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Temporal changes in species composition affect a ubiquitous species' use of habitat patches

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Abstract. Across landscapes, shifts in species composition often co-occur with shifts in structural or abiotic habitat features, making it difficult to disentangle the role of competitors and environment on assessments of patch quality. Using over two decades of rodent community data from a long-term experiment, we show that a small, ubiquitous granivore (*Chaetodipus penicillatus*) shifted its use of different experimental treatments with the establishment of a novel competitor, *C. baileyi*. Shifts in residency, probability of movement between patches, and the arrival of new individuals in patches altered which treatment supported the highest abundances of *C. penicillatus*. Our results suggest that the establishment of a new species worsened the quality of the originally preferred treatment, likely by impacting resource availability. Paradoxically, the presence of the new species also increased *C. penicillatus'* use of the less preferred treatment, potentially through shifts in the competitive network on those plots.

Key words: habitat selection; metacommunity; patch preference; patch quality; species composition; species interactions.

INTRODUCTION

Species often exist in landscapes consisting of a patchwork of habitats, some of which are conducive to a species' survival and reproduction and others that are less suitable. Building upon intraspecific habitat selection (Fretwell and Lucas 1969) and optimal patch use theory (Charnov 1976, Brown 1988), numerous studies have shown that interspecific habitat selection can act as a potential mechanism of species coexistence (e.g., Grant 1971, Schoener 1974, Morris 1989, 2003). Landscape heterogeneity creates niche opportunities (Comins and Noble 1985) while variability in patch connectivity supports scenarios where populations can be rescued from extinction by dispersal (Brown and Kodric-Brown 1977) or where species can find isolated refuges when they would otherwise be driven extinct (Sedell et al. 1990). However, changes in patch conditions also take place through time (Ernest et al. 2008), resulting in patches

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that vary in their suitability for a species as conditions change. Despite the fact that population dynamics and regional processes (i.e., dispersal, colonization, extinction) are inherently both spatial and temporal, temporal variation in patches is rarely incorporated into studies on patch preference.

While many studies on habitat selection focus on differences between patches in structural habitat (e.g., vegetation structure) or abiotic conditions (e.g., temperature, soil conditions), species density and composition can also affect patch preference (Grant 1971, Danielson and Gaines 1987, Morris 1989, Abramsky et al. 1992). Understanding a species' response to species composition is complicated because shifts in species composition often co-occur across landscapes with shifts in structural or abiotic habitat features (Whittaker 1967, Tews et al. 2004). Species may be less abundant or absent from certain patches, but whether that absence is due to the patch having an incompatible environment, the isolation of the patch from other patches, the presence of superior competitors, or a combination of any of the above reasons is often unclear. Thus, in determining how a species uses the landscape through time, it is often difficult to disentangle the roles of structural or abiotic habitat qualities from species interactions (Grant 1971, Kraft et al. 2015).

In this study, we use time-series data from a desert rodent community in southeastern Arizona, USA, to show how both spatial and temporal variation in abundances and species composition in patches affect species and their use of habitat patches. Our system has experimentally created patches in the form of control plots (all rodents have access) and manipulated plots in which kangaroo rats, the behaviorally dominant genus in the system, are selectively excluded. Recent studies have shown only minimal impacts of the treatment on the plant community (Supp et al. 2012); thus, this system creates a landscape with patches of differing quality due primarily to differences in rodent species composition.

In the mid-1990s, a species of large pocket mouse (*Chaetodipus baileyi*) colonized and exhibited a preference for kangaroo rat exclosures. Here, we ask whether the patch preference of a small, subdominant pocket mouse, *C. penicillatus*, was impacted by the arrival of the larger pocket mouse across this landscape of patches with and without kangaroo rats. Because congeners are expected to compete more strongly due to their shared evolutionary history, we hypothesized that (1) *C. penicillatus'* use of treatment would change with the establishment of *C. baileyi*, (2) the magnitude of change would be correlated with *C. baileyi* abundance, and (3) *C. penicillatus* residency, probability of moving between treatments, and recruitment of new individuals would show corresponding changes with the establishment of *C. baileyi*.

METHODS

Study system and data

We used a 22-yr time series (1988–2010) of capture–mark–recapture rodent data collected at a long-term experimental study called the Portal Project (Brown 1998) to assess how habitat use of *C. penicillatus* over time was impacted by the arrival of a novel competitor, *C. baileyi*. The Portal Project is located in the Chihuahuan desert near Portal, Arizona, USA, on unceded land of the Chiricahua Apache currently under jurisdiction of the U.S. Bureau of Land Management. The site consists of 24 50 × 50 m fenced plots with three treatments. In control plots ($n = 10$), holes cut in the fence are large enough to allow all rodent species access while full rodent removal plots ($n = 6$) have no holes. Kangaroo rat exclosures ($n = 8$) have small holes in the fences that allow passage of all rodents except for kangaroo rats (*Dipodomys* genus), which are behaviorally dominant in the system (Brown and Heske 1990).

In this study, we primarily use data from 18 plots—controls and kangaroo rat exclosures—though we include data from full removals in calculations of residency and probability of movement between treatments to increase estimate accuracy (Appendix S1). Each plot consists of 49 evenly-spaced, permanent trapping stations in a 7 × 7 grid. Rodent abundance and

composition data are collected monthly using Sherman live traps (Ernest et al. 2018). We identify trapped individuals to species and give each rodent an individualizing marker (previously toe and ear tags, now exclusively passive integrated transponder [PIT] tags).

Over the 22 yr used in this study, many species exhibit major shifts in abundances, driven by regional process (e.g., landscape shifts and climate events) that impacted all treatment plots (Brown 1998). *C. penicillatus*, which was present from the beginning of the study, experienced a population increase across the site. *C. baileyi* was first captured in 1995; it became a dominant species in the system but crashed in the late 2000s and did not rebound (see Appendix S1 for details; Fig. 1a). Due to these dynamics, we focus primarily on analyses comparing how treatments change relative to each other over time. We also only use data through 2010 because this is when *C. baileyi* was no longer dominant in the system, but using data through 2014 produced qualitatively similar results (Appendix S1: Figs. S1–S3).

Patch use of C. penicillatus in response to C. baileyi abundance

We assessed changes in relative abundance of *C. penicillatus* between control plots and kangaroo rat exclosures by fitting a linear model along the 1:1 line of mean *C. penicillatus* per plot by year in kangaroo rat exclosures against control plots. We then fit a linear generalized least squares model (*nlme*; Pinheiro et al. 2018) of mean *C. baileyi* per plot by year against the resulting residuals from the previous model, accounting for temporal autocorrelation (see Appendix S1), to evaluate how *C. penicillatus'* habitat use shifted with increases in *C. baileyi* abundance.

Population-level metrics of C. penicillatus

For *C. penicillatus* in each treatment, we calculated apparent survival, transition probability, and the average number of new individuals per treatment. Both survival and transition probability were estimated through a multistate capture–mark–recapture model using the RMark package, an R interface for the MARK software (White and Burnham 1999, Laake 2013). Different strata represented treatment types, and each time step was a trapping period. We designated each time period as being either before or after the establishment of *C. baileyi*; the first trapping period in which *C. baileyi* was caught in all eight kangaroo rat exclosures (July 1997) was used as the differentiating time point. We assumed that recapture probabilities were equal between the treatments. Our data do not allow for differentiation between permanent emigration and death, so these two processes are not differentiated in our survival estimates; we believe that any differences in apparent survival are driven primarily by emigration and, therefore, will hereafter refer to this metric as residency. We used Program
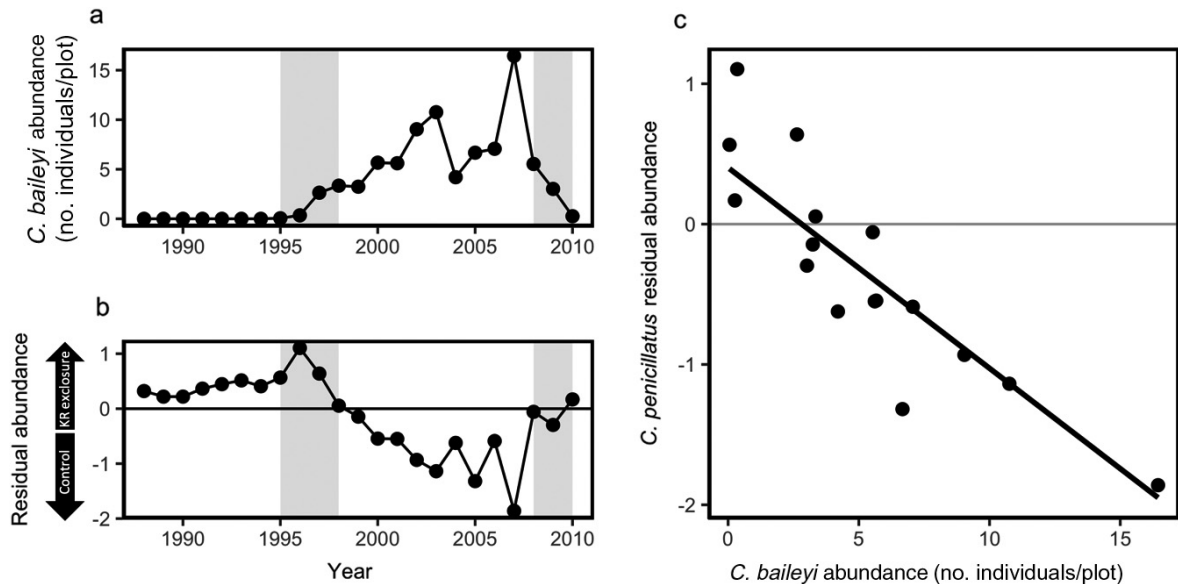
FIG. 1. Relationship between *Chaetodipus penicillatus* abundances on treatments and *Chaetodipus baileyi* abundance. (a) Mean *C. baileyi* abundance through time. (b) Residual mean *C. penicillatus* abundance (individuals per plot) through time. The zero line indicates equal numbers of *C. penicillatus* on both treatments. Points are residuals from a linear model run against a 1:1 line of mean *C. penicillatus* abundance on kangaroo rat (KR) exclosures against controls. Points above the zero line (positive residuals) indicate higher mean *C. penicillatus* abundance on kangaroo rat exclosures; points below the line (negative residuals) indicate higher mean *C. penicillatus* on controls. In panels a and b, gray bars indicate the colonization period (1995–1998) and subsequent decline (2008–2010) of *C. baileyi*. (c) Generalized least squares regression of *C. penicillatus* differences from equal (*y*-axis from panel a) against mean *C. baileyi* density per year (*y*-axis from panel b). As mean *C. baileyi* abundances increase, the mean abundance of *C. penicillatus* shifts from more individuals on kangaroo rat exclosures to more on controls.

CONTRAST, a program designed specifically for comparing survival estimates (Hines and Sauer 1989), to run chi-squared tests to determine the significance of differences in residency and transition probabilities between *C. baileyi* establishment and treatments.

We calculated the number of new *C. penicillatus* individuals, defined as individuals caught and given identification tags for the first time, in each treatment. Using mean new *C. penicillatus* individuals per plot by year, we used a linear mixed effects model (*nlme*; Pinheiro et al. 2018) to assess the interaction between treatments and *C. baileyi* establishment.

System-level aspects of patch preference

Changes in species composition can substantially impact energy use in a system (Ernest and Brown 2001). To determine how this aspect of ecosystem functioning might have contributed to *C. penicillatus* use of patches through time, we calculated the ratio of total energy use by rodents per year between the kangaroo rat exclosures and controls (*portalr*; Yenni et al. 2018).

Analyses

Analyses were performed using R 3.5.0 (R Core Team 2018). Data and code are available online (see *Data Availability*).

RESULTS

Patch use of C. penicillatus in response to C. baileyi abundance

After its arrival in 1995, *C. baileyi* increased in abundance until the late 2000s (Fig. 1a) and was found far more frequently on the kangaroo rat exclosures than the control plots (Appendix S1: Fig. S4). *C. penicillatus'* use of the two treatment types also shifted through time (Fig. 1b). *C. penicillatus* had a higher average abundance in the kangaroo rat exclosures before *C. baileyi* arrived; during the time *C. baileyi* was established, however, *C. penicillatus* had a higher average abundance on controls. *C. penicillatus*'s preference for control plots increased with increases in *C. baileyi* abundance (Fig. 1c; $y = -0.14x + 0.40$, df = 16, RSE = 0.40, $P < 0.001$).

Population-level metrics of C. penicillatus

Residency of *C. penicillatus* depended on treatment and *C. baileyi* status ($\chi^2 = 10.72$, df = 3, $P = 0.01$). Before *C. baileyi* colonized the site, residency for *C. penicillatus* was significantly higher on kangaroo rat exclosures than on controls (Fig. 2a). This difference completely disappeared after *C. baileyi* established, at which point residency became statistically indistinguishable between treatments.
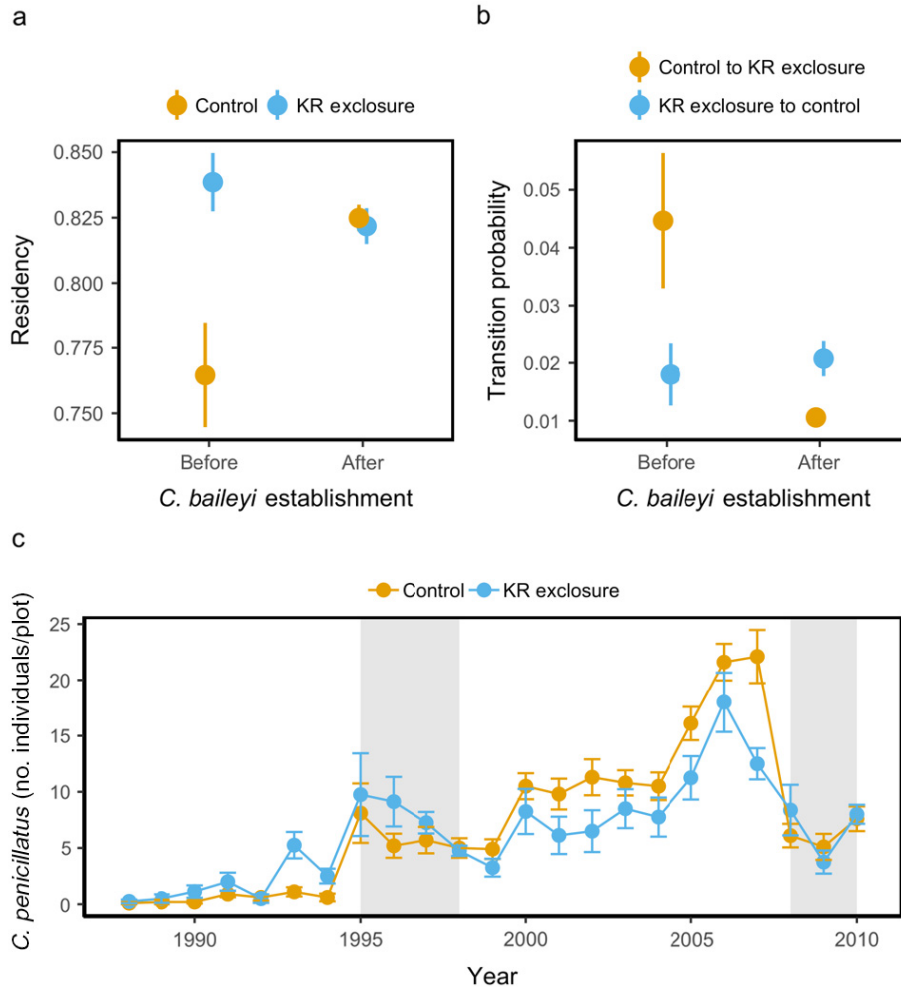
Fig. 2.   Population-level metrics of *Chaetodipus penicillatus* by treatment type. (a) Residency of *C. penicillatus* by treatment and *C. baileyi* establishment in the system. (b) Probability of *C. penicillatus* individuals moving from one treatment to the other, also based on *C. baileyi* establishment. (c) Mean abundance of new *C. penicillatus* individuals through time. Gray bars indicate the period of establishment (1995–1998) and subsequent decline (2008–2010) of *C. baileyi.*

The transition probability of *C. penicillatus* also depended on treatment and *C. baileyi* status ($\chi^2 = 16.53$, df = 3, $P < 0.001$). The probability of a *C. penicillatus* individual moving from a kangaroo rat exclosure to a control plot was low, regardless of *C. baileyi* establishment (Fig. 2b). When a *C. penicillatus* individual moved before *C. baileyi*'s arrival, it was more likely to move from a control plot to a kangaroo rat exclosure. Afterwards, however, the probability of a *C. penicillatus* individual moving from a control plot to a kangaroo rat exclosure was not only significantly lower than before *C. baileyi* establishment but also significantly lower than the probability of movement in the other direction (Fig. 2b).

The significant interaction between treatments and *C. baileyi* establishment on new (i.e., untagged) *C. penicillatus* individuals also supports changes in patch preference (Fig. 2c). Before the arrival of *C. baileyi*, kangaroo rat exclosures had significantly higher numbers of new individuals appearing ($F_{1,389} = 24.87$, $P < 0.001$); after *C. baileyi* established in the system, new individuals were consistently found on control plots in higher average numbers until the period of *C. baileyi* decline in the late 2000s.

System-level aspects of patch preference

Prior to *C. baileyi* fully establishing in the system, the energy use on kangaroo rat exclosures was only a fraction of that on control plots (Fig. 3). With the arrival of *C. baileyi*, however, the average energy used on kangaroo rat exclosures reached over 80% of the energy used on control plots, even with *C. penicillatus* individuals moving to the controls.
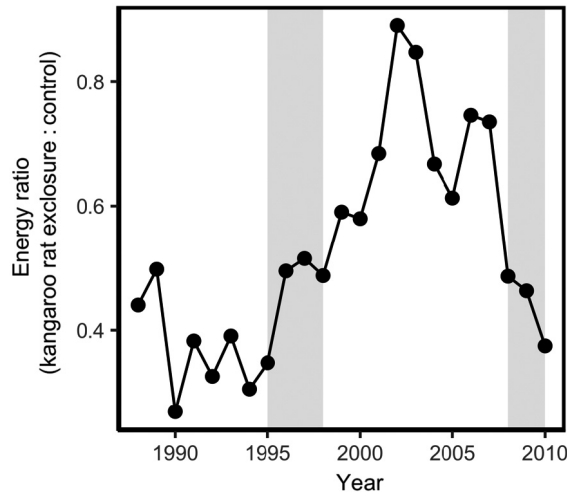
Fig. 3. Ratio of total rodent energy in kangaroo rat exclosures to controls though time. Gray bars indicate establishment (1995–1998) and subsequent decline (2008–2010) of *Chaetodipus baileyi.*

Discussion

Our results suggest that the arrival of a congener changed perceptions of patch quality for one of the abundant rodent species in our ecosystem, *C. penicillatus.* Changes in patch use can be driven by perceived declines in quality of an individual's current patch or perceived increases in quality of another patch. Increases in new *C. penicillatus* individuals on the controls and declines in residency on kangaroo rat exclosures suggest that both of these mechanisms may have occurred with the arrival of *C. baileyi,* ultimately shifting patch use by *C. penicillatus.*

Declines in the perceived quality of kangaroo rat exclosures, as evidenced by declines in *C. penicillatus* residency, could have been caused by changes in resource availability after the arrival of *C. baileyi* (Fig. 1). Before *C. baileyi* established, rodent energy use on the kangaroo rat exclosures was never more than half of that found in controls (Fig. 3). With the preferential establishment of *C. baileyi* on the kangaroo rat exclosures, however, the energy ratio between the exclosure and control plots increased considerably. If patches have roughly the same amount of resources, patches with lower rates of energy use should have more resources that are not being fully exploited (MacArthur and Pianka 1966). Because the two species are congeners, niche similarities due to a shared evolutionary history may have increased the possibility of substantive overlap in their resource preferences. Thus, the colonization of *C. baileyi* on kangaroo rat exclosures in concert with increased numbers of *C. penicillatus* may have had an effect on rates of resource use on those plots, thus altering foraging and fitness expectations for *C. penicillatus.* This could explain the corresponding declines in residency for

C. penicillatus (Fig. 2a) on kangaroo rat exclosures. However, while this explains why kangaroo rat exclosures may have been perceived as worse environments after the arrival of *C. baileyi,* this does not explain why controls were suddenly able to support higher numbers of *C. penicillatus.*

While *C. penicillatus* increased in abundance on both plot types after the arrival of *C. baileyi,* its greater increase on controls than on kangaroo rat exclosures suggests that *C. penicillatus* perceived relative improvements in the quality of those patches. Since *C. penicillatus'* residency and transition probabilities were similar between treatments after the arrival of *C. baileyi,* increases in abundance appear to be due to higher numbers of new individuals arriving on controls (Fig. 2c). These new individuals could be due to increases in birth rates, immigration rates, or juvenile survivorship or decreases in juvenile dispersal rates, but we unfortunately do not have the data to discern the source of the new individuals.

Higher immigration rates into some patches over others can reflect differences in distances to source populations (i.e., mass effects or source–sink dynamics; Holt 1985, Pulliam 1988) or active decisions by individuals based on their expected fitness or resource intake rate in a patch, which is indicative of density-dependent habitat selection (e.g., Grant 1971, Brown and Munger 1985, Morris 1987, Abramsky et al. 1992, Morris and MacEachern 2010). Because our patches are interspersed in a matrix that is suitable habitat for *C. penicillatus,* all patches should be equidistant from a *C. penicillatus* source population. We also see no reason *C. penicillatus* should perceive control plots as improved based on abiotic conditions, habitat structure, or resource availability. At the scale of the site, all plots experience the same weather and our measure of rodent energy use suggests that resource availability on the two plot types is very similar (Fig. 3). Furthermore, while the site has experienced vegetation changes (Brown 1998), there is no indication that this has differed by treatment (Ernest 2001).

The higher abundance of *C. penicillatus* on controls relative to kangaroo rat exclosures after the establishment of *C. baileyi* presents an interesting dilemma. If there were ecological opportunities (e.g., resource availability, territory, etc.) for *C. penicillatus* in the controls after *C. bailey* become established on the kangaroo rat exclosures, why was *C. penicillatus* not utilizing them previously? After *C. baileyi* established in the system, controls tended to have a higher abundance of competitors (*Dipodomys* spp. and *C. baileyi*) than kangaroo rat exclosures ($P < 0.001$, Appendix S1: Fig. S5). Resource competitors that would be unable to coexist if they interacted only with each other can actually benefit each other when they share a common competitor (Levine 1976, Stone and Roberts 1991, Allesina and Levine 2011). At our site, while *C. baileyi* showed a preference for kangaroo rat exclosures over controls, they were

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still present on controls in considerable numbers (Appendix S1: Fig. S4; Thibault and Brown 2008). Both natural history and observed dynamics at our site have shown that *C. baileyi* also competes with smaller kangaroo rats such as *D. merriami* and *D. ordii* (Thibault and Brown 2008), probably due to its similar size and dietary overlap (Reichman 1975). Thus, in this "enemy of my enemy is my friend" scenario, the shifts in the competitive network caused by adding *C. baileyi* to controls may have altered the interspecific density dependence experienced by *C. penicillatus* in such a way that it paradoxically resulted in higher vital rates, more new individuals, and higher abundances for *C. penicillatus* on controls.

Species' perceptions of patch quality can vary depending on a variety of factors, such as resource availability (MacArthur and Pianka 1966), biotic interactions (Grant 1971, Abramsky et al. 1992), and other habitat properties (Brown 1988). Changes in patch quality and selection can also affect communities and metacommunities through landscape-level processes (e.g., dispersal, colonization/extinction; Pulliam and Danielson 1991, Resetarits and Silberbush 2016). In this study, we used an experimental long-term study to show how species colonization and resulting shifts in species composition can affect a species' perception of patch quality and patch preference. This is not to suggest that changes in structural habitat or abiotic factors do not impact patch preference; much work in landscape ecology and metacommunity theory has shown that they can (Leibold and Chase 2018); rather, we use time series data and experimentally manipulated patches to tease apart the effects of species composition and abundance from those of structural or abiotic habitat differences, changes that frequently occur together spatially. This method allows us to still assess habitat selection and space use—key aspects of metacommunity theory—while also allowing changes through time to inform observations. We suggest that time is a key component in any holistic study of patch preference in community structure and metacommunity dynamics.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2869/suppinfo

Data Availability

Data and code are available on Zenodo: https://doi.org/10.5281/zenodo.3371466

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