Santa Rosa were both characterized by extremely high levels of development and low levels of canopy cover as expected from an urban landscape. The mean estimate of proportional canopy cover and development cover was 0.05 (SE = 0.01) and 0.96 (SE = 0.01) respectively for the city of Santa Cruz. The mean estimate of proportional canopy cover and development cover was 0.06 (SE = 0.01) and 0.95 (SE = 0.01) respectively for the city of Santa Rosa.

We conducted 108 observational surveys and 35 hair snare surveys at UCSC (Table 2). Regression results comparing tree squirrel abundance with canopy and development cover are presented in Table 3 for all study areas. At UCSC, canopy cover had a significant effect in shaping the tree squirrel community composition. We observed *S. griseus* most commonly on the outside north, west, and east edges of the UCSC study area where the proportion canopy cover was highest and development cover was lowest, while *S. carolinensis* was observed most commonly near the interior of the study area where canopy cover was lowest and development cover was highest. Observational surveys at UCSC indicate that canopy cover had a significantly positive effect on the abundance of *S. griseus* ($p = 0.04$) (Fig. 3a), but did not affect *S. carolinensis* ($p = 0.29$) (Fig. 3b). Observations of *S. griseus* and *S. carolinensis* were not affected by

Fig. 2 Development cover correlates negatively with canopy cover estimated as a proportion of area (R = −0.84; $p < 0.01$)
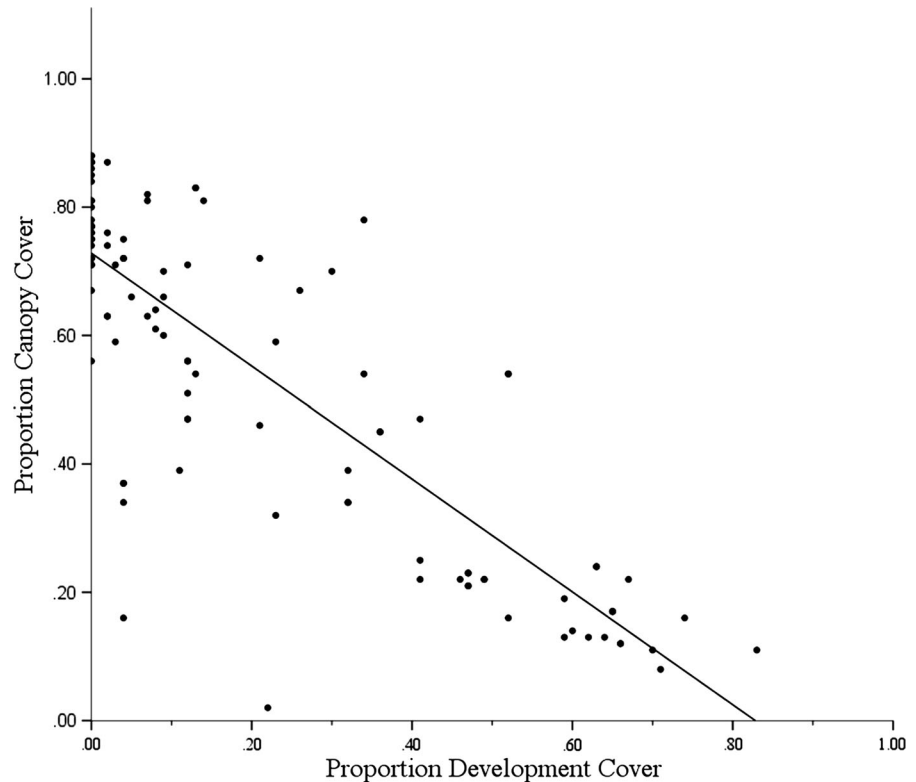
Table 2 Summary of observational and hair snare transect data for all methods and study areas, listing the method used, location of the surveys, total transects completed, species present, number of tree squirrels detected, and mean Kilometer Index of Abundance (KIA)

Method	Location	Transects	Species	N	Mean KIA
Observational surveys	UCSC	108	S. griseus	37	0.69
			S. carolinensis	48	0.89
Hair snare surveys	UCSC	35	S. griseus	19	1.09
			S. carolinensis	23	1.31
Observational surveys	Santa Cruz	82	S. griseus	0	0
			S. carolinensis	30	0.73
Observational surveys	Santa Rosa	87	S. griseus	26	0.60
			S. carolinensis	0	0

Table 3 Negative binomial regressions with log-link function of tree squirrel counts and proportional estimates of canopy and development cover for observational and hair snare surveys in all study locations

Method	Location	Species	Parameter	B	SE	Wald χ^2	p
Observational Survey	UCSC	S. griseus	Can. cover	3.92	1.89	4.31	0.04*
			Dev. cover	−1.45	2.13	0.46	0.5
		S. carolinensis	Can. cover	−1.45	1.36	1.12	0.29
			Dev. cover	1.56	1.31	1.42	0.23
Hair snare survey	UCSC	S. griseus	Can. cover	2.5	1.21	4.22	0.04*
			Dev. cover	−0.04	0.42	0.01	0.92
		S. carolinensis	Can. cover	−2.06	0.9	5.2	0.02*
			Dev. cover	−0.35	0.48	0.51	0.48
Observational survey	Santa Cruz	S. carolinensis	Can. cover	0.37	0.21	3.08	0.08
			Dev. cover	−0.27	0.42	0.42	0.52
Observational survey	Santa Rosa	S. griseus	Can. cover	0.37	0.23	2.62	0.11
			Dev. cover	−0.82	0.49	2.81	0.09

Significant results are highlighted with asterisks

development cover ($p = 0.50$ and 0.23 respectively) (Fig. 3c, d). Forest type also had no effect on the abundance of *S. griseus* ($F(3, 104) = 2.26$, $p = 0.09$) and *S. carolinensis* ($F(3, 104) = 0.57$, $p = 0.64$), suggesting that there are no significant effects of forest composition on observations of tree squirrels. These trends in observational surveys were observed year-round and therefore seasonal effects on tree squirrel abundance are negligible.

Similar to the observational studies, *S. griseus* was detected by hair snare tubes most often on the outside north, west, and east edges of the UCSC study area where the proportion canopy cover was highest and development cover was lowest. Canopy cover was again found to have a significantly positive effect on the abundance of *S. griseus* ($p = 0.04$) (Fig. 4a), while development cover had little effect ($p = 0.96$) (Fig. 4b). In contrast, *S. carolinensis* was detected most commonly near the interior of the study area where canopy cover was lowest and development cover was highest. Observations of *S. carolinensis* decreased with increasing canopy cover ($p = 0.02$) (Fig. 4c) and were unaffected by development cover ($p = 0.48$) (Fig. 4d). We detected a slightly higher KAI with the hair snares for both species, but this is likely due to hair tubes having a slightly higher detection probability due to the bait.
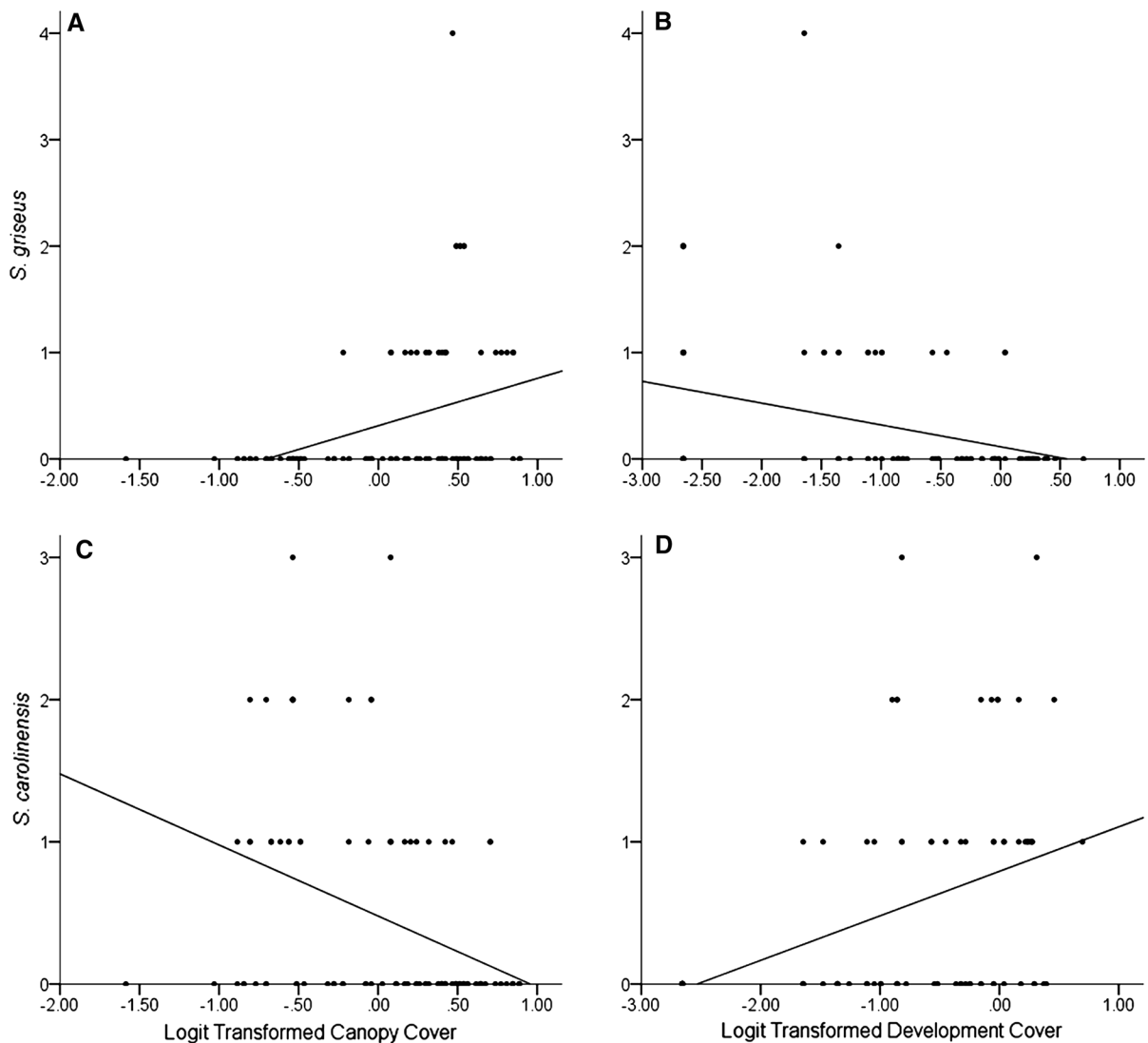
Fig. 3 Observations of *S. griseus* at UCSC increased with increasing canopy cover (**a**) ($p = 0.04$) and were unaffected by development cover (**b**) ($p = 0.50$). Observations of *S. carolinensis* were independent of canopy cover (**c**) ($p = 0.29$) and development cover (**d**) ($P = 0.23$)

We conducted 82 and 87 observational surveys in the cities of Santa Rosa and Santa Cruz respectively (Table 2). In the city of Santa Rosa, *S. griseus* was the only species of tree squirrel observed, while *S. carolinensis* was the only species of tree squirrel observed in the city of Santa Cruz. Regression results show that observations of *S. griseus* and *S. carolinensis* were unaffected by development cover and marginally affected by canopy cover (p ranging from 0.08 to 0.52) (Fig. 5a–d).

Discussion

In the context of biological invasions, novel species may rapidly exclude native species from viable habitat through a variety of means, including competition. Declines in native species associated with environmental change and the presence of an invasive species are summarized in the "driver-passenger" model, which proposes mechanisms to explain declines in native species in the face of both invasive species and environmental change (Didham et al. 2005). This
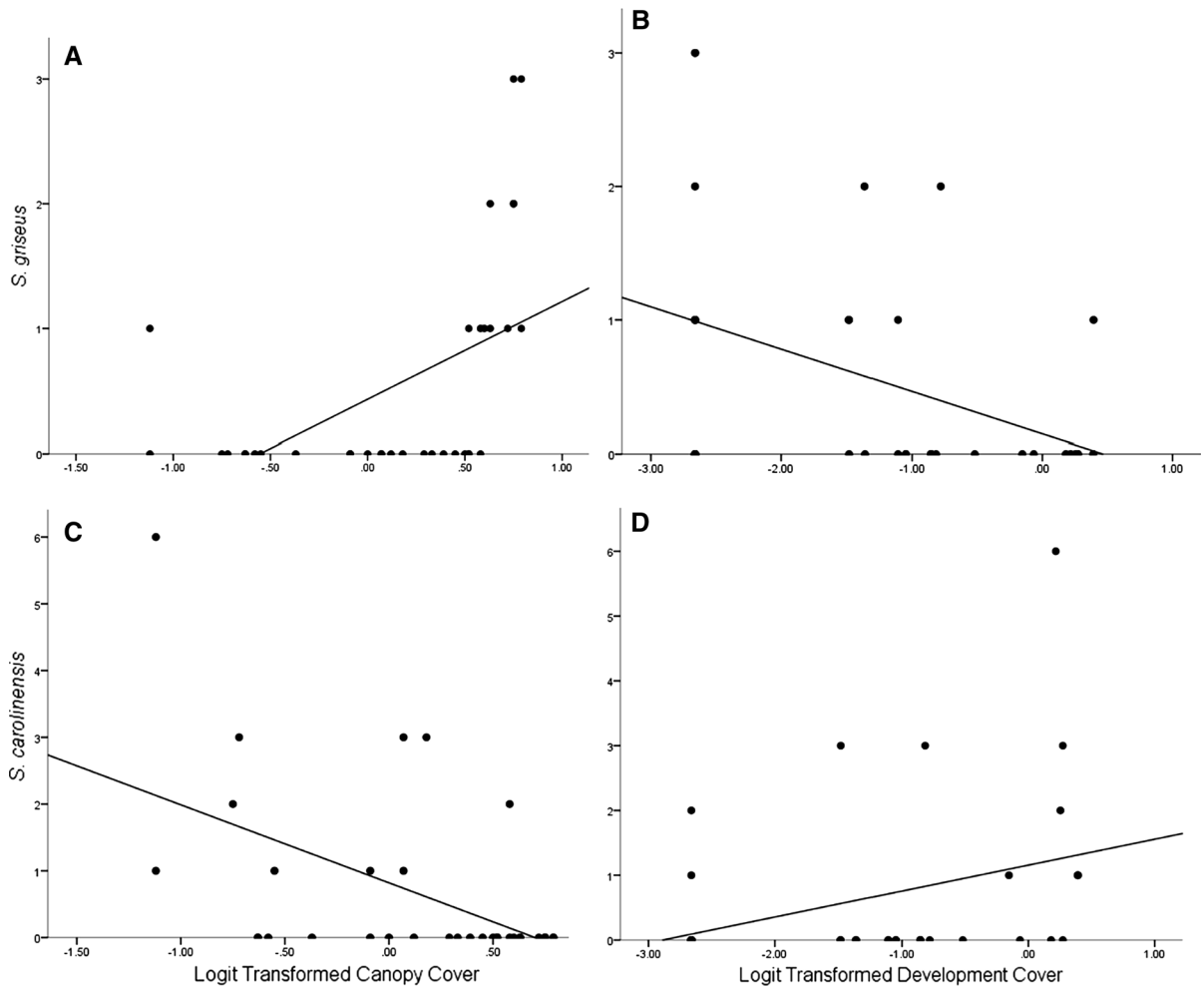
Fig. 4 Hair snare surveys show similar results to observational surveys at UCSC. Observations of *S. griseus* increased with increasing canopy cover (**a**) ($p = 0.04$) and were unaffected by development cover (**b**) ($p = 0.92$). Conversely, observations of *S. carolinensis* decreased with increasing canopy cover (**c**) ($p = 0.02$) were unaffected by development cover (**d**) ($p = 0.48$)

study provides evidence that habitat fragmentation alters the competitive dynamics between two species of tree squirrel, and that non-native eastern gray tree squirrels are a "driver" of the decline of native tree squirrels only after this environmental change.

Results from our observational surveys in Santa Rosa and Santa Cruz demonstrate that both *S. griseus* and *S. carolinensis* are capable of inhabiting highly developed urban areas. Neither tree canopy cover nor development cover significantly affected observations of tree squirrels suggesting that populations of *S. carolinensis* and *S. griseus* are not meaningfully affected by the presence of buildings, roads, and low canopy cover. However, we did observe a marginally

significant positive relationship between tree canopy cover and observations of each species in both cities, indicating that there is likely to be selection within urban areas for areas with relatively higher tree density for *S. carolinensis* and *S. griseus*. We therefore conclude that human development, and the associated loss of canopy cover, is not a driver of decline in native *S. griseus*, but rather that it modifies the competitive hierarchy of these two species by providing a competitive advantage to *S. carolinensis*.

In western Washington State, USA, Johnston (2013) reported that there was little spatial overlap between *S. griseus* and *S. carolinensis*, indicating that there may be interspecific avoidance in areas of
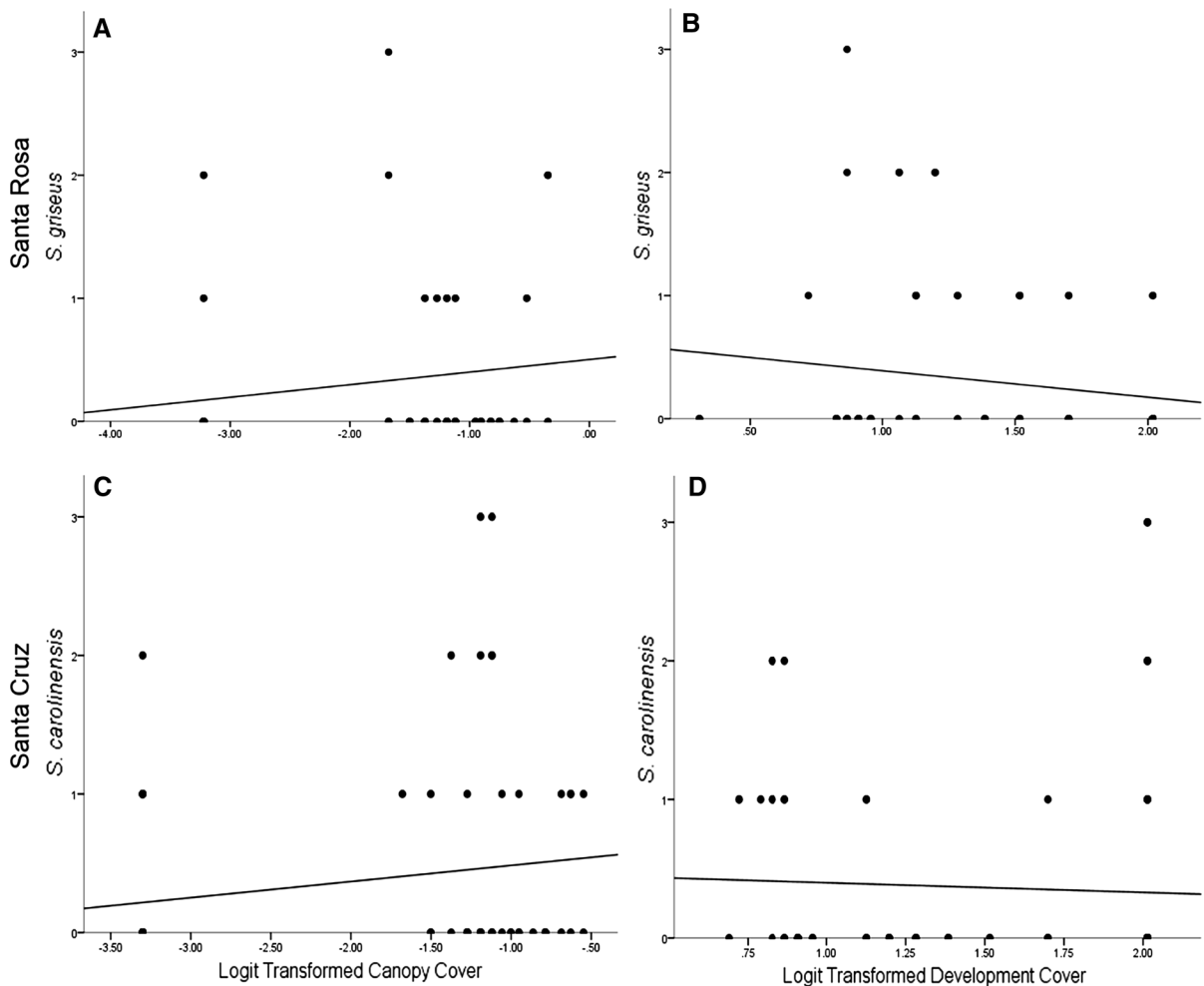
Fig. 5 Observations of *S. griseus* were unaffected by canopy cover and development cover in the city of Santa Rosa (**a** and **b**) (p = 0.11 and 0.09 respectively). Similarly, observations of *S. carolinensis* were unaffected by development cover but tended to be positively associated with increasing canopy cover in the city of Santa Cruz (**c** and **d**) (p = 0.08 and 0.52 respectively)

sympatry. Additionally, *S. griseus* rarely used areas that were formerly inhabited by *S. carolinensis* following removal treatments (Johnston 2013). Johnston (2013) found that *S. griseus* typically occurred in upland coniferous forests while *S. carolinensis* was found more often in riparian areas with deciduous trees. We found no association between forest type and observations of *S. griseus* and *S. carolinensis* in our study however. This could be due to differences in the habitat preferences of tree squirrels in our study area and Washington, or because our observational surveys were not able to detect fine-scale habitat preferences. Regardless, the results of this study and Johnston (2013) suggest that a removal of dense stands of

conifer trees in conjunction with competition will likely reduce the habitat available to *S. griseus* in areas where *S. carolinensis* is also present.

In our study, competition between *S. griseus* and *S. carolinensis* at UCSC is likely to be occurring for seed caches stored underground during winter as there is no evidence of significant dietary niche partitioning between these squirrels (Wauters et al. 2002b, Johnston 2013). Previous studies have shown that introduced *S. carolinensis* can exclude native tree squirrels from seed caches through interference and exploitation competition (Reynolds 1985; Wauters et al. 2002a, b; Gurnell et al. 2004). Since *S. carolinensis* appears to be better adapted to fragmented areas, it

may be more easily harvesting seed caches than *S. griseus* in developed areas.

In eastern England, *S. carolinensis* is known to be a more terrestrial squirrel compared to the more agile native red squirrels that are better adapted to moving through tree canopies (Gurnell 1987). In this case, both species' body size reflects their adaptation to ground or canopy specialization. Changes in landscape characteristics such as habitat fragmentation may therefore provide competitive advantages to one species depending on their evolutionary history. For example, Gonzales et al. (2008) showed that non-native *S. carolinensis* gained a competitive advantage in developed areas over native Douglas (*Tamiasciurus douglasii*) and northern flying squirrels (*Glaucomys sabrinus*) in western Canada. In central California, our study shows that *S. carolinensis* may have a competitive advantage over *S. griseus* in areas with high tree canopy fragmentation. Most of the size difference between these two species can be attributed to the larger tail size of *S. griseus* which is an adaptation for balance and counterweighting during running and jumping among other uses (Gurnell 1987). This could be a result of an evolutionary history in the dense canopy forests of western North America. In undeveloped forest areas, this adaptation could provide *S. griseus* a competitive advantage over other species, but is less effective in fragmented areas such as the city of Santa Cruz.

Sparse tree canopy cover may also increase interspecific interactions. Previous studies have shown that the presence of *S. carolinensis* can increase interspecific competition among closely related species (Wauters et al. 2000). Gray squirrel agonistic behavior is difficult to observe, since it is short lived and usually occurs in peaks mostly during the spring and autumn when tree squirrel activity is highest (Gurnell 1987). Additionally, observing interspecific interactions are rare at UCSC because the geographic ranges of these species on the campus show only slight overlap suggesting that there is little coexistence. Alternatively, the competitive advantage of *S. carolinensis* could be a result of coexisting with high density human settlements for a longer time and thereby learning to better exploit outcomes of development such as food waste and coping with other anthropogenic disturbances such as noise, traffic, pets, etc. The mechanisms of competitive exclusion between these species remain unknown, but this study demonstrates that habitat fragmentation elicits a shift in tree squirrel community composition in Central California.

Conclusions

Further habitat fragmentation in western North America in conjunction with the expansion of the range of *S. carolinensis* will very likely continue this process of native tree squirrel replacement, although more research is needed to identify the specific mechanisms of tree squirrel competitive exclusion. The results from this study show that competitive dynamics between native and non-native species can be affected by the process of habitat fragmentation and may result in an altered community composition. We provided a spectrum of invasion: from no invasion (Santa Rosa), to partial invasion mediated by habitat fragmentation (UCSC), to full invasion (Santa Cruz). Ultimately, competition can be viewed on this spectrum, and the tree canopy cover is a strong predictor of who will win. More broadly, we provide a field study that demonstrates the case of an invasive species that becomes a "driver" of native species decline following habitat fragmentation. We suggest that existing competitive structures be considered by wildlife managers in areas where land use change is planned, especially where there is potential for invasion by non-native species.

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