Popul Ecol (2013) 55:95–106
DOI 10.1007/s10144-012-0357-y

THE SOCIETY
OF
POPULATION
ECOLOGY

ORIGINAL ARTICLE

Alternate attractors in the population dynamics of a tree-killing bark beetle

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Received: 31 July 2011 / Accepted: 18 November 2012

Abstract Among the most striking changes in ecosystems are those that happen abruptly and resist return to the original condition (i.e., regime shifts). This frequently involves conspicuous changes in the abundance of one species (e.g., an oubreaking pest or keystone species). Alternate attractors in population dynamics could explain switches between low and high levels of abundance, and could underlie some cases of regime shifts in ecosystems; this longstanding theoretical possibility has been difficult to test in nature. We compared the ability of an alternate attractors model versus two competing models to explain population fluctuations in the tree-killing bark beetle, *Dendroctonus frontalis*. Frequency distributions of abundance were distinctly bimodal, a prediction of the alternate attractors model, strongly indicating the lack of a single, noisy equilibrium. Time series abundance data refuted the existence of strong delayed density-dependence or non-linearities, as required by the endogenous cycles model. The model of alternate attractors was further supported by the existence of positive density-dependence at intermediate beetle abundances. Experimental manipulations show that interactions with competitors and shared enemies could create a locally stable equilibrium in small populations of *D. frontalis*. High variation among regions and years in the abundance of predators and competitors could permit switches between alternate states. *Dendroctonus frontalis* now provides the strongest case that we know of for alternate attractors in natural population dynamics. The accompanying demographic instability appears to underlie spatially extensive outbreaks that have lasting impacts on forest ecosystems. Understanding feedbacks in populations with alternate attractors can help to identify thresholds underlying regime shifts, and potentially manage them to avoid undesirable impacts.

Keywords Alternate stable states · *Dendroctonus* · Multiple equilibria · *Pinus* · Regime shift · Shared predators

Introduction

Recent decades have been notable for diverse but collectively extensive changes in ecosystems (Tylianakis et al. 2008; Jiao 2009). Some of these changes are consequential for human welfare and may be regarded as negative (Chapin et al. 2003; Scheffer and Carpenter 2003). Those that can be referred to as regime shifts are particularly consequential because they resist return to initial

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Electronic supplementary material The online version of this article (doi:10.1007/s10144-012-0357-y) contains supplementary material, which is available to authorized users.

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conditions even after the forcer has been removed (Scheffer and Carpenter 2003; Collie et al. 2004; Contamin and Ellison 2009). Regime shifts frequently arise from large changes in the abundance of one or few populations (e.g., Resilience Alliance, http://www.resalliance.org/index.php/thresholds_database; Schroder et al. 2005). The existence of alternate attractors (which can create multiple equilibria, i.e., alternate stable states, when certain demographic criteria are met) in the feedback systems that regulate population abundance is a long standing hypothesis for persistent conspicuous fluctuations in population abundance (Lewontin and Cohen 1969; Holling 1973; Southwood and Comins 1976; Sutherland 1990; Beisner et al. 2003) and could be a general mechanism for regime shifts in ecological systems (Collie et al. 2004; Weijerman et al. 2005; Biggs et al. 2009; Jiao 2009). Although there has been sustained interest in the theoretical possibility of alternate attractors in population dynamics, and it has become textbook paradigm in pest management (Edmonds et al. 2000), empirical tests have been rare and limited (Elkinton and Liebhold 1990; Angeli et al. 2004).

The classical model of alternate attractors in population dynamics includes two regions of negative feedback that each produce a stable equilibrium and which are separated by a region of positive feedback that yields an unstable equilibrium (Southwood and Comins 1976; Beisner et al. 2003; Angeli et al. 2004). Three non-trivial predictions follow from this model: (1) there is meaningful negative feedback on population growth even when abundance is relatively low, (2) there must be destabilizing positive feedback in population dynamics at intermediate abundances, and (3) the frequency distribution of abundances will be bimodal (Morris 1963; Liebhold 1992). Additionally, all models of alternate attractors require some form of stochastic perturbation to move the system between attractors. Sufficient stochastic perturbations could take three general forms; (1) density-independent emigration or immigration could change abundance such the population moves from the regulatory domain of one attractor to the other; (2) density-independent variation in per capita reproduction (e.g., due to effects on survival of interannual variation in winter temperatures) creates a frequency distribution of possible reproductive rates around the density-dependent relationship; and (3) stochastic variability in the environment could change the form of the density-dependent function (e.g., reduction of predators, for reasons independent of the focal species, can cause the lower equilibrium to shift or even disappear; S1 in Electronic Supplementary Material (ESM).

There are two prominent alternative hypotheses for extreme fluctuations in abundance. The first is that populations might have a single attractor but fluctuate with high variance due to density-independent (stochastic, exogenous) variation in resources, weather (Moran effects), community interactions, etc. Under this "noisy equilibrium" model, the frequency distribution of abundances should be log-normal around a mean population size, with a variance that reflects the exogenous effects (Bellows 1981). The second hypothesis is that extreme fluctuations (even chaotic dynamics) result from delays and/or nonlinearities in density-dependence (Turchin 2003).

We employed analyses and experiments to compare these three models with a well-studied species (*Dendroctonus frontalis* Zimmermann, southern pine beetle or SPB) that is notorious for large population fluctuations that exert strong, broad effects on forest ecosystems (Coulson and Klepzig 2011). Detailed population studies from the past several decades permitted a set of tests with existing data and provided the background for new critical experiments. Previous analyses of abundance time series and predator exclusion experiments have suggested that a delay in the numeric response of predators to *D. frontalis* populations caused *D. frontalis* populations to cycle, and was the chief driver in population fluctuations (Turchin et al. 1999). However, the addition of subsequent years of data to the same time series has weakened the signal of cycles (Friedenberg et al. 2008), and data from a broader spatial scale seem to lack cycles (Thatcher et al. 1980; Price et al. 1997). So, although this is one of the best studied forest insects in the world, we still lack a satisfactory, theoretical explanation for their population dynamics.

Methods

Study system

When *D. frontalis* are abundant, they kill healthy pine trees via pheromone-mediated mass attacks that overwhelm resin defense systems. Female adults oviposit within the phloem, where larvae feed before pupating in the outer bark and then emerge to join attacks on other trees. In large populations, outbreaks are limited by strong intraspecific competition within the phloem of host trees (Reeve et al. 1998), local depletion of suitable host trees within a landscape (Cairns et al. 2008), and negative feedback from human suppression efforts (Clarke and Billings 2003; Billings 2011). By comparison, little is known about the population ecology of *D. frontalis* when they are rare. Small populations are unable to overwhelm healthy trees and instead reproduce within weakened trees (especially those that have been struck by lightning), where they become part of a larger community of less aggressive bark beetles (Hodges and Pickard 1971; Coulson et al. 1983; Lovelady et al. 1991; Flamm et al. 1993). Insect predators, especially *Thanasimus dubius* Fabricius (Coleoptera:

Cleridae) can be a significant demographic force in large populations of *D. frontalis* (Reeve 1997; Turchin et al. 1999; Reeve and Turchin 2002; Reeve 2011) and also prey on bark beetles in general within isolated trees (e.g., ones struck by lightning).

Abundance data from southwide monitoring program

Since 1987, there has been a growing program coordinated by the Texas Forest Service to monitor the annual abundance of *D. frontalis* in forests throughout the southeastern U.S. (http://txforestservice.tamu.edu/). By 2005, this network had accumulated time series of at least 7 years for 133 forests [averaging $\approx$ 400 km^2 of pine forest, mainly *Pinus taeda* (L.)] in 13 states spanning 1,931 km (from Texas through Virginia; S2 & S3 in ESM). The database contained 1,905 independent annual measurements of beetle abundance (unique forest-year combinations).

The data included two separate measures of *D. frontalis* abundance: (1) number of *D. frontalis* (and the predator *T. dubius*) captured in replicated pheromone-baited funnel traps ($N = 3$ traps per forest-year, separated by 1–10 km within forests) during beetle dispersal in the spring, and (2) the number of localized infestations of four or more beetle-killed trees ("beetle spots") that were detected in systematic aerial surveys during the remainder of the year [see Friedenberg et al. (2007) for a description of initial spot size]. Twelve-unit, Lindgren funnel traps were deployed for 4 weeks in the spring (locally timed to match the flowering of *Cornus florida* L.), and baited with frontalin (two vials of racemic frontalin, 99 % cp; 400 μl centrifuge vial; 3.3 μg/day @ 20 °C) and a pinene lure (currently CLIN 0002 Sirex Lure, 70:30 blend of alpha:beta pinene, 75 % (+) enantiomer, packed for ultra high release; Synergy Corp.). We used these replicated time series to evaluate the strength and form of density-dependent feedbacks on beetle population growth, and to test for bimodality in abundance.

These data are uniquely valuable in that they are temporally extensive and encompass most of the distribution of *D. frontalis* in the United States. A constraint is that data collection involved many people, and the main objective was to aid forest managers, i.e., they were operational data. However, analyses indicated that the program yielded good estimates for each forest-year of the abundance of *D. frontalis* and *T. dubius*. For both *D. frontalis* and *T. dubius*, the variance among forests was highly significant and accounted for 78 and 79 %, respectively, of the total variance in captures [$\ln(N \times \text{trap}^{-1} \times 14\ \text{days}^{-1} + 1)$; $F_{942,\ 1715} > 10.80$, $P < 0.0001$, MSE = 0.541 and 0.904, respectively, from 943 forest-year combinations during 1987–1999 when captures were recorded separately for each trap]. Further evidence of the quality of the data came from the strong correlation between independently collected measures of beetle abundance from funnel traps and subsequent formation of beetle spots (see our Results below).

Testing for bimodality in the frequency distributions of beetle abundance

For analysis of 1,905 annual forest-specific estimates of *D. frontalis* abundance (beetles $\times$ trap^{-1} $\times$ 14 days^{-1} during spring), and 1,827 beetle spots (observed during the subsequent summers), we compared the best fits of alternative theoretical models of beetle population dynamics to empirical frequency distributions. Equation S1 (S1 in ESM) describes a simple form of linear density-dependence with a stochastic component that allows for variable noise around an equilibrium. This model predicts a log-normal frequency distribution of abundance. Thus, for the possibility of a single noisy equilibrium we fit our empirical frequency distribution of abundance to the two parameter model:

$$\mathrm{Prob}(X) = \mathrm{NormDist}(\mu, \sigma) \tag{1}$$

where X = log-transformed abundance, μ = mean and σ = standard deviation. To compare the goodness of fit of alternate models, we calculated χ^2 statistics comparing observed and expected frequencies of beetle abundances. We recognized 18 bins of ln-transformed beetle abundance: −0.25 to <0.25, 0.25 to <0.75, 0.75 to …, ≥8.75, which provided satisfactory resolution (numerous bins) while still yielding expected values of ≥5. Later, we evaluated the sensitivity of conclusions to the binning rules by repeating the analyses with different bins.

Under the competing model of alternate attractors (Eq. S3, S1 in ESM), the expected probability density function for beetle abundance can be described with five parameters:

$$\begin{aligned}\mathrm{Prob}(X) = {} & (\mathrm{NormDist}(\mu_{\mathrm{R}}, \sigma_{\mathrm{R}}))(1 - p) \\ & + (\mathrm{NormDist}(\mu_{\mathrm{A}}, \sigma_{\mathrm{A}}))(p)\end{aligned} \tag{2}$$

with symbols as in Eq. 1 but allowing for two modes representing rare (R) and abundant (A) populations, and p indicating the proportion of forest-years when beetles were abundant. As with Eq. 1, we estimated parameters to maximize the goodness of fit using a generalized reduced gradient algorithm (via solver in Microsoft Excel©); exploration of other algorithms showed these solutions to be robust.

Tests for negative feedback when populations are large

We tested for 1st and 2nd order density-dependence in the southwide monitoring data (Turchin 2003). From each of the 133 time series of *D. frontalis* abundance, we estimated interannual per capita population growth rates from beetle captures in spring and beetle spot counts during the summer as:

$$R_t = \ln(N_{t+1}) - \ln(N_t) \qquad (3)$$

where N_t equaled beetle captures × trap^{-1} × 14 days^{-1} in year '*t*' (+1 to allow for years when captures were 0) or number of spots in year '*t*' (+0.1 to allow for years with no spots), and N_{t+1} equaled abundance the subsequent year. Then we evaluated the general linear models where R_t = function of forest (categorical variable), current abundance = $\ln(N_t)$, and previous abundance = $\ln(N_{t-1})$. In this model, the strength of stabilizing 1st order feedback is represented by the regression coefficient for N_t, and the presence of potentially destabilizing 2nd order feedbacks are represented by nonzero coefficients for N_{t-1}. We examined the residuals for lack of fit. Finally, to be certain that we were not missing any notably better, but less parsimonious, models of endogenous feedbacks, we evaluated all models that included any possible subsets of $\ln(N_t)$, $\ln(N_{t-1})$, $\ln(N_t)^2$, $\ln(N_{t-1})^2$, and $\ln(N_t) \times \ln(N_{t-1})$ (Turchin 2003). Throughout this model selection process we treated the *F* statistics and *P* values as approximations because of complications with statistical tests for density-dependence and autocorrelations (Brook and Bradshaw 2006), and relied on AIC to make comparisons between models with varying numbers of parameters (Burnham and Anderson 2002). Additionally, while there is some spatial autocorrelation in beetle abundance among study forests (potential Moran effects), our unit of study (USFS Ranger Districts) was chosen such that the distance between forests was well beyond beetle dispersal distance (Peltonen et al. 2002); Turchin and Thoeny (1993) estimated that 99 % of *D. frontalis* dispersed less than 3.3 km, whereas the mean nearest neighbor distance among our study forests was 39 km (range = 18–146 km).

Tests for positive demographic feedback

Previous studies have revealed positive density-dependence in *Dendroctonus* spp. from increased efficacy of tree attacks, and decreased probability of local extinctions, when beetles are abundant (Berryman et al. 1989; Friedenberg et al. 2007). Here we tested for the additional mechanism that efficiency with which *D. frontalis* aggregate to initiate beetle spots (local infestations) might increase with increasing abundance of dispersing beetles (Tobin et al. 2007). We evaluated this with the southwide monitoring data by testing for (1) acceleration in the relationship between the number of beetle spots formed during summer and the abundance of dispersing beetles in spring and (2) increases in the average size of spots at the time of their formation. For the latter, we added data from the U.S. Forest Service SPBIS program (SPBIS = southern pine beetle information system). Within ranger districts experiencing *D. frontalis* outbreaks, forest service personnel usually ground-checked beetle spots shortly after the aerial detection. Ground surveys verified that *D. frontalis* were the cause of tree mortality and recorded the number of red or fading trees, which represented the number of trees killed by the beetles that formed the spot and is correlated with the number of beetles that made up the initial aggregation. Most spots are formed during beetle dispersal in late spring, and become evident in aerial surveys during summer as the crown color fades in killed trees. Thus we analyzed the 26,143 spots within the SPBIS database that were detected between 15 May and 31 August, when surveying activity is most intense, and which were ground-checked within 15 days of detection (same data as analyzed for another purpose by Friedenberg et al. (2007). This yielded 174 forest-year combinations with paired estimates of beetle captures in spring and the initial sizes of subsequent beetle spots. The initial size of spots approximated a lognormal distribution, so we estimated the average for each forest in each year of the log-transformed numbers of red and fading trees at detection. Then we tested for a relationship between average initial size of spots and abundance of dispersing beetles.

Tests for negative feedback when populations are small

The model of alternate attractors predicts that rare populations tend to remain rare by virtue of negative density-dependence. A priori, this was the most improbable postulate because *D. frontalis* can be so uncommon when they are rare that it is difficult to envision ecologically realistic mechanisms for negative feedback. We hypothesized that interactions with other bark beetle species (especially *Ips* species) and shared predators could stabilize *D. frontalis* populations around a lower attractor (S1 in ESM). *Ips* species co-attack and reproduce simultaneously with *D. frontalis* in lightning struck trees, and the reproductive success of *D. frontalis* in those trees is reduced by intense interspecific competition with *Ips* for limited phloem resources (Hodges and Pickard 1971; Flamm et al. 1987, 1993). But for interspecific interactions to produce density-dependent feedback, the abundance of competitors and/or predators within trees must increase as a function of *D. frontalis*. We hypothesized that this could arise via heterospecific attraction to the aggregation pheromones of *D. frontalis*. The predator *T. dubius* is strongly attracted to frontalin, a primary component of *D. frontalis* pheromones (Pureswaran et al. 2006). There is also evidence, though less well validated in the field, that other predators and competitors perceive frontalin (Smith et al. 1990; Salom et al. 1992; Ascoli-Christensen et al. 1993; Aukema and Raffa 2005). In this case, since the size of the pheromone plume coming from a tree increases with the number of *D. frontalis,* the abundance of competitors and predators could increase in an appropriately density-dependent fashion. We evaluated this mechanism by comparing the attractiveness of lightning-struck trees to which we added frontalin, relative to paired control trees, to competitors and predators. We also tested for dosage-dependent attraction of heterospecifics and predators to frontalin, which is a further requirement of the hypothesized mechanism.

We chose the Kisatchie National Forest (Louisiana, USA) for our experimental study of lightning struck trees. At this time, *D. frontalis* was so rare in this forest as to be regarded by some as locally extinct (not a single beetle or spot detected in annual surveys since 1998). In that forest, during the summers of 2004–2006, we located 11 pairs of similarly-sized trees that had been struck by lightning during the same storm and discovered by us within 5 days (5 pairs in 2005 and 6 in 2006). Paired trees were separated by >10 m but <1 km (range necessitated by natural availability of tree pairs, but falls well within the dispersal distance of flying beetles) and were the same species (7 pairs of *Pinus palustris* Mill., 4 pairs of *Pinus taeda*). Immediately following discovery, we placed two sticky traps (transparent acetate sheets, 22 × 28 cm, coated with Tanglefoot$^{\mathrm{TM}}$ and permethrin) on opposite sides of each tree trunk at 4 m to capture landing insects. One randomly assigned tree in each pair was baited at 5 m height on the main stem with a frontalin lure (elution = 5 mg/day). Sticky traps were checked weekly for captures (and refreshed or replaced).

To assess the background community of bark beetles and predators in the vicinity of study trees, we deployed four 12-unit (Lindgren) funnel traps, arranged in the general area near each pair of trees, but always >20 m from the nearest study tree. In each array of four traps, every trap was baited with a host volatile of *Pinus*, alpha-pinene (at 28 mg/day), and with one of three bark beetle pheromones (frontalin with elution = 5 mg/day, ipsenol at 230 µg/day, or ipsdienol at 110 µg/day), and one with no pheromone. These lures represent the main attractant pheromones for all common bark beetles and predators in this region and the presence of alpha-pinene is a known pheromone synergist (Aukema and Raffa 2005; Miller et al. 2005). Ipsenol and ipsdienol lures were racemic mixtures (20 mg bubble caps from Pherotech Inc, now Contech Enterprises Inc., British Columbia, Canada). Alpha-pinene and frontalin lures were made by us and eluted from 400 µl polyethylene Eppendorf tubes, which were replaced every week when traps were emptied and lures were rotated between traps.

In September 2005 we were permitted to fell five pairs of our experimental trees. We counted the number of bark beetle attacks (indicated by pitch tubes on the outer bark; all from *Ips calligraphus*) on one side of the bole from the ground to the base of the live crown. Two 1-m bolts were cut (one from 3 m and one at 70 % to the live crown) and censused for insect bodies to identify which species made the pitch tubes, to measure egg gallery, and quantify larval feeding activity within the phloem. Using a 2 × 3 cm grid overlay we classified all phloem as unused, destroyed from the lightning strike, absent (unreadable due to feeding by cerambycid and buprestid beetle larvae), or filled with bark beetle gallery. We calculated the percent phloem used by bark beetles as a proportion of the area not erased by borers or destroyed by the lightning. In September 2006 we also counted pitch tubes (attacks) on one side of the open bole of each tree (6 pairs), but in this case a pair of observers used binoculars (validated by climbing a subset of trees to make detailed observations of removed bark to ascertain the attacking species).

To characterize heterospecific dosage responses to frontalin, we deployed 29 arrays of four 12-unit (Lingren) funnel traps in pine forests within four regions of three states during 2004 and 2005 (S4 in ESM). Traps were configured as a 50 × 50 m square and baited with frontalin at elution rates of 0, 5, 15, or 55 mg/day and with host volatiles (racemic alpha-pinene at 28 mg/day). We emptied traps weekly (and rotated lures to preclude spurious spatial effects) for 4 weeks. For analyses, we summed captures across time for each lure within each array, and analyzed beetles × trap^{-1} × 7 days^{-1} (ln-transformed). Arrays within the same forest, season (spring or summer), and year were regarded as replicate measures from the same regional community. Thus the general linear model included the term SFY (representing the six unique combinations of season, forest, and year), array nested within SFY (as a random effect), frontalin dosage as a continuous variable (ln-transformed), and SFY × dosage.

A mechanism for moving between attractors

If a system has alternate attractors, stochastic perturbations are required to move the population from one state to another. One way that this could happen is if density-dependence in rare populations arises from interactions with predators and/or interspecific competitors. Then stochastic perturbations that causes variation in the abundance of predators and/or competitors could permit transitions between alternate states of abundance (by moving the unstable equilibrium or even erasing the lower attractor when predators and competitors become rare; S1 in ESM). We tested for variability in the abundance of *T. dubius* and

Ips spp. using records from the southwide monitoring program and our own trapping data.

Results

Comparing goodness-of-fit to frequency distributions of beetle abundance

The empirical frequency distributions of beetle abundance were distinctly bimodal (Fig. 1) and could not be satisfactorily fit based upon the theoretical model of a single point equilibrium with noise. For trap captures, with $\mu \pm \sigma = 3.17 \pm 2.29$ (estimated as mean and standard deviation from empirical distribution), the goodness of fit was very poor ($\chi^2 = 1,866$); for beetle spots, with $\mu \pm \sigma = 0.67 \pm 2.87$, the fit was similarly poor ($\chi^2 = 2,326$); compare dashed lines to actual frequency distributions in Fig. 1). The lack of fit was partly because trap captures with zero beetles were very high compared to the theoretical model. Estimates of zero abundance are likely over-represented in the monitoring data for beetles because of detection limits (i.e., estimates of zero abundance in trap captures probably do not mean that there were no *D. frontalis* in the forest that year—greater sampling effort could yield a longer tail in the estimates of low abundance). Thus, we also evaluated a noisy equilibrium model that recognized lower detection limits (with the expected frequency for the lowest abundance class calculated including the cumulative lower tail of the theoretical probability density function). The fit to a single equilibrium was improved by allowing for lower detection limits but was still poor (estimated $\mu \pm \sigma = 3.37 \pm 3.27$, $\chi^2 = 260$; compare dotted line to actual frequency distribution in Fig. 1, upper). Thus, the pattern of bimodal abundance was not an artifact of detection limits. Detection limits were not appropriate for beetle spots/100 km^2 because the aerial surveys are essentially a census.

In contrast to the single equilibrium model, the data were a good match with the theoretical possibility of alternate attractors. For trap captures, the best fit model was $\mu_R \pm \sigma_R = 0.81 \pm 3.05$, $\mu_A \pm \sigma_A = 4.86 \pm 1.24$, and $P = 0.48$, $\chi^2 = 20.58$ (solid lines in upper Fig. 1). For beetle spots, the fit was almost perfect with $\mu_R \pm \sigma_R = -1.97 \pm 2.94$, $\mu_A \pm \sigma_A = 3.41 \pm 1.64$, and $P = 0.40$, $\chi^2 = 4.38$ (lower Fig. 1). Thus, beetle trap captures have tended to be near 1 or 128 captures × trap^{-1} × 14 days^{-1}, with about 48 % being near the upper value, and beetle spots have tended to be near 0 or 30 spots/100 km^2, with about 40 % near the upper value.

These conclusions were robust to how the data were binned. We repeated analyses with bins shifted by 50 %, expanded by 50 % to 13 bins, and contracted by 30 % to 24 bins). For trap captures, with alternative binning decisions, $\chi^2 = 1,283–2,796$ for the log-normal model, $\chi^2 = 232–292$ for the log-normal model with detection limits, and $\chi^2 = 11.8–41.4$ for the bimodal log-normal model. For beetles spots and alternative binning, $\chi^2 = 2,326–8,378$ for the log-normal model, and $\chi^2 = 4.4–20.1$ for the bimodal log-normal model.

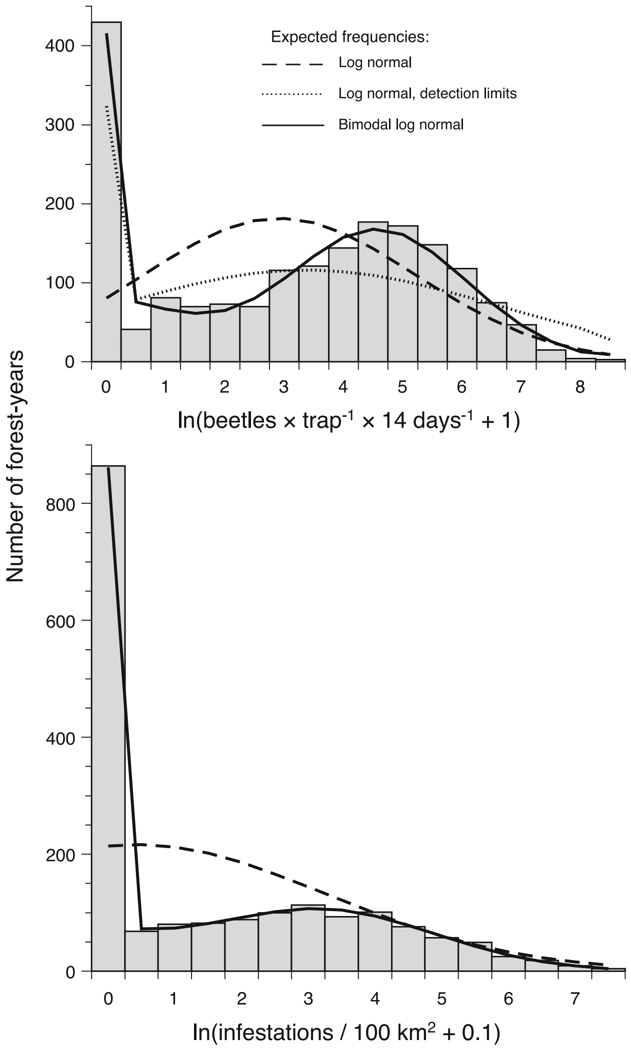

Fig. 1 *Histograms* indicate frequency distributions of *D. frontalis* captures during spring sampling (*upper*, $n = 1,905$ forest-years) and *D. frontalis* spots detected in aerial surveys (*lower*, $n = 1,827$ forest-years). *Lines* indicate expected frequencies under statistical models of a single noisy point equilibrium (log-normal or log-normal with detection limits) versus two locally stable attractors (bimodal log-normal)

A bimodal pattern could also appear if our dataset were dominated by sites where beetle abundance was usually high, and other sites where it was usually low; instead of individual sites switching between high and low abundance. However, this was not the case. There was striking interannual variability in beetle abundance throughout the subcontinental study area (S3 in ESM, note range between minima and maxima and SD in log abundance). For example, the median minimum annual abundance across 131 forests was 0 beetles × trap^{-1} × 14 days^{-1}, while the median maximum abundance was 423 beetles × trap^{-1} × 14 days^{-1}. In 51 of 131 forests, the factor of change from ±1 SD in annual variance in beetle captures was >100-fold, and it was >10-fold in 90 % of the forests (from back-transforms of means and SDs in S3 in ESM). The interannual variance in beetle spots per forest-year was even more dramatic: spots were completely absent in some years in nearly all forests (125 of 131), but most forests also had years with hundreds of spots (median maximum = 280). This signal of high interannual variation in *D. frontalis* is also dramatically evident in the much longer time series that is available for East Texas (Friedenberg et al. 2008). These data show that population levels within a single site fluctuate across time.

Tests for negative feedback when populations are large

Analyses of abundance time series revealed strong 1st order density-dependence for both beetles (spring trap captures) and spots (aerial surveys). There was also strong evidence for additional effects from nonlinearity for beetles (trap captures) and delays in spot growth (aerial surveys) in density-dependence (S5 in ESM). However, the 2nd order effects had only modest effects on the dynamical behavior of the model, and did not generate cyclical behavior, because the coefficients were small relative to the first order effects (Royama 1992; Klapwijk et al. 2012). Both models produced simple endogenous dynamics with rapid convergence on the equilibrium abundances of 18 beetles × trap^{-1} × 14 days^{-1} (Eq. 4) or 1.4 beetle spots/100 km^2 of host forest (Eq. 5; S6 in ESM).

$$R_t = 1.16 - 0.31 \times \ln(N_t + 1) - 0.0285 \times \ln(N_t + 1)^2 \sqrt{\text{MSE}} = 1.42 \tag{4}$$

$$R_t = 0.25 - 0.50 \times \ln(N_t + 0.1) - 0.096 \times \ln(N_{t-1} + 0.1) \sqrt{\text{MSE}} = 2.08 \tag{5}$$

For spring trap captures (Eq. 4), the first order effect was dominant (-0.31 ± 0.05, ±SE, AIC = 5040.89, $w_i = 0.004$, $\overline{R}^2 = 0.377$). Adding the quadratic term ($(\ln(N_t))^2$, -0.0285 ± 0.0083; ±SE) improved the model (AIC = 5030.02, $w_i = 0.996$, $R^2 = 0.382$). For beetle spots (Eq. 5), the first order effect was similarly dominant (-0.50 ± 0.03, AIC = 5558.29, $w_i = 0.005$, $R^2 = 0.370$), and the coefficient for delayed density-dependence, $\ln(N_{t-1})$, was also distinguishable from zero (-0.096 ± 0.027) and improved the model (AIC = 5547.55, $w_i = 0.995$, $R^2 = 0.377$). Both of the more complex models [for beetles, adding $\ln(N_t)^2$, and for spots, adding $\ln(N_{t-1})$] accounted for slight but significant differences in average population growth rate among forests ($F_{132,\ 1284} = 1.89$, $P = 0.0004$ and $F_{130,\ 1156} = 1.46$, $P = 0.001$, for beetles and spots, respectively). In neither case were there any models involving any other combination of linear and quadratic terms for present and past abundance that improved the goodness of fit beyond $\overline{R}^2 = 0.39$ or $\triangle\text{AIC} > 1$.

Tests for positive demographic feedback

Data from the *D. frontalis* monitoring program revealed positive demographic feedback in landscape population dynamics. The average number of beetle spots that developed per forest during the summer increased more than linearly with increases in the abundance of dispersing beetles during the spring (Fig. 2):

$$\text{Spots} = -0.49 + 0.041 \times \text{SPB} + 2.12\text{E} - 5 \times \text{SPB}^2 \tag{6}$$

where Spots = number of local infestations detected in aerial surveys per 100 km^2 of pine forest, and SPB = number of *D. frontalis* individuals captured per trap per 2 weeks. Both regression coefficients were highly significant ($F_{1,\ 12} > 11$, $P < 0.005$) and the model provided good fit ($R^2 = 0.99$). The acceleration in the efficacy of beetle aggregation into spots was appreciable: e.g., as average spring trap captures increased from 100 to 200 SPB × trap^{-1} × 14 days^{-1}, the average number of spots increased by 4.7 (8.6–13.7 spots/100 km^2), whereas when trap captures increased by the same amount from 600 to 700, the number of spots increased by 7.3 (31.8–38.7 spots/

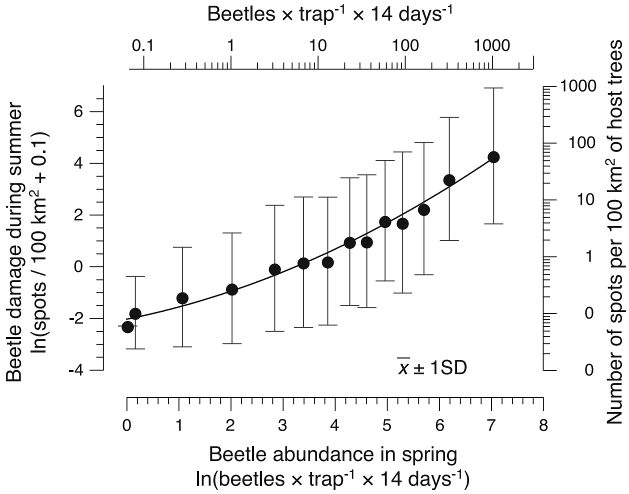

Fig. 2 The number of beetle spots that were formed during the summer increased more than linearly as a function of the abundance of beetles during spring dispersal. Figure shows data in 15 bins of 102 samples (each sample representing one forest in 1 year) sorted by beetle abundance in spring

100 km^2, Fig. 2). The average initial size of spots (number of red trees), which is strongly related to the probability of spot growth versus spot extinction (Friedenberg et al. 2007), also increased with increasing abundance of beetles during spring; initial spot size (# red trees) ranged from 16.0 to 21.8 red trees as average spring trap captures increased from 100 to 1,000 SPB × trap^{-1} × 14 days^{-1} [analyzed as, $\ln(\# \text{ SPB} + 1) = 2.15 + 0.135 \times \ln(\# \text{ red trees})$ ($F_{1,\,171} = 20.07$, $P < 0.0001$, $R^2 = 0.10$)].

Positive density dependence, as described above, could result in populations being driven to extinction if there were no stable attractor at low levels of abundance (S1 in ESM). The lower spike in our frequency distributions of abundance data would be an evanescent snapshot of beetles as they were going extinct. However, low abundances of *D. frontalis* were not usually because they were extinct (or going extinct); in 427 forest-years, there were no multi-tree aggregations of *D. frontalis* (0 spots), yet beetles were still common enough (n = 1–3,415) to be detected in the spring trapping. In some forests, these low but detectable levels of abundance lasted as many as 8 years (>35 beetle generations), before the population was large enough to again create beetle spots. In only 2 % of 1905 forest-years were no *D. frontalis* detected for more than 2 years in a row, implying that even though they escaped detection for 1 or 2 years, they were still present. Thus it is common for *D. frontalis* populations to be stable at low abundances.

Tests for negative feedback when populations are small

Results indicated that behavior of the predator, *T. dubius*, could produce stabilizing density-dependence in small populations of *D. frontalis*. Consistent with a theoretical mechanism involving predators (S1 in ESM, upper), *T. dubius* was strongly attracted to frontalin. There were >7 times more *T. dubius* landing on frontalin-baited trees than on unbaited trees ($t_4 = 3.31$, $P = 0.007$, ln-transformed) and *T. dubius* captures in funnel traps increased as a function of frontalin elution rate [$\ln\ y = \ln\ x\ \ 0.55\ (\pm 0.17) + 0.86\ (\pm 0.50)$, $R^2 = 0.10$, $F_{1,\,43} = 28.81$, $P < 0.0001$; S7 in ESM].

Consistent with a mechanism involving competitors, lightning-struck trees baited with frontalin sustained >2 times more *Ips* attacks than unbaited trees (59 ± 10 vs. 27 ± 8 attacks/tree, respectively (mean ± SE, adjusted to average tree area of 4 m^2; Fig. 3 upper; $t_{10} = 3.58$, $P = 0.005$). Attacks were predominantly *I. calligraphus*, but with very occasional *Ips grandicollis* (*Ips avulsus* were common in the crown, but above the area used by *D. frontalis* and therefore outside of our sampling zone). In accord with the higher attack densities, trees baited with frontalin had more phloem occupied by *Ips* gallery than unbaited trees (92 ± 2 vs. 78 ± 5 % phloem with *Ips* gallery, respectively, Fig. 3 lower; $t_4 = 3.32$, $P = 0.03$).

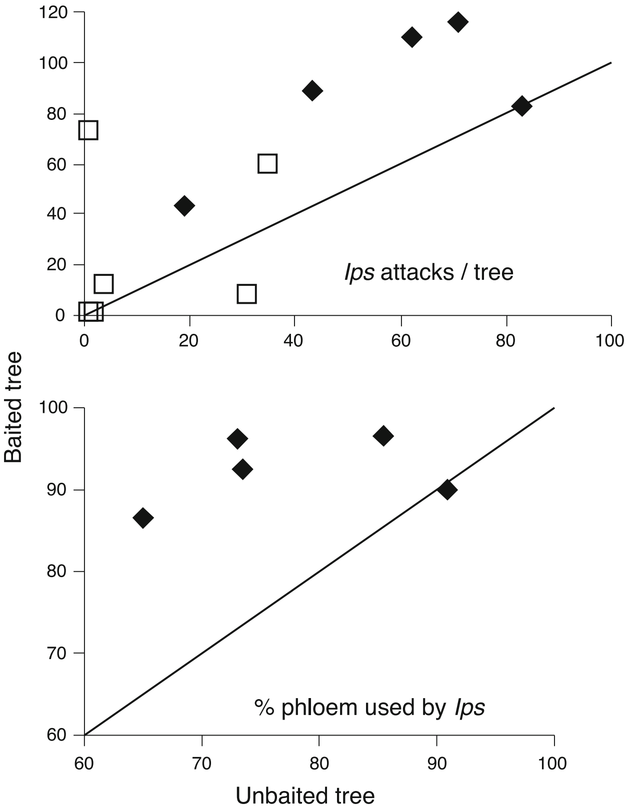

Fig. 3 Number of *Ips* attacks (*upper*) and percentage of phloem used by *Ips* (*lower*) in pairs of lightning-struck trees in which one tree was experimentally baited with the aggregation pheromone of *D. frontalis* (frontalin). *Points* above the *line* of equality indicate attraction to frontalin (diamonds and squares = 2005 and 2006, respectively)

The increased attack densities of *Ips* in frontalin-baited trees was apparently due to post-landing behavior because sticky traps on these trees showed landing rates to be unaffected by frontalin for both *I. grandicollis* ($t_4 = 0.03$, $P = 0.98$) and *I. calligraphus* ($t_4 = 0.98$, $P = 0.35$); e.g., *Ips* were equally likely to land on either lightning-struck tree, but were more likely to attack and produce gallery in a tree that had frontalin (a signal of SPB) associated with it. The higher attacks by *Ips* in frontalin-baited trees could also not have been predicted from funnel trap captures: *I. calligraphus* displayed no attraction to frontalin in funnel traps (<10 captures total from 29 trap arrays across four forests where *I. calligraphus* were common); *I. grandicollis* captures were only slightly higher and unrelated to frontalin dose ($F_{1,\,29} = 0.22$, $P = 0.64$). During this study, no *D. frontalis* attacked any of the experimental trees nor were they found in any of the funnel or sticky traps.

A mechanism for moving between attractors

One hypothetical mechanism for moving between attractors requires high variation in the abundance of predators and/or competitors. This condition was easily satisfied in our study system. Abundance of the predator *T. dubius* varied by more than three orders of magnitude (range = 0–342 beetles × trap^{-1} × 7 days^{-1}; 10–90th percentile = 1.0–92 beetles × trap^{-1} × 7 days^{-1}) through time and space (scale of states) as measured by our captures in baited funnel traps (S8 in ESM, upper panel; $F_{4, 21} = 22.82$, $P < 0.0001$). This was consistent with 16 years of trap captures from the southwide monitoring program where *T. dubius* abundance varied by nearly four orders of magnitude: range = 0–972 beetles × trap^{-1} × 14 days^{-1}; 10–90th percentile = 5.4–192 beetles × trap^{-1} × 14 days^{-1}; $n = 273$ forest-years (analysis restricted to forest-year combinations where *D. frontalis* had been absent or rare (<2 beetles × trap^{-1} × 14 days^{-1}) for the current and previous year to exclude numeric responses of *T. dubius* to *D. frontalis*).

Abundance of the competitors, *Ips*, was also highly variable in space in time. From captures in arrays of ipsenol- and ipsdienol-baited traps near lightning-struck trees in 2004 and 2005, *I. grandicollis* abundance ranged from 0 to 229 beetles × trap^{-1} × 7 days^{-1}, (10–90th percentile = 1.0–64 beetles × trap^{-1} × 7 days^{-1}, S8 in ESM). We were unable to judge variation in *I. calligraphus* because they rarely appeared in our traps even when they were abundant in lightning-struck trees (range = 0–11 beetles × trap^{-1} × 7 days^{-1}; 10–90th percentile = 1.0–5.6 beetles × trap^{-1} × 7 days^{-1}).

Discussion

Our results support the existence of alternate attractors in *D. frontalis* population dynamics by satisfying all of the essential theoretical requirements (S1 in ESM). Empirical frequency distributions matched a bimodal model (Fig. 1). Time series data revealed negative density-dependence at high abundance (S5 in ESM). There was positive density dependence; increases in beetle abundance in spring produced disproportionate increases in the number and size of beetle aggregations that subsequently formed (Fig. 2). Experiments validated a mechanism for negative density dependence to regulate populations at a lower equilibrium via predation and competition (Fig. 3). High spatiotemporal variation in predator and competitor abundance provides a mechanism for populations to escape the lower equilibrium (S1 & S8 in ESM). This is an especially likely mechanism in this system where predators are known to exert strong effects on *D. frontalis* populations (Reeve et al. 1995; Turchin et al. 1999).

Measurements of beetle abundance were distinctly bimodal (Fig. 1) due to populations fluctuating between low and high levels of abundance over time within space. We describe frequent cases of *D. frontalis* being rare but present, which is consistent with the existence of a lower stable attractor in their population dynamics. For example, since 2000 there have been no beetle spots in Louisiana, yet between 2000 and 2006, in 7 of 17 ranger districts, a few beetles were captured some years during spring trapping, and our own more intensive sampling captured five individual *D. frontalis* in a district where no beetles were captured during spring trapping (in 2005, Evangeline Ranger District, Kisatchie National Forest). However, it could be that some cases of zero beetle captures do represent actual extinction of *D. frontalis* within areas as large as National Forest Ranger Districts (e.g., in East Texas, there have been no beetle spots since 2000, and between 2000 and 2006, in only 2 of 18 districts was even a single beetle captured). We expect that stochastic effects on populations that are regulated at very low levels (K_R in S1 in ESM) should sometimes pull those populations below an extinction threshold. It remains difficult to know how often *D. frontalis* reach true extinction in habitat patches as large as we studied.

Our hypothetical mechanisms for regulation of rare *D. frontalis* populations, and for escape from that regulation, involved cross-species attraction to frontalin, an aggregation pheromone of *D. frontalis*. As predicted, the competitors (*Ips* spp.) colonized trees more densely and dominated phloem use when frontalin was present. Apparently, frontalin synergizes the attraction of *Ips* to volatiles emitted by lightning-struck trees (Coulson et al. 1983), even if frontalin alone is only weakly attractive to some *Ips* species. Furthermore, the predator *T. dubius* was attracted in larger numbers to trees with frontalin. This was consistent with the view that *T. dubius* prefer *D. frontalis* as prey but are sustained by *Ips* when *D. frontalis* are rare (Reeve et al. 2009). Variation in the abundance of shared predators and/or competitors, which is conspicuous in this study system, could make the lower equilibrium appear and disappear (S1 in ESM). Specifically, high abundance of *Ips* is expected to limit escapes of *D. frontalis* populations to outbreak levels—partly by direct competition and partly by supporting more robust *T. dubius* populations. It follows that environmental conditions or management practices that favor relatively high abundance of *Ips* may limit outbreaks of *D. frontalis* (Clarke et al. 2000).

We note that frontalin is only one component of the *D. frontalis* aggregation pheromone. It would be informative to measure the heterospecific community response to trees experimentally baited with live *D. frontalis*. In our lightning tree study, *Ips avulsus* were found in the crown of baited trees, and *Ips calligraphus* were found attacking the trees with frontalin at much higher densities, even though *I. calligraphus* were found in equal numbers landing on the trunks. Perhaps the pheromone eavesdropping story is more complex; *I. avulsus* is attracted to frontalin—*I. avulsus* pheromones are attractive to *I. calligraphus*—therefore

I. calligraphus is a strong competitor for phloem resources with *D. frontalis*, even though *I. calligraphus* does not have a direct attraction to frontalin.

While supporting the existence of alternate attractors, our results weakened the case for both leading alternative models (noisy equilibrium and endogenous cycles), although we show that there are significant (albeit weak) second order endogenous effects (S6 in ESM). Nonetheless, there remained some difficulties for the alternate attractors model. The empirical relationship between beetle abundance and per capita growth rate (S5 in ESM) did not display the strong nonlinearities expected for alternate attractors when populations are rare (S1 in ESM); there was no clear signal of a region of positive density dependence at abundances near the hypothetical unstable equilibrium. We think it likely that the southwide monitoring program lacks sufficient sampling intensity to capture dynamics of rare populations. There are several strong independent lines of evidence for social facilitation (positive density-dependence) in *Dendroctonus* bark beetles: higher attack rates on trees lead to more rapid depletion of tree defenses and higher per capita reproduction (Raffa and Berryman 1983; Martinson et al. 2007); potential for swamping the functional response of predators (Reeve and Turchin 2002); and increased success with increasing abundance in initiating and sustaining local infestations (spots) in forest landscapes (Fig. 2; Friedenberg et al. 2007). We assume that the empirical density-dependent relationship from the southwide time series data mainly describe the upper equilibrium when beetles are sufficiently common to be readily sampled. However there still remains some mismatch because the upper modes in Fig. 1 (95 SPB × trap^{-1} × 14 days^{-1} and 24 spots/100 km^2) were higher than the equilibria predicted by the density-dependent functions in S5 in ESM (18 SPB × trap^{-1} × 14 days^{-1} and 1.4 spots/100 km^2). These discrepancies notwithstanding, our results make a strong case that there is some element of alternate attractors in the population dynamics of *D. frontalis* and it is more challenging than before to identify alternative, comparably satisfying models (compare the dynamical behavior of the alternate attractors model in S9 in ESM to the best single equilibrium model in S6 in ESM).

Although the theoretical possibility of alternate equilibria in population dynamics has been recognized for decades (Morris 1963; Ludwig et al. 1978), critical tests and explicit comparisons with competing models have been rare. This must be partly because it is hard to test: rare populations are difficult to study, experiments are complicated, and the most common analyses for endogenous dynamics do not allow for alternate attractors (Turchin 2003). Or, alternate equilibria may simply be rare in nature. Our case invoked heterospecific attraction to semiochemicals, which is infrequently described outside of bark beetles. However our mechanism also invoked prey switching by a generalist predator, which is common in outbreak populations. Models of alternate attractors in spruce budworm (Morris 1963; Ludwig et al. 1978) gypsy moth (Elkinton et al. 2004), and moose (Messier and Crete 1985) have also invoked predators to maintain the lower equilibrium. Mechanisms by which predators can regulate prey include a Type III functional response (Holling 1973) and shared predators (Holt and Lawton 1994). Type III responses are difficult to evaluate at the appropriate spatial scale but have not been evident in *T. dubius* (Reeve 1997; Aukema and Raffa 2004). Theory for shared predators permits a stable equilibrium for *D. frontalis* if its maximal per capita growth exceeds the product of predator attack rate and predator abundance ($r > aP$). Because predator abundance varies greatly in our system (probably an indirect response to resource pulses in its alternative prey, *Ips*) the lower, predator-controlled equilibrium for *D. frontalis* can be expected to vary – and even disappear – when predators become so rare that positive density-dependence begins to be realized from increased efficacy in attacking healthy trees (S1 in ESM and Fig. 2; Raffa 1988). This supports the notion that resource pulses can promote the existence of alternate stable states (Holt 2008). In addition to fluctuations in the supply rate to *Ips* of naturally dying trees, there is reason to expect exogenous effects on the density-dependent function for *D. frontalis* from temperature (Friedenberg et al. 2008) and the abundance of the fungal antagonist, *Ophiostoma minus* (Hofstetter et al. 2006).

Dendroctonus frontalis population dynamics may be more complicated than implied by the alternate attractors in S1 and S9 in ESM, because there is apparently delayed density-dependence when populations are high. *Dendroctonus frontalis* outbreaks rarely persist for more than a few years, presumably due to depletion of host trees (Cairns et al. 2008), numeric increases in *T. dubius* (Turchin et al. 1999), and human suppression efforts (Billings 1994). In contrast, the state of being rare may persist for many years (Price et al. 1997; Friedenberg et al. 2008).

Dendroctonus frontalis now provides the strongest case of which we know for alternate attractors in natural population dynamics. The extreme dynamics that result from this type of demography underlie episodic, spatially extensive outbreaks that have lasting impacts on forest ecosystems (i.e., regime shifts; Lafon and Kutac 2003; Coleman et al. 2008; Xi et al. 2008). Many bark beetle species share characteristics with *D. frontalis* that may predispose their populations to similar dynamic behavior: strong interactions when rare with a guild of less aggressive phloeophages and their shared enemies; aggregation pheromones that are exploited by competitors and predators; and positive density-dependence during mass attacks of trees (Berryman 1982; Raffa 1988, 2001; Ayres et al. 2001; Okland and Bjornstad 2006; Boone et al. 2008). Because many bark beetles share these commonalities, this may explain why, as a guild, they are the most destructive biotic forest pest worldwide (Raffa et al. 2008; Seppala 2009). One benefit of identifying this type of feedback system, is that it allows us to identify systems that are on the brink of a regime shift, and to manage critical conditions so as to avoid undesirable impacts (Biggs et al. 2009).

Acknowledgements Maria Lombardero was instrumental in teaching SJM how to identify the hundreds of insects we found in our traps. Colleagues at the Southern Research Station provided critical assistance: James Barnett, Calvin Meier, and Forrest Oliveria assisted in the development of this study, and Brian Strom, Rich Goyer, Tessa Bauman, Erich Vallery, and Kier Klepzig provided intellectual and logistical support. Paul Marino, Liz Wilson, Milica Milunovic, Luke Evans, and Harvey Carreras were excellent field assistants. Morale was spirited by musical acts across the South, and by The Littlest Birds. We gratefully acknowledge the generous cooperation of U.S.F.S. personnel in the Talladega, Kisatchie and De Soto National Forests. The manuscript benefited from comments by Kathy Cottingham, David Peart, Andrew Storer and many anonymous reviewers. Research was financially supported by NRI/AFRI 2009-65104-05731 and a cooperative agreement with the Southern Research Station.

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