Amphibian and reptile declines over 35 years at La Selva, Costa Rica

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Amphibians stand at the forefront of a global biodiversity crisis. More than one-third of amphibian species are globally threatened, and over 120 species have likely suffered global extinction since 1980. Most alarmingly, many rapid declines and extinctions are occurring in pristine sites lacking obvious adverse effects of human activities. The causes of these "enigmatic" declines remain highly contested. Still, lack of long-term data on amphibian populations severely limits our understanding of the distribution of amphibian declines, and therefore the ultimate causes of these declines. Here, we identify a systematic community-wide decline in populations of terrestrial amphibians at La Selva Biological Station, a protected old-growth lowland rainforest in lower Central America. We use data collected over 35 years to show that population density of all species of terrestrial amphibians has declined by ≈75% since 1970, and we show identical trends for all species of common reptiles. The trends we identify are neither consistent with recent emergence of chytridiomycosis nor the climate-linked epidemic hypothesis, two leading putative causes of enigmatic amphibian declines. Instead, our data suggest that declines are due to climate-driven reductions in the quantity of standing leaf litter, a critical microhabitat for amphibians and reptiles in this assemblage. Our results raise further concerns about the global persistence of amphibian populations by identifying widespread declines in species and habitats that are not currently recognized as susceptible to such risks.

conservation | long-term studies | tropical wet forest

Global declines in amphibian populations rank among the most critical issues in conservation biology (1, 2). Over one-third of amphibian species are globally threatened, and over 120 amphibian species have likely become extinct since 1980 (1). Amphibian populations worldwide are negatively affected by anthropogenic factors such as habitat modification or invasive predators, yet many rapid population declines and extinctions have occurred even in habitats lacking obvious anthropogenic disturbances. Such "enigmatic" declines have aroused particular alarm (1, 3), and much research and controversy have surrounded factors contributing to these declines (3–5).

The impacts of enigmatic declines have been particularly problematic in Central and South America (2, 3, 5). Within the Neotropics (and elsewhere), the primary large-scale trend observed surrounding enigmatic declines is that population declines and extinctions occur almost exclusively in regions >400 m above sea level (3, 6). These montane declines have been associated with outbreaks of chytridiomycosis, a potentially lethal infection of the amphibian epithelium by the chytrid fungal pathogen *Batrachochytrium dendrobatidis*. Chytridiomycosis is now widely viewed as the leading causative factor of enigmatic amphibian declines (3, 5, 7). There are no reports of *B. dendrobatidis* in Central America before 1986 (8), and first emergence of *B. dendrobatidis* at a site has been linked with rapid extirpations of up to 50% of resident amphibian species and total declines in amphibian density of 80% (5). Both laboratory and field evidence indicate that growth and pathogenicity of *B. dendrobatidis* are inhibited by warm temperatures (9, 10), presumably explaining why most observed amphibian decline events have occurred in montane areas. The recently proposed "climate-linked epidemic hypothesis" suggests that severe outbreaks of chytridiomycosis are triggered by extreme climatic events (3).

Despite the growing amount of research investigating ultimate causes of amphibian declines, a pronounced lack of long-term data still makes it impossible to determine the status of most populations. Approximately 22.5% of amphibian species are listed as data deficient by the International Union for the Conservation of Nature and Natural Resources (IUCN), and this knowledge deficit is concentrated in tropical regions where the overwhelming proportion of biodiversity is located (1). Those declines that are generally reported are strongly biased toward "rapid" declines, which may include populations that decline from stable to extinct in a matter of months (5).

In contrast to the lack of long-term data for most tropical amphibian assemblages, amphibians have been sampled since the 1950s at La Selva Biological Station, a 16-km^2 primarily old-growth wet forest reserve in the Caribbean lowlands of Costa Rica (11). We compiled data obtained from several studies (1970–2005) that estimated density of amphibians and reptiles at La Selva by using a standard method (12). The available data focused specifically on the leaf litter herpetofauna, which at La Selva includes ≈26 species of frogs and 2 species of salamanders, but also 13 species of lizards and many species of snakes (11). The leaf litter guild of the lizard fauna represents the vertebrate group most ecologically similar to litter amphibians, and both terrestrial frogs and terrestrial lizards use similar habitats, microhabitats, and prey (13, 14). Because these two groups differ in physiological susceptibility to factors associated with amphibian declines (e.g., pesticide exposure or emerging infectious diseases), these ecologically similar lizards provide an invaluable contrast for sorting hypotheses about mechanisms driving amphibian declines.

Our primary goals were to determine whether amphibians at La Selva show evidence of population declines, whether population trends vary between terrestrial amphibians and terrestrial lizards, and whether population trends vary among habitat disturbance regimes. Given current knowledge of global trends in amphibian population declines (1), as well as detailed patterns for montane regions in the Neotropics (3, 6, 15), there is no *a*

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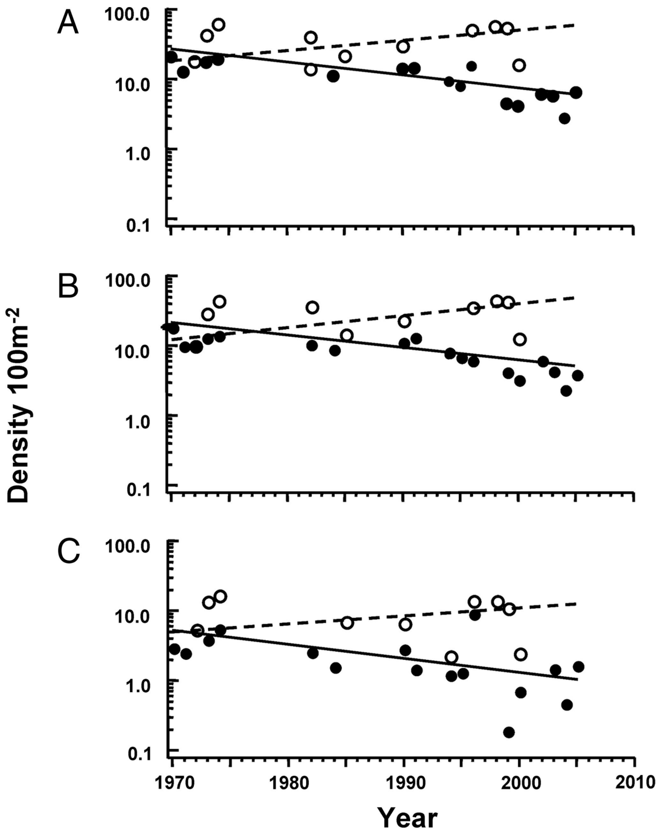

Fig. 1. Amphibian and reptile density over 35 years at La Selva Biological Station, Costa Rica. Each point indicates mean density for all quadrats in a given year. The closed symbols and solid line indicate data from primary forest. The open symbols and dashed line indicate data from abandoned cacao plantations. (*A*) Trends for all terrestrial amphibians and reptiles. (*B*) Trends for frogs only. (*C*) Trends for lizards only.

priori reason to expect widespread population declines to have occurred for the site or assemblage we examine.

Results

Our data indicate a 75% decline in total densities of leaf litter amphibians and reptiles in primary forest since 1970 (Fig. 1). Total frog density has declined by an average rate of 4.1% per year since 1970, and, unexpectedly, total lizard density has decreased by an average of 4.5% per year over the same period. Every individual species of frog or lizard for which we detected a significant trend (n = 17) decreased in density over the study period in primary forest (Table 1). Population trends differed markedly between primary forest and abandoned cacao plantations ($F_{1,12}$ = 104.6, P < 0.0001). In cacao, total density of amphibians and reptiles increased by an annual average of 4.0% and 2.7%, respectively. Although all species declined significantly in primary forest, in cacao, seven species declined and four increased in density; this habitat by taxon interaction was significant ($F_{1,12}$ = 17.44, P = 0.001). Even species that increased in density in cacao declined significantly in primary forest. Temporal trends in density did not differ between frog species and lizard species in forest ($F_{1,19}$ = 0.05, P = 0.82), in cacao ($F_{1,13}$ = 0.95, P = 0.35), or when habitat types were pooled ($F_{1,12}$ = 0.001, P = 0.95). Although individual species' temporal trends were statistically significant only for common species with adequate statistical power, there was no association between ranked abundance and slope of trend (r = 0.029, P = 0.801, n = 77).

Discussion

Our data indicate dramatic declines in total density of terrestrial amphibians since 1970, and nearly identical trends for lizards, but also indicate opposite trends in some species in adjacent abandoned cacao groves. Declines of similar magnitude to those we report for La Selva's primary forests have been widely reported for other tropical sites in Central and South America and Australia, but the trends we identify are distinct from all other recorded population declines in at least three major ways. First, community-wide amphibian population declines of the magnitude that we report herein have only been reported from cool climates: temperate regions or montane regions of the tropics (3, 15, 16). Second, amphibian decline events in the montane tropics have occurred rapidly, often in as little as 6 months (5). Third, declines in montane sites are only rarely reported to accompany declines in populations of other faunal elements such as reptiles or birds (17, 18). Hence, the widespread declines we describe appear fundamentally different from all other enigmatic population declines that have been reported previously.

Differentiating problematic declines from natural fluctuations in populations is an issue of particular difficulty in applied ecology (19, 20), yet community-wide unidirectional declines of the duration and intensity we report here are not consistent with reported data on population fluctuations at other tropical sites (21, 22). Dramatic fluctuations in amphibian population density may occur, but appear to be driven primarily by unpredictable aquatic environments (20, 23, 24). However, amphibian species with terrestrial direct development, including the majority of this assemblage (11), are independent from standing water and do not show such dramatic fluctuations in population size (24, 25). Finally, our data for primary forest suggest simultaneous declines among all common species without apparent intermittent years of high recruitment, an unlikely pattern for stochastic population fluctuations.

Habitat modification cannot provide a satisfactory explanation for our trends because these declines have occurred in protected old-growth rainforests (26). Because of short dispersal distances, high site fidelity, and the spatial configuration of forest types at La Selva, we consider it exceptionally unlikely that amphibians and reptiles are moving from old-growth habitats into abandoned cacao plantations. Habitat fragmentation has been linked to extirpations of several species of understory insectivorous birds at La Selva (27). However, fragmentation is an unlikely mechanism for our trends because most species of amphibians and reptiles at La Selva historically existed in very large populations that are unlikely to be susceptible to fragmentation-driven processes such as genetic drift, inbreeding, or demographic stochasticity. The declines we report are inconsistent with any reported declines attributable to chytridiomycosis because of either recent invasion of *B. dendrobatidis* (5) or emergence of *B. dendrobatidis* due to shifting climate (3). We are aware of no evidence that *B. dendrobatidis* can affect reptiles. Although *B. dendrobatidis* has been confirmed in the vicinity of La Selva (8), our preliminary testing of 140 individuals of *Oophaga pumilio*, *Craugastor bransfordii*, and *Dendropsophus ebraccatus* between June and November 2006 showed no evidence of infection by *B. dendrobatidis* (J. Wood, personal communication). We are aware of no reports of the presence of agrochemical pesticides within the La Selva reserve despite proximity to agricultural areas. Critically, neither habitat fragmentation nor chytridiomycosis nor pesticide drift can explain population increases in abandoned cacao groves among the same species experiencing declines in adjacent primary forest [these factors are discussed in supporting information (SI) *Text*].

We suggest that the most parsimonious explanation for declines at La Selva is that climate shifts in the past 35 years have reduced standing litter mass, a major proximate determinant of

Table 1. Population trends for leaf litter amphibians and reptiles at La Selva Biological Station

Taxon	1970s forest density, individuals 100 m^{-2}	Mean yearly percentage change	95% confidence limits	1970s cacao density, individuals 100 m^{-2}	Mean yearly percentage change	95% confidence limits	*F*	*P*
Entire herpetofauna	19.01	**−4.10**	(−4.6, −3.6)	54.46	**3.42**	(2.0, 4.9)	180.6	<0.0001
All frogs	14.24	**−4.01**	(−4.5, −3.5)	38.30	**3.99**	(2.5, 5.5)	168.6	<0.0001
All lizards	4.57	**−4.54**	(−5.4, −3.7)	14.81	**2.68**	(1.0, 4.5)	79.4	<0.0001
All salamanders	0.13	**−14.52**	(−17.0, −12.2)	0.64	**−17.10**	(−19.0, −15.2)	2.3	0.13
All snakes	0.03	1.90	(−0.1, 4.1)	0.72	−2.95	(−6.0, 0.5)	8.1	0.0047
Frogs								
Rhaebo haematiticus	0.23	**−5.93**	(−7.4, −4.4)	0.32	**−5.69**	(−8.4, −2.6)	0.03	0.86
Chaunus marinus	0.00			0.00	3.19	(−1.1, 8.0)		
Oophaga pumilio	3.20	**−1.18**	(−2.0, −0.4)	14.33	**8.75**	(7.3, 10.3)	146.8	<0.0001
Craugastor bransfordii	7.41	**−5.22**	(−6.0, −4.5)	20.46	**−4.45**	(−6.0, −2.8)	1.2	0.27
Craugastor fitzingeri	0.00	1.95	(−0.1, 4.1)	0.00				
Craugastor megacephalus	0.56	**−9.97**	(−11.2, −8.8)	1.27	**−7.35**	(−9.5, −5.0)	5.9	0.016
Craugastor mimus	0.39	**−13.49**	(−15.7, −11.5)	0.00				
Craugastor noblei	0.13	**−10.42**	(−13.3, −7.7)	0.00				
Craugastor talamancae	0.42	**−6.78**	(−8.2, −5.4)	0.00				
Eleutherodactylus caryophyllaceus	0.16	**−2.27**	(−3.8, −0.6)	0.00				
Eleutherodactylus cerasinus	0.10	−0.74	(−2.4, 1.0)	0.00	−1.27	(−4.5, 2.4)	0.11	0.74
Eleutherodactylus cruentus	0.10	**−3.51**	(−5.2, −1.8)	0.00				
Eleutherodactylus diastema	0.46	**−6.69**	(−8.0, −5.4)	0.64	**−5.41**	(−9.5, −0.4)	0.58	0.45
Eleutherodactylus ridens	0.20	**−5.77**	(−7.3, −4.2)	0.72	**−14.44**	(−19.1, −9.6)	22.3	<0.0001
Gastrophryne pictiventris	0.26	−2.10	(−4.7, 0.7)	0.08	**−3.52**	(−6.4, −0.3)	0.54	0.46
Lithobates warszewitschii	0.16	**−5.06**	(−6.7, −3.3)	0.00				
Lizards								
Ameiva festiva	0.13	**−3.05**	(−4.9, −1.1)	0.40	6.14	(−2.9, 17.4)	8.5	0.0037
Lepidoblepharis xanthostigma	0.82	**−8.05**	(−9.4, −6.8)	5.41	**−9.05**	(−10.8, −7.2)	0.78	0.38
Norops capito	0.07	−0.73	(−2.5, 1.1)	0.08	−0.24	(−4.0, 4.1)	0.08	0.78
Norops humilis	2.12	**−4.44**	(−5.5, −3.4)	6.13	**5.68**	(3.9, 7.5)	116.2	<0.0001
Norops limifrons	0.85	**−3.05**	(−4.4, −1.7)	1.27	**5.73**	(2.7, 9.0)	43.3	<0.0001
Sphenomorphus cherriei	0.42	**−10.03**	(−12.2, −7.9)	1.27	**6.51**	(2.8, 10.6)	69.0	<0.0001

Density (1970s) for forest and cacao represent mean number of individuals per 100 m^2 derived from studies in the early 1970s for forest and cacao habitats, respectively. Mean percentage change indicates mean yearly percentage change in population status for forest and cacao habitats, respectively; trends in bold are significant at the 0.05 significance level. Confidence limits indicate 95% confidence limits about the mean percentage change. *F* and *P* values indicate differences in trends between forest and cacao habitats. Entire herpetofauna includes frogs, lizards, salamanders, and snakes.

abundance for leaf litter amphibians and reptiles (13, 28–30). The annual mean of daily minimum temperature increased between 1982 and 2004 (Fig. 2*A*). Although total rainfall did not increase, the proportion of days with no rainfall decreased between 1970 and 2004 (Fig. 2*B*) (*SI Text*). The annual mean daily minimum temperature is negatively correlated with tree growth during the same period (31), indicating that these climatic shifts are of sufficient intensity to influence ecosystem processes. The increasingly warm and wet conditions of the past two decades could negatively influence standing litter mass by affecting rates of litterfall or litter decomposition (32). Litterfall in tropical forests may be stimulated by drought stress (33), and litter decomposition rates may be constrained by dry season moisture limitation (34). Therefore, an increase in precipitation and temperature may decrease quantity of litter stocks. Standing leaf litter depth has been positively associated with density of leaf litter amphibians and reptiles among microhabitats (28), forest types (13, 29), biomes (30), and between seasons (13). Additionally, litter dynamics can explain the difference in trends between habitat types: because cacao trees have several leaf-flushing events each year, litter accumulation is greater in cacao plantations than it is in old-growth forests (13). Furthermore, rates of litterfall may increase as early succession progresses in abandoned plantations (35). Because depth of leaf litter appears to strongly influence the density of both terrestrial amphibians and terrestrial reptiles, and because litter dynamics are controlled by climate, increases in temperature and precipitation frequency could decrease litter mass and reduce critical microhabitat resources for amphibians and reptiles.

Regardless of which factor (or combination of factors) has contributed to La Selva declines, we identify what we believe to be the strongest available evidence that amphibian declines in pristine habitats may be accompanied by simultaneous declines in other taxa. Cross-taxa declines have been documented elsewhere, yet not emphasized. Declines in populations of anoline lizards and forest birds accompanied well documented amphibian declines in Monteverde, Costa Rica (18). Populations of reptiles declined in conjunction with amphibians in the western United States (36) and in Panama (17). These simultaneous declines have been either attributed to wide-acting environmental changes (18) or posited as indirect consequences of amphibian declines manifested through trophic links (17). Yet because very few studies have documented population trends of other taxa when reporting amphibian declines, it is impossible to determine how frequently simultaneous declines of several taxa occur. Our data urge that attention be devoted to understanding how often other faunal groups decline in conjunction with amphibian populations, and what processes cause these simultaneous declines.

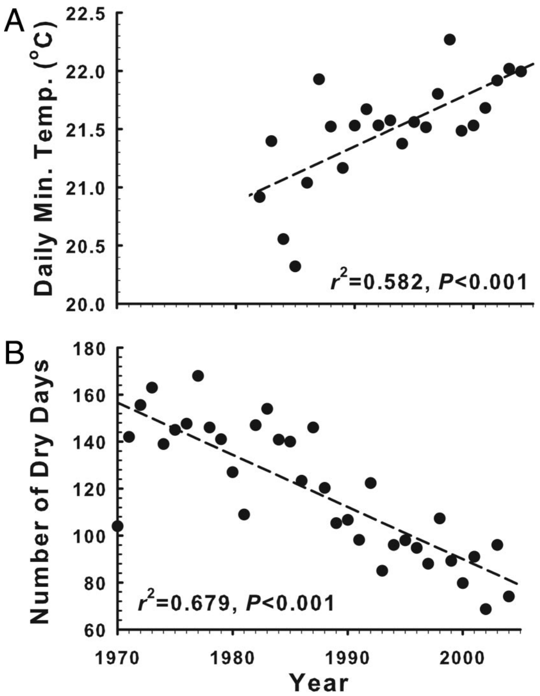

Fig. 2. Climate data for 35 years at the La Selva Biological Station indicates that the climate is getting warmer and more consistently wet. The annual mean of daily mean temperature (*A*) has increased and the number of days with zero rainfall has decreased since 1970 (*B*).

Amphibian decline events reported in the literature, particularly those from the Neotropics, are dominated by mass mortality events and rapid extirpations that occur over a period of a few months (3, 5). In contrast to these sudden decline events, we demonstrate in this report that community-wide gradual declines also may occur. Sadly, the dramatic declines we report here can only be considered slow in comparison to these nearly instantaneous extinction events. It is currently impossible to determine how often gradual community-wide declines such as the one we report here are actually occurring, because trends such as those we report are impossible to detect without long-term abundance-based data on population densities collected by using consistent methodology. Although such datasets are exceptionally rare, they will be critical to understanding the full extent of the amphibian decline crisis.

Furthermore, the lack of historic data on population densities may lead to naive or inappropriate assessments of conservation status, a phenomenon known as shifting baselines syndrome (37). Even in 2005, the last year for which we include data, population densities of terrestrial amphibians and reptiles at La Selva may be greater than densities from sites where similar methodologies have been used. Without robust historical datasets indicating precipitous declines, current densities of amphibians and reptiles could be used to suggest that amphibian and reptile populations at La Selva are free from conservation risks. Indeed, all but one of the amphibian species for which we report persistent decade-long declines in protected old-growth rainforests are listed as "least concern" in the IUCN Red List (38).

Our data raise the worrying possibility that systematic declines in amphibian populations do not occur only in cool climates, but that because declines occurring in cooler sites occur more quickly, these are the only habitats where they are detected. Our data indicate that even populations of amphibians for which specific threats have not been identified may nonetheless be suffering dramatic decline, and that such populations may be considered stable because of lack of long-term data, not lack of threats.

Materials and Methods

La Selva Biological Station (10° 25′ N, 84° 00′ W) is a 1,615 hectare evergreen tropical wet forest reserve in the Caribbean lowlands of Heredia Province, Costa Rica (26). Elevation ranges from 30 to 135 m above sea level. Mean monthly temperature ranges from 24.7°C in January to 27.1°C in August, and annual precipitation averages ≈4,000 mm with a short mild dry season from January to April (39). Approximately 53% of the La Selva reserve consists of old-growth forests, and <4% of the reserve consists of several small abandoned agricultural tracts. These former plantations of cacao (*Theobroma cacao*) were abandoned in part in 1963 and the remainder in 1986 (26). Secondary succession followed abandonment of these plantations. Although many *Theobroma* trees remain in these sites, in some cases there were efforts to remove trees from former plantation sites. Our data from former cacao plantations therefore reflect complicated histories of anthropogenic forest disturbance.

We compiled published and unpublished reports of density of leaf litter amphibians and reptiles at La Selva (SI Table 2). We included only data collected by using a single standard method, day-sampled litter quadrats (12). Briefly, sampling litter quadrats involves the demarcation of an area of the forest floor of fixed size followed by an exhaustive search for all amphibians and reptiles (12). This method is widely used for sampling of terrestrial amphibians and reptiles throughout the tropics. Size of quadrats used in this study range from 4 to 144 m^2. Plots were sampled in both primary forest and in abandoned cacao plantations undergoing secondary succession. In the case of studies that conducted experimental manipulations of study quadrats, only unmanipulated control quadrats were used. A component of our data (≈11% of area sampled) was collected by students in graduate and undergraduate courses and represents small studies with limited sample sizes. These student studies were supervised by experienced professional ecologists or herpetologists. Inclusion of these studies may increase variance because of observer effects, but are the only data available for many of the years in which data were collected.

The fundamental data from each census are the numbers of individuals of each species captured in exhaustive sampling of a quadrat. Of the 5,280 amphibian and reptile samples, 93 were unidentified frogs (e.g., *Eleutherodactylus* sp.) and 17 were unidentified salamanders (*Oedipina* sp.); total reptiles included 27 snakes. For tests of frogs and lizards, only species with at least five individuals were included. Individual studies included from 1 to 98 separate plots, typically within the same month but occasionally spread over an entire year. Not all studies recorded data separately by plot. Therefore, studies or plots were weighted by area sampled rather than equally by study, which produced estimates unaffected by the level of aggregation.

These data were analyzed with generalized linear mixed models with Poisson error and log-link, with log (quadrat size) included as an offset to correct for varying quadrat size (40). Temporal trends were estimated as linear slopes across years; with the log-link, these parameter estimates translate to multiplicative changes in abundance per year. For each species and habitat with five or more individuals, we report the multiplicative change per year as a percentage: $(1 - \beta_{\mathrm{year}}) \times 100\%$. Habitat (cacao vs. forest) and taxon (frog vs. lizard) were treated as fixed effects; species within taxon were considered random effects. Differences between taxa or habitats in temporal trends were tested as taxon × year or habitat × year interactions. Denominator degrees of freedom were computed by the containment method, so the taxon × year term was tested against the species (taxon) × year random effect. Preliminary analyses including wet season vs. dry season found no interactions of season with other factors, and there was no trend in season of sampling across years, so season was dropped from the analyses reported. The overdispersion parameter of the overall model including species, habitat, and year was 0.85, indicating reasonable fit with the Poisson error. Results similar to those we report were obtained when data collected by graduate or undergraduate courses were excluded from the analyses.

There is a significant negative trend in quadrat size over these 35 years, primarily a shift from 25 × 25 feet (58.06-m^2) and 8 × 8 m (64-m^2) quadrats toward larger numbers of 5 × 5 m (25-m^2) quadrats within a survey. Although smaller quadrats are expected to have higher capture efficiency, if they have lower capture efficiency (perhaps because of edge effects), quadrat size could artefactually contribute to the estimated declines. However, including an additional linear quadrat size term in the analyses strengthened the magnitude and statistical significance of the estimated declines, so these declines cannot be explained by the shift in quadrat sizes.

We used meteorological data collected on site at La Selva to explore long-term shifts in climate at this site (*SI Text*). We examined a number of climate variables in an exploratory search for long-term shifts in local climate. We report results only for variables for which long-term shifts in climate have been previously reported for this site (31), or for which we detected significant changes over our study period.

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