Effects of ENSO-linked climate and vegetation on population dynamics of sympatric rodent species in semiarid grasslands of Inner Mongolia, China

G. Jiang, T. Zhao, J. Liu, L. Xu, G. Yu, H. He, C.J. Krebs, and Z. Zhang

Abstract: El Niño Southern Oscillation (ENSO) linked climate has been known to be associated with several rodent species, but its effects on rodent community at both spatial and temporal scales are not well studied. In this study, we investigated the possible causal chain relating ENSO, precipitation, temperature, and vegetation index (normalized difference vegetation index, NDVI) to rodent abundance for 14 sympatric rodent species in 21 counties of semiarid grasslands in Inner Mongolia, China, from 1982 to 2006. We found that both precipitation and temperature showed a generally direct positive effect on rodent abundance in many species in the current year, but indirect effects that operate through NDVI in the current or following year could have a reverse effect on abundance. We described one ENSO-linked precipitation bottom-up chain and three ENSO-linked temperature bottom-up chains. These observed bottom-up links reveal that in El Niño years, or 1 year after La Niña years, or 2 years after El Niño years, ENSO-driven climate or vegetation factors tend to increase population abundances of many sympatric rodent species in this region. We also found time-lag effects and the life-history strategy (i.e., functional groups of hibernating behavior, activity rhythm, or food habits) also contribute to the observed complicated effects of SOI on precipitation, temperature, NDVI, and ultimately rodent abundance.

Résumé : On a établi un lien entre le climat associé à El Niño et à l'oscillation australe (ENSO) et plusieurs espèces de rongeurs, mais les effets du climat sur la communauté de rongeurs n'ont pas été bien étudiés aux échelles temporelles et spatiales. Nous examinons, dans notre recherche, la possible chaîne causale reliant ENSO, les précipitations, la température et l'indice de la végétation (indice d'activité végétale, NDVI) à l'abondance des rongeurs de 14 espèces sympatriques dans 21 comtés de prairies semi-arides de la Mongolie Intérieure, Chine, de 1982 à 2006. Tant les précipitations que la température ont en général un effet positif direct sur l'abondance des rongeurs de plusieurs espèces durant l'année courante, mais les effets indirects qui agissent à travers le NDVI au cours de l'année courante ou de l'année suivante peuvent avoir des effets inverses sur l'abondance. Nous décrivons une chaîne ascendante des précipitations liées à ENSO et trois chaînes ascendantes de la température liée à ENSO. Ces chaînes ascendantes montrent que durant les années El Niño, ou 1 an après les années La Niña, ou 2 ans après les années El Niño, le climat influencé par ENSO ou les facteurs de la végétation ont tendance à faire augmenter les abondances des populations de plusieurs espèces sympatriques de rongeurs dans cette région. Il y a aussi des effets à action retardée et les stratégies démographiques (groupes fonctionnels de comportement d'hibernation, rythmes d'activité ou habitudes alimentaires) contribuent aussi aux effets complexes observés de SOI (indice d'oscillation australe) sur les précipitations, la température, NDVI et, en bout de ligne, l'abondance des rongeurs.

[Traduit par la Rédaction]

Introduction

The El Niño Southern Oscillation (ENSO) has been recognized as a significant factor affecting climatic variation globally (Diaz et al. 2001; Holmgren et al. 2006). ENSO-associated climatic factors may facilitate population outbreaks of pests or diseases directly or indirectly (Zhang and Wang 1998). Recently, ENSO-linked precipitation changes have been shown to affect the population dynamics of several rodent species (e.g., Jaksic et al. 1997; Lima et al. 1999*a*, 1999*b*; Zhang et al. 2003). Theses studies were mostly conducted based on localized and single-species populations, the responses of rodent populations to ENSO-linked climatic and vegetation factors have not been investigated at regional and rodent community levels.

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Climatic variation may result in closely correlated responses of population changes and spatial synchrony in rodent species (Stenseth et al. 1996; Ranta et al. 1997), and may influence population fluctuations of rodents through changes in food supplies (Ernest et al. 2000; Brown and Ernest 2002). Previous studies have revealed that consumers respond to pulsed rainfall induced by ENSO events in many terrestrial and aquatic ecosystems (Ostfeld and Keesing 2000; Brown and Ernest 2002); such associations need to be tested using long-term data (but see Brown and Ernest 2002). Sympatric rodent species with different life histories may have different responses to pulsed rainfall and food resources produced by ENSO events (Stapp and Polis 2003). Some studies have shown that population outbreaks of omnivorous or granivorous murids in desert and semiarid environments are closely associated with ENSO events (Jiménez et al. 1992; Meserve et al. 1995). Precipitation may impose direct and indirect impacts on small rodents because moderate precipitation may benefit plant growth and then rodents, whereas heavy precipitation may kill rodents by flooding their burrows and nests (Brown and Ernest 2002). Rainfall may benefit rodents through increases of plant growth and food supplies, but may disadvantage some rodent species that prefer open vegetation (Zhang et al. 2003). In addition, time lags may be present in ENSO-driven effects, but these have rarely been considered.

ENSO, as a climate driver, has complex effects on the biota. It not only affects the amount of rainfall, it also affects temperature (Cochrane and Barber 2009). Temperature, together with precipitation, may affect reproduction and survival of small rodents (Pennycuik et al. 1986; Koontz et al. 2001). Impact of temperature on small mammals have been studied in some previous literatures (e.g., Stapp et al. 1991; Bowman et al. 2005; Myers et al. 2009); however, studies of impact of ENSO-driven temperature on small rodents are still lacking.

The purpose of this study is to investigate the causal chain of ENSO, precipitation, temperature, and normalized difference vegetation index (NDVI) as drivers of change in rodent abundance for 14 sympatric rodent species in 21 locations (or counties) of semiarid grasslands in Inner Mongolia, China, from 1982 to 2006. Precipitation and temperature in this region have been suggested to be linked to ENSO (e.g., Zhao 1989; Zhang and Xue 1994; Qian 1997), and population abundances of a few rodent species (e.g., Mongolian jird, Brandt's vole) have previously been found to be associated with precipitation or ENSO (e.g., Xia et al. 1982; Zhang et al. 2003). This study aims to test two hypotheses. First, ENSO-driven climate may affect population abundance of different sympatric species differently owing to differences in life histories of these species. Second, bottom-up causal chain from SOI to rodent abundance through climate and vegetation index may exist in some symaptric species in this region.

Materials and methods

Study areas

The Inner Mongolia Autonomous Region (IMAR) is located in northern China (37°24′N~53°23′N, 97°12′E~126°04′E). The mean elevation of the IMAR is 1000~1200 m above sea level. A continental temperate monsoon prevails in this region. The annual mean temperature range is –5 to ~9 °C with a mean of 3.8 °C and the precipitation is 150~500 mm with a mean of 326 mm. Annual mean temperature decreases, while precipitation increases, from the southwest to the northeast. The winter ambient temperature has steadily increased by 0.5–0.9 °C per decade during the past 40 years (Zhai and Ren 1997). Desert grassland, typical grassland, and meadow grassland are the major landscapes of this plateau. We analyzed the long-term time series of rodent populations collected from 21 sites located in 21 counties of central Inner Mongolia, covering an area of 257 900 km^2 (Fig. 1). The dominant plant species of the meadow grassland include baical needlegrass (*Stipa baicalensis* Roshevitz), Siberian filifolium (*Filifolium sibiricum* (L.) Kitam.), and *Aneurolepidium chinense* (Trinius ex Bunge) Kitagawa (= *Leymus chinensis* (Trinius ex Bunge) Tzvelev); those of the typical grassland include Smirnov needlegrass (*Stipa grandis* P. Smirnov), Krylov needlegrass (*Stipa krylovii* Roshevitz), *A. chinense*, and bunge needlegrass(*Stipa bungeana* Trinius), whereas those of the desert grassland include Klemenz needlegrass (*Stipa klemenzii* Roshevitz), sandy needlegrass (*Stipa glareosa* (P. Smirnov) Tzvelev), and short flower needlegrass (*Stipa breviflora* Grisebach) (Ma et al. 2008).

Rodent abundances

The abundance of rodent populations have been surveyed twice a year by the Inner Mongolia Center for Endemic Diseases Control and Research since 1982 (Table 1). The survey was conducted over an area of about 25 ha; the predominant habitat or vegetation type of each county was selected for estimating relative abundances of rodents. From the middle of April to the middle of May and from the middle of September to the middle of October every year, 1~3 sampling plots were selected in each of the 21 locations to capture rodents. At each plot, 100 snap-traps were baited with flour pie mixed with bean oil spaced at an interval of 5 m along a transect line. The transect lines were about 200 m apart. Traps were set after sunset and collected in the morning for 2 successive days at each plot. The captured animals were identified, weighed, and dissected to check for pathogens. The trap sites were rotated to minimize the negative effect of successive trapping on population dynamics. Only the pooled spring and autumn data of county stations were available to us for analysis. The relative abundance is defined as the total number of captured animals/total number of snap-traps × 100 (i.e., percentage of trap success).

We classified the rodent species into the following species groups: hibernating or nonhibernating species; nocturnal or diurnal species; granivorous, folivorous, or omnivorous species by referring to previous studies of their life histories (see Table 2) (e.g., Zhao 1981; Luo et al. 2000).

Climate and vegetation data

The yearly Southern Oscillation Index (SOI) data during 1980–2006 was calculated based on the monthly SOI data obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/current/soi2.shtml; accessed 20 December 2007). The SOI is defined as the normalized pressure difference between Tahiti and Darwin stations, which is closely associated with global precipitation and temperature

Fig. 1. Illustrations of study sites in Inner Mongolia Autonomous Region of China.

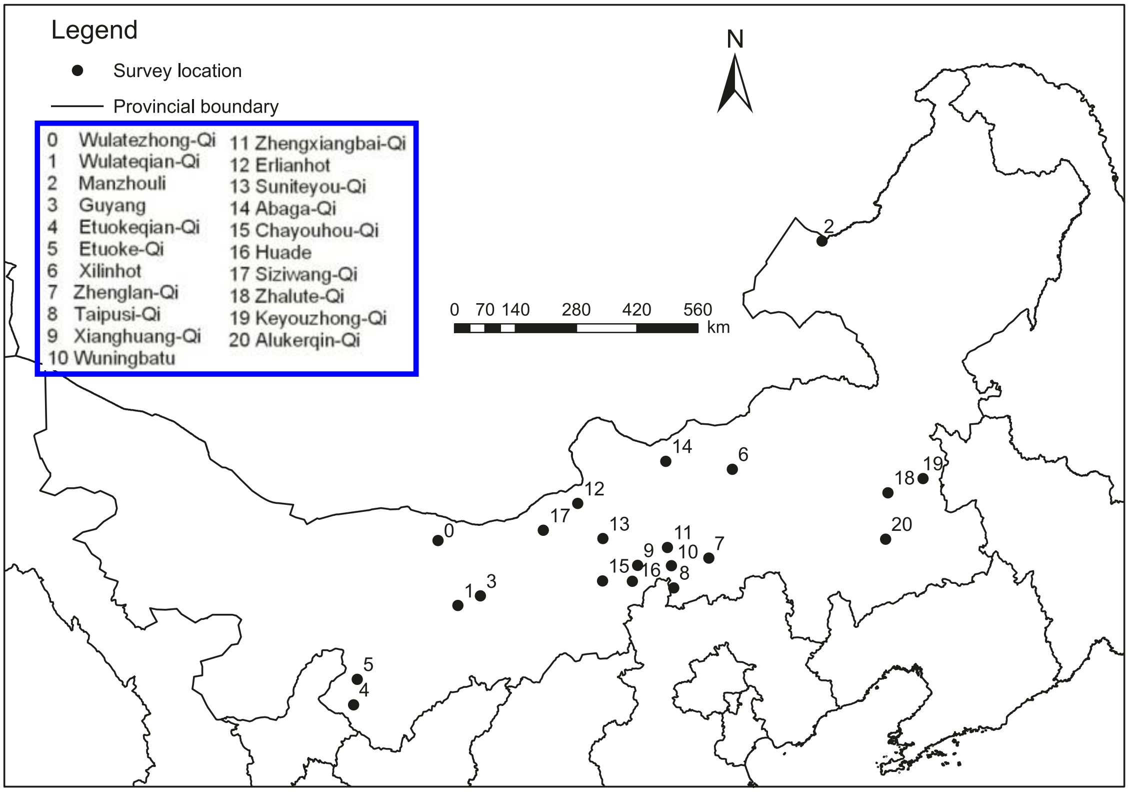


Table 1. The 21 study locations, survey durations, and number of rodent species.

Location name	Longitude (E)	Latitude (N)	Time period	Number of species	Total number of individuals captured
Wulatezhong-Qi	108.4850	41.9556	1984–2006	12	2591
Wulateqian-Qi	109.4031	40.7829	1984–2006	8	1397
Manzhouli	117.6592	49.4612	1984–2006	7	973
Guyang	109.9218	41.0697	1985–2006	8	790
Eqian-Qi	107.3786	38.3743	1982–2006	9	3884
Etuoke-Qi	107.3186	38.8849	1984–2006	8	2725
Xinlinhot	116.0681	44.5687	1986–2006	6	221
Zhenlan-Qi	115.8053	42.7003	1985–1998	1	58
Taipusi-Qi	114.9839	41.9889	1989–2006	5	199
Xianghuang-Qi	113.9085	42.3134	1984–2006	7	1335
Wunibatu	114.8226	42.4205	1984–2006	6	802
Zhengbai-Qi	114.6304	42.7783	1985–2006	7	561
Erlianhot	111.9600	43.3075	1984–2006	12	1588
Suniteyou-Qi	112.8324	42.7138	1984–2006	12	1576
Abaga-Qi	114.1584	44.4940	1984–2006	6	678
Chayouhou-Qi	113.0456	41.8717	1988–2006	4	49
Huade	113.8419	41.9768	1982–2006	9	402
Siziwang-Qi	111.1936	42.6344	1982–2006	10	825
Zhalute-Qi	120.5739	44.5087	1985–2006	5	994
Keyouzhong-Qi	121.5443	44.8722	1985–2006	5	1211
Alukerqin-Qi	120.6480	43.5535	1982–2006	6	963

(Stone et al. 1996; Tsonis et al. 2005). We calculated the yearly SOI based on the monthly SOI data (see Zhang et al. 2003).

The yearly temperature and precipitation data covering all trapping sites during 1980–2006 had a resolution of 10 km × 10 km (http://www.cerndata.ac.cn/; accessed 20 May 2008). The spatial temperature and precipitation data were calculated based on the monitoring data from 722 weather stations using a linear interpolation resampling technique and ArcGIS spatial analysis model that accounted for effects of slope gradient, slope aspect, and altitude (ESRI 1996). The accuracy of the spatial interpolation method was assessed using root-mean-square-standardized predication error (RMSDE) (Yu et al. 2004).

The monthly NDVI measures the amount or greenness of vegetation, which is related to the photosynthetic levels

Table 2. The 16 rodent species, mean rodent abundance (number of individuals/100 trap-nights), their life-history characteristics, and the number of locations used for analysis during 1982–2006.

		Life-history characteristics					
Species code	Species name	Dormancy	Activity	Feeding strategy	No. of locations	Total no. of individuals caught	Mean abundance (SE)
1	Mid-day jird, *Meriones meridianus* (Pallas, 1773)	Nonhibernation	Nocturnality	Granivorous	10	3918	1.043 (0.189)
2	Northern three-toed jerboa, *Dipus sagitta* (Pallas, 1773)	Hibernation	Nocturnality	Omnivorous	12	2151	0.518 (0.043)
3	Mongolian five-toed jerboa, *Allactaga sibirica* (Forster, 1778)	Hibernation	Nocturnality	Omnivorous	20	5057	0.973 (0.048)
4	Thick-tailed jerboa, *Stylodipus telum* (Lichtenstein, 1823)	Hibernation	Nocturnality	Omnivorous	4	123	0.300 (0.046)
5	Five-toed pygmy jerboa, *Cardiocranius paradoxus* Satunin, 1903	Hibernation	Nocturnality	Granivorous	3	56	0.070 (0.017)
6	Desert hamster, *Phodopus roborovskii* (Satunin, 1903)	Nonhibernation	Nocturnality	Granivorous	15	2699	0.531 (0.054)
7	Dzhungarian hamster, *Phodopus sungorus* (Pallas, 1773)	Nonhibernation	Nocturnality	Granivorous	13	984	0.418 (0.050)
8	Eversman's hamster, *Cricetulus eversmanni* (Brandt, 1859)	Nonhibernation	Nocturnality	Granivorous	12	797	0.286 (0.038)
9	Gray dwarf hamster, *Cricetulus migratorius* (Pallas, 1773)	Nonhibernation	Nocturnality	Granivorous	7	388	0.179 (0.037)
10	Striped dwarf hamster, *Cricetulus barabensis* (Pallas, 1773)	Nonhibernation	Nocturnality	Granivorous	21	4188	0.961 (0.087)
11	Daurian pika, *Ochotona dauurica* (Pallas, 1776)	Nonhibernation	Crepuscular and diurnality	Folivorous	1	67	0.558 (0.301)
12	Mongolian jird, *Meriones unguiculatus* (Milne-Edwards, 1867)	Nonhibernation	Crepuscular and diurnality	Granivorous	14	1426	0.498 (0.115)
13	House mouse, *Mus musculus* L., 1758	Nonhibernation	Nocturnality	Omnivorous	10	366	0.000 (0.014)
14	Daurian suslik, *Spermophilus dauricus* Brandt, 1843	Hibernation	Crepuscular and diurnality	Folivorous	4	216	0.198 (0.056)
15	Brandt's vole, *Lasiopodomys brandtii* (Radde, 1861)	Nonhibernation	Crepuscular and diurnality	Folivorous	4	775	1.705 (0.613)
16	Large Japanese field mouse, *Apodemus speciosus* (Temminck, 1844)	Nonhibernation	Nocturnality	Granivorous	1	520	0.862 (0.221)

Note: Life-history characteristics from Zhao (1981) and Luo et al. (2000). Abundance is expressed as the number of animals captured/100 trap-nights.

(Tucker et al. 1991). The NDVI data with the size of NDVI pixel (64 km^2) for the period of 1980–2006 was obtained from the Environmental and Ecological Science Data Center for west China (EESDCWC), National Natural Science Foundation of China (NSFC) (http://westdc.westgis.ac.cn; accessed 27 January 2008). The NDVI data is produced by the Global Inventory Monitoring and Modeling Studies (GIMMS) group from measurements of the advanced very high resolution radiometer (AVHRR) onboard the National Oceanic and Atmospheric Administration (NOAA) satellites. We calculated the yearly NDVI of each location based on the monthly NDVI by using the spatial analysis tool (zonal statistics) in ArcGIS (ESRI 1996). In addition, we obtained data on annual grass production (1991–2003) from four locations sampled by the Grass Station of Xinlinguole Meng. Using the data from these four locations (Xinlinhot, Abaga-Qi, Taipusi-Qi, and Zhengbai-Qi) during 1991–2003, we found that the yearly grass production (kg/acre) was significantly and positively associated with NDVI of the current year (mean CCF = 0.18; 95% CI = 0.002 and 0.37), suggesting NDVI can be taken as an indicator of grass production. However, because the cross-correlation function (CCF) values are relatively small, NDVI does not fully represent grass biomass.

Statistical analysis

We used the CCF method to investigate associations among ENSO, climate factors (precipitation and temperature), NDVI, and rodent abundance of the current (lag 0) and previous (lag –1) years. To satisfy the CCF analysis, the data on population abundance were first log$_e$-transformed to stabilize the variance and then detrended using linear regression models with generalized least squares (Venables and Ripley 2002); the climate and vegetation data were also detrended, but without log-transformation. We did not analyze the time series for a species if the data covered less than 5 successive years. We replaced a few missing data for some time series by using the mean values of the previous and next years.

Because time-series data is often autocorrelated, the conventional models are often not suitable to deal with these data. The alternative method is to increase the number of replicates in space and to calculate the mean value and confidence interval (CI) of the CCF, and to determine the significance of a CCF association between two time series (Efron and Tibshirani 1993; Lillegrd et al. 2005; Cheal et al. 2007). The CCF method is able to solve the autocorrelation problems associated with time-series data, whereas CI is able to solve the problem of covariations between variables by taking different sites as replicates. These two issues are very hard problems associated with many conventional models.

We calculated CCF coefficients based on Shumway and Stoffer (2006), and we calculated the mean CCF coefficients using bootstrap confidence intervals (CI) (based on 10 000 replications) to examine if the CCF coefficients overlap zero (Efron and Tibshirani 1993). We calculated the mean CCF and 95% CI of each rodent species based on CCF values in different locations (counties) for each species. To explore the relationship between grass production and NDVI, we also calculated the mean CCF and 95% CI and checked if NDVI can serve as an index for grass production. The significant in-phase (positive) association between two time series is defined as both the mean CCF and its 95% CI being larger than zero; the out-of-phase (negative) association is defined as both the mean CCF and its 95% CI being smaller than zero (Lillegrd et al. 2005; Cheal et al. 2007). Data from 16 species were used to calculate CCF, but only data from 14 species were used to calculate CI (number of locations ≥3).

To figure out the bottom-up causal links on each species, we assume the following causal relationships: SOI affects precipitation (P) and temperature (T); climate affects NDVI; climate affects rodent (R); and NDVI affects rodents (R). In theory, there are 38 possible causal links from SOI to P and T, to NDVI, and to R considering the effect of the current year and the following year, including 6 one-level links (P→R; T→R; NDVI→R), 16 two-level links (SOI→P→R; SOI→T→R; P→NDVI→R; T→NDVI→R), and 16 three-level links (SOI→P→NDVI→R; SOI→T→NDVI→R). We only present the causal links if five or more species show the same significant CCFs along the links. All statistical analyses were conducted using the R software packages (R Development Core Team 2006).

Results

Rodent abundance and richness

Both abundance and species richness of rodents varied greatly among different locations (Table 1). Three locations (Wulatezhong-Qi, Erlianhot, and Suniteyou-Qi) showed high species richness ($n = 12$), while one location (Zhenlan-Qi) had only one species (Table 1). Twenty-seven rodent species were captured over the past 25 years, but data from only 16 species were sufficient for calculating CCF, 14 species for calculating the CI of CCFs (Fig. 2, Table 2). Among the 16 species, the predominant species were Mid-day jirds, striped dwarf hamsters, and Mongolian five-toed jerboas; 69% were nonhibernating species, 31% were hibernating species; 75% were nocturnal species; 56% were granivorous, 19% were folivorous, and 25% were omnivorous species.

Of the total 59 associations between every two species (based on calculation of CCF at each location), we found 31 significant positive associations and 5 significant negative associations. These results suggest that sympatric species showed strong synchronous responses to external forces at the regional scale, implying a regional impact of climate on rodent communities.

Effect of SOI on climate

As shown in Fig. 3*b* (left panel), SOI had a significant positive effect on precipitation for locations of six species in the current year. As shown in Fig. 3*b* (right panel), SOI had a negative effect on precipitation for locations of 14 species in the previous year. SOI showed a significant negative effect on temperature for locations of 13 species in the current year (Fig. 3*a*, left panel), whereas SOI showed a positive effect on temperature for locations of 14 species in the previous year (Fig. 3*a*, right panel).

Effect of climate on vegetation

As shown in Fig. 3*d* (left panel), precipitation had a significant positive effect on NDVI for locations of 14 species in the current year. As shown in Fig. 3*d* (right panel), precipitation had a positive effect on NDVI for locations of only three species in the previous year. Temperature showed a significant negative effect on NDVI for locations of four species in the current year (Fig. 3*c*, left panel), whereas temperature showed a positive effect on NDVI for locations of only 14 species in the previous year (Fig. 3*c*, right panel).

Effect of climate on rodent abundance

Temperature showed a significant positive effect on rodent abundance for six species and a negative effect on rodent abundance for one species in the current year (Fig. 4*a*, left panel), whereas temperature showed a few significant effects on rodent abundance, only two positive effects and one negative effect in the previous year (Fig. 4*a*, right panel). Of the six species showing positive associations between abundance and temperature in the current year, four of them are hibernating species. Of the six species showing positive associations between abundance and temperature in the current year, four of them are nocturnal species, two of them were granivorous species, and two of them were folivorous species. Of the two species showing positive association between abundance and temperature in the following year, one of them is a folivorous species. These results suggest that temperature tends to have a positive effect on abundances of hibernating and nocturnal species.

Precipitation showed significant positive correlations with abundances of four species and negative correlations with abundances of two species in the current year (Fig. 4*b*, left panel), whereas precipitation had only a negative effect on abundances of three species in the following year (Fig. 4*b*, right panel). Of the four species showing positive association between abundance and precipitation in the current year, three are nonhibernating species and two species are crepuscular and diurnal species. These results suggest that precipitation tends to have a positive effect on abundances of nonhibernating species.

Effect of vegetation on rodent abundance

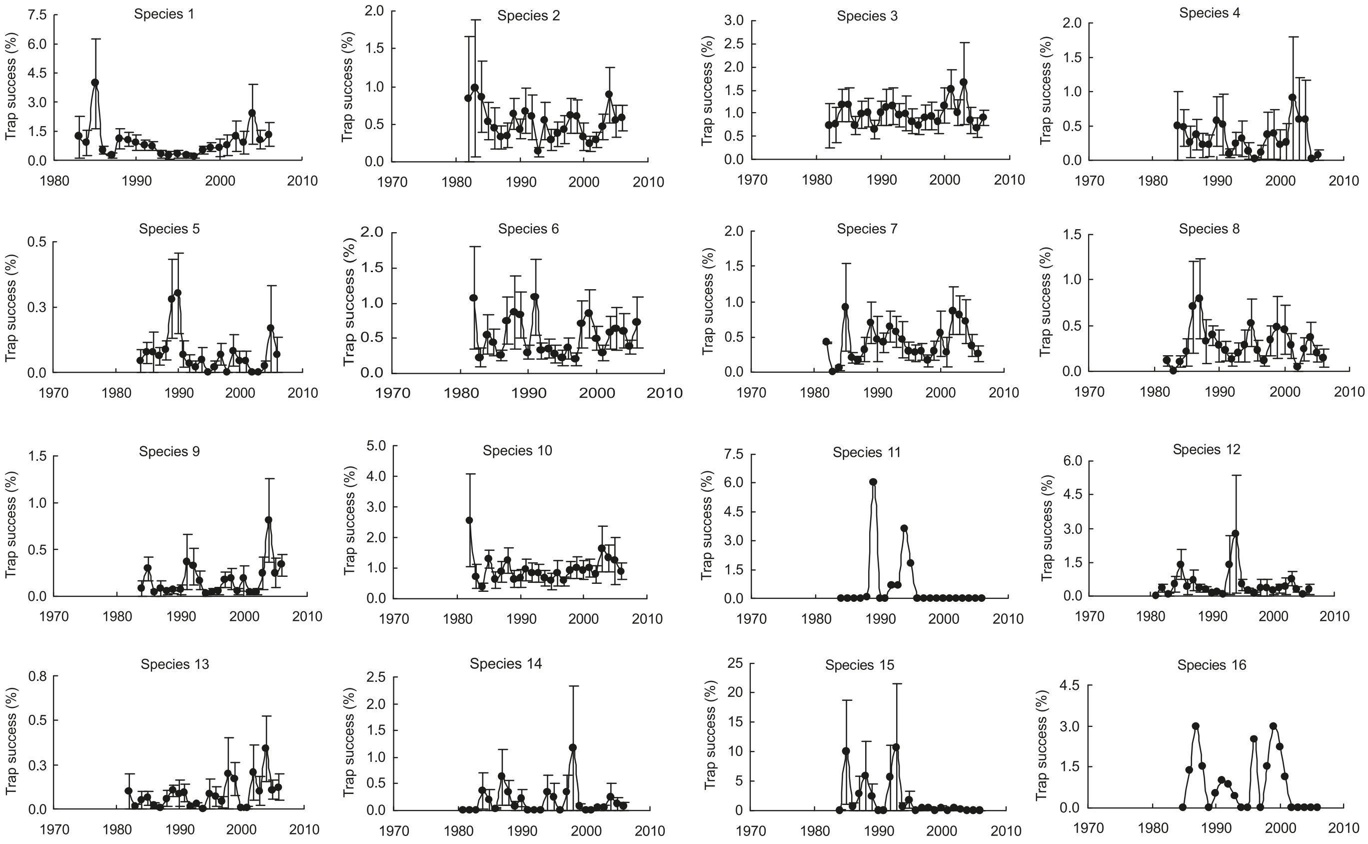
By contrast, NDVI showed only one significant positive correlation and five negative effects on rodent abundance in the current year (Fig. 4*c*, left panel), whereas NDVI showed positive correlations with four species and negative correlations with two species in the previous year (Fig. 4*c*, right panel). Of the five species showing negative associations between abundance and NDVI in the current year, four species are nonhibernating rodent species, four species are granivorous rodent species, and three species are nocturnal rodent species. Of the four species showing positive association between abundance and NDVI in the following year, four are nonhibernating species and three are nocturnal species. NDVI tends to have a negative effect on nonhibernating or granivorous rodent species.

Effect of climate and NDVI on function groups

Hibernating

Temperature showed significant positive effect on abundance of the hibernating rodent species in the current year (Fig. 5*a*). In contrast with temperature, precipitation showed significant positive effects on the abundance of nonhibernating rodent species in both the current and the following years (Figs. 5*a*, 5*b*, respectively). NDVI showed significant negative effects on the abundance of nonhibernating rodent

Fig. 2. The mean abundance and its SE (based on variations among the locations) of the 16 species of rodents in the study region. Species 11 and 16 have only a single population, which were not used to calculate the confidence interval (CI). The relative abundance is defined as the total number of captured animals/total number of snap-traps × 100 (i.e., percentage of trap success).



species in the current year (Fig. 5*a*), but positive effect on nonhibernating rodent species in the following year (Fig. 5*b*).

Activity rhythm

Temperature showed a significant positive effect on the abundance of both nocturnal and crepuscular and diurnal rodent species in the current year (Fig. 5*c*). Precipitation showed a significant positive effect on abundance of crepuscular and diurnal rodent species in the current year (Fig. 5*c*). NDVI showed a significant negative effect on abundance of nocturnal rodent species in the current year (Fig. 5*c*), but a positive effect on nocturnal rodent species in the following year (Fig. 5*d*).

Food habits

Temperature showed significant positive effect on abundances of both granivorous and folivorous rodent species in the current year (Fig. 5*e*). Precipitation showed significant positive effect on abundance of granivorous rodent species in the following year (Fig. 5*f*). NDVI showed a significant negative effect on abundance of both granivorous and folivorous rodent species in the current year (Fig. 5*e*), but a positive effect on granivorous rodent species and a negative effect on the ominivorous rodent species in the following year (Fig. 5*f*).

Bottom-up links

A total of six paths showing climatic and vegetation effects on rodent abundances were identified. Two of the six paths involve SOI–precipitation–NDVI–rodent links (P1 and P2 in Fig. 6*a*) and four of the six paths involve SOI–temperature–NDVI–rodent links (T1, T2, T3, and T4 in Fig. 6*b*). Species 1, 5, 9, 12, and 15 showed significant associations in the SOI–precipitation–NDVI–rodent links, whereas species 1, 2, 4, 5, 8, 9, 14, and 15 showed significant associations in the SOI–temperature–NDVI–rodent links. In the other possible causal paths, there were less than five species showing significant positive or negative associations.

As illustrated in Fig. 6*a*, precipitation showed indirect negative effects on rodent abundance in the current year through path P1, whereas SOI showed indirect positive effects on rodent abundance in the following year through path P2. Temperature showed direct positive effects on rodent abundances in the current year through path T1, shown in Fig. 6*b*. SOI showed indirect positive effects on rodent abundance in the following year through path T3. In contrast, SOI also produced indirect negative effects on rodent abundance in the current year through path T2, whereas SOI showed indirect negative effects on rodent abundance with a 2-year time lag through path T4.

Fig. 3. Estimated mean correlations between climate variable time-series pairs (*a*–*d*) at 0-year time lag (left-side panels; year *t*) and 1-year time lag (right-side panels; year *t* – 1) for each species in their own regions and bootstrapped 95% CI (confidence interval) for the cross-correlation coefficient (CCF). The CIs of species 11 and 16 were not available because they only occurred in one location and the climate variable values were yearly means. SOI, the Southern Oscillation Index; P, precipitation; T, temperature. Asterisks indicate the mean CCF and its 95% CI were larger or less than zero ($P < 0.05$).

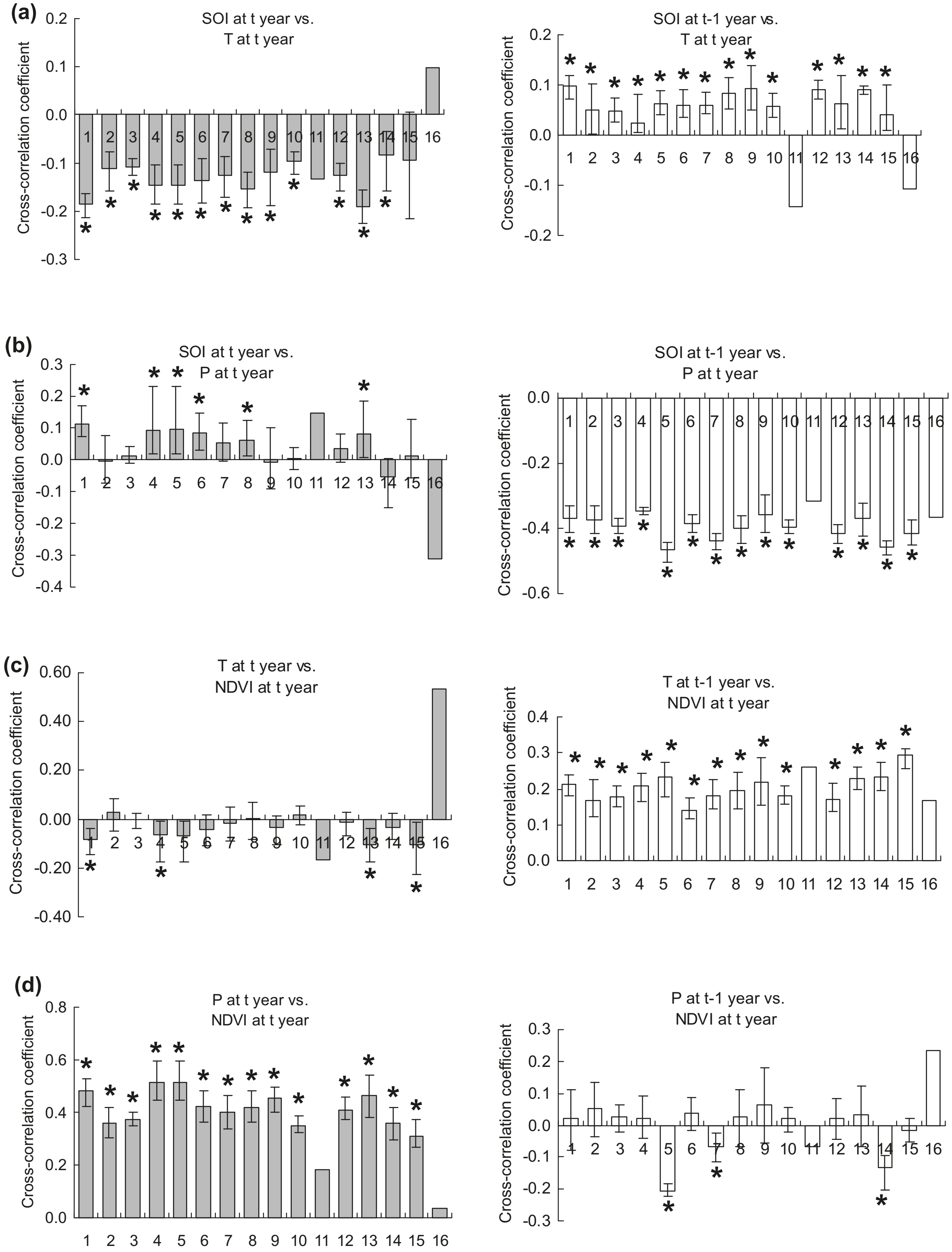


Fig. 4. Estimated mean correlations between the population abundance time series (ln $(N + 1)$-transformed; *a*–*d*) of the 16 rodent species and climate variables at 0-year time lag (left-side panels; year *t*) and 1-year time lag (right-side panels; year $t - 1$) for each species in their own regions and bootstrapped 95% CI (confidence interval) for the cross-correlation coefficient (CCF). The CIs of species 11 and 16 were not available because they only occurred in one location and the climate variable and population abundance values used in this analysis were yearly means. P, precipitation; T, temperature. Asterisks indicate the mean CCF and its 95% CI were significantly different from zero ($P < 0.05$).

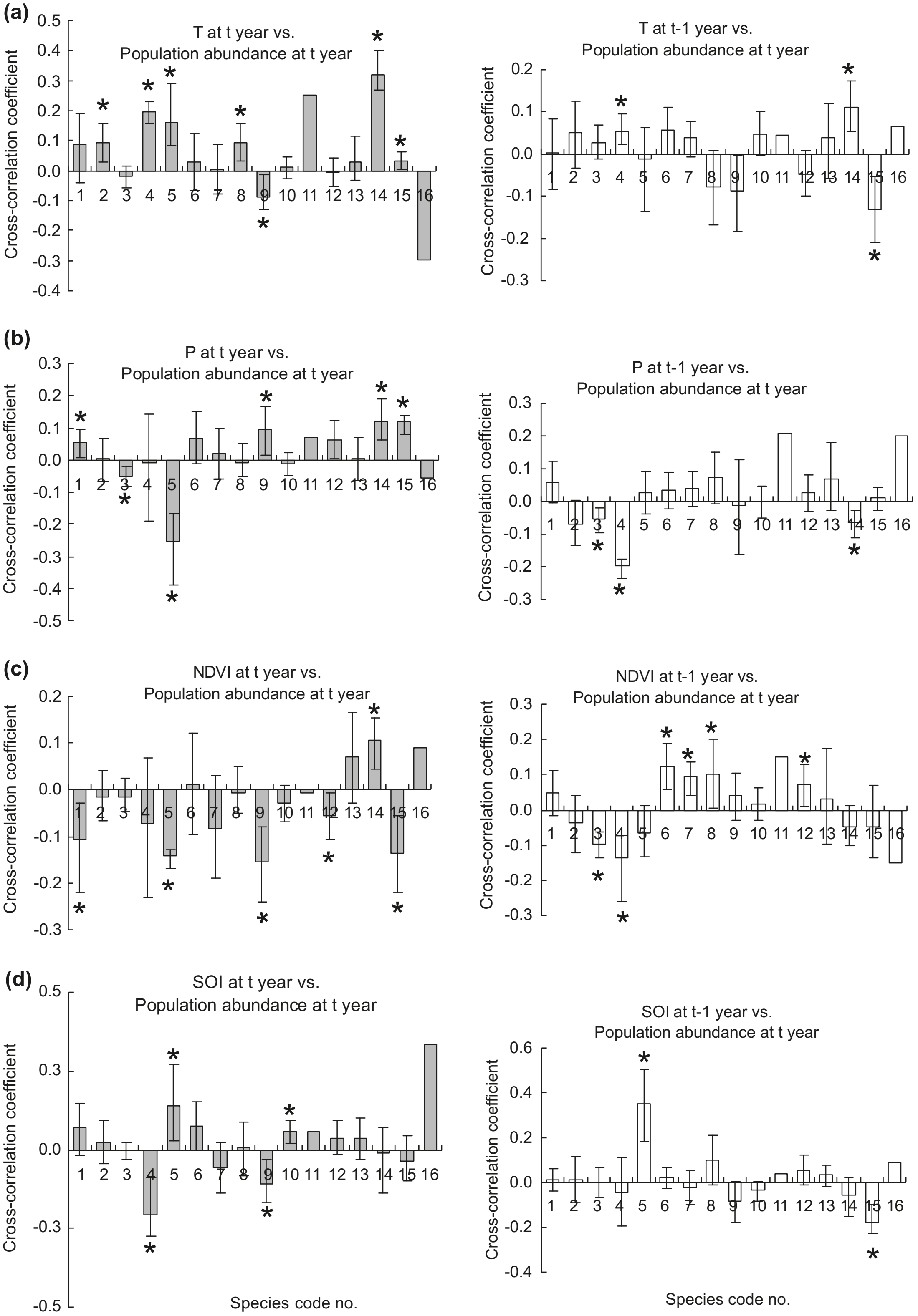
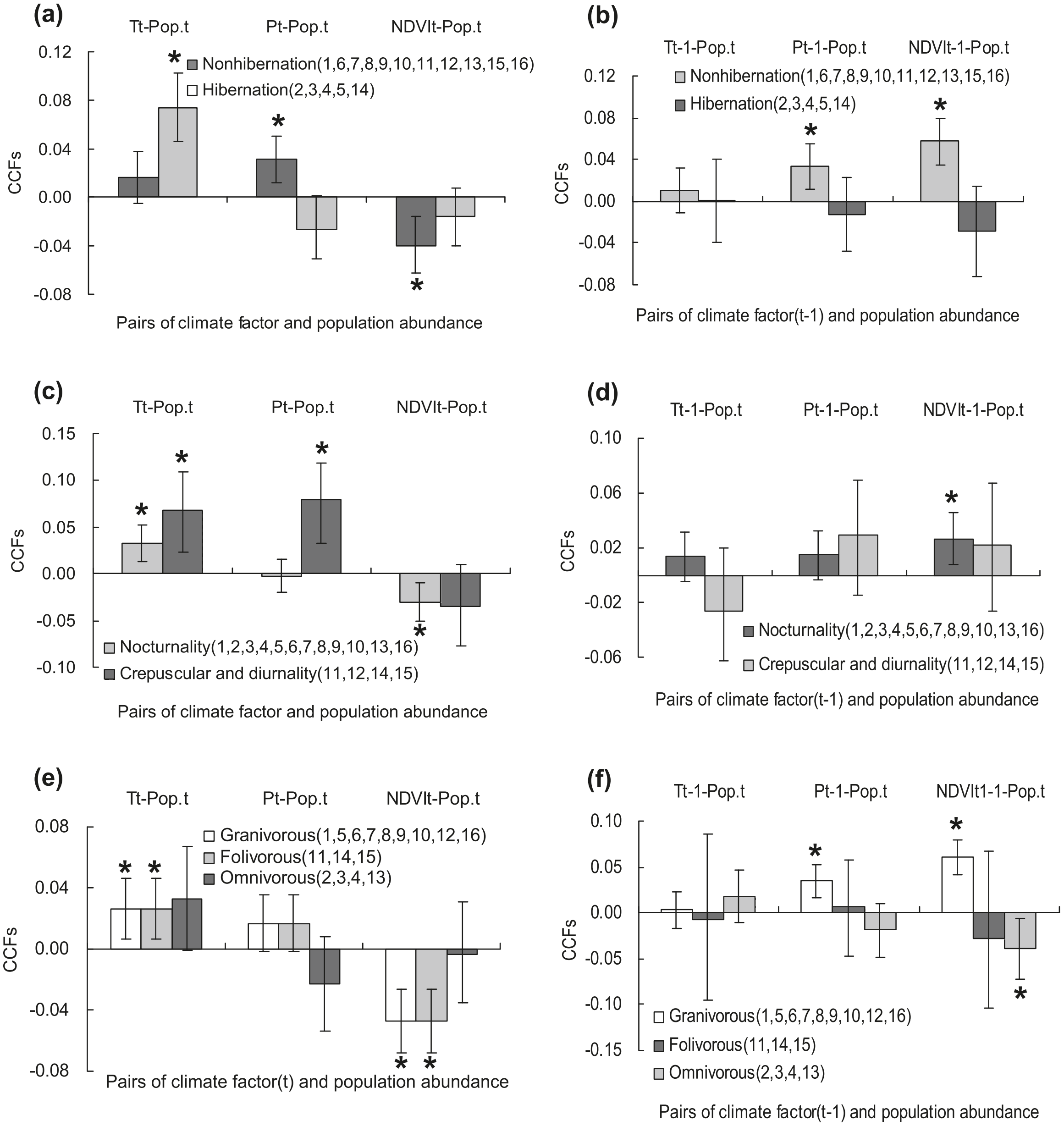


Fig. 5. Relationship between abundance of hibernating or nonhibernating rodent population and climate factors with 0-year (*a*; year *t*) and 1-year (*b*; year $t - 1$) time lags. Relationship between abundance of nocturnal or non-nocturnal rodent population and climate factors with 0-year (*c*; year *t*) and 1-year (*d*; year $t - 1$) time lags. Relationship between abundance of granivorous, folivorous, or omnivorous rodent population and climate factors with 0-year (*e*; year *t*) and 1-year (*f*; year $t - 1$) time lags. The mean values are bootstrapped 95% CI (confidence interval) for the correlation coefficients. P, precipitation. Pop., population relative abundance; T, temperature. There are 108 populations of 11 nonhibernating species and 43 populations of 5 hibernating species. There are 128 nocturnal populations for 12 species and 23 crepuscular and diurnal populations for 4 species. There are 97 granivorous populations for 9 species, 9 folivorous populations for 3 species, and 45 omnivorous populations for 4 species. Asterisks indicate that the mean CCF and its 95% CI were larger or less than zero ($P < 0.05$).

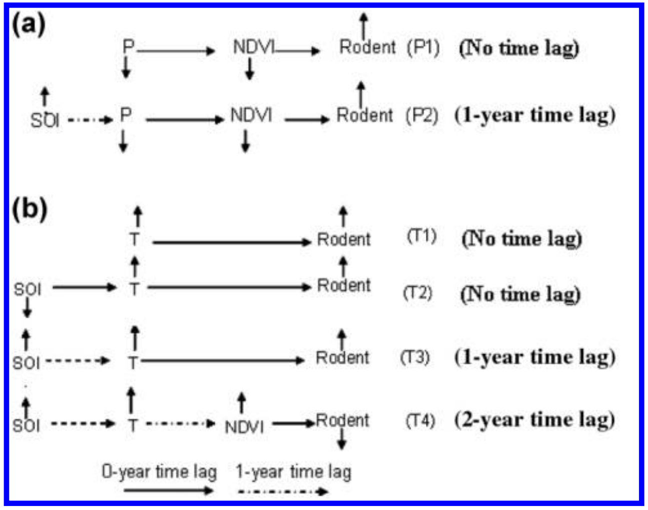


Discussion

Effect of precipitation

Abundant precipitation has been well demonstrated to increase the population growth of small rodents in southern and eastern Australia (Singleton 1989; Pech et al. 1999), western South America (Jaksic et al. 1997; Lima et al. 1999*a*, 1999*b*), and Inner Mongolia, China (Xia et al. 1982; Li and Zhang 1993). The causal mechanism behind the impact of precipitation on rodent abundance appears to be an increased primary production, both as herbage production and seed-bank storage (Ostfeld and Keesing 2000; Brown and Ernest 2002). Our results reveal that an increase of precipitation shows a significant positive effect on the abundance of five species, but also shows a negative effect on the abundance of two species in the current year. In general, increased precipitation shows a positive effect on rodent abundance of many species at the regional and rodent community

Fig. 6. Bottom-up links of climatic and vegetation factors on rodent abundances. Only medium or above effect (species number or with their locations is larger than 5 showing significant CCF values between two variables) were presented here, based on path analysis in Figs. 7*a* and 7*b*.



levels in the current year, consistent with the previous studies listed above. However, the discovery of negative effects of precipitation on other species differs from the previous results. This could be caused by differences in the response of different species to precipitation, owing to difference in life histories.

Our results on functional group indicate that increased precipitation has positive effect on nonhibernating rodent species in both the current and the following years, not on hibernating species (Figs. 5*a*–5*f*). Wet weather or heavy snow does not favor the hibernating species that positively depend on warm weather (Inouye et al. 2000, also see below). Precipitation shows positive effect on crepuscular and diurnal rodent populations in the current year. Crepuscular and diurnal activity may require more water intake (Chew 1951). Thus, abundant rainfall may be more important for non-nocturnal rodent species. Precipitation shows significant positive effect on abundance of granivorous rodent species in the following years, suggesting that abundant precipitation may increase seed production, and thus benefit survival over the winter of granivorous rodent species. Most granivorous rodent species store food for survival through the overwintering period in Inner Mongolia (Zhao 1981; Zhong et al. 2008). These results support our first hypothesis that sympatric rodent species may show different responses to ENSO-linked climate because of the differences in life histories.

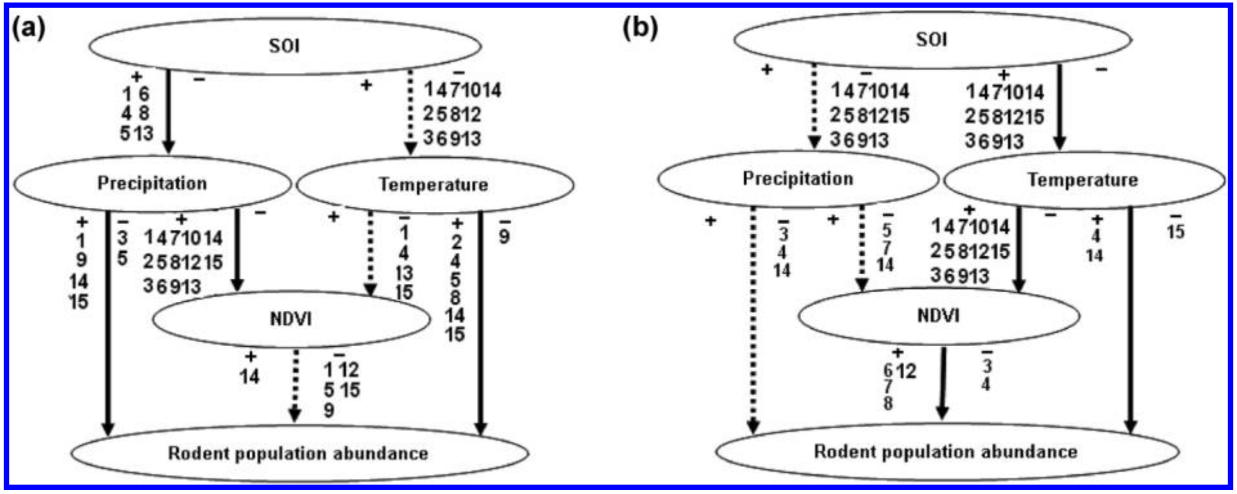
Effect of temperature

Compared with precipitation, effects of temperature on rodent population are relatively less investigated. Previous studies suggest that warm temperature may benefit population growth of rodents directly or indirectly. Pucek et al. (1993) reported that the warm June–July climate of the previous year (good for bud formation) resulted in seed masting of European hornbeam (*Carpinus betulus* L.), English oak (*Quercus robur* L.), and Norway maple (*Acer platanoides* L.), and then outbreaks of bank vole (*Clethrionomys glareolus* (Schreber, 1780)) and yellow-necked mice (*Apodemus flavicollis* (Melchior, 1834)) in the following year. Inouye et al. (2000) reported that hibernating yellow-bellied marmots (*Marmota flaviventris* (Audubon and Bachman, 1841)) appeared aboveground 38 days earlier than observed 23 years ago, apparently owing to warmer spring air temperatures. An increase in temperature may significantly advance the beginning of the plant growing season (Chmielewski and Rotzer 2001; Li et al. 2007) and fresh green plants may trigger early spring reproduction for hibernating rodents (Linn 1991; Negus and Pinter 1966). Our results indicate that temperature has positive effects on the abundance of six species and a negative effect on one species, suggesting that temperature has a predominant positive effect on rodent species at the regional level in the current year, but its effect on rodent abundance is much weaker in the following year (Figs. 7*a*, 7*b*).

In general, the effects of temperature on many rodent species are positive (Figs.7*a*, 7*b*). Temperature shows a significant positive effect on hibernating species but not on nonhibernating species. This is probably because hibernating species are more sensitive to temperature. Vickery and Bider (1981) reported that variation in activity of nocturnal rodents was more likely associated with predator avoidance than with physiological restrictions under temperature changes. But, our results indicate that both nocturnal and non-nocturnal species showed the same positive association between abundance and temperature, suggesting that this effect may not be related to such activity. An increase of temperature is more obvious in winter in Inner Mongolia (Zhai and Ren 1997), which may benefit overwintering survival and spring breeding of rodents (Schmidt-Nielsen 1975). Besides, an increase in temperature may benefit plant growth in spring and extend the growing season. Chmielewski and Rotzer (2001) showed that an early spring warming by 1 °C caused an advance in the beginning of the plant growing season by 7 days, the extension of the growing season was mainly the result of an earlier onset of spring, and an increase in the mean annual air temperature by 1 °C led to an extension of the plant growing season by 5 days. Stapp and Polis (2003) reported that granivorous and omnivorous rodent species may respond differently to pulsed variations of resources. According to the results of the functional group, we found that temperature showed a significant positive effect on both granivorous and folivorous rodent species in the current year, and nonsignificant effect on omnivorous rodent species (Figs. 5*a*–5*f*). These results also support our first hypothesis.

The obvious positive association of population abundance with temperature in many rodent species of Inner Mongolia suggests that global warming may increase the abundance of small rodents in this region. Zhai and Ren (1997) reported that the minimum temperature has been warming by 0.5~0.9 °C per decade over the past 40 years in northern China. In Inner Mongolia, Pei et al. (2009) reported that mean annual temperature increased all over the region during the past 40 years; increased by 0.5 °C per decade from 1964 to 1983 and by 0.9 °C per decade from 1984 to 2003. Li et al. (2007) reported that annual NDVI also exhibited a slightly increasing trend from 1983 to 1997 in the desert grassland and meadow grassland of Inner Mongolia. However, extreme high temperatures may be detrimental to some rodent species and can be lethal, especially in a hot summer (Beck and Anthony 1971). Kausrud et al. (2008) reported that global

Fig. 7. Simple linear net models showing how climate pulses the dynamics of rodent populations. "+" and "–" indicate significant positive and negative species codes. The solid arrows represent the main positive effects among species, whereas the dashed arrows represent the main negative effects among species. The number of species represents the indicators of the defined main responses. Panel *a* is the result of 0-year time lag (year *t*) summarized by the left-side panels of Figs. 3*a*–3*d* and 4*a*–4*d* and panel *b* is the result of 1-year time lag (year *t* – 1) summarized from right-side panels of Figs. 3*a*–3*d* and 4*a*–4*d*.



warming may be the cause of disappearing outbreaks of Norway lemmings (*Lemmus lemmus* (L., 1758)) because snow cover, which is important for keeping lemmings warm, lasts a shorter time at present than it did in previous years.

Effect of NDVI

Studies of the relationship between rodent abundance and NDVI are relatively rare. In central Argentina, population dynamics of Azara's grass mouse (*Akodon azarae* (J. Fischer, 1829)) (Muridae: Sigmodontinae) seems to be strongly influenced by human land use, indexed by NDVI (Andreo et al. 2009). Whereas rates of population growth of great jirds exhibit greater variability in areas with low NDVI in April, the mean population density is not strongly related to the mean vegetation productivity (NDVI) (Kausrud et al. 2007). Though precipitation and temperature show predominant positive effects on NDVI in the current or in the following year, associations between rodent abundance and NDVI are relatively weak.

Besides, small mammals are likely to be highly sensitive to changes in plant quality as well. Studies have shown that warming reduces plant quality in this ecoregion (Klein et al. 2007). Thus, temperature and precipitation may have the potential confounding effect on plant quality. There is high potential for shifts in species composition in vegetation, which can have an influence on the composition of the rodent community. But, we do not have data on plant composition in many spatial study sites, so we cannot assess this plant-shift effect.

Based on results of the functional group, NDVI showed significant negative effects on nonhibernating species, nocturnal species, and granivorous population in the current year, but positive effect on all of them in the following year (Figs. 5*a*–5*f*). The negative effect of NDVI on several rodent species may be due to improvements in vegetation cover and may not be due to additional food in the current year. Vegetation cover or height may play an important role in predator avoidance of many rodent species. High vegetation prohibits movement and antipredation efficiency of small rodents in the grassland (Arenz and Leger 1999). High or dense vegetation may suppress population growth of rodent species requiring low and sparse plant cover in grassland or alpine meadow ecosystems (Zhong et al. 1999; Wang and Zhong 2006). However, abundant vegetation may provide more food sources for rodent to store, benefiting the population of the following year by promoting the overwintering survival of the population, which may explain why NDVI showed positive effects on several species in the following year (Figs. 5*a*–5*f*).

NDVI has been used as an index of food or vegetation resources (see Kausrud et al. 2007). In our study, we found a weak positive association between grass production and NDVI in four locations, suggesting that NDVI may be used to explain more than just food abundances. Our study suggests that NDVI acts more as an index of vegetation than as an index of food resources in the current year. High NDVI apparently corresponds with reduced abundance of several rodent species. However, NDVI is more of an index of food resources (i.e., more grass seeds or grass for overwintering period) than of vegetation resources because it has a positive effect on the abundance of several species in the following year.

Bottom-up links

The ENSO-driven precipitation related bottom-up model has been supported by several short-term studies, but not by long-term studies (Ostfeld and Keesing 2000; Brown and Ernest 2002). Our studies reveal one obvious bottom-up trophic chain from SOI, precipitation, NDVI, to rodent abundance (Figs. 6*a*, 6*b*). The one path was from precipitation to NDVI, and then to rodent abundance (Fig. 6*a*). It is notable that the positive effect of SOI on the abundance of rodent population in the following year is through precipitation and NDVI. These results support our second hypothesis that the bottom-up effect of SOI on climate, vegetation, and rodent abundance may exist in this region for some sympatric species.

The direct associations between rodent abundance and SOI are very weak in both the current and the following year. We only found that SOI had a significant positive effect on rodent abundances of two species and a negative effect on on rodent abundances of two species in the current year, whereas SOI had a positive effect on one species and a negative effect one one species in the following year (Fig. 4*d*). A few prior studies also reported that significant associations exist between rodent abundances and ENSO (e.g., Zhang et al. 2003). ENSO-linked precipitation has been found to increase the abundance of several rodent species (e.g., Jaksic et al. 1997; Lima et al. 1999*a*, 1999*b*), which is supported by our observations (P2 in Fig. 6*a*). However, in an Amazonian savanna, densities of hairy-tailed bolo mouse (*Necromys lasiurus* (Lund, 1841)) were positively associated with SOI and the extent of fire in the region, not to rainfall (Magnusson et al. 2010). To reveal the bottom-up effect of ENSO using long-term data, it may be essential to study the association of ENSO with rodent abundances at the regional scale and at the rodent community scale.

The ENSO-linked temperature bottom-up model has not been tested before. Magnusson et al. (2010) suggest that changes in temperature caused by El Niño periods may have drastic consequences on population fluctuations of hairy-tailed bolo mouse. In this study, we showed three obvious ENSO-linked temperature bottom-up chains through or not through NDVI (T2, T3, and T4 in Fig. 6*b*). For paths not through NDVI, rodent abundance is positively associated with SOI of the previous year (T3 in Fig. 6*b*), but negatively associated with the SOI of the current year (T2 in Fig. 6*b*). This is probably because temperature is low in high SOI years, whereas the temperature is high in the following year of high SOI. High temperature (especially in the spring and winter seasons) promotes breeding and survival. For paths through NDVI, SOI showed a negative effect on rodents with a 2-year time lag (T3 and T4 in Fig. 6*b*). This is because high temperatures decrease NDVI in the current year, whereas they increase NDVI, which decreases the rodent abundance, in the following year. Tang and Chen (2003) showed that an increase in winter temperature was an important factor affecting yearly mean NDVI in northeastern China. High NDVI often stops population growth of many rodent species, but increases the population growth during the following year. Thus, the 1-year-time-lag effects of SOI on rodent abundances are positive through temperature.

ENSO generally appears irregularly every 2–7 years (Zhang et al. 2003). Peak or trough SOI year often correspond with La Niña or El Niño years. According to our models in Figs. 6*a* and 6*b*, ENSO should affect population abundances of many sympatric rodent species simultaneously. As shown in Fig. 6*b*, in SOI-peak years or La Niña years, rodent abundances of many species tend to be low in the current year through T2, to be high in the following year through P2 and T3, to be low 2 years later through T4. In other words, those associations were reversed in SOI-trough years or El Niño years. Thus, we conclude that ENSO-driven climate or vegetation tend to increase rodent abundance of many sympatric species in grasslands of Inner Mongolia in El Niño years, or 1 year after La Niña years, or 2 years after El Niño years.

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