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# Compensatory recruitment allows amphibian population persistence in anthropogenic habitats

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**Habitat anthropization is a major driver of global biodiversity decline. Although most species are negatively affected, some benefit from anthropogenic habitat modifications by showing intriguing life-history responses. For instance, increased recruitment through higher allocation to reproduction or improved performance during early-life stages could compensate for reduced adult survival, corresponding to “compensatory recruitment”. To date, evidence of compensatory recruitment in response to habitat modification is restricted to plants, limiting understanding of its importance as a response to global change. We used the yellow-bellied toad (*Bombina variegata*), an amphibian occupying a broad range of natural and anthropogenic habitats, as a model species to test for and to quantify compensatory recruitment. Using an exceptional capture–recapture dataset composed of 21,714 individuals from 67 populations across Europe, we showed that adult survival was lower, lifespan was shorter, and actuarial senescence was higher in anthropogenic habitats, especially those affected by intense human activities. Increased recruitment in anthropogenic habitats fully offset reductions in adult survival, with the consequence that population growth rate in both habitat types was similar. Our findings indicate that compensatory recruitment allows toad populations to remain viable in human-dominated habitats and might facilitate the persistence of other animal populations in such environments.**

global change | recruitment | survival | senescence | amphibians

Habitat anthropization is a worldwide phenomenon and one of the major causes of biodiversity decline (1). Typically, anthropization involves various types of land-use change (e.g., urbanization, intensive agriculture, mining, logging, and deforestation), whereby natural habitats are converted into seminatural or human-dominated environments. The composition of animal communities is altered by these changes (2–4), with species being extirpated or favored according to their life-history strategies (3, 5). Species that benefit from habitat anthropization may exhibit adaptive modifications of their life histories (6, 7), behavior (8), and physiology (9). However, understanding of these mechanisms among animals is currently restricted to a few study systems, mainly birds along gradients of urbanization (7), which limits our ability to predict the effects of habitat anthropization on population viability.

Life-history theory provides a conceptual framework to predict the influence of habitat anthropization on the dynamics of populations. This theory, rooted in the principle of allocation (10), is based on the tenet that during an individual lifetime, limited resources (i.e., nutrients and energy) are allocated to competing functions (i.e., growth, reproduction, and survival [11, 12]). Resource limitation leads to trade-offs among life-history traits (for instance between survival and reproduction [13]). Across species, these trade-offs between fitness components lead to the “slow–fast continuum” (14, 15), an axis of life-history variation along which organisms range from “live-fast/die-young” strategies with a short lifespan and a high annual fecundity to “live-slow/die-old” strategies with the opposite attributes. The strength of actuarial senescence (i.e., the increase in mortality with increasing age, hereafter “senescence”) also contributes to the species/populations’ position along the slow–fast continuum and becomes greater as the life history accelerates (16, 17).

Following this theoretical background, two demographic scenarios can be proposed about the impact of habitat anthropization on populations within a species. First,

## Significance

Our study demonstrates that anthropogenic habitat modification results in higher adult mortality and accelerated actuarial senescence in yellow-bellied toad populations across Europe. However, higher mortality is offset by increased recruitment, which accelerates individual life cycles in anthropogenic habitats. We show that compensatory recruitment allows amphibian populations to persist even in highly modified landscapes.

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The authors declare no competing interest.

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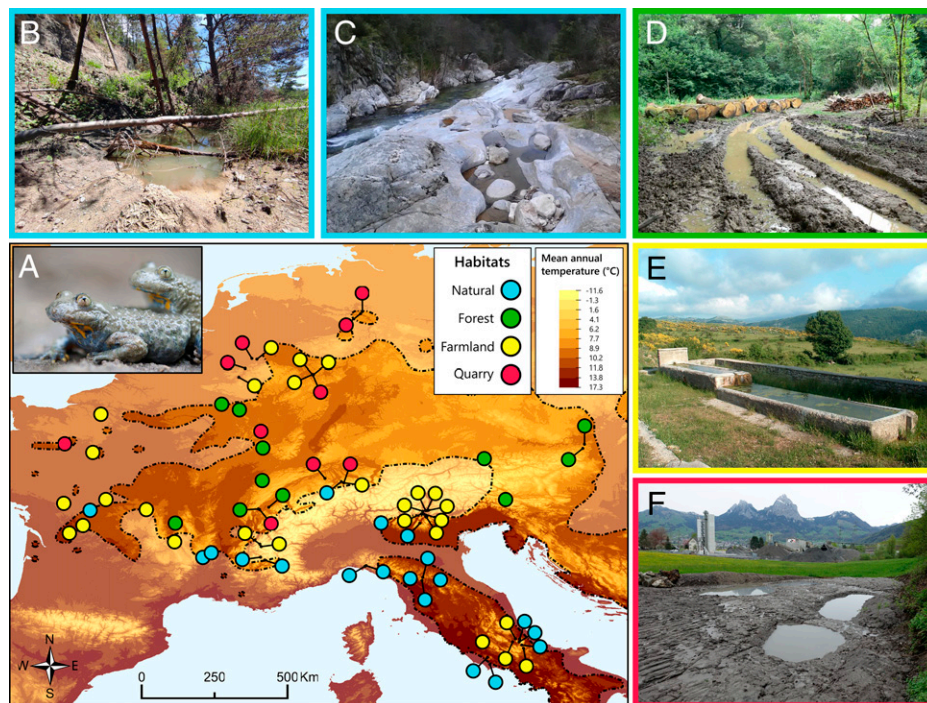
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anthropization can decrease environmentally driven risks of adult mortality (e.g., predation or parasitism), promoting a slow life-history strategy through reduced annual reproductive allocation and increased lifespan (18). Birds along urbanization gradients match this scenario (7). However, in most cases, habitat anthropization and related human activities cause increased adult mortality (19, 20), which can be offset by increased recruitment through elevated reproductive effort and/or improved early-age performance (e.g., higher juvenile survival and faster growth). This phenomenon, termed “compensatory recruitment” (reviewed by Valenzuela-Sánchez et al. [21] in the context of disease ecology), might lead to an accelerated life cycle in anthropogenic habitats.

To date, empirical investigations of compensatory recruitment in relation to habitat anthropization among animals are scarce (for plants, see refs. 22 and 23), and two questions remain unresolved: 1) does compensatory recruitment arise as a response to human activities in anthropogenic habitats? If so, 2) does this phenomenon allow the long-term persistence of populations in anthropogenic environments? We addressed these issues using the yellow-bellied toad (*Bombina variegata*) as a model organism. This pond-breeding amphibian is a good model to test for compensatory recruitment because it is widely distributed in Europe and occupies diverse natural and anthropogenic habitats (24) (Fig. 1). *B. variegata* breeds in small waterbodies that are affected by frequent disturbances; consequently, they remain at an early-successional stage with low densities of aquatic predators, with the result that tadpole survival and adult recruitment in these anthropogenic habitats are increased (25–27). Natural habitats correspond to environments where the main disturbance sources that determine the presence and renewal of breeding waterbodies (i.e., rocky pools on riverbanks and puddles associated with intermittent streams and springs) are natural phenomena, such as floods, desiccation, and landslides (25, 28). By contrast, anthropogenic habitats designate environments where the principal sources of creation and disturbance of breeding waterbodies

(i.e., ruts, ditches, seminatural ponds, and drinking troughs) are human activities, such as quarrying, livestock farming, and logging (29–31). Natural disturbances such as floods generally have only a minor influence on the survival of adult *B. variegata* (32), whereas anthropogenic disturbances (including vehicle traffic in waterbodies, cleaning of ditches, and filling of ruts for the maintenance of unpaved pathways) increase adult mortality (31, 33) and reduce body condition (34). Nonetheless, anthropogenic habitats currently host large and healthy populations of *B. variegata* (8, 35), while the extent of natural habitat has been greatly reduced in most European landscapes during the 20th century (36). This suggests that increased recruitment could offset human-induced adult mortality, allowing the persistence of *B. variegata* in human-dominated environments.

Using a large capture–recapture dataset (21,714 individuals), we estimated adult recruitment, adult survival, lifespan, and senescence rate across 67 populations of *B. variegata* in western Europe (Fig. 1A). We tested whether populations from anthropogenic habitats displayed compensatory recruitment using a two-step approach (SI Appendix, Fig. S1). First, we examined differences in demographic parameters of populations in natural (Fig. 1B and C) and anthropogenic habitats (i.e., quarries, farmland, and logged forest; Fig. 1D–F). Specifically, we tested the hypothesis that adult survival was lower, lifespan was shorter, and senescence was faster in anthropogenic habitats than in natural habitats due to harmful human activities. We also tested the hypothesis that increased adult recruitment in anthropogenic habitats compensates for decreased adult survival, leading to an accelerated life cycle in viable populations. Second, we tested for compensatory recruitment within anthropogenic habitats by comparing sites where quarrying and logging activities had been attenuated within protected areas (i.e., protected forests and abandoned quarries in nature reserves) with those where human activities continued unabated outside protected sites (e.g., forests managed for timber production and active quarries). We



**Fig. 1.** (A) Map showing the 67 western European populations of *B. variegata* monitored using capture–recapture methods. The distributional range of this species according to IUCN data (24) is displayed, although a few of the study populations occurred outside this range. (B and C) Examples of natural habitats: natural pond created by landslides (B) and rocky pools on riverbanks (C). (D–F) Examples of anthropogenic habitats: ruts in a logged forest (D), drinking trough in farmland (E), and puddles in a quarry (F).

expected populations exposed to intense human activities in unprotected anthropogenic habitats to have the lowest adult survival and highest rate of senescence. Third, we tested whether increased recruitment was able to compensate for higher adult mortality in such highly modified human-dominated habitats.

## Results

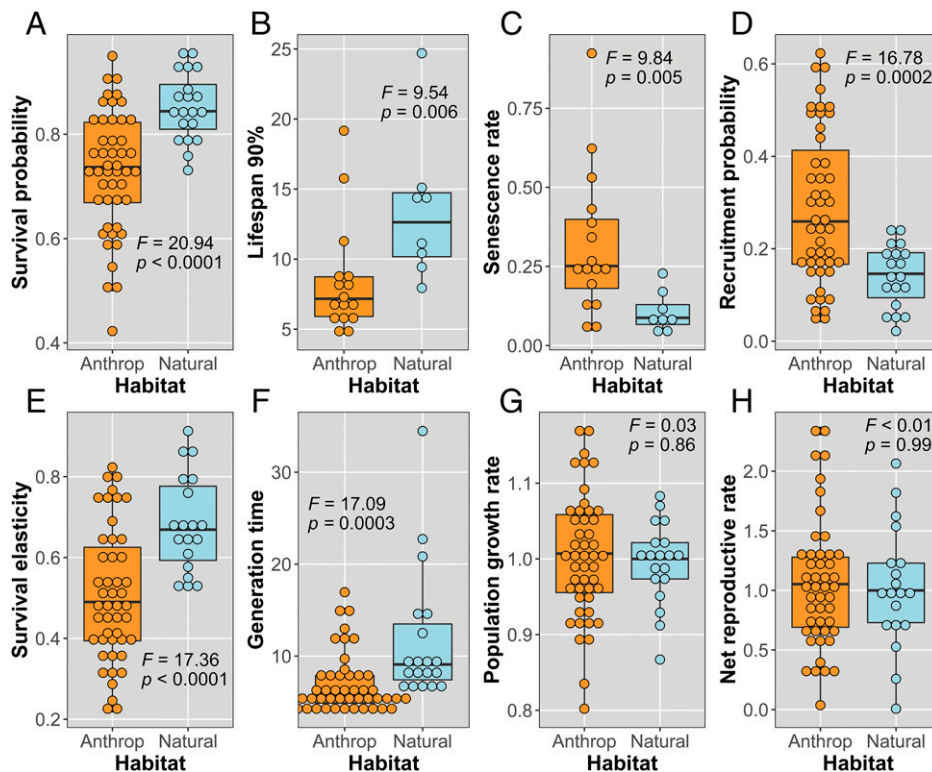
Our analyses focused on 67 populations of *B. variegata* across Europe from The Netherlands to Central Italy. The demographic studies were conducted between 1994 and 2021, and the average length of capture–recapture monitoring was  $7.5 \pm 5$  y (minimum: 3, maximum: 23). The annual population size varied considerably among populations, ranging from a few individuals (<10) to 4,595 individuals (population F1; *SI Appendix, Dataset S2*).

We tested whether demographic parameters estimated using population-specific capture–recapture models (*SI Appendix, Figs. S1–S5*) differed between natural and anthropogenic habitats using meta-regression analyses (37) that take into account sampling variance of demographic parameters (*SI Appendix, Section 7*). Adult survival probability was lower in anthropogenic (mean  $\pm$  SE:  $0.73 \pm 0.018$ ) habitats than in natural ( $0.85 \pm 0.017$ ) habitats ( $F_{1,55.6} = 20.94$ ,  $P < 0.0001$ ; unique variance explained  $R^2_{\beta} = 0.2$ , on the logit scale; Fig. 2A). Further analyses indicated that the effect of habitat anthropization (a two-modality factor: natural versus anthropogenic habitats) on adult survival persisted after controlling for the effect of the spatial proximity among populations ( $F_{1,55} = 19.95$ ,  $P < 0.0001$ ). In addition, the elasticity of adult survival (i.e., the impact of a given proportional change of adult survival on population growth rate  $\lambda$ ) was lower in

anthropogenic habitats than in natural habitats ( $0.50 \pm 0.02$  versus  $0.68 \pm 0.03$ ;  $F_{1,62} = 17.36$ ,  $P < 0.0001$ ,  $R^2_{\beta} = 0.21$ ; Fig. 2E). Additional analyses examining whether habitat anthropization explained variation in demographic parameters among natural habitats, logged forests, quarries, and farmland (*SI Appendix, Fig. S6*) also supported these findings (*SI Appendix, Table S11*).

Senescence rate (measured as the exponential rate of increase in mortality risk with age, the  $b_1$  parameter in the Siler model [38]; *Materials and Methods*) was higher in anthropogenic ( $0.29 \pm 0.05$ ) habitats than in natural ( $0.10 \pm 0.03$ ) habitats ( $F_{1,22} = 9.97$ ,  $P = 0.005$ ,  $R^2_{\beta} = 0.31$ , on the log scale; Fig. 2C). In addition, the lifespan (i.e., the age at which 90% of individuals were alive after the first overwintering died) was lower in anthropogenic ( $7.73 \pm 0.74$  y) habitats than in natural ( $12.68 \pm 1.72$  y) habitats ( $F_{1,21} = 9.54$ ,  $P = 0.006$ ,  $R^2_{\beta} = 0.24$ , on the log scale; Fig. 2B). The same pattern was found for lifespan 80% and lifespan 50%, although not with a statistically significant difference for lifespan 50% (*SI Appendix, Fig. S11*), which might suggest that the effect of habitat on mortality was stronger late in life when senescence occurs. Generation time ( $T_b$ ) was also shorter in anthropogenic habitats ( $6.26 \pm 0.33$  versus  $10.37 \pm 1.14$  y;  $F_{1,26.7} = 17.09$ ,  $P = 0.0003$ ,  $R^2_{\beta} = 0.37$ , on the log scale; Fig. 2F).

Our analyses provide strong evidence that an increase in adult recruitment—namely the proportion of new adults recruited annually into the population (39)—compensated for higher mortality in anthropogenic habitats. Adult recruitment, which was negatively correlated to adult survival ( $r = -0.83 \pm 0.04$ , on the logit scale), was almost twofold higher in anthropogenic ( $0.27 \pm 0.03$ ) than in natural ( $0.14 \pm 0.01$ ;  $F_{1,46.4} = 16.78$ ,  $P = 0.0002$ ,  $R^2_{\beta} = 0.26$ , on the logit scale;



**Fig. 2.** (A–G) Demographic parameters of 67 *B. variegata* in natural and anthropogenic (“Anthrop”) habitats (farmland, quarry, and logged forest combined) in western Europe: annual survival probability (A), lifespan (i.e., the age at which 90% of the individuals alive after the first overwintering were dead) (B), senescence rate (i.e., the increase in mortality with age) (C), annual recruitment (D), survival elasticity (E), generation time ( $T_b$ , in years) (F), population growth rate ( $\lambda$ ) (G), and net reproductive rate ( $R_0$ ) (H). The plots were produced from raw demographic estimates.  $F$  statistics and  $P$  values are from meta-regression models where demographic variables were log transformed and where survival and recruitment probabilities were on the logit scale. The models also accounted for differences in variance between anthropogenic and natural habitats (*SI Appendix*).

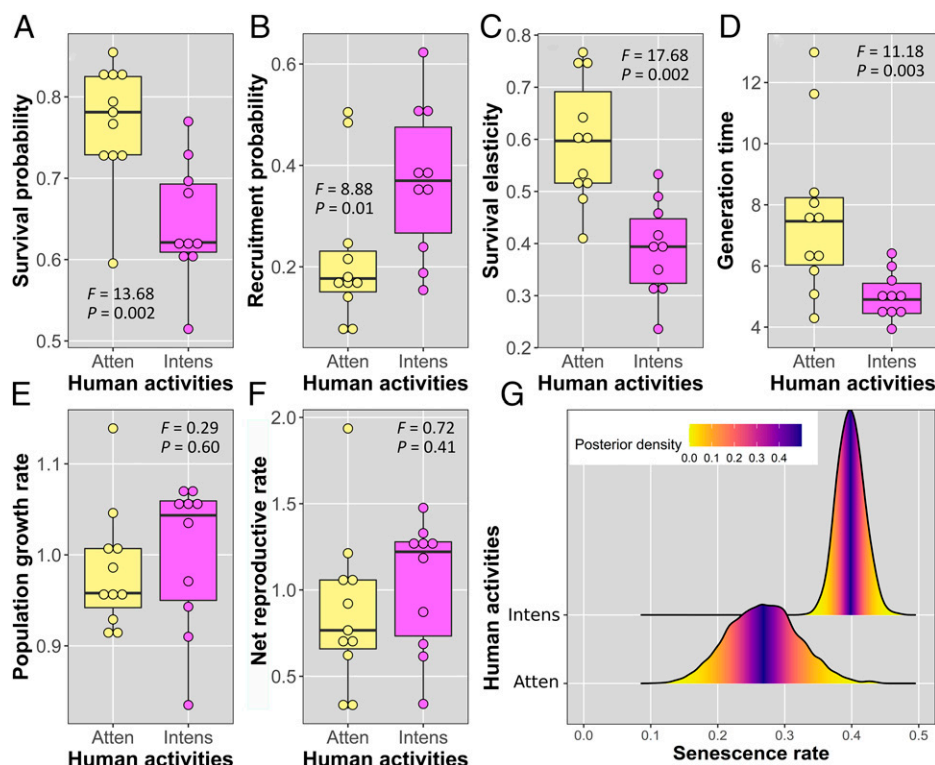
Fig. 2B) habitats. This association persisted when accounting for the influence of the spatial proximity among populations in the model ( $F_{1,55.5} = 11.65$ ,  $P = 0.001$ ). Population growth rates ( $\lambda$ ) were almost identical in natural ( $0.99 \pm 0.02$ ) and anthropogenic ( $1.0 \pm 0.01$ ) habitats ( $F_{1,62} = 0.03$ ,  $P = 0.86$ ; Fig. 2G), and the net reproductive rate ( $R_0$ ) did not differ between them ( $1.02 \pm 0.12$  versus  $1.01 \pm 0.08$ ;  $F_{1,62} < 0.01$ ,  $P = 0.99$ ; Fig. 2H). Lastly, a life table response experiment (LTRE)—a retrospective approach aiming to partition the difference of population growth rate between two situations (e.g., populations, treatments, or contexts) into contributions of the different vital rates (40)—was applied to quantify compensatory recruitment. Using populations from natural habitats as the reference, the LTRE revealed that the difference in adult survival between habitats reduced  $\lambda$  by 0.09 in anthropogenic environments. However, this was almost entirely offset by a greater adult recruitment, which increased  $\lambda$  by 0.08 in anthropogenic habitats, ensuring the long-term persistence of *B. variegata* populations (with  $\lambda = 1.00$ ). Population sizes in natural and anthropogenic habitats were quite similar (SI Appendix, Section 11).

**Effects of the Intensity of Human Activity on Demographic Variation within Anthropogenic Habitats.** We investigated whether demographic rates were associated with the level of intensity of human activities (“attenuated” versus “intense”; Materials and Methods) in anthropogenic habitats and tested for the existence of compensatory recruitment in this context (SI Appendix, Fig. S1). Our analyses focused on forest (forests managed for timber production versus forests in protected areas) and quarries (active quarries versus abandoned quarries in

protected areas), that is, 21 populations in total. Metaregression analyses showed that the adult survival probability was lower in habitats with intense human activities ( $0.66 \pm 0.03$ ) than in those where activities had been attenuated ( $0.78 \pm 0.02$ ;  $F_{1,18.7} = 13.68$ ,  $P = 0.002$ ,  $R^2_\beta = 0.42$ , on the logit scale; Fig. 3A). The elasticity of adult survival was also lower in habitats with intense human activities ( $0.39 \pm 0.03$  versus  $0.60 \pm 0.03$ ;  $F_{1,19} = 20.11$ ,  $P < 0.0001$ ,  $R^2_\beta = 0.51$ ; Fig. 3C).

Senescence was likewise influenced by the intensity of human activities within anthropogenic habitats. We obtained estimates of senescence rates from five populations with attenuated human activities (two from abandoned quarries and three from protected forests) and five populations with intense activities (two from active quarries and three from forests managed for timber production). We compared the averaged posterior distribution of senescence rates, which showed little overlap (Fig. 3G), indicating that senescence rates were higher in habitats with intense activities ( $0.40 \pm 0.02$ ) than in those where activities had been attenuated ( $0.27 \pm 0.05$ ). Moreover, generation time was shorter when populations experienced intense activities ( $4.97 \pm 0.41$  y versus  $7.27 \pm 0.57$  y;  $F_{1,19} = 11.18$ ,  $P = 0.003$ ,  $R^2_\beta = 0.37$ , on the log scale; Fig. 3D).

Our analyses provide evidence for the existence of compensatory recruitment in response to the intensity of human activities. Adult recruitment was higher in habitats with intense activities ( $0.36 \pm 0.04$  versus  $0.21 \pm 0.03$ ;  $F_{1,12} = 8.88$ ,  $P = 0.01$ ,  $R^2_\beta = 0.42$ , on the logit scale; Fig. 3B). The average population growth rate ( $\lambda$ ) was similar in populations experiencing intense ( $1.0 \pm 0.02$ ) and attenuated ( $0.98 \pm 0.02$ ) activities ( $F_{1,19} = 0.29$ ,  $P = 0.60$ ,  $R^2_\beta = 0.01$ ; Fig. 3E). In addition,



**Fig. 3.** (A–F) Demographic rates of 21 *B. variegata* populations in anthropogenic habitats where human activities (quarrying and logging) were attenuated (“Atten”, 10 populations) or intense (“Intens”, 10 populations): annual survival probability (A), annual recruitment probability (B), survival elasticity (C), generation time ( $T_b$ , in years) (D), population growth rate ( $\lambda$ ) (E), net reproductive rate ( $R_0$ ) (F), and senescence rate (G). Sites with attenuated activities correspond to protected areas (i.e., protected forests and abandoned quarries in nature reserves), whereas sites with intense activities designate areas where logging and quarrying operations continued unabated outside protected zones (e.g., forests managed for timber production and active quarries). The plots were produced from raw demographic estimates. F statistics and P values are from metaregression models, where demographic variables were log transformed and where survival and recruitment probabilities were on the logit scale (SI Appendix).

there was negligible difference in net reproductive rate ( $R_0$ ) in habitats with intense ( $1.03 \pm 0.13$ ) and attenuated activities ( $0.88 \pm 0.13$ ;  $F_{1,19} = 0.72$ ,  $P = 0.41$ ,  $R^2_{\beta} = 0.03$ , on the log scale; Fig. 3F). Moreover, the LTRE revealed that intense human activities reduced  $\lambda$  by 0.09. However, this was offset by a rise in recruitment, increasing  $\lambda$  by 0.08, which allowed populations to persist over the long term ( $\lambda = 1.01$ ). Lastly, population size varied marginally according to the intensity of human activities, depending on habitat type (SI Appendix, Section 11). Mean population sizes were higher in forest populations exposed to intense activities than in those with attenuated activities, but this effect was not seen in quarries.

## Discussion

Our study provides clear evidence that compensatory recruitment allows the sustainability of *B. variegata* populations in anthropogenic environments. In these habitats, individuals have lower adult survival, shorter lifespan, and quicker senescence than those in natural habitats. Yet, increased recruitment fully compensates for the higher adult mortality, including in anthropogenic habitats with intense human activities. This leads to contrasting life-history strategies among habitats and a spectacular acceleration of life cycles in human-dominated environments.

**Anthropogenic Habitats Are Associated with Increased Adult Mortality and Accelerated Senescence.** On average, mean adult survival of *B. variegata* was 14% lower, and lifespan was 39% shorter in anthropogenic habitats, where loss and degradation of breeding sites are major causes of adult mortality. In logged forests, for example, the destruction of breeding waterbodies due to harvesting operations may reduce annual survival of adults by 45% (33). In addition, frequent vehicle traffic through breeding waterbodies along unpaved roads is associated with smaller body size and lower body condition in quarries (34). Our results are consistent with previous findings that human activities dramatically increase adult mortality of anurans (41–43) and other vertebrates (19, 20) in anthropogenic environments. Nevertheless, we found considerable variation in adult survival among populations within logged forests, farmland, and quarries. Habitats with intense quarrying and logging activities were associated with lower adult survival than habitats where these activities had been attenuated by appropriate conservation management. Our results indicate that the reduction of anthropogenic disturbances and amphibian-specific management result in survival rates of adult toads that are comparable to those in some natural habitats.

Senescence rates in anthropogenic habitats were 167% higher than in natural habitats and were highest in sites with intense human activities. Accelerated senescence in anthropogenic habitats may arise from three nonexclusive pathways that cannot be disentangled from our study. First, increased senescence rate may result from the decreased force of natural selection on adult survival caused by the overall acceleration of the life cycle we observed. This indirect pathway is congruent with the higher senescence rates reported in vertebrate species with fast life histories than in those with slower life histories (16). Second, the acceleration of senescence could be a direct consequence of compensatory recruitment through the occurrence of increased reproductive costs. In anthropogenic habitats where the risk of adult mortality is high, selection might favor individuals investing heavily in reproduction at the expense of somatic maintenance, which could result in the deterioration of some

physiological functions, thereby accelerating senescence and shortening lifespan (44). Third, stressful environmental conditions brought about by human activities could have a direct detrimental impact on organisms' physiology (e.g., accelerated telomere attrition [45], as recently reported in common lizard [*Zootoca vivipara*] in the context of climate warming [46]), which may intensify senescence and shorten lifespan in the long run. Irrespective of the pathway involved, we provide evidence of a close link between habitat anthropization and senescence of *B. variegata*, which supports the hypothesis that anthropogenic global change is a critical driver of aging in animal populations (47, 48).

**Anthropogenic Habitats Are Associated with Increased Adult Recruitment.** Average recruitment of adult *B. variegata* was 93% higher in anthropogenic habitats than in natural habitats. This result could reflect the operation of two processes that may have synergic effects on recruitment. First, higher recruitment in anthropogenic habitats could be due to increased reproductive allocation. In support of this, females from logged forests and farmland produce, on average, more juveniles per year than those from natural habitats (31). Second, human disturbance that is detrimental to adult survival could increase reproductive success by modifying the conditions prevailing in waterbodies during larval growth. For instance, vehicle traffic on unpaved roads causes disturbance to temporary waterbodies that form in ruts, reducing submerged aquatic vegetation and the density of predatory insects (such as Odonate larvae), thereby increasing tadpole survival and reproductive success (27, 49, 50). Likewise, logging operations that destroy extant breeding sites may also create new ones where breeding probability and success are higher than before due to increased exposure to sunlight (36) and a relative scarcity of predatory aquatic insects (27).

Our analyses highlighted considerable variation in recruitment among *B. variegata* populations within anthropogenic habitats, reflecting, in part, the intensity of human disturbances. Attenuated quarrying and decreased logging activities were associated with lower recruitment than in habitats where intense activities occurred. This striking and rather nonintuitive result indicates that changes in management practices may have contrasting effects on *B. variegata* demography. By reducing habitat alterations within protected areas, wildlife managers can reduce rates of mortality of adult toads, but this may have the undesirable effect of decreasing adult recruitment, most likely because predator densities in ponds increase predation on tadpoles (25, 27). Our findings are congruent with previous studies showing that human disturbance plays an essential role in maintaining suitable artificial breeding waterbodies (49, 50) and contributes to the persistence of *B. variegata* populations in quarries, farmland, and logged forests (8, 25). More broadly, current evidence shows that population viability of animals and plants using early-successional habitats often relies on anthropogenic disturbance (51), especially in human-dominated landscapes where natural disturbance regimes have been profoundly modified.

**Compensatory Recruitment Leads to an Accelerated Life Cycle in Anthropogenic Habitats.** On average, increased recruitment counterbalanced decreased adult survival of *B. variegata* in anthropogenic habitats, providing strong evidence of a compensatory recruitment. The net reproductive rate was similar in both natural and anthropogenic habitats where, on average, populations were close to demographic stationarity (i.e.,  $\lambda = 1$ ). However, the existence of compensatory recruitment did not always prevent *B. variegata* populations from declining. Almost

half (47% or 22 out of 47) of populations from anthropogenic habitats had a negative population growth rate ( $\lambda < 1$ ), and this was similar to that seen in natural habitats (42% or 8 out of 19 populations with  $\lambda < 1$ ). Although the population growth rate estimates were more variable in short-term than in long-term studies (*SI Appendix*, Fig. S10), our findings suggest that the potential for compensatory recruitment might be limited in some populations. A combination of extreme weather events (32, 52), emerging diseases (53), and a reduction in the number of breeding sites due to certain management practices (33) reduce the production of juveniles and/or prereproductive survival of *B. variegata*. The subsequent decrease in adult recruitment diminishes the potential to compensate for adult mortality and thereby increases the risk of local extinction of populations.

We demonstrated that compensatory recruitment leads to a spectacular acceleration of the *B. variegata* life cycle since average generation time in anthropogenic habitats (6.3 y) was as much as 39% shorter than in natural habitats (10.4 y) and 52% shorter (5.0 y) in man-made habitats experiencing intense human activity. Interestingly, while a demographic response to habitat anthropization occurs in both amphibians and birds, the demographic parameter involved and the change in life cycle speed differ. Thus, increased adult survival in urban birds is associated with a slower life cycle (7), whereas the occurrence of compensatory recruitment speeds up the life cycle of *B. variegata* in various human-dominated habitats. Regardless of the direction of the change, these works demonstrate that habitat anthropization can cause marked within-species changes of life history that are at least as large as those generated by variations in latitude, altitude, or temperature (47, 54, 55).

The evolutionary mechanisms underlying life-history acceleration and compensatory recruitment in our study system are still unknown. Increased recruitment could be enabled by nucleotide or structural variations in the genome, which have allowed rapid adaptation to habitat anthropization and human disturbances in other vertebrates (56, 57). Furthermore, compensatory recruitment could be facilitated by a strong plasticity of demographic traits (21, 58), which could have epigenetic bases [e.g., DNA methylation (59)] facilitating the transgenerational inheritance of accelerated life cycles in anthropogenic habitats. Quantifying the respective contribution of phenotypic plasticity and adaptation to compensatory recruitment remains a crucial challenge to better understand the evolutionary significance of demographic compensation (21).

## Conclusions

Our study demonstrates that habitat anthropization, especially when accompanied by intense human activities, is associated with a dramatic reduction of adult survival and lifespan of adult *B. variegata* and accelerated senescence. Strikingly, however, increased recruitment compensates for this greater adult mortality, with the consequence that life cycles are completed more quickly in these novel anthropogenic habitats. The compensatory recruitment we observed is similar to that previously reported in vertebrates (including other amphibians) affected by infectious diseases that increase the risk of adult mortality (21). Here, we present evidence that animal populations affected by human disturbance exhibit compensatory recruitment and associated life-history shifts similar to the demographic responses previously reported for plants (22, 23). Compensatory recruitment is likely a key mechanism ensuring the long-term persistence of populations in degraded, unstable, or frequently disturbed anthropogenic habitats, which are likely to become increasingly prevalent in the near term.

## Materials and Methods

**Study Populations.** We gathered capture–recapture data from 67 populations of *B. variegata* across the western part of the species' range (Fig. 1A). Our general analyses comparing demographic parameters in natural and anthropogenic habitats were performed on the entire dataset. Twenty populations were located in natural habitats (Fig. 1B and C), and 47 populations were associated with three types of anthropogenic habitats (Fig. 1D–F): quarries (10 populations), farmland (26 populations), and logged forests (11 populations). Our analyses on the influence of the intensity of human activity focused on quarries and logged forest habitats (i.e., 21 populations in total), where the regulation of logging and quarrying activities could be readily assessed—the situation is more complicated in farmland that is often used by multiple landowners in very different ways. Quarries that had been abandoned for at least 10 y and/or where breeding sites were protected (e.g., by inclusion within a nature reserve) and actively managed for wildlife protection were classified as having attenuated human activities. Forest habitats were regarded as experiencing attenuated human activities if they were located within a protected area (such as a nature reserve) where logging continued but habitats were managed in such a way that *B. variegata* breeding sites were protected from logging operations. Where there was no environmental protection of any sort, quarries and logged forest were regarded as experiencing intense human activities.

The characteristics of each surveyed population (i.e., study period, duration, number of individuals captured, and number of captures performed during the study period) are set out in *SI Appendix*, Table S1. The capture–recapture sampling protocol was the same for all 67 populations and has been described in previous studies (31, 53, 60, 61). Briefly, several capture sessions were performed each year during which individuals were caught by hand or by using dipnets. The belly of each individual, which has unique markings allowing individual recognition using image-matching software (62), was photographed at every capture.

**Estimating Adult Survival and Recruitment.** We estimated annual survival of adults and annual recruitment using observations of individuals 3 y old (i.e., the age at sexual maturity) and older in the 67 *B. variegata* populations (*SI Appendix*, Fig. S1). We used goodness-of-fit (GOF) tests to assess transience (i.e., individuals captured for the first time have a lower expectation of being reobserved in the future than individuals of the same sample that had been captured previously), trap dependence (i.e., individuals behaviorally respond to capture and become harder to catch [trap shyness]), and recapture heterogeneity (i.e., individuals differ in their capture rate). We built models taking these effects into account whenever necessary. A stepwise approach was adopted to choose a model structure appropriate for each population. First, we used the tests 2CT and 3SR implemented in the program U-CARE (63) to assess trap dependence and transience, respectively, and the global test for recapture heterogeneity. If the global test was significant ( $P < 0.05$ ), we checked the presence of recapture heterogeneity using the GOF test proposed by Jeyam et al. (64). In cases where the test failed to run because of a too small sample size or short time series, we tested for recapture heterogeneity by comparing the AICc (Akaike information criterion adjusted for small samples) of models with and without Pledger's heterogeneity mixtures (65) (see model description below). We detected transience only, trap dependence only, and recapture heterogeneity in four, two, and eight populations, respectively (*SI Appendix*, Table S3).

Annual adult survival and recruitment were estimated separately for each population. Recruitment, namely the proportion of "new" adults in the population at time  $t$ , was quantified using a reverse-time capture–recapture model (39). The capture–recapture models were implemented in the program E-SURGE (66). When the GOF test was significant ( $P < 0.05$ ) for transience, we built the transience model (parametrization B) proposed by Genovart and Pradel (67), which allows transience, survival, and recapture probabilities to be estimated simultaneously (*SI Appendix*, Figs. S2–S5). We adapted this model to estimate recruitment along with recapture and transience probabilities using the matrices presented in *SI Appendix*, Figs. S2–S5. For the populations where recapture heterogeneity was detected, we used multievent models including Pledger's heterogeneity mixtures (65) (for recruitment model with heterogeneity mixtures, see ref. 68). When trap dependence was detected, we used the model described in Pradel and Sanz-Aguilar (69) to estimate survival

and adapted this parametrization to estimate recruitment (*SI Appendix, Figs. S2–S5*). We allowed for annual variation in recapture probability for all 67 populations. We obtained reliable estimates of annual adult survival and recruitment for 67 and 66 populations, respectively (*SI Appendix, Dataset S1*); in one case (population N13), recruitment probability was 0 due to an “edge effect” and was removed from further analyses. For eight populations (*SI Appendix, Table S3*), we simplified the model structure by removing trap dependence or heterogeneity effects to facilitate model convergence and thereby obtain accurate estimates of survival and recruitment.

**Estimating Senescence Rate and Lifespan.** Population-specific senescence rates and lifespans were estimated using Bayesian survival trajectory analyses implemented in the R package BaSTA (70, 71). Simulations by Colchero and Clark (70) showed that BaSTA models are robust to uncertainty in birth and death dates when estimating age-dependent mortality. BaSTA therefore allowed us to take into account imperfect detection, left-truncated (i.e., unknown birth date [age]), and right-censored (i.e., unknown death date) capture-recapture data in our analyses. We considered a year-dependent recapture probability for all populations. We ran four Markov chain Monte Carlo chains with 50,000 iterations and a burn-in period of 5,000. Chains were thinned by a factor of 50. Model convergence was evaluated using diagnostic analyses implemented in BaSTA, which calculate the potential scale reduction for each parameter to assess convergence. These analyses were performed on a restricted set of 24 populations in which the year of birth of individuals was partially known (on average, for  $53 \pm 14\%$  of the individuals, range of 18 to 80%; *SI Appendix, Table S2*), and the minimum study duration was 7 y. The age mortality curve drawn for each population is presented in *SI Appendix, Fig. S7*.

We fitted a Siler (38) model for modeling age-specific mortality in every population to obtain comparable metrics. The five-parameter Siler model is given by

$$\mu(x) = a_0 \exp(-a_1x) + c + b_0 \exp(b_1x),$$

where  $a_0$ ,  $a_1$ ,  $b_0$ ,  $b_1$ , and  $c \geq 0$  are the parameters of the mortality function,  $\mu$  is mortality rate, and  $x$  is the age in years. The first exponential function, with  $a$  parameters, describes mortality during the immature stage (in our case, between 1 and 3 y old), whereas  $c$  gives the lower limit of mortality during the early adult stage. The second exponential function, with  $b$  parameters, corresponds to the mortality increase late in life. The parameter  $b_1$  of the Siler model measures the exponential increase in mortality rate with age during the senescent stage, and it is therefore commonly used to measure senescence rate (e.g., ref. 72 in mammals); the posterior distribution of  $b_1$  calculated for the 24 populations is shown in *SI Appendix, Fig. S8*. We estimated lifespan (in years) corresponding to the age at which 90% of the individuals that had survived the first overwintering (i.e., 1-y-old juveniles) were dead. This was calculated from Siler model parameters by solving the following equation:

$$e^{\frac{a_0}{a_1}(e^{-a_1x}-1)} - \frac{c}{a_1} + \frac{b_0}{a_1}(1-e^{-b_1x}) = 0.9.$$

**Population Projection Models and LTRE Analyses.** Using adult survival and recruitment estimates, we built population projection models (40) to quantify elasticities, population growth rate ( $\lambda$ ), generation time ( $T_b$ , a reliable measure of the speed of the life cycle (73)), and the net reproductive rate ( $R_0$ ) of each population—for details about life cycle and model structure, see *SI Appendix, Section 6*. We then performed two LTREs to evaluate whether recruitment effectively compensates survival loss quantified using our capture-recapture data. A first LTRE aimed to assess whether recruitment offsets decreased adult survival in anthropogenic habitats as a whole (demographic parameters averaged among the three habitat types). Demographic parameters from natural habitats were used in the reference matrix. In the second LTRE, we assessed whether recruitment compensated for any reduction in survival associated with intense logging and quarrying. Demographic parameters from those managed or protected habitats with attenuated activities were used in the reference matrix.

**Examining the Influence of Habitat Anthropization and Intensity of Human Activities on Demographic Parameters.** We examined if mean adult survival, adult recruitment, lifespan, and senescence rate, generation time ( $T_b$ ), annual growth rate ( $\lambda$ ), and the net reproductive rate ( $R_0$ ) were associated with habitat anthropization and human activity intensity. For survival and

recruitment, the logit scale estimates (from the E-SURGE outputs) were directly used as the dependent variables. Lifespan, senescence rate, and generation time estimates were log transformed, while the two other demographic parameters (i.e.,  $\lambda$  and  $R_0$ ) were kept untransformed. All the analyses are detailed in *SI Appendix, Section 7*. For adult survival, adult recruitment, and senescence rate, we performed meta-regression analyses implemented in linear mixed effects models (37). More specifically, we used the inverse variance weighting method to take into account sampling error related to the demographic estimates, and we used a random effect to estimate the residual variance among populations (i.e., the among-population variance remaining after accounting for the sampling error and the fixed effects introduced in the model). In the case of survival and recruitment, a distinct residual variance was specified for each habitat type in the initial model and subsequently reduced if the difference in variance among habitat types was found to be negligible (*SI Appendix, Section 8*). For all other demographic parameters, sampling variances were not available, and analyses were controlled for differences in variance among habitat types only (except for lifespan given the reduced dataset). In all analyses, mean annual temperature (after Z-transformation) was included as a control covariate because of its effects on anuran demography (48)—nevertheless, temperature had only marginal effects on any demographic parameters (*SI Appendix, Table S12*). To investigate the effect of habitat anthropization on demographic parameters, all habitat types (i.e., logged forests, quarries, farms, and natural) were introduced as a nominal variable in the fixed part of the model (except for analyses on the aging rate and lifespan given the reduced sample size), and both a contrast test and a customized  $F$  test were used to the effect of habitat anthropogeny (*SI Appendix, Section 7*). To investigate the effect of human activity level on demographic parameters in anthropogenic habitats, both the habitat type and the activity level and their interactive effect were introduced in the fixed part of the model. An  $F$  test was also used to assess the effect of activity level. We also examined associations between adult survival and recruitment and between senescence rate and other demographic traits (*SI Appendix, Table S10* and *Section 7*).

**Data, Materials, and Software Availability.** All study data are included in the article and/or supporting information.

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