

SOURCE–SINK DYNAMICS IN A TEMPORALLY HETEROGENEOUS ENVIRONMENT

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Abstract. In traditional source–sink models, vital rates and movement probabilities are assumed to be temporally homogeneous. Numerous studies, however, have demonstrated that temporal heterogeneity is the rule rather than the exception in natural systems. A case of particular interest is an expanding and contracting population where determination of source and sink populations is dependent on the timing and duration at which population growth rates are measured. Thus, ecologists have been perplexed about what is the proper scale to test for source–sink dynamics. In this study, I present a temporally variable source–sink dynamic driven by flooding disturbance. I measured population growth rates of an herbivorous neotropical rolled-leaf beetle, *Cephaloleia fenestrata* (Chrysomelidae), at different temporal scales in this expanding and contracting population. I demonstrate that flooding created a strong sink, but the system lacked source–sink dynamics during nonflood periods. The sink is caused by a flood-related sevenfold decrease in survival probability. There was no evidence for effects of flooding on recruitment. Migration was directional from the upland to the flood zone habitat, supporting the conclusion that the population in the flood zone is a sink. A Monte Carlo simulation demonstrated that whether the population in the flood zone is a sink, and the intensity of the sink, ultimately depend on the flooding frequency. Given an observed flood frequency of approximately once per year, the flood zone population was determined to be a long-term sink. This study provides evidence of high temporal variability resulting in fluctuations in and out of a source–sink dynamic and implicates a causal factor (increased mortality due to flooding). These results illustrate the importance of considering temporal variability in source–sink dynamics, and in choosing the proper temporal scale at which to test for source–sink dynamics.

Key words: *Cephaloleia fenestrata*; dispersal; disturbance; flooding; mark–recapture; *Pleio-stachya pruinosa*; source–sink dynamics; survival; temporal heterogeneity.

INTRODUCTION

Classic source–sink dynamics occur in spatially heterogeneous, but temporally constant, environments (Pulliam 1988). Numerous studies, however, have demonstrated that temporal heterogeneity is the rule rather than the exception in natural systems. Temporal heterogeneity takes a number of forms including seasonality (Andrewartha and Birch 1954), year-to-year environmental variation (Andrewartha and Birch 1954), El Niño events (Schreiber and Schreiber 1984), climate change (Glynn 1991), and disturbances (Connell 1978). Determination of source–sink dynamics requires calculating premigration population growth rates (λ), where $\lambda > 1$ indicates a source and $\lambda < 1$ indicates a sink population. Ecologists have been perplexed about what is the proper scale to detect source–sink dynamics because, in temporally variable systems, determining source and sink habitat is dependent on the timing and duration at which population growth rates are mea-

ured. This dilemma is clear in the case of an expanding and contracting population in which λ s may fluctuate above and below unity. Herein, I measure λ s of an expanding and contracting population of a neotropical rolled-leaf beetle, *Cephaloleia fenestrata* Weise (Chrysomelidae), at multiple temporal scales. Population contractions are associated with flood events, while population expansions are associated with nonflood periods. I distinguish between short-term (25 d) and long-term (1 yr and indefinite) source–sink dynamics in the system and demonstrate that understanding temporal variation in population demography is crucial to determining long-term source–sink dynamics.

In a source habitat, reproductive output exceeds mortality, while in a sink habitat mortality exceeds reproductive output and population density is maintained by net migration from a source habitat. Herein, I will use “sink” as a general term referring to both true sinks and pseudosinks. I define a true sink as one that, without immigration, has an equilibrium density of zero. A pseudosink is a viable population, but where deaths exceed births and immigrants exceed emigrants, thus, inflating population size above a nonzero equilibrium which would be realized if the population was isolated (Watkinson and Sutherland 1995). Distinguishing between the two requires experimental manipulation or

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information on density dependence in vital parameters. Because I have neither, I will use the general term "sink" hereafter.

There are several potential consequences of temporal variation in source–sink dynamics. An extreme example is a source–sink inversion, where a source switches to a sink and vice versa. Theoretical pursuits and anecdotal evidence suggest that such an inversion may occur on an evolutionary time scale, where an organism's adaptation to habitat of a sink population turns it into a source (Dias 1996). Source–sink inversions could hypothetically occur on an ecological time scale as well, caused by relatively rapid (i.e., seasonal) temporal variation in environmental factors. In another example, variation in environmental factors was shown to inflate the effects of sources on sinks, raising population sizes in sinks higher than if there were no variation. This has implications on community structure, potentially increasing the population size (thus, the community-wide impact) of a species that otherwise would have been rare or excluded (Holt et al. 2003). Also, numerous studies have demonstrated that variability, especially in conjunction with spatial synchrony (i.e., the Moran effect), can reduce population persistence times. Thus, studies that discount temporal variation in source–sink dynamics risk missing the complex dynamics of a system and its effects on community structure.

There is a paucity of empirical studies on temporal variation in source–sink dynamics, probably because of the difficulty in identifying the cause of temporal change and separating its effect from demographic variation. Boughton (1999), however, found a decline in quality of butterfly habitat over time, causing the population in the habitat to shift from a source to a sink. In a theoretical framework, Walters (2001) demonstrated how shifting patterns of resource productivity could alter the source–sink dynamics of deer in the north-eastern United States.

Stochastic flooding of the Puerto Viejo River in Costa Rica completely inundated a subset of patches of a prayer plant, *Pleiostachya pruinosa* (Marantaceae), the host plant of *C. fenestrata*. In this study, I estimate survival and movement probabilities and per capita recruitment of *C. fenestrata* during both flood and non-flood periods. I ask the following questions. (1) Does flooding induce short- and long-term source–sink dynamics in this system? (2) If so, is this dynamic caused by flood-induced decreases in survival and recruitment? (3) Does observed directional movement of *C. fenestrata* support the presence of a source–sink dynamic? (4) Are the observed effects of flooding on population dynamics of *C. fenestrata* consistent among patches in the study area?

METHODS

Study site and study system

This study was carried out at La Selva Biological Station in the lowland tropical wet forest of Costa Rica

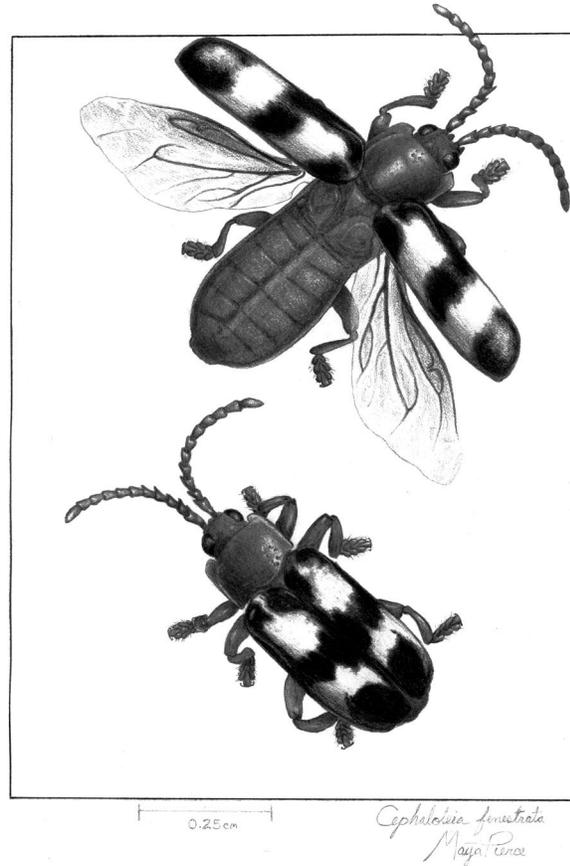


PLATE 1. *Cephaloleia fenestrata* Weise (Hispininae: Chrysomelidae: Coloptera). Illustration by Maya Pierce.

(10°26' N, 83°59' W). La Selva is a 1500-ha reserve on the Caribbean slope contiguous with Braulio Carrillo National Park to the south. Mean (± 1 SD) yearly rainfall at La Selva was 4242 ± 785 mm from 1958 to 2002 (La Selva Biological Station, meteorological data). Yearly rainfall during this study, 4152 mm (1999), 4465 mm (2000), and 5163 mm (2001), was within the normal range (0.11, 0.28, and 1.17 standard deviations from the mean, respectively).

Cephaloleia fenestrata (see Plate 1) is a member of the guild of rolled-leaf hispinines that feed on plants in the order Zingiberales and family Arecaceae (Staines 1996). Rolled-leaf beetles are so named because they live and feed primarily in the immature rolled leaves of their host plants. *C. fenestrata* is a specialist herbivore, spending its entire lifetime on *P. pruinosa* plants. Adults feed primarily on the tender tissue in rolled leaves. Females lay eggs and larvae feed and pupate in the concavity of the leaf petioles. Larval dispersal is minimal, probably limited to plants of which the leaves are touching (Strong 1977; D. Johnson, *personal observation*). Generation time of *C. fenestrata* is ~ 6 mo (Johnson 2003).

P. pruinosa grows in discrete patches ranging from one to 735 ramets in and near the floodplain of the Puerto Viejo River at La Selva Biological Station. I defined a patch as a group of *P. pruinosa* that are at least 17 m away from the nearest conspecifics (a distance determined in a concurrent metapopulation study so interpatch migration was below 20% [Johnson 2003]).

Flood frequency

The probability of a flood event in any 25-d period was estimated based on three years of data from December 1998 to October 2001 (D. Johnson, *unpublished data*). The 95% confidence interval was estimated based on the binomial distribution (Zar 1999). A definition of the flood zone that is most relevant to this study is an area covered by at least 1.5 m of water. This is deep enough to cover rolled leaves and leaf petioles, and thus, to inundate adults and immature stages.

Adult population dynamics

To detect the effects of flooding on adult *C. fenestrata* survival and movement, I conducted a mark-recapture study from January 1999 to January 2000 with 14 sample periods ~25 d apart. The sample area consisted of 75 *P. pruinosa* patches distributed primarily along a 1.5-km stretch of the Puerto Viejo River. Plants in 17 of the 75 patches were located in the flood zone of the river.

During each sampling period, all of the 75 patches were censused. *C. fenestrata* were removed from all rolled leaves with a diameter of 2 cm or greater at the apex. Each adult beetle was given a unique mark with a series of gentle punctures of the elytra. This marking method does not appear to harm the beetles (Unruh and Chauvin 1993; D. Johnson, *personal observation*). The leaves were carefully rerolled, and the beetles were released into the same rolled leaves from which they were removed.

To estimate parameters for survival, capture, and movement probability, analyses were run in the program MARK, version 1.8 (White and Burnham 1999). I estimated probabilities of survival (S), capture (p), and movement between the two strata (ψ ; flood zone and upland) from a multistrata model. The product of survival and movement probabilities is represented by ϕ (Fig. 1). For example, the probability of a beetle in the upland (u) at time t being alive in the flood zone (f) at time $t + 1$ is expressed as $\phi_{uf} = S_u \psi_{uf}$. This model assumes that the survival of a beetle that moves between strata is the same as that of a beetle remaining in the donor stratum. Capture probability is defined as the probability of capturing an organism conditional on it being present in that stratum during that sample period.

I derived the most parsimonious two-stratum model by starting with the simplest model. The simplest mod-

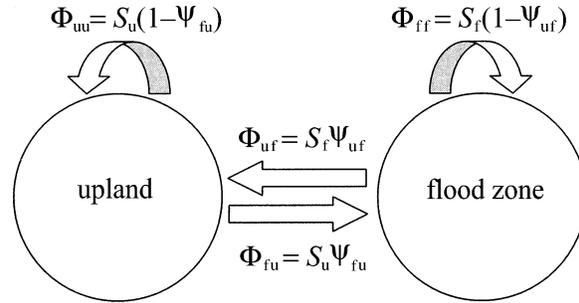


FIG. 1. Graphical illustration of a two-stratum mark-recapture model. The transition probability ϕ is the product of the survival probability S and the movement (or lack of movement) probability (ψ is the probability). Subscripts u and f refer to the upland and flood zone, respectively.

el is denoted $S(\cdot)p(\cdot)\psi(\cdot)$ in which the population pattern is explained by the three constant parameters: survival, recapture, and movement probabilities. A “.” indicates that the parameter is constant in all factor dimensions (time [t], habitat [h], and flood [f]). Then, in a forward step-wise fashion (i.e., t , $t + h$, $t + h + f$) for each of these parameters, I added functional dependency on the three factors. For example, the model described by $S(t)p(\cdot)\psi(h,f)$ includes time-dependent survival, constant capture probability, and movement probability dependent upon both habitat and flood status. The model with the lowest Akaike's Information Criterion value (AIC, Akaike 1973) is the best fit model. Herein I report the Δ AIC value, which is the difference between the lowest AIC value and the AIC value of the generalized model.

Recruitment

I surveyed immature stages of *C. fenestrata* on eight occasions at three-month intervals from March 1999 to December 2000. Immature stages (eggs, larvae, and pupae) were surveyed in the concavity of the leaf petioles of ramets in each patch. Mean and standard deviations of the stage-specific ratios (eggs:adult, larvae:eggs, pupae:larvae, and adults:pupae) were calculated to detect habitat specific differences in egg production and transition probabilities (an indicator of stage-specific survival probabilities).

The effects of flooding on larval *C. fenestrata* were investigated with a simulated flooding experiment. Flooding of *P. pruinosa* was simulated in a 1.5 m deep tub. Unchlorinated well water was pumped into the tub such that the water level rose at ~1 m/h until full. There were four treatments: 6 h, 12 h, 24 h, and a control (not flooded). Twelve to 14 potted *P. pruinosa* plants were used per treatment, each with one to 13 larvae.

Patch-level analyses

The source-sink analysis described in the next subsection treats the flood zone and upland each as one population. Each habitat, however, is composed of mul-

multiple patches (17 flood zone and 58 upland), both categories of which are distributed from one end of the somewhat linear study area to the other. Thus, each can be treated as an independent measure of the effects of flooding on population dynamics as compared to the other habitat. Numbers of adults and immatures in each patch were classified either as increasing, decreasing, or remaining the same following a flood. Fisher's exact test was used to test for significant differences in the numbers of increases and decreases between the upland and flood zone habitat concurrent with a flood.

Source–sink analysis

Following the birth-immigration-death-emigration (BIDE) model (Pulliam 1988), one must decouple local (recruitment and survival probability) and regional (immigration and emigration) sources to a population to detect source–sink dynamics. Herein, I first estimate habitat-specific population sizes and then decouple local and regional sources of these populations. Then I investigate source–sink dynamics in the system by calculating population growth rates with migration excluded from the estimations.

I estimated adult *C. fenestrata* abundance in habitat *i* at time *t* [$\hat{n}_i(t)$] by dividing the number of captures [$n_i(t)$] by the estimate of capture probability $\hat{p}_i(t)$,

$$\hat{n}_{\text{tot},i}(t) = \frac{n_i(t)}{\hat{p}_i(t)} \quad (1)$$

for each habitat: upland and flood zone. The total number of individuals in upland habitat *i* at time *t* can be separated into three categories (survivors, recruits, and immigrants from patch *j*):

$$n_{\text{tot},i} = n_{\text{surv},i}(t) + n_{\text{recr},i}(t) + m_{ij}(t). \quad (2)$$

The number of beetles moving from habitat *j* to *i* [$\hat{m}_{ij}(t)$] was estimated by multiplying the abundance [$\hat{n}_j(t-1)$] and probability of survival [$\hat{S}_j(t-1)$] in patch *j*, and movement probability from *j* to *i* [$\hat{\psi}_{ij}(t-1)$]:

$$m_{ij}(t) = \hat{n}_{\text{tot},j}(t-1)\hat{S}_j(t-1)\hat{\psi}_{ij}(t-1). \quad (3)$$

The number of survivors from time *t* – 1 to *t* in habitat *i* is estimated by the product of estimated population size at time *t* – 1 and the probability of surviving and staying within the habitat:

$$\hat{n}_{\text{surv},i}(t) = \hat{n}_{\text{tot},i}(t-1)\hat{\phi}_{ii}(t-1). \quad (4)$$

The number of recruits in habitat *i* at time *t* could then be estimated by subtracting the estimated number of survivors and immigrants from the total estimated in Eq. 1:

$$\hat{n}_{\text{recr},i}(t) = \hat{n}_{\text{tot},i}(t) - \hat{n}_{\text{surv},i}(t) - \hat{m}_{ij}(t). \quad (5)$$

The time-specific population growth rate in a given habitat was estimated by dividing the estimated number of beetles “produced” in the habitat (survivors, emi-

grants, and recruits) by the estimated number of beetles in the habitat during the previous time step:

$$\begin{aligned} \lambda_i(t) &= \frac{\hat{n}_{\text{surv},i}(t) + \hat{m}_{ji}(t) + \hat{n}_{\text{recr},i}(t)}{\hat{n}_{\text{tot},i}(t-1)} \\ &= \frac{\hat{n}_{\text{tot},i} + \hat{m}_{ji}(t) - \hat{m}_{ij}(t)}{\hat{n}_{\text{tot},i}(t-1)}. \end{aligned} \quad (6)$$

Variance for the numerator and denominator of Eq. 6 was calculated assuming a binomial distribution (Zar 1999). Variances of λ s were calculated based on the delta method for calculating the variance of a ratio (Lynch and Walsh 1998) assuming independence of the estimates of the numerator and denominator. Standard error in a binomial distribution is the square root of the variance (Zar 1999).

To estimate long-term population growth rates at different flooding probabilities, simulations were run where the flood probability in any 25-d period was varied from 0 to 0.3. For each of 1000 time steps, a flood or nonflood period was randomly selected based on the given flood probability. When a flood period was randomly sampled, the population growth rate from the corresponding flood period was selected. During a simulated nonflood period, the population growth rate was randomly selected from the empirical distribution of population growth rates during nonflood periods. The long-term population growth rate for each flood probability was estimated by calculating the geometric mean of the series of 1000 population growth rates.

RESULTS

Flood frequency

The Puerto Viejo River flooded in four out of 44 25-d periods over the course of this study: December 1998, November 1999, December 2000, and June 2001. The estimated probability of a flood event in a 25-d period is 0.091 with a 95% confidence interval of 0.025–0.216. The Puerto Viejo River flooded on two occasions that affected the mark–recapture study: in December 1998 (one month prior to initiation of the mark–recapture study), and in late November 1999 (between the 12th and 13th sampling periods).

Adult population dynamics

Over the year-long study, I uniquely marked 1199 adult beetles and recorded a total of 2019 captures. An average of 144 ± 31 (mean \pm 1 SD) adult beetles was captured per sampling period. In the upland, the numbers of captures ranged from 88 to 163 per sampling period. The numbers of captures in the flood zone ranged from 0 to 71. The upland contained an estimated 2508 ramets of *P. pruinosa* compared to 642 ramets in the flood zone. Thus, based on estimated capture probabilities (see next paragraph), there was a range of 0.109–0.203 captures per ramet in the upland (coeffi-

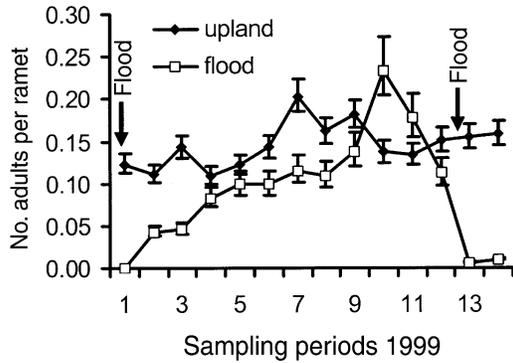


FIG. 2. *Cephaleia fenestrata* density (mean \pm 1 SE) in the upland and flood zone. A flood preceded the first and 13th sampling periods. Arrows indicate flood events.

cient of variation = 0.18) and 0.000 to 0.230 captures/ramet in the flood zone (coefficient of variation = 0.74; Fig. 2). Following the December 1998 flood, no adult beetles were captured in the flood zone. In the subsequent sample periods, density in the flood zone continued to increase and by the 10th sample period surpassed that of the upland (0.23 vs. 0.14 adult beetles per ramet, respectively). However, by the 12th sample period, density in the flood zone had dropped below that of the upland, and by the 13th sampling period, after the November 1999 flood, density in the flood zone dropped to fewer than 0.01 captures per ramet.

The most parsimonious multistrata model [$(S(t,f)p(h)\psi(h,f)$, 25 parameters] was a significantly better fit than the generalized model [$(S(t,h)p(t,h)\psi(t,h)$, 71 parameters] as indicated by a Δ AIC = 17.79. In the most parsimonious model, survival probability was significantly dependent on time (Likelihood ratio test, $\chi^2 = 40.241$, $df = 12$, $P = 0.0001$), but not on habitat, except for during the flood period. During the flood period, survival in the flood zone ($S = 0.11 \pm 0.07$) was reduced to 1/7 of the survival in the upland ($S = 0.76 \pm 0.09$; $\chi^2 = 23.34$, $df = 1$, $P < 0.0001$; Fig. 3). All

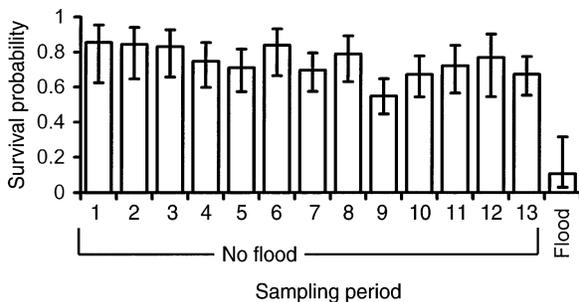


FIG. 3. Survival probability (mean \pm 1 SE) of *C. fenestrata* adults over 13 sampling periods in 1999. Sampling periods 1–11 and 13 represent the combined survival probability in the upland and flood zone. The sampling period labeled “12” is the survival probability in the upland only. The survival probability labeled “Flood” occurred in the flood zone during the 12th sampling period (when the habitat flooded).

TABLE 1. Pairwise likelihood ratio tests for significance of fits of the independent variables (time, habitat, and flood) to dependent variables (survival, capture probability, and movement) in the selected model.

Dependent variable	Independent variable	χ^2	df	P
Survival	time	40.24	12	0.0001
Survival	flood	23.34	1	<0.0001
Capture probability	habitat	17.35	1	<0.0001
Movement	habitat	8.38	1	0.0038
Movement	flood	6.37	1	0.0116

probabilities reported herein are for any 25-d period. Except in the flood zone during a flood, survival probability ranged from 0.55 to 0.86. Beetles were 1.7 times more likely to be captured in the flood zone than in the upland ($p_f = 0.47 \pm 0.03$; $p_u = 0.32 \pm 0.02$; $\chi^2 = 17.35$, $df = 1$, $P < 0.0001$). Movement was affected by habitat ($\psi_{uf} = 0.015 \pm 0.003$ and $\psi_{fu} = 0.05 \pm 0.02$ during nonflood periods; $\chi^2 = 8.38$, $df = 1$, $P = 0.0038$) and movement from the flood zone to the upland was affected by flooding (during a flood $\psi_{fu} = 0.76 \pm 0.23$; $\chi^2 = 6.37$, $df = 1$, $P = 0.01$). A summary of likelihood ratio statistics testing the significance of effects in the selected model is provided in Table 1.

Recruitment

The mean densities of immature stages were all higher in the upland than in the flood zone, while the coefficient of variation was higher in the flood zone (Table 2). Immature density was always lower in the flood zone than in the upland immediately following a flood (sign test; $P < 0.05$; Ambrose and Ambrose 1987). Egg densities in the flood zone increased and matched those of the upland by 3–6 mo following floods. Larval density in the flood zone increased and matched those of the upland following the first flood; but after the second flood they remained below that in the upland. Pupal density in the flood zone required 6–9 mo after a flood to recover to nonflood levels.

To test for stage-specific differences in *C. fenestrata* egg production and immature transition probabilities, I compared ratios of successive stages between the upland and flood zone habitat. There were no detectable between-habitat differences in egg:adult (t test, $df = 4$, $P = 0.80$), larvae:eggs (t test, $df = 10$, $P = 0.63$), pupae:larvae (t test, $df = 10$, $P = 0.053$), and recruits:

TABLE 2. Densities (per ramet), standard deviations, and coefficients of variation (cv) of immature *Cephaleia fenestrata* (a rolled-leaf beetle) on *Pleiostachya pruinosa* (a prayer plant) in the upland and flood zone habitats.

Stage	Upland				Flood zone			
	Mean \pm 1 SD	cv	N	Mean \pm 1 SD	cv	N		
Eggs	0.09 \pm 0.04	0.47	8	0.06 \pm 0.05	0.92	8		
Larvae	0.21 \pm 0.04	0.21	8	0.14 \pm 0.09	0.62	8		
Pupae	0.03 \pm 0.02	0.70	8	0.01 \pm 0.01	1.50	8		

TABLE 3. Effects of three simulated flooding regimes (24 h, 12 h, and 6 h of submersion) and respective controls on the survival of *C. fenestrata* larvae.

Treatment	No. larvae	Survival probability	No. plants with:		Contingency table analyses		
			Increase/same no. larvae	Decrease in no. larvae	χ^2	df	<i>P</i>
24-h flood	33	0.00	0	14	16.09	3	0.002
Control	47	0.96	9	3			
12-h flood	39	0.00	0	14	13.49	3	0.007
Control	45	0.98	8	4			
6-h flood	33	0.94	8	4	0.00	3	1.000
Control	44	0.68	8	4			

pupae (*t* test, *df* = 4, *P* = 0.68) ratios. Thus, there was no evidence for differences in per capita recruitment or stage-specific immature survival probabilities between habitats.

There was, however, evidence for flooding reducing survival probability in larvae. In the flooding experiment, one-day survival probability of the larvae in the 12- and 24-h treatments was 0% (*N* = 39 and 33, respectively) compared to 96% and 98% in the respective controls (Table 3; contingency table analysis; *P* = 0.002 and 0.007, respectively). There was no difference in changes in the number of larvae between the 6-h flood and the control (*P* = 1.00).

Patch-level analyses

To demonstrate that the effect of the flood was consistent throughout the flood zone, I compared the number of beetles in the flood zone and in the upland on a patch-by-patch basis before and after the November 1999 flood. The patches were sampled one week after the flood, leaving little time for beetles to recolonize the area. In the sampling that followed the flood, immature population size decreased in a significantly higher proportion of patches in the flood zone (10 decreased and zero increased) than in the upland (17 decreased and 12 increased; Fisher's exact test, *P* = 0.03).

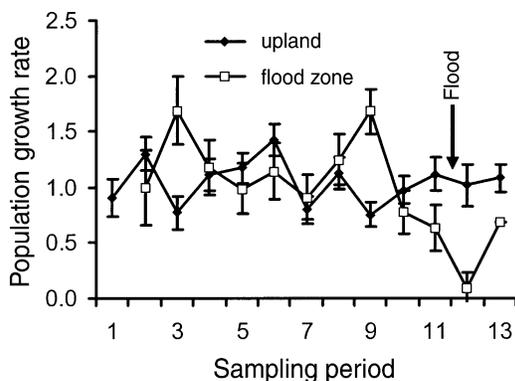


FIG. 4. Time-specific population growth rates (and 95% confidence intervals) in the upland and flood zone habitat. The flood zone flooded between the 11th and 12th sampling periods.

Likewise, adult population size decreased in a significantly higher proportion of the patches in the flood zone (eight decreased and zero increased) than in the upland (six decreased and eight increased, Fisher's exact test, *P* = 0.03).

Source-sink analysis

Time-specific population growth rates for a 25-d period were calculated for the upland and flood zone habitats (Fig. 4). With a Bonferroni correction for the number of lambdas estimated, none of the population growth rates were significantly different from 1 except for that for the flood zone in sampling period 12 just before the flood ($\hat{\lambda}_f = 0.63 \pm 0.10$ [mean \pm 1 SE], *Z* = 3.62, *P* = 0.0001) and that for sampling period 13 just after the flood ($\hat{\lambda}_f = 0.08 \pm 0.04$, *Z* = 21.28, *P* < 0.0001). This suggests that the flood zone becomes a sink habitat when it is flooded. When the habitats were not flooded, the population growth rates in the upland and the flood zone were similar ($\hat{\lambda}_u = 1.02 \pm 0.06$, *n* = 14 sampling periods; $\hat{\lambda}_f = 1.03 \pm 0.11$, *n* = 13 sampling periods; *t* test, *P* > 0.05). Thus, during non-flood periods, there appears to be no source-sink dynamics between the upland and flood zone habitats.

The low numbers of beetles in the flood zone after the flood resulted in a migration imbalance, meaning that a greater number of beetles migrated from the upland to the flood zone than vice versa (Fig. 5A). As the time since that flood lengthened, the population attained approximately balanced dispersal. Nonetheless, overall, significantly more beetles dispersed from the upland to the flood zone than vice versa (*t* test, *df* = 13, *P* = 0.006; Fig. 5B).

Bootstrap estimates of the population growth rate with different flood frequencies are provided in Fig. 6. Above, I calculated the 95% confidence interval the probability of flooding to be 0.025–0.216 in any 25-d period. The estimated population growth rate within this range of flood probabilities is less than one, suggesting that the population in the flood zone is a sink in the long term (in the order of years). The analysis suggests that the flood zone could be a source habitat if flooding frequency were less than 0.01 floods per 25-d period (or ~ 0.14 floods per year).

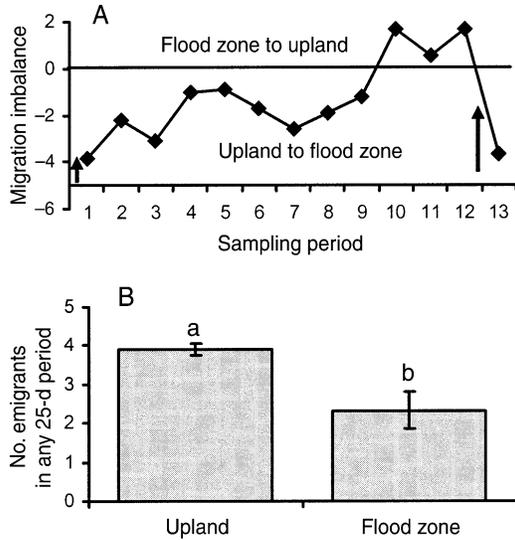


FIG. 5. (A) Estimated migration imbalance over time (total number of migrants between upland and flood zone per time step) and (B) number of emigrants in any 25-d period (± 1 SE) between the upland and flood zone habitats. Migration imbalance is the net movement of beetles between the two habitats (i.e., a negative value indicates that more beetles moved from the upland to the flood zone than the opposite direction). Lowercase letters indicate that the overall direction of movement was significant between the upland and the flood zone. Arrows indicate flood events.

DISCUSSION

Despite theorists' focus on source-sink dynamics (Holt 1985, Pulliam 1988, Watkinson and Sutherland 1995, Loreau and DeAngelis 1997), few empirical studies have provided strong evidence for sources and sinks in nature. Although comparative movement across habitats is an integral part of source-sink theory (Pulliam 1988), field studies with information on immigration and emigration are generally lacking (but see Breininger and Carter 2003, De Bruijn 1994, and for a laboratory system see Donahue et al. 2003). Some studies circumvented the problem of measuring migration by assuming that migration had negligible effects on population sizes (Brawn and Robinson 1996, Boughton 1999), or that differences in net migration between habitats were zero (Walters 2001). These essentially assumed balanced dispersal, a postulate counter to fundamental source-sink theory (Diffendorfer 1998). Source-sink dynamics can be demonstrated without observing actual movement events if habitats are closed systems in which two habitats can be experimentally connected and isolated (Kadmon and Tielbörger 1999, Amezcua and Holyoak 2000). In such a case, sources, true sinks, and pseudosinks are distinguishable. In the present study, I individually marked adult *C. fenestrata*; thus, recapture data provided both immigration and emigration data. The data indicated that ~80% more beetles dispersed from the upland to the flood zone than vice versa over the course of a year.

Movement rates of *C. fenestrata* for a 25-d period were low (<5%) except during flood events when the probability of migration from the flood zone to the upland increased to 76%. Doak (1995) demonstrated that the viability of a source-sink population of grizzly bears is sensitive to movement rates, in which low movement rates between habitats facilitate high population viability, and high rates of movement endangered the population. Thus, if movement from the source to the sink is too great, the source cannot maintain its own population density. The population density of *C. fenestrata* in the upland remained near an equilibrium level, suggesting that the population growth rate of this source habitat is sufficient to maintain even with the observed levels of emigration.

The data indicate that a nearly sevenfold reduction in *C. fenestrata* adult survival probability in the flood zone during a flood event was the primary cause of the flood zone being a sink. In periods without flooding, survival probability did not differ between upland and flood zone habitat. Nor did per capita recruitment differ between habitats. These findings are similar to those of the Iberian lynx in which a sink was characterized by a reduction in survival but there was no difference in fecundity (Gaona et al. 1998).

The present study empirically demonstrates temporally variable source-sink dynamics (as do Virgl and Messier [2000] and Walters [2001]). Boughton (1999) found that the same population acted as a source for resident butterflies, but as a sink for immigrant butterflies. The difference was caused by a difference in the timing of oviposition between residents and immigrants. Timing is important in the *C. fenestrata* system as well. Beetles in the flood zone during flood periods suffered high mortality, thus making the flood zone a sink. Conversely, in periods without flooding, population growth rates were no different between habitats.

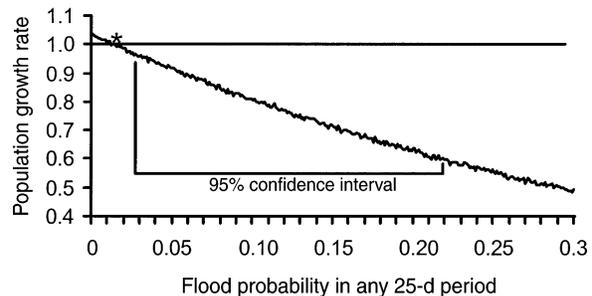


FIG. 6. Projected population growth rate in the flood zone as a function of flood frequency. Population growth rate was estimated by bootstrapping observed population growth rates during flood and nonflood periods. The 95% confidence interval was calculated from the binomial distribution based on four observed flood events over 44 sampling periods ($N = 44$, mean = 0.091, 95% confidence interval 0.025–0.216). The asterisk indicates the threshold for becoming a source habitat.

Floods greatly reduced the densities of *C. fenestrata* adults in the flood zone. A simulated flood experiment showed that larvae suffer nearly 100% mortality when their host plants are flooded for 12 h or more, conditions that occurred during the November 1999 flood (D. Johnson, *personal observation*). In accordance, immature densities were lower in the flood zone than in the upland in this study.

In this study, source–sink dynamics were driven by flooding. Source–sink dynamics were expected in a population of Sitka mice in and near a floodplain, but instead it was found that differences in demographic parameters were greater between replicate sites than between the floodplain and upland (Hanley and Barnard 1999). Doak (1995) demonstrated how habitat degradation due to disturbance can significantly affect source–sink dynamics of grizzly bears. The patch-level analysis in my study demonstrates that the negative effects of flooding on *C. fenestrata* are consistent across patches in the flood zone.

In source–sink theory, the population growth rate (λ) in a source is greater than one and in a sink is less than one in the absence of immigration (Pulliam 1988). Based on these criteria, the flood zone is a long-term sink habitat for *C. fenestrata*. The sink seems to be caused mainly by high mortality of both adults and larvae during a flood. While determining that the flood zone was a sink habitat suggests that the upland is a source, this cannot be confirmed by this study because the estimated population growth rate in the upland was not significantly different from one. An alternative possibility is that a *C. fenestrata* population outside the study area acts as the source. This is unlikely because known dispersal distances (Johnson 2003) are less than the distance to the nearest *C. fenestrata* populations outside the study area. The more likely explanation is that the population growth rate in the upland actually is above 1. This explanation is supported by the observed overall directional migration of *C. fenestrata* from the upland to the flood zone.

Distinguishing between true sinks and pseudosinks is not a trivial task. A pseudosink will look like a true sink in that its level of population density is maintained by immigration from a source habitat (e.g., Holt 1985). The difference between the two is that in the absence of immigrants from a source, a true sink will go extinct while a pseudosink will still be viable, just at a lower population size. A pseudosink has density dependence in vital rates where, for example, if survival probability is negatively related to population density then immigration would be required to maintain a high density, but would not be required to maintain a low density. I do not have information on density dependence of vital rates for *C. fenestrata*. Mortality caused by flooding, however, was the primary cause of sink dynamics in the flood zone and would likely act in a density-independent fashion, thus, suggesting that the flood zone is a true sink rather than a pseudosink.

Asking whether a system displays source–sink dynamics requires stating a time scale and moment at which population growth rates are measured. In this study, I demonstrated that population growth rates varied above and below unity in an expanding and contracting population. During flood periods the flood zone acted as a strong sink while during non-flood periods there was no sink dynamic in the flood zone. Whether the flood zone was a long-term sink or not was dependent on the frequency of flooding. These results illustrate the importance of accounting for temporal variation and explicitly defining the time scale examined when investigating source–sink dynamics.

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