

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

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12 Running head: Timescale analyses of squirrel populations

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

42 1 INTRODUCTION

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

53 An example where a native species is threatened in some habitats by competition from an
54 invasive species occurs in Southern California, where the western gray squirrel (*Sciurus griseus*,
55 WGS, Fig. 1A) is facing increasing competition from the fox squirrel (*Sciurus niger*, FS, Fig,
56 1B), a non-native, invasive congener. WGSs are native to the western coast of North America
57 with a historical distribution extending from central Washington to Baja California (Carraway &
58 Verts 1994; Escobar-Flores *et al.* 2011). Populations of WGSs have been declining in areas of
59 Washington, Oregon, and California (Muchlinski *et al.* 2009; Stuart 2012; Cooper 2013; Cooper
60 & Muchlinski 2015). In Washington, they are listed as a state-threatened species (Linders &
61 Stinson 2007), while in Oregon they are an Oregon Conservation Strategy Species (Oregon
62 Department of Fish and Wildlife 2016). While there have been only a few studies regarding
63 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

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

91 Many factors can influence population persistence, but one that has received
92 comparatively less attention is the timescale of environmental fluctuations. By analogy with the
93 spectrum of visible light, time series fluctuations that occur over long timescales are referred to
94 as having a *red spectrum* and those occurring over short timescales as having a *blue spectrum*
95 (Lawton 1988). These are distinguished from *white noise* random fluctuations which have no
96 serial autocorrelations. In general, theoretical analyses from single-species unstructured
97 population models suggest that reddened environmental spectra increase extinction risk for
98 slowly growing populations and blue spectra increase extinction risk for rapidly growing
99 populations (Ripa & Lundberg 1996; Petchey *et al.* 1997; Ripa & Heino 1999; Schwager *et al.*
100 2006; Ruokolainen *et al.* 2009; García-Carreras & Reuman 2011; Mustin *et al.* 2013; Danielian
101 2016), although these conclusions often depend on modeling details (Heino 1998; Heino *et al.*
102 2000). In their simulations of three competing species, Ruokolainen and Fowler (2008) found
103 that extinction risk increased with reddened environmental noise when species responded
104 independently to the environment but decreased when there was a strong correlation between
105 species-specific responses. On the empirical side, Pimm and Redfearn (1988) looked at 100 time
106 series from insects, birds, and mammals, and found that the variance of the population
107 fluctuations increased with the window of time used in the calculation, suggesting that these
108 populations have red spectra. García-Carreras & Reuman (2011) analyzed the dynamics of 147
109 animal populations and climate data for the population locations and found a positive correlation

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

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

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

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

138 Wavelet analyses have been used in ecology to identify changes in the spectral
139 distributions of population and environmental fluctuations over time (Cazelles *et al.* 2008).
140 Whereas spectral analyses assume that the statistical properties of the time series do not vary
141 with time, wavelet analysis can be applied to non-stationary time series. A filtering function is
142 applied to the time series signal to allow a local estimation of spectral characteristics of the
143 signal at a point in time. The filtering function can be adjusted to look at different times and
144 frequencies. The result is a two-dimensional picture of the wavelet power as a function of
145 frequency and time. Wavelets can be used, for example, to investigate the impact on ecological
146 populations of climate regime shifts, such as the North Atlantic Oscillation (Sheppard *et al.*
147 2016), or changes in the timescale of environmental fluctuations due to climate change.

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

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

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

167 **2 MATERIALS AND METHODS**

168 **2.1 Collection of census data**

169 We established three transect lines within a 11.3 ha section of the California Botanic Garden
170 (CBG) in Claremont, CA during October of 2009. We defined sampling points along transect
171 lines at 40 m intervals providing 35 viewpoints within the study area. Two researchers conducted
172 a census along the transect lines once per month from October 2009 through May 2021. The
173 researchers spent 3 minutes at each sampling point, with each researcher responsible for counting
174 animals within a separate 180-degree arc from the viewpoint. We began each monthly census at
175 0800 hrs and ended at approximately 1030 hrs. We switched the starting transect line for the
176 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,

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

207 We conducted computations to detect significant ($P < 0.05$) peaks or valleys in the
208 observed spectra for the null hypothesis that there is no frequency dependence in the variance
209 and covariance of the time series fluctuations (i.e., independent “white noise” time series). We
210 shuffled the temporal order of the bivariate time-series by generating a random permutation of
211 the integers 1 through n , where $n = 140$ is the number of monthly observations. We then used the
212 permutation to reorder the bivariate monthly censuses of the two species. Next, we computed
213 two smoothed normalized spectra and a smoothed normalized cospectrum in the same way as the
214 correctly ordered data. We repeated this random reshuffling process 2000 times and used the
215 2.5th and 97.5th percentiles at each frequency to define 95% confidence limits for the null
216 hypothesis that there are no timescale components to the variance and covariance of the observed
217 time series. This method of generating the spectra preserves the time-independent statistical
218 properties of the two time-series (means, variances, distribution, correlation, etc.), while varying
219 only the time-dependence of the bivariate data values.

220 **2.3 Analyses of weather data**

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

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

230 Since annual seasonal changes dominated the temperature time series, we used the
231 MATLAB “bandstop” function to attenuate cyclic components with periodicities in the range of
232 9-15 months. This produced a filtered time series with annual effects removed. We then
233 produced a smoothed normalized spectrum for the filtered temperature time series. We also
234 generated smoothed normalized cospectra between the filtered temperature time series and both
235 the WGS and EF census time series. Using the methods described above, we obtained 95%
236 confidence intervals for these spectra and cospectra.

237 **2.4 Model simulations**

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

$$\begin{aligned} 241 \quad N_1(t+1) &= N_1(t) \exp\left(r_1 (K_1 - N_1(t) - \alpha N_2(t)) / K_1 + \sigma_1 \varepsilon_1(t)\right), \\ N_2(t+1) &= N_2(t) \exp\left(r_2 (K_2 - N_2(t) - \beta N_1(t)) / K_2 + \sigma_2 \varepsilon_2(t)\right), \end{aligned} \quad (1)$$

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

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

248 We introduced frequency-specific biases into the noise variables using an algorithm
249 devised by Chambers (1995). This method generates a multivariate random time series based on
250 any specified theoretical spectral matrix that is a function of frequency. The diagonal elements of
251 that matrix are the theoretical spectra (frequency decompositions of the variances) and the off-
252 diagonal elements are theoretical cross-spectra (complex numbers). The real parts of the cross-
253 spectra are the theoretical cospectra (frequency decompositions of the covariances) and the
254 complex parts are the quadrature spectra (frequency-specific phase shifts). For the model (1), we
255 used identical spectra that were linear functions of frequency for the two species. High-
256 frequency-biased blue noise was represented with a linear spectrum that varied from a power of
257 0.0 for a frequency of $f=0.0$ to a power of 1.0 for a frequency of $f=0.5$ (maximum possible
258 frequency). Low-frequency-biased red noise was represented with a linear spectrum that varied
259 from a power of 1.0 for a frequency of $f=0.0$ to a power of 0.0 for a frequency of $f=0.5$.
260 Unbiased white noise had a constant power of 0.5 across all frequencies. A gradual shift from
261 blue to white to red noise was accomplished by varying the slope of the noise spectrum in 101
262 increments while keeping the average of the spectrum constant at 0.5. This produced a constant
263 total variance of $\varepsilon_1(t)$ and $\varepsilon_2(t)$ equal to 0.5 while changing only its frequency-specificity. For the
264 covariance between the random variables $\varepsilon_1(t)$ and $\varepsilon_2(t)$, we used a cospectrum function that was
265 equal to a constant fraction, 0.9, of the spectrum. This resulted in a frequency-specific correlation
266 of 0.9 across all frequencies. A high correlation was used since it was assumed that the native
267 and invasive species are ecologically similar and occupy the same habitat. The quadrature

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

272 In addition to the spectral frequency of the environmental noise, the simulation protocol
273 also involved varying the intensity of the competitive effects of the invasive species on the native
274 species. We set the value of the competition coefficient α to 0.25 (weak competition), 0.50
275 (moderate competition), and 0.75 (strong competition). We kept the competitive effects of the
276 native species on the invasive species at a value of $\beta = 0.25$. The remaining model parameters
277 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
278 extinction risk, when the population density of a species fell below 5% of its carrying capacity,
279 we set it to zero. For simulations not involving extinction risk, the threshold was set to zero. We
280 ran each simulation for 200 time steps.

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

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

297 **2.5 Analyses of climate data**

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

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

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

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

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

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

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

348 **3 RESULTS**

349 **3.1 Census data**

350 Figure 2 shows the time series of monthly census values for the WGS and the FS. The large
351 increase in census numbers during 2013 and 2014 corresponded with production of a large acorn
352 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
353 trees used to assess acorn production, Appendix A). Mean acorn production measured in the
354 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
355 $+ 35.5$ g/m² in 2012. Availability of acorns appears to have a major impact on the number of
356 WGSs and FSs in the CBG.

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

364 **3.2 Population spectra and cospectrum**

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

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

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

384 3.3 Spectral analyses of weather data

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

395 There is a negative correlation between the filtered temperature time series and the
396 squirrel census data. For the WGS, the correlation is statistically significant ($r = -0.194$, $P =$
397 0.022) and, as indicated by the smoothed normalized cospectrum (Fig. 5A), is distributed at long
398 timescales and at a timescale of 6 months. The correlation between the filtered temperature time
399 series and the FS census data is also negative, but not statistically significant overall ($r = -0.146$,
400 $P = 0.085$). The cospectrum between the filtered temperature time series and FS census data
401 shows a large significant peak a 6-month timescale (Fig. 5B). These results suggest that the

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

404 3.4 Simulation results

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

408 Figure 6A shows the protocol we used for the random environmental noise. We assumed
409 a linear spectrum which varied from short timescale fluctuations (slope = 2, blue noise), to
410 fluctuations with no autocorrelation (slope = 0, white noise), to long timescale fluctuations (slope
411 = -2, red noise). The random time series generated by these spectra have the same mean of zero
412 and same variance, the latter being proportional to the total area under the spectrum; they differ
413 only in their timescale properties. For the simulations involving the computation of spectral
414 exponents and extinction probabilities, we varied the spectral slope of the environmental noise in
415 small increments from +2 to -2, as indicated by the curved arrow in Fig. 6A.

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

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

440 Figure 6C shows how the population spectral exponents change as the environmental
441 noise is shifted gradually from blue, to white, to red (arrow in Fig. 6A). Positive spectral
442 exponents indicate spectra which are biased towards short timescales and negative spectral
443 exponents are indicative of long timescale fluctuations. The population spectral exponents
444 decrease monotonically as the spectra for the environmental noise redden. However, the
445 population spectral exponent first becomes negative while the environmental spectrum is still
446 strongly blue. The bluest linear spectrum for environmental noise begins with a linear slope of
447 2.00 and the first negative population spectrum appears when the linear slope has decreased to

448 1.72. As mentioned above, with the model parameter values used in our simulations, the
449 dynamics of the two competing species acts as a “reddening filter,” producing population spectra
450 that are more biased towards long timescales.

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

467 **3.5 Climate data**

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

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

476 To investigate evidence for change in the color of the mean annual temperature spectra
477 over time, we divided the 100-year record from each station into four 25-year intervals and
478 computed the spectral exponents for each time interval (see section 2.5). Figure 8 shows the
479 histograms of spectral exponents for the 1218 stations. The dashed line represents the zero value
480 (white noise environmental fluctuations); spectral exponents to the left indicate a red noise bias
481 and those to the right represent a blue noise bias. The arrow at the top of each histogram shows
482 the mean. The mean values are 0.500, 0.313, 0.432, and -0.160 for the range of years 1915-1939,
483 1940-1964, 1965-1989, and 1990-2015, respectively. It appears that there was a shift from 1990-
484 2014 from blue-shifted spectra to red-shifted spectra. The significance values for the changes
485 between adjacent time intervals are $P = 0.046$, $P = 0.654$, and $P = 1.676 \times 10^{-10}$.

486 The spectral analyses conducted for Fig. 8 assume that the residual deviations from the
487 fitted quadratic trends for each 25-year time period are stationary, that is, the probability
488 distribution and timescale properties of the residual time series are invariant. A mean field
489 wavelet analysis which relaxes the stationarity assumption is presented in Fig. 9 for the entire
490 100-year time period. The regions of statistically significant wavelet power are outlined in black.
491 They indicate that the timescale of the fluctuations in mean annual temperature, when averaged
492 over all weather stations, has shifted to long timescale values of approximately 3.5-7 years for

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

495 **4 DISCUSSION**

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

501 Changes in population numbers on a long timescale could be due to variation in the
502 supply of food resources on multi-year, highly variable timescales. For example, acorns provide
503 a valuable source of food for tree squirrels (Steele & Yi 2020), but a very large ($> 600 \text{ g/m}^2$)
504 mast crop was only produced in one of the nine years in which we measured relative acorn
505 production (Appendix A). We observed production of a very large mast crop within our study
506 area in the fall of 2013 (Table A1). Census counts for both species began to increase in the late
507 spring and summer of 2013 and continued to increase through the spring of 2014 (Fig. 2). A
508 precipitous decrease in abundance was observed throughout the summer of 2014 which may
509 have been brought about by dispersal of animals out of our study site. A very small acorn crop ($<$
510 6 g/m^2) was produced in the fall of 2014. A modest sized crop of acorns ($\sim 35 \text{ g/m}^2$) produced in
511 the fall of 2015 was followed by an increase in census counts for both species through the
512 summer of 2016. Acorn production was very low in the fall of 2016, 2017, 2018, and 2019, and
513 this long time-period without a modest to large sized acorn crop corresponded to relatively low
514 census counts for both species (≤ 20 animals). A modest acorn crop produced in the fall of 2020
515 again corresponded to an increase in census counts for both species during the summer and fall

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

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

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

534 Two distinct periods of potential reproduction for the FS in Southern California were
535 documented by King's (2004) study of 135 litters submitted to three wildlife rehabilitation
536 centers during 2002. Approximately 60% of litter production documented by King (2004) was
537 associated with the months of February, March, and April, with the largest number of litters born
538 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

562 sites. (Sites with a high height of ground cover, a high percentage canopy cover, and a low
563 percentage deciduous trees were identified as “exclusion habitats” where only the WGS is found,
564 but the FS exists in adjacent habitats.) For example, Muchlinski *et al.* (2009) reported that the FS
565 replaced the WGS in four years at a short-term coexistence habitat, California State Polytechnic
566 University, Pomona, which contained manicured and more natural areas on the campus with
567 paved pathways and buildings surrounded by a mixture of *Juglans*, *Eucalyptus*, *Washingtonia*,
568 *Pinus*, and other tree species. In contrast, the two species have coexisted within longer-term
569 coexistence habitats of Griffith Park in Los Angeles, CA for more than 60 years, which were
570 more natural in appearance consisting of *Pinus*, *Quercus*, *Umbellularia*, *Sequoia*, and *Ulmus*
571 species, but with human-influenced aspects such as picnic tables, a playground, and restrooms
572 (King 2004; King *et al.* 2010; DeMarco *et al.* 2020). The study area at CBG has been classified
573 as a longer-term coexistence habitat by Muchlinski *et al.* (2012). How long coexistence can
574 continue in longer-term coexistence habitats is unknown. Many longer-term coexistence sites are
575 fragments of habitat where the FS, but not the WGS, exists in surrounding habitats. The WGS is
576 also subject to loss of genetic diversity in these habitat fragments as described by DeMarco *et al.*
577 (2020).

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

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

593 After the annual changes in mean monthly temperature were removed from the ONT data
594 using a band-stop filter, the remaining variation in temperature fluctuations were composed of a
595 strong six-month cycle and significant variation on timescales that exceeded 30 months (Fig.
596 4C). Meteorologists and climate scientists have used harmonic analysis to document semi-annual
597 cycles in rainfall and temperatures whose amplitude and phase shift vary by geographical
598 location, with moderate amplitudes for the southwest United States (Hsu & Wallace 1976; White
599 & Wallace 1978). Analyzing North American temperature data from 1979-2018, North *et al.*
600 (2021) used Bayesian analysis to fit a model with annual and semi-annual harmonics that vary
601 over space and time. They identify geographical regions with significant changes in the
602 contributions of the two harmonics to seasonal cycles. In Appendix C, we use least squares to fit
603 a model with annual and semi-annual harmonics to the unfiltered mean monthly temperature data
604 in Fig. 4A and show that a model that includes both annual and semi-annual cycles provides a
605 significantly better fit to the data than a model based on the annual cycle alone. The cospectra of
606 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

630 autoregressive process and was added to the carrying capacity for each species. Third, and most
631 importantly, in their models the intrinsic rate of increase for each species was set to $r_i = 1.8$,
632 whereas in our model we chose $r_1 = r_2 = 0.5$, which is more consistent with the reproductive
633 capabilities of tree squirrels. In deterministic models of the type used our simulations and those
634 of Ruokolainen & Fowler (2008), values of $1 > r > 2$ lead to overcompensating dynamics, where
635 the approach to equilibrium exhibits damped oscillations. Although Ruokolainen & Fowler
636 (2008) claimed that their results are qualitatively similar for values of $r < 1$, previous work with
637 single-species models (e.g., Danielian 2016) has shown that extinction risk increases with a
638 reddening of environmental noise when the deterministic model, like ours, has
639 undercompensating dynamics ($r_i < 1$), but decreases with a reddening of environmental noise
640 when the deterministic model has overcompensating dynamics ($1 < r_i < 2$). Since the apparent
641 contradiction between our results and those of Ruokolainen & Fowler (2008) occurred when
642 there was a strong synchrony among the three species due to the high correlation of the effects of
643 environmental noise, their result is consistent with what one would expect from a single-species
644 model. When we repeated our simulations using values of $r_1 = r_2 = 1.8$, we observed a result
645 consistent with Ruokolainen & Fowler (2008).

646 Our simulation results were limited in their scope. They were motivated by our analyses
647 of timescale differences in the variability of population fluctuations for two sympatric species of
648 tree squirrels. Simulation analyses of the type conducted in this paper could be expanded to
649 include a broader examination of parameter space, other ecological interactions such as predator
650 and prey, and larger communities of interacting species. Our approach could also be adapted to
651 applied conservation models where environmental variability is a part of the simulation
652 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.

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

683 **5 CONCLUSIONS**

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

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

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711 **CONFLICT OF INTEREST**

712 None declared.

713 **AUTHORS' CONTRIBUTIONS**

714 A. E. M. and R. A. D. conceptualized the project and were responsible for the methodology. A.
715 E. M., J. L. O., R. I. A., and B. P. G. participated in the investigation. A. E. M. was responsible
716 for data curation, project administration, and project supervision. R. A. D. performed the data
717 analysis and visualization. All authors were responsible for the preparation, reviewing and
718 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=e13155-sup-0001-Supinfo.pdf>.

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