

**Timescale Analyses of Fluctuations in Coexisting Populations of a Native and
Invasive Tree Squirrel**

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13 Abstract

- 14 1. Competition from invasive species is an increasing threat to biodiversity. In Southern
15 California, the western gray squirrel (*Sciurus griseus*, WGS) is facing increasing competition
16 from the fox squirrel (*Sciurus niger*, FS), an invasive congener.
- 17 2. We used spectral methods to analyze 140 consecutive monthly censuses of WGS and FS
18 within a 11.3 ha section of the California Botanic Garden. Variation in the numbers for both
19 species and their synchrony was distributed across long timescales (> 15 months).
- 20 3. After filtering out annual changes, concurrent mean monthly temperatures from nearby
21 Ontario Airport (ONT) yielded a spectrum with a large semiannual peak and significant
22 spectral power at long timescales (> 30 months). Squirrel-temperature cospectra showed
23 significant negative covariation at long timescales (> 35 months) for WGS and smaller
24 significant negative peaks at 6 months for both species.
- 25 4. Simulations from a Lotka-Volterra model of two competing species indicates that the risk of
26 extinction for the weaker competitor increases quickly as environmental noise shifts from
27 short to long timescales.
- 28 5. We analyzed the timescales of fluctuations in detrended mean annual temperatures for the
29 time period 1915-2014 from 1218 locations across the continental USA. In the last two
30 decades, significant shifts from short timescales to long timescales have occurred, changing
31 from less than 3 years to 4-6 years.
- 32 6. Our results indicate that (i) population fluctuations in co-occurring native and invasive tree
33 squirrels are synchronous, occur over long timescales, and may be driven by fluctuations in
34 environmental conditions; (ii) long timescale population fluctuations increase the risk of
35 extinction in competing species, especially for the inferior competitor; and (iii) the timescales

36 of interannual environmental fluctuations may be increasing from recent historical values.
37 These results have broad implications for the impact of climate change on the maintenance of
38 biodiversity.

39 **KEYWORDS**

40 Western gray squirrel, fox squirrel, population timescales, spectral analysis, invasive species,
41 climate change

1 INTRODUCTION

Competition from non-native, invasive species is an increasing threat to the biodiversity of native species in a globalized world. Invasive species are often considered one of the most important threats to ecological function and a top driver of species extinctions (Flory & Lockwood 2020; Dueñas *et al.* 2021). The presence of invasive species can alter animal communities, trigger trophic cascades, displace native species, and even lead to hybridizations with similar or related species (Huxel 1999; Doody *et al.* 2017). The ability to be more competitive over limited resources is one of the characteristics that enables invasive species to be successful. In addition, they are often characterized by having life history traits with colonizer characteristics: short generation times, high reproduction rates, and fast growth rates (Sakai *et al.* 2001). With this competitive edge, they can invade and displace native species.

An example where a native species is threatened in some habitats by competition from an invasive species occurs in Southern California, where the western gray squirrel (*Sciurus griseus*, WGS, Fig. 1A) is facing increasing competition from the fox squirrel (*Sciurus niger*, FS, Fig. 1B), a non-native, invasive congener. WGSs are native to the western coast of North America with a historical distribution extending from central Washington to Baja California (Carraway & Verts 1994; Escobar-Flores *et al.* 2011). Populations of WGSs have been declining in areas of Washington, Oregon, and California (Muchlinski *et al.* 2009; Stuart 2012; Cooper 2013; Cooper & Muchlinski 2015). In Washington, they are listed as a state-threatened species (Linders & Stinson 2007), while in Oregon they are an Oregon Conservation Strategy Species (Oregon Department of Fish and Wildlife 2016). While there have been only a few studies regarding populations of WGSs in California, there is a noticeable trend in the decline of these squirrels in

64 areas below an elevation of 457m (Cooper 2013; Cooper & Muchlinski 2015). As of now, the
65 WGS does not have special conservation status in California.

66 The FS has a historical native range in the eastern and central United States and the
67 southern prairie provinces of Canada, south of approximately 48°N latitude (Koprowski 1994),
68 where they are known to live in forests, woodlands, agricultural landscapes, and urban areas
69 (Kleiman *et al.* 2004). Through both natural and human-assisted range expansion, the FS is now
70 common in many areas west of its historical range (iNaturalist accessed 24 July 2021,
71 <https://www.inaturalist.org/taxa/46020-Sciurus-niger>). FSs have been introduced or have
72 expanded their range into Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon,
73 Utah, Washington, and Wyoming (Wolf & Roest 1971; Flyger & Gates 1982; Koprowski 1994;
74 Jordan & Hammerson 1996; Steele & Koprowski 2001; Brady *et al.* 2017).

75 FSs have dispersed from original points of introduction through natural dispersal and
76 through intentional movement of animals by humans (Frey & Campbell 1997; Geluso 2004;
77 King *et al.* 2010). Since the original introduction to Los Angeles County (Becker & Kimball
78 1947), the FS has expanded its range at a rate of 1.60 to 3.00 km/yr in heavily suburbanized
79 areas of Southern California (Garcia & Muchlinski 2017). Although the FS has generally
80 remained restricted to areas of human habitation, with continued range expansion the FS has
81 become sympatric in some isolated suburban habitat fragments and in certain foothill areas with
82 the native WGS (Hoefler & Harris 1990).

83 FSs may compete with native WGSs for resources such as nesting sites and food, and the
84 FS has replaced the WGS within certain habitats in Southern California (Muchlinski *et al.* 2009;
85 Cooper & Muchlinski 2015). Los Angeles County can be considered an ideal location for
86 invasion by the FS given the mild Mediterranean climate and year-round food supply offered by

exotic plant species, accompanied by the absence of the native WGS throughout much of the Los Angeles Basin. The FS is both morphologically, ecologically, and behaviorally similar to this native species, thus these overlaps in form, function, activity, and presence provides a situation where interactions between the two species can be studied (Ortiz 2021).

Many factors can influence population persistence, but one that has received comparatively less attention is the timescale of environmental fluctuations. By analogy with the spectrum of visible light, time series fluctuations that occur over long timescales are referred to as having a *red spectrum* and those occurring over short timescales as having a *blue spectrum* (Lawton 1988). These are distinguished from *white noise* random fluctuations which have no serial autocorrelations. In general, theoretical analyses from single-species unstructured population models suggest that reddened environmental spectra increase extinction risk for slowly growing populations and blue spectra increase extinction risk for rapidly growing populations (Ripa & Lundberg 1996; Petchey *et al.* 1997; Ripa & Heino 1999; Schwager *et al.* 2006; Ruokolainen *et al.* 2009; García-Carreras & Reuman 2011; Mustin *et al.* 2013; Danielian 2016), although these conclusions often depend on modeling details (Heino 1998; Heino *et al.* 2000). In their simulations of three competing species, Ruokolainen and Fowler (2008) found that extinction risk increased with reddened environmental noise when species responded independently to the environment but decreased when there was a strong correlation between species-specific responses. On the empirical side, Pimm and Redfearn (1988) looked at 100 time series from insects, birds, and mammals, and found that the variance of the population fluctuations increased with the window of time used in the calculation, suggesting that these populations have red spectra. García-Carreras & Reuman (2011) analyzed the dynamics of 147 animal populations and climate data for the population locations and found a positive correlation

between the biotic and climatic spectral exponents (a measure of spectral color), with most spectra being red-shifted. Inchausti & Halley (2003) directly examined the relationship between population variability and quasi-extinction time (measured as the time required to observe a 90% decline of population abundance) for a large set of data comprised of 554 populations for 123 animal species that were censused for more than 30 years. The results showed that the quasi-extinction time was shorter for populations having higher temporal variability and redder dynamics.

Spectral methods are a powerful tool for characterizing the timescales of fluctuations in a time series (Brillinger 2001). A univariate time series can be transformed into a *power spectrum*, which describes the distribution of the variance of the time series at different frequencies. The sum of the spectral powers across frequencies is proportional to the total variance of the time series. If the time series is multivariate, in addition to the spectra, there are also cross-spectra for each pair of time-series variables. The cross-spectrum is a complex-valued function of frequency. The real part is the *cospectrum*, which describes the distribution of the in-phase covariance between the time series at different frequencies, and the imaginary part is the *quadrature spectrum*, which is a phase-shifted covariance. The sum of the cospectral powers across frequencies is proportional to the total covariance of the two time series. The cospectrum can also be viewed as the distribution of the correlation coefficient across frequencies. Since frequency, f , is the inverse of the period, the spectral and cospectral power provide information on the variance and correlation, respectively, at the timescale $1/f$.

The color of a power spectrum can be characterized using a *spectral exponent* (Vasseur & Yodzis 2004; García-Carreras & Reuman 2011). If S_f is the power of the spectrum at frequency f , the spectral exponent can be computed as the slope of a least squares linear regression of $\log(S_f)$

versus $\log(f)$. Negative spectral exponents are characteristic of spectra dominated by long timescale variation (red spectra) and positive values are indicative of short timescale variation (blue spectra). White noise spectra will have a spectral exponent of zero. When applied to environmental and population time series, spectral color allows one to better assess the risk of ecological extinction.

Wavelet analyses have been used in ecology to identify changes in the spectral distributions of population and environmental fluctuations over time (Cazelles *et al.* 2008). Whereas spectral analyses assume that the statistical properties of the time series do not vary with time, wavelet analysis can be applied to non-stationary time series. A filtering function is applied to the time series signal to allow a local estimation of spectral characteristics of the signal at a point in time. The filtering function can be adjusted to look at different times and frequencies. The result is a two-dimensional picture of the wavelet power as a function of frequency and time. Wavelets can be used, for example, to investigate the impact on ecological populations of climate regime shifts, such as the North Atlantic Oscillation (Sheppard *et al.* 2016), or changes in the timescale of environmental fluctuations due to climate change.

Global climate is undergoing rapid changes (Pachauri *et al.* 2014). While the threats to biodiversity have focused mostly on increasing temperatures, it is feasible that disruptions to climate patterns may also affect the timescale of environmental fluctuations, and, if so, this may have ecological implications for population persistence. For example, García-Carreras & Reuman (2011) analyzed detrended mean summer temperature time series from weather stations on six continents and found significant shifts to shorter timescales (blue shifts) in the spectral exponents for the years 1951-1990 compared to 1911-1950. For conservation purposes, it is important to gain a better understanding of how changes in climate may be associated with

changes in the timescale of environmental fluctuations and how this may impact extinction risks for natural populations.

The objectives of the present study were (1) to evaluate, using spectral methods, the timescale of population fluctuations in a long time series (140 months) where the WGS and FS have coexisted together, (2) to determine the extent to which the timescale of the squirrel population fluctuations are determined by environmental factors, (3) to infer, using model simulations, how changes in the timescale of environmental fluctuations could impact the timescale of population fluctuations and the risk of extinction in a system of two competing species, and (4) to assess the extent to which the timescale of year-to-year environmental fluctuations around their trends are changing, possibly as a result of human impacts on climate, and to assess the implications of these results on the potential loss of native biodiversity.

2 MATERIALS AND METHODS

2.1 Collection of census data

We established three transect lines within a 11.3 ha section of the California Botanic Garden (CBG) in Claremont, CA during October of 2009. We defined sampling points along transect lines at 40 m intervals providing 35 viewpoints within the study area. Two researchers conducted a census along the transect lines once per month from October 2009 through May 2021. The researchers spent 3 minutes at each sampling point, with each researcher responsible for counting animals within a separate 180-degree arc from the viewpoint. We began each monthly census at 0800 hrs and ended at approximately 1030 hrs. We switched the starting transect line for the monthly census between Line 1 and Line 3 on alternate months.

177 Researchers conducting each census were conservative in counting the number of
178 squirrels observed, thereby giving an estimate of observable population size at a point in time. If
179 there was any chance that a squirrel observed at a sampling point had been counted at a previous
180 sampling point, that individual was not counted as a new observation unless the animal was
181 obviously different from the animal previously observed (a juvenile instead of an adult or a male
182 instead of a female, when gender could be assessed). Numbers may vary due to factors such as
183 natality, mortality, dispersal, and activity levels which could change due to seasonality or
184 reproductive activity.

185 The four corners of the 11.3 ha study area were defined by the following GPS
186 coordinates: SE 34.110262 & -117.714651, SW 34.110258 & -117.715921, NE 34.115883 & -
187 117.714419, NW 34.115684 & -117.715891. CBG is a native California garden, meaning all
188 plants are native to California, but not specifically Southern California. At the beginning of the
189 study in 2009, the habitat within the study area included 1,048 trees along with numerous shrubs
190 and bushes. Of the trees, 31% were deciduous species, 17% were coniferous species, 42% were
191 in the genus *Quercus*, and 6% were in the genus *Pinus*. The composition of the study area did
192 change over the time period of the censuses with the death and removal of several trees. Death of
193 trees in the study area was due mainly to a prolonged drought within Southern California from
194 2011 through 2016.

195 2.2 Spectral analyses of census data

196 We used spectral methods to analyze the monthly census data. We used fast Fourier transforms
197 to compute the raw spectra and cross-spectrum of the bivariate time series. Computations were
198 conducted using the spec.pgram algorithm from R modified to run in MATLAB. No trends were
199 removed from the data prior to analysis. Since raw spectra and cross-spectra are usually jagged,

we applied two iterations of a window-averaging smoothing Daniell kernel with spans of 5 and 7 data points, modified with clipped windows at the endpoints to preserve the number of data values. We divided the spectral powers by their sum across frequencies. This yielded a normalized spectral power plot for each species which shows the distribution of variation across timescales. We used the real part of the cross-spectrum to obtain a smoothed cospectral power plot for the covariance between the two species. We normalized the cospectrum so that its sum equals the correlation coefficient.

We conducted computations to detect significant ($P < 0.05$) peaks or valleys in the observed spectra for the null hypothesis that there is no frequency dependence in the variance and covariance of the time series fluctuations (i.e., independent “white noise” time series). We shuffled the temporal order of the bivariate time-series by generating a random permutation of the integers 1 through n , where $n = 140$ is the number of monthly observations. We then used the permutation to reorder the bivariate monthly censuses of the two species. Next, we computed two smoothed normalized spectra and a smoothed normalized cospectrum in the same way as the correctly ordered data. We repeated this random reshuffling process 2000 times and used the 2.5th and 97.5th percentiles at each frequency to define 95% confidence limits for the null hypothesis that there are no timescale components to the variance and covariance of the observed time series. This method of generating the spectra preserves the time-independent statistical properties of the two time-series (means, variances, distribution, correlation, etc.), while varying only the time-dependence of the bivariate data values.

2.3 Analyses of weather data

We obtained weather data for Ontario Airport (ONT) from the Climate Data Online web site of NOAA’s National Centers for Environmental Information (<https://www.ncdc.noaa.gov/cdo->

[web/](#)). ONT is located about 12 km from the CBG and should be an accurate representation of the temperature profile of the study site. We focused on the reported “average monthly temperature,” which is computed by averaging the daily maximum and minimum temperatures for each month. We avoided rainfall totals because many months have zeros, which is a problem for spectral analyses, and much of the vegetation in the CBG is irrigated. We obtained a temperature time series for the same months as the census data and applied the same spectral methods to obtain a smoothed normalized power spectrum.

Since annual seasonal changes dominated the temperature time series, we used the MATLAB “bandstop” function to attenuate cyclic components with periodicities in the range of 9-15 months. This produced a filtered time series with annual effects removed. We then produced a smoothed normalized spectrum for the filtered temperature time series. We also generated smoothed normalized cospectra between the filtered temperature time series and both the WGS and EF census time series. Using the methods described above, we obtained 95% confidence intervals for these spectra and cospectra.

2.4 Model simulations

We conducted model simulations to obtain a better understanding of the implications of timescale-specific environmental variation on the dynamics of two competing species. We used the following discrete-time version of the Lotka-Volterra competition equation:

$$\begin{aligned} N_1(t+1) &= N_1(t) \exp\left(r_1 \left(K_1 - N_1(t) - \alpha N_2(t)\right) / K_1 + \sigma_1 \varepsilon_1(t)\right), \\ N_2(t+1) &= N_2(t) \exp\left(r_2 \left(K_2 - N_2(t) - \beta N_1(t)\right) / K_2 + \sigma_2 \varepsilon_2(t)\right), \end{aligned} \quad (1)$$

where r_1 and r_2 are the intrinsic rates of population increase, K_1 and K_2 are the carrying capacities, and α and β are the competition coefficients for the two species. The variables $\varepsilon_1(t)$ and $\varepsilon_2(t)$ represent random environmental noise with a mean of zero and variance of 0.5. We

used the coefficients σ_1 and σ_2 to scale the magnitude of the noise. For the purposes of discussion, species 1 will represent a native species and species 2 will represent an invasive species.

We introduced frequency-specific biases into the noise variables using an algorithm devised by Chambers (1995). This method generates a multivariate random time series based on any specified theoretical spectral matrix that is a function of frequency. The diagonal elements of that matrix are the theoretical spectra (frequency decompositions of the variances) and the off-diagonal elements are theoretical cross-spectra (complex numbers). The real parts of the cross-spectra are the theoretical cospectra (frequency decompositions of the covariances) and the complex parts are the quadrature spectra (frequency-specific phase shifts). For the model (1), we used identical spectra that were linear functions of frequency for the two species. High-frequency-biased blue noise was represented with a linear spectrum that varied from a power of 0.0 for a frequency of $f=0.0$ to a power of 1.0 for a frequency of $f=0.5$ (maximum possible frequency). Low-frequency-biased red noise was represented with a linear spectrum that varied from a power of 1.0 for a frequency of $f=0.0$ to a power of 0.0 for a frequency of $f=0.5$. Unbiased white noise had a constant power of 0.5 across all frequencies. A gradual shift from blue to white to red noise was accomplished by varying the slope of the noise spectrum in 101 increments while keeping the average of the spectrum constant at 0.5. This produced a constant total variance of $\varepsilon_1(t)$ and $\varepsilon_2(t)$ equal to 0.5 while changing only its frequency-specificity. For the covariance between the random variables $\varepsilon_1(t)$ and $\varepsilon_2(t)$, we used a cospectrum function that was equal to a constant fraction, 0.9, of the spectrum. This resulted in a frequency-specific correlation of 0.9 across all frequencies. A high correlation was used since it was assumed that the native and invasive species are ecologically similar and occupy the same habitat. The quadrature

spectrum was set to zero (no frequency-specific phase shifts). To summarize, the timescales of the random environmental noise were varied from short (blue) to uniform (white) to long (red) with a frequency-independent correlation in the effects of the noise on the growth of the two species.

In addition to the spectral frequency of the environmental noise, the simulation protocol also involved varying the intensity of the competitive effects of the invasive species on the native species. We set the value of the competition coefficient α to 0.25 (weak competition), 0.50 (moderate competition), and 0.75 (strong competition). We kept the competitive effects of the native species on the invasive species at a value of $\beta = 0.25$. The remaining model parameters had constant values of $r_1 = r_2 = 0.5$, $K_1 = K_2 = 50$, and $\sigma_1 = \sigma_2 = 0.75$. For the assessment of extinction risk, when the population density of a species fell below 5% of its carrying capacity, we set it to zero. For simulations not involving extinction risk, the threshold was set to zero. We ran each simulation for 200 time steps.

For every set of parameter values and environmental noise color, we conducted 2000 replicate simulations. For blue, white, and red environmental noise, we computed smoothed normalized power spectra and cospectrum of the species and averaged these over replicates to see how the timescale for population fluctuations are affected by different colors of noise. To investigate gradual shifts in the effects of frequency-biased environmental noise on the population spectra and probability of extinction, we chose a slope for the environmental spectra, varying the slopes in 101 gradual increments, beginning at blue noise (slope = 2) and ending at red noise (slope = -2). For each choice of the environmental spectra, we simulated the population trajectories of the two species, estimated the unsmoothed normalized population spectra, computed the two spectral exponents and averaged them. We repeated these

computations for each of the 2000 replicate simulations and computed an overall average for the spectral exponent. To investigate the effects of frequency-biased environmental noise on the population persistence, the number of instances where the native species went extinct was divided by 2000 to yield an estimate of the extinction risk. The extinction risk for the invasive species was always less than or equal to the risk for the native species and was not considered in the analyses.

2.5 Analyses of climate data

We obtained climate data from the U.S. Historical Climatology Network (USHCN) which is freely available online (<https://www.ncei.noaa.gov/products/land-based-station/us-historical-climatology-network>). We used version 2.5 of the monthly temperature records which contains long-term data from 1218 stations across the continental United States. Menne *et al.* (2009) describe the adjustments used to remove biases due to factors such as relocation of recording stations, changes in instrumentation, and urbanization. USHCN monthly average temperatures were computed as the average over the month of the daily maximum and daily minimum temperatures. The mean annual temperature for each year is the average of the 12 mean monthly temperatures. We used the mean temperatures for the 100-year range from 1915 through 2014, the latter being the latest year available.

We looked at changes in the distribution of spectral exponents for the fluctuations in the mean annual temperatures. First, we broke the 100-year range into four 25-year spans. Next, we detrended the temperature time series for each 25-year span by fitting a quadratic polynomial using least squares regression and computed the standardized residuals. Then we computed an unsmoothed spectrum for each residual time series and estimated the spectral exponent as the

slope of a linear regression of $\log(\text{spectral power})$ versus $\log(\text{frequency})$. Histograms were created with the 1218 spectral exponents (one per station) for each of the 25-year time spans.

Although it would be tempting to analyze the changes in the spectral exponents using a repeated measures ANOVA, with stations as the subjects, spatial autocorrelations exist among stations that are in the same geographical proximity, inflating the Type I error rates. A solution to this problem was suggested by Clifford *et al.* (1989) and modified by Dutilleul (1993), which yields an “effective sample size” based on the spatial structure of the data. It is appropriate for paired observations distributed in space. We used the software package SAM (Spatial Analysis in Macroecology; Rangel *et al.* 2006) to compute effective sample sizes for the following three sets of paired data: [1915-1939] vs. [1940-1964], [1940-1964] vs. [1965-1989], and [1965-1989] vs. [1990-2014]. We conducted paired sample *t*-tests for the spectral exponents from these three paired data sets and adjusted the standard errors for the test statistics and degrees of freedom for the statistical significance values using the effective sample sizes. We then applied a Bonferonni correction to account for the multiple comparisons.

We also conducted a mean field wavelet analysis on the 100-year time series of mean annual temperatures. For each station, we detrended the time series using a quadratic polynomial and computed the standardized residuals. Next, we used the MATLAB continuous wavelet transform function “cwt” to compute wavelet powers for the residual time series using the analytic Morse filter (Olhede & Walden 2002) with the default values of 3 for the symmetry parameter and 60 for the time-bandwidth product. Lastly, we averaged the wavelet powers across all stations for each time-frequency combination. We chose the Morse wavelet because it is useful for analyzing signals with time-varying amplitude and frequency. We investigated varying the symmetry and time-bandwidth product parameters, but the results were not much different

from what was obtained using the default values. We also used a Morlet wavelet which has equal variance in time and frequency, but, again, the results were like the Morse wavelet with default parameters. We experimented with cubic and quartic polynomials for detrending, but these gave mean field wavelets that were much like the one obtained with a quadratic function.

To identify wavelet powers that were statistically significant, we used the surrogate time series approach (Schreiber & Schmitz 2000). We took a random permutation of the mean annual temperature time series for all stations in tandem and computed a mean field wavelet as described above. We repeated this process 2000 times and computed the upper 95th percentile of the wavelet powers for each combination of time and frequency. This provided a set of critical values for identifying “hot spots” on the mean field wavelet under the null hypothesis of no timescale dependence in the fluctuations of the mean annual temperature residuals around the trends.

3 RESULTS

3.1 Census data

Figure 2 shows the time series of monthly census values for the WGS and the FS. The large increase in census numbers during 2013 and 2014 corresponded with production of a large acorn crop during the fall of 2013 (mean \pm SE of 608.3 ± 120.1 g/m² in a 1 m² plot under each of six trees used to assess acorn production, Appendix A). Mean acorn production measured in the same 1 m² plots during other years ranged from a low of 5.7 ± 2.7 g/m² in 2014 to a high of $67.5 + 35.5$ g/m² in 2012. Availability of acorns appears to have a major impact on the number of WGSs and FSs in the CBG.

The fluctuations in census numbers show signs of synchrony. The estimated Pearson correlation coefficient in animal numbers is $r = 0.581$ which is statistically significant from zero ($P = 5.20 \times 10^{-14}$). The total variation in the numbers for each species and their synchrony seems to be distributed across different time scales. Long intervals can be seen where the numbers of both species are elevated and depressed (Fig. 2). Superimposed on this long timescale variation are random short timescale fluctuations. We quantify this timescale component of variation with the spectral analyses in the next section.

3.2 Population spectra and cospectrum

Figures 3A and 3B show the smoothed normalized spectra for the WGS and the FS. For both the WGS and the FS, the spectra suggest that the largest variation in numbers occurs at frequencies below 0.0833 which corresponds to a timescale of more than 12 months. The WGS spectrum crosses the upper significance threshold at timescale of around 15 months. The FS spectrum crosses the upper significance threshold at timescale of around 19 months. The spectrum for the FS shows a small peak at 6 months, but that peak is not statistically significant. Since the total variation remains constant across frequencies for the confidence bands from the randomly ordered data, the larger variation in WGS and FS at long timescales is compensated for by significantly smaller variation at timescales of about 4 months or less.

The smoothed normalized cospectrum (Fig. 3C) shows how the total correlation in population numbers between the two species is distributed across timescales. Covariance between WGS and FS is significantly biased towards long timescales, with a smaller nonsignificant peak at a timescale of around 6 months. The cospectrum crosses the upper significance threshold at timescale of about 18 months. The total correlation between the numbers of the WGS and FS is $r = 0.581$. Using the unsmoothed cospectrum, we can partition

this total correlation by timescale intervals: $r_1 = 0.409$ for >12 months, $r_2 = 0.162$ for 4–12 months, and $r_3 = 0.010$ for ≤ 4 months, where $r = r_1 + r_2 + r_3$. Thus, 70% of the total correlation occurs at timescales exceeding one year. We can infer that population synchrony for these two species occurs mostly at long timescales.

3.3 Spectral analyses of weather data

Figure 4A shows the time series of mean monthly temperatures for Ontario Airport (ONT), which is 12 km from the study site. As one would expect, there is a strong seasonal component to these temperatures. Figure 4B shows the smoothed normalized spectrum for the mean monthly temperatures, which is dominated by a strong peak for the annual cycle. Since the squirrel spectra show no indication of an annual cycle (Fig. 3), we applied a band-stop filter to remove the annual cycle and plotted the resulting time series (Fig. 4A, dashed line). The smoothed normalized spectrum for the filtered mean monthly temperatures appears in Fig. 4C. There is a peak at low frequencies which begins to increase at a timescale of about 12 months and crosses the upper threshold for statistical significance at a timescale of approximately 30 months. There is also a large spectral peak at 6 months.

There is a negative correlation between the filtered temperature time series and the squirrel census data. For the WGS, the correlation is statistically significant ($r = -0.194$, $P = 0.022$) and, as indicated by the smoothed normalized cospectrum (Fig. 5A), is distributed at long timescales and at a timescale of 6 months. The correlation between the filtered temperature time series and the FS census data is also negative, but not statistically significant overall ($r = -0.146$, $P = 0.085$). The cospectrum between the filtered temperature time series and FS census data shows a large significant peak a 6-month timescale (Fig. 5B). These results suggest that the

distribution of variation in the squirrels' population fluctuations may be driven, in part, by fluctuations in weather and climate outside of the annual seasonal cycle.

3.4 Simulation results

Our analyses of the simulations of the Lotka-Volterra competition model (1) are summarized in Fig. 6. Our focus was on the effects of the timescale of environmental fluctuations on the spectral properties of population numbers and the probability of extinction for the native species.

Figure 6A shows the protocol we used for the random environmental noise. We assumed a linear spectrum which varied from short timescale fluctuations (slope = 2, blue noise), to fluctuations with no autocorrelation (slope = 0, white noise), to long timescale fluctuations (slope = -2, red noise). The random time series generated by these spectra have the same mean of zero and same variance, the latter being proportional to the total area under the spectrum; they differ only in their timescale properties. For the simulations involving the computation of spectral exponents and extinction probabilities, we varied the spectral slope of the environmental noise in small increments from +2 to -2, as indicated by the curved arrow in Fig. 6A.

Figure 6B shows the population spectrum and cospectrum for the simulations involving blue noise, white noise, and red noise (Fig. 6A). Since the parameter values for the two competing species are identical, and the properties of their environmental noise inputs are the same, the mean curves shown apply to both populations. As described in section 2.4, we used a cospectrum function that was equal to a constant fraction, 0.9, of the spectrum, so, for each color of environmental noise, the population spectrum and cospectrum are similar. For blue environmental noise, the smoothed normalized spectrum and cospectrum have low power at long timescales which increases and levels off at frequencies exceeding 0.1. This reflects the fact that, for the intrinsic rates of increase used in the simulations ($r_1 = r_2 = 0.5$), population growth is

undercompensating, that is, perturbations from a stable equilibrium do not show damped oscillations in the deterministic version of the model. Previous work for single species population models has shown that undercompensating populations are sensitive to long timescale environmental noise, whereas overcompensating populations are sensitive to short timescale noise (e.g., Danielian 2016). In effect, the slower response times of populations with small intrinsic rates of increase “filter out” the short timescale components of the environmental noise (Desharnais *et al.* 2018). This phenomenon can also be seen in the smoothed normalized spectrum and cospectrum for the populations subjected to white environmental noise. The population fluctuations are less sensitive to the shorter timescale components of the flat environmental spectrum producing a population spectrum and cospectrum that is biased towards long timescales (Fig. 6B). Lastly, when the populations are subjected to environmental noise biased towards long timescales, the longer timescale components of the noise are enhanced and the shorter timescale components are suppressed, producing a smoothed normalized spectrum and cospectrum that is more strongly biased towards long timescales than the environmental noise (Fig. 6B).

Figure 6C shows how the population spectral exponents change as the environmental noise is shifted gradually from blue, to white, to red (arrow in Fig. 6A). Positive spectral exponents indicate spectra which are biased towards short timescales and negative spectral exponents are indicative of long timescale fluctuations. The population spectral exponents decrease monotonically as the spectra for the environmental noise redden. However, the population spectral exponent first becomes negative while the environmental spectrum is still strongly blue. The bluest linear spectrum for environmental noise begins with a linear slope of 2.00 and the first negative population spectrum appears when the linear slope has decreased to

1.72. As mentioned above, with the model parameter values used in our simulations, the dynamics of the two competing species acts as a “reddening filter,” producing population spectra that are more biased towards long timescales.

Of interest for conservation purposes is how the timescale of the fluctuations in the environmental noise influences the persistence of the native species. Figure 6D is based on simulations where an extinction threshold has been set arbitrarily to 5% of the carrying capacity. All other model parameter values are identical to the ones used for the simulations in Figs. 6B and 6C. When the competition coefficients are equal ($\alpha = \beta = 0.25$), the extinction probability for both species remains close to zero until the color of the environmental noise begins to redden (Fig. 6D). For the reddest environmental spectrum, both species have about a 42% probability of extinction. If the non-native species has a competitive advantage, the influence of reddened environmental spectra on population persistence becomes more pronounced. Figure 6D shows how increasing the competition coefficient for the invading species to $\alpha = 0.75$ increases the likelihood that the native species will be lost. A reddening of the environmental spectrum quickly elevates the probability of extinction from a value of about 6% for the bluest environmental noise to a value which asymptotes at about 98% for the reddest environmental noise (Fig. 6D). This suggests the possibility of a synergy between the effects of reddening environmental noise and competition from non-native species for the risk of extinction for native populations.

3.5 Climate data

We know that human impact on the climate system has resulted in an increasing trend of warming temperatures (Pachuri *et al.* 2014). Given the observations and results of the previous sections, an important related question is whether there have been changes in the timescale of

random environmental fluctuations around these trends. Our analyses make use of a 100-year record (1915-2014) of mean annual temperatures from 1218 weather stations obtained from the U.S. Historical Climatology Network (Menne *et al.* 2009). Figure 7 shows the locations of the weather stations. Although not uniform in their distribution, they cover every state and region in the continental United States.

To investigate evidence for change in the color of the mean annual temperature spectra over time, we divided the 100-year record from each station into four 25-year intervals and computed the spectral exponents for each time interval (see section 2.5). Figure 8 shows the histograms of spectral exponents for the 1218 stations. The dashed line represents the zero value (white noise environmental fluctuations); spectral exponents to the left indicate a red noise bias and those to the right represent a blue noise bias. The arrow at the top of each histogram shows the mean. The mean values are 0.500, 0.313, 0.432, and -0.160 for the range of years 1915-1939, 1940-1964, 1965-1989, and 1990-2015, respectively. It appears that there was a shift from 1990-2014 from blue-shifted spectra to red-shifted spectra. The significance values for the changes between adjacent time intervals are $P = 0.046$, $P = 0.654$, and $P = 1.676 \times 10^{-10}$.

The spectral analyses conducted for Fig. 8 assume that the residual deviations from the fitted quadratic trends for each 25-year time period are stationary, that is, the probability distribution and timescale properties of the residual time series are invariant. A mean field wavelet analysis which relaxes the stationarity assumption is presented in Fig. 9 for the entire 100-year time period. The regions of statistically significant wavelet power are outlined in black. They indicate that the timescale of the fluctuations in mean annual temperature, when averaged over all weather stations, has shifted to long timescale values of approximately 3.5-7 years for

the period after 1980, again suggesting that there has been a recent reddening of the timescale for random fluctuations in mean annual temperatures around their changing trends.

4 DISCUSSION

Our spectral analyses of the WGS and FS census data suggest that most of the variation in animal numbers occurs on timescales that exceed 15 months. In the case of the FS, there is also evidence for variation on a six-month timescale. This timescale-specific variation may be due to changes in resource abundance, the timing and frequency of reproduction, and reproductive output.

Changes in population numbers on a long timescale could be due to variation in the supply of food resources on multi-year, highly variable timescales. For example, acorns provide a valuable source of food for tree squirrels (Steele & Yi 2020), but a very large ($> 600 \text{ g/m}^2$) mast crop was only produced in one of the nine years in which we measured relative acorn production (Appendix A). We observed production of a very large mast crop within our study area in the fall of 2013 (Table A1). Census counts for both species began to increase in the late spring and summer of 2013 and continued to increase through the spring of 2014 (Fig. 2). A precipitous decrease in abundance was observed throughout the summer of 2014 which may have been brought about by dispersal of animals out of our study site. A very small acorn crop ($< 6 \text{ g/m}^2$) was produced in the fall of 2014. A modest sized crop of acorns ($\sim 35 \text{ g/m}^2$) produced in the fall of 2015 was followed by an increase in census counts for both species through the summer of 2016. Acorn production was very low in the fall of 2016, 2017, 2018, and 2019, and this long time-period without a modest to large sized acorn crop corresponded to relatively low census counts for both species (≤ 20 animals). A modest acorn crop produced in the fall of 2020 again corresponded to an increase in census counts for both species during the summer and fall

of 2020. Acorns are present in the trees for a prolonged period before they appear in significant quantities on the ground, so this food resource is also available to the animals prior to the fall of the year which may account for the high census counts in the summers prior to our acorn crop sampling periods.

The yearly record of observations of juvenile and sub-adult individuals for both species shown in Appendix B illustrates the effect that long-term variability of food resources may have on reproduction by the WGS and the FS over long timescales. As stated above, production of acorns varied widely between years and the production of other food supply items could certainly vary widely between years. Variability in the availability of food items each year along with changes in the number of juvenile and subadult animals could lead to population variability on long timescales, as observed in the spectral analyzes of our data (Fig. 3).

The availability of food in our study site also varied on a six-month timescale. Items such as catkins from oak and walnut trees, flowers on *Fremontodendron* spp. and *Arctostaphylos* spp., and male cones on pine trees became available in the spring. Items such as acorns, walnuts, and fruit bodies from the California Bay Laurel (*Umbellularia californica*) and California Buckeye (*Aesculus californica*) became available in the fall of the year (Ortiz & Muchlinski 2015). The timings (spring and fall) of the first availability of these food items on a yearly basis fit well with the potential timing of reproduction on a yearly basis by both the FS and WGS.

Two distinct periods of potential reproduction for the FS in Southern California were documented by King's (2004) study of 135 litters submitted to three wildlife rehabilitation centers during 2002. Approximately 60% of litter production documented by King (2004) was associated with the months of February, March, and April, with the largest number of litters born in March. A second pulse of litter production occurred during the months of August, September,

539 and October with the largest number of litters born in September, six months after the largest
540 pulse of litters born during the spring. Although production of litters by the FS on a semi-annual
541 basis is possible, thus leading to an increase in observed population size on a semi-annual basis,
542 the number of juvenile/subadult animals observed during census counts in this study varied
543 widely among years (Fig. A1).

544 The WGS appears to exhibit a yearly pattern of reproduction different than the FS. Most
545 research documents breeding activity in late fall and early winter months with birth of most
546 litters in spring and early summer months (Carraway & Verts 1994; King 2004). A few pregnant
547 females were observed in June, July, August, and September (Fletcher 1963) and lactating
548 females have been observed as late as October in Californian (Swift 1977). However, no definite
549 records of multiple pregnancies not attributable to intrauterine loss of the first litter are available
550 (Bailey 1936; Fletcher 1963; Swift 1977; Jameson & Peeters 1988). The difference in
551 reproductive patterns between the FS and the WGS could bring about the presence of a 6-month
552 cycle in abundance of the FS and the absence of a similar 6-month cycle in the WGS. The
553 difference in reproductive patterns could also give a competitive advantage to the FS in certain
554 habitats through higher natality in years of good resource production.

555 Muchlinski *et al.* (2012) produced a Habitat Suitability Model (HSM) for the WGS and
556 the FS which allowed short-term and longer-term coexistence habitats to be identified using a
557 linear combination of three habitat variables: percent canopy cover, percent of deciduous trees,
558 and average height of ground cover. Habitats with a low percentage of canopy cover, a high
559 percentage of deciduous trees, and a low height of ground cover were classified as short-term
560 coexistence habitats. Locations with a high percentage of canopy coverage, a low percentage of
561 deciduous trees, and a low height of ground cover were classified as longer-term coexistence

sites. (Sites with a high height of ground cover, a high percentage canopy cover, and a low percentage deciduous trees were identified as “exclusion habitats” where only the WGS is found, but the FS exists in adjacent habitats.) For example, Muchlinski *et al.* (2009) reported that the FS replaced the WGS in four years at a short-term coexistence habitat, California State Polytechnic University, Pomona, which contained manicured and more natural areas on the campus with paved pathways and buildings surrounded by a mixture of *Juglans*, *Eucalyptus*, *Washingtonia*, *Pinus*, and other tree species. In contrast, the two species have coexisted within longer-term coexistence habitats of Griffith Park in Los Angeles, CA for more than 60 years, which were more natural in appearance consisting of *Pinus*, *Quercus*, *Umbellularia*, *Sequoia*, and *Ulmus* species, but with human-influenced aspects such as picnic tables, a playground, and restrooms (King 2004; King *et al.* 2010; DeMarco *et al.* 2020). The study area at CBG has been classified as a longer-term coexistence habitat by Muchlinski *et al.* (2012). How long coexistence can continue in longer-term coexistence habitats is unknown. Many longer-term coexistence sites are fragments of habitat where the FS, but not the WGS, exists in surrounding habitats. The WGS is also subject to loss of genetic diversity in these habitat fragments as described by DeMarco *et al.* (2020).

The predictions of the competition model presented in section 3.4 can be interpreted in terms of the HSM developed by Muchlinski *et al.* (2012). The HSM implies that the competitive effects of the FS on the WGS is high in a short-term coexistence site such as California State Polytechnic University, Pomona, and other former lowland coexistence sites (Cooper & Muchlinski 2015). In terms of the competition model presented in Fig. 6, the value of the competition coefficient α would be large relative to the coefficient β , and extinction of the WGS could occur under conditions of blue as well as red environmental noise. Conversely, a lower

level of competition in a longer-term coexistence site implies the values of α and β are similar and a higher level of reddened environmental noise would be needed to bring about extinction of the WGS (Fig. 6D). Our results from section 3.5 suggest that climate changes are increasing the timescale of yearly environmental fluctuations. Our spectral analyses of monthly census data suggest that most of the variation in numbers of the WGS and FS occurs over timescales of more than 15 months (Fig. 2). Thus, aside from the effects of a warming climate, any changes in the timescale of temperature fluctuations around the increasing trend could represent an additional risk factor for the persistence of the WGS in some of its native range.

After the annual changes in mean monthly temperature were removed from the ONT data using a band-stop filter, the remaining variation in temperature fluctuations were composed of a strong six-month cycle and significant variation on timescales that exceeded 30 months (Fig. 4C). Meteorologists and climate scientists have used harmonic analysis to document semi-annual cycles in rainfall and temperatures whose amplitude and phase shift vary by geographical location, with moderate amplitudes for the southwest United States (Hsu & Wallace 1976; White & Wallace 1978). Analyzing North American temperature data from 1979-2018, North *et al.* (2021) used Bayesian analysis to fit a model with annual and semi-annual harmonics that vary over space and time. They identify geographical regions with significant changes in the contributions of the two harmonics to seasonal cycles. In Appendix C, we use least squares to fit a model with annual and semi-annual harmonics to the unfiltered mean monthly temperature data in Fig. 4A and show that a model that includes both annual and semi-annual cycles provides a significantly better fit to the data than a model based on the annual cycle alone. The cospectra of Fig. 5 indicate a significant negative correlation between the squirrel census data and the ONT

607 filtered weather data at a timescale of six months. While we cannot demonstrate a causal
608 mechanism for this correlation, this observation could motivate further research.

609 It was not possible to specify an estimated peak value for the timescale of low frequency
610 variation in the squirrel numbers or mean monthly temperatures. The 140 months of the time
611 series represent less than 12 years. In spectral analyses, estimates of long period, low frequency
612 cycles are less precise since they cannot be as readily observed as short period, high frequency
613 oscillations. In the estimated spectra of Figs. 3 and 4, the spectral power continues to increase as
614 the frequency decreases. However, the record of mean annual temperatures for Ontario Airport
615 extends back to 1999, providing a 22-year time series. In Appendix D we show that a significant
616 peak in the spectrum of annual temperatures occurs on a timescale of about 7 years, which is
617 consistent with the wavelet analysis in Fig. 9. If annual changes in environmental conditions are
618 driving the long-term variation in squirrel numbers, which seems to be the case for the WGS
619 (Fig.5A), this estimate could also represent the timescale of those fluctuations.

620 We presented simulation results in section 3.4 that were designed to explore the effects of
621 changes in the timescale of environmental noise on the outcome of competition between
622 ecologically similar native and non-native species. We showed that an increase in the timescale
623 of environmental noise reddens the spectrum of population fluctuations and decreases the
624 likelihood of coexistence, especially when the non-native is a better competitor. This result
625 differs from one of the findings of Ruokolainen & Fowler (2008), who concluded that extinction
626 risk decreased with a reddening of environmental noise when, like in our model, there was a
627 strong correlation in the species response to the environmental fluctuations. However, their
628 simulation protocols differed from ours in several ways. First, they looked at a community of
629 three competing species. Second, their environmental noise was generated using an

autoregressive process and was added to the carrying capacity for each species. Third, and most importantly, in their models the intrinsic rate of increase for each species was set to $r_i = 1.8$, whereas in our model we chose $r_1 = r_2 = 0.5$, which is more consistent with the reproductive capabilities of tree squirrels. In deterministic models of the type used our simulations and those of Ruokolainen & Fowler (2008), values of $1 > r > 2$ lead to overcompensating dynamics, where the approach to equilibrium exhibits damped oscillations. Although Ruokolainen & Fowler (2008) claimed that their results are qualitatively similar for values of $r < 1$, previous work with single-species models (e.g., Danielian 2016) has shown that extinction risk increases with a reddening of environmental noise when the deterministic model, like ours, has undercompensating dynamics ($r_i < 1$), but decreases with a reddening of environmental noise when the deterministic model has overcompensating dynamics ($1 < r_i < 2$). Since the apparent contradiction between our results and those of Ruokolainen & Fowler (2008) occurred when there was a strong synchrony among the three species due to the high correlation of the effects of environmental noise, their result is consistent with what one would expect from a single-species model. When we repeated our simulations using values of $r_1 = r_2 = 1.8$, we observed a result consistent with Ruokolainen & Fowler (2008).

Our simulation results were limited in their scope. They were motivated by our analyses of timescale differences in the variability of population fluctuations for two sympatric species of tree squirrels. Simulation analyses of the type conducted in this paper could be expanded to include a broader examination of parameter space, other ecological interactions such as predator and prey, and larger communities of interacting species. Our approach could also be adapted to applied conservation models where environmental variability is a part of the simulation protocols. The inference in section 3.5 that timescale shifts in environmental fluctuations may be

653 occurring due to climate change would be a motivation to explore the impacts for populations of
654 interest to conservationists and natural resource managers.

655 Our analyses of spectral exponents for mean annual temperatures suggest that there has
656 been a reddening of the timescale of climate fluctuations for the continental United States during
657 the time period 1990-2014. García-Carreras & Reuman (2011) conducted a global analysis of
658 spectral exponents for the time period 1911-1990. They split the time series into two halves and
659 concluded that, while most of the spectral exponents were red-shifted, the red shift was smaller
660 in 1951-1990 compared to 1911-1950. This was true for all continents except Asia, which was
661 redder in 1951-1990 than it was in 1911-1950. Thus, in general, they observed a shift to shorter
662 timescales in more recent times, while we observed the opposite. This inconsistency may be due
663 to differences in our analyses. García-Carreras & Reuman (2011) used a linear function to
664 detrend their data, while we used a quadratic function. They divided their time series into two
665 segments of 40 years each, while we divided ours into four segments of 25 years each. Most
666 importantly, our last time series segment covered 1990-2014 which went beyond the latest year
667 that they examined. It was in this last 25-year period that we saw a strongly significant shift from
668 blue-tinged fluctuations to red-tinged fluctuations (Fig. 8). It may be the case that the
669 lengthening of the timescale of mean annual temperature fluctuations is a relatively recent
670 phenomenon.

671 Our analyses of changes in climate fluctuations could be extended in several ways. The
672 distributions in Fig. 8 shows that there is variation in the values of the spectral exponents among
673 weather stations. The sampling locations, which are scattered across the continental United
674 States (Fig. 7), could be subdivided by region (e.g., northeast, southwest, etc.) to see if there are
675 significant differences in the values of the spectral exponents due to geographic location.

Following García-Carreras & Reuman (2011), our analyses could be expanded to include sampling stations on other continents and other measures, such as mean seasonal temperatures, could be analyzed. Total annual precipitation could also be included in the analyses. Further research is needed to see if our inference that climate changes are lengthening the timescales for environmental fluctuations is robust. This could have implications, not only for conservation biology and resource management, but also for other areas such as forest fire management and agriculture.

5 CONCLUSIONS

Using spectral analyses, we have shown that the variations in monthly fluctuations of population numbers for native and non-native tree squirrels coexisting in the same habitat are distributed mostly over long timescales (> 15 months) and their numbers are synchronous over long timescales. After annual cycles are filtered from the time series for mean monthly temperatures from nearby Ontario Airport, there remains a strong six-month cycle and significant fluctuations at timescales that exceed 15 months. There was a significant negative correlation between the temperature data and squirrel numbers for both WGS and EF at a six-month timescale and a significant amount of long timescale correlation between mean monthly temperatures and WGS numbers. We used model simulations to show that environmentally-induced long timescale variation in population numbers for two competing species with moderate rates of reproduction greatly increases the probability of extinction of the inferior competitor. Finally, we conducted spectral and wavelet analyses for 100 years of mean annual temperatures from 1218 weather stations across the continental United States. Our results suggest that the timescale of fluctuations around the changing climate trends have increased in the last few decades, providing another environmental aspect that could threaten the maintenance of biodiversity.

This study documents long timescale variation in natural populations of conservation interest, shows that long timescale variation can accelerate the loss species diversity, and provides evidence that the timescales of environmental fluctuations have increased in recent times. We hope this serves as a cautionary message for conservationists and natural resource managers that an examination of timescales for environmental and population fluctuations are factors worthy of consideration.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

A. E. M. and R. A. D. conceptualized the project and were responsible for the methodology. A. E. M., J. L. O., R. I. A., and B. P. G. participated in the investigation. A. E. M. was responsible for data curation, project administration, and project supervision. R. A. D. performed the data analysis and visualization. All authors were responsible for the preparation, reviewing and editing of the manuscript. All authors gave final approval for publication.

719 **DATA ACCESSIBILITY**

720 Squirrel census data are archived on Dryad (URL to be determined). Weather and climate data
721 are accessible at the Climate Data Online web site of NOAA's National Centers for
722 Environmental Information (<https://www.ncdc.noaa.gov/cdo-web/>). MATLAB code used for
723 computing and smoothing the spectra and cospectra is available online at
724 [https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Ffele.13155&file=e1](https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Ffele.13155&file=e13155-sup-0001-Supinfo.pdf)
725 [e13155-sup-0001-Supinfo.pdf](https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Ffele.13155&file=e13155-sup-0001-Supinfo.pdf).

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