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Viewpoint

Fitness in animals correlates with proximity to discontinuities in body mass distributions



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ABSTRACT

Discontinuous structure in landscapes may cause discontinuous, aggregated species body-mass patterns, reflecting the scales of structure available to animal communities within a landscape. Empirical analyses have shown that the location of species within body mass aggregations, which reflect this scale-specific organization, is non-random with regard to several ecological phenomena, including species extinctions. The propensity of declining species to have body masses proximate to discontinuities suggests that transition zones between scaling regimes ultimately decreases the ecological fitness for some species. We test this proposition using vulnerable and unthreatened fish species in Mediterranean streams with differing levels of human impact. We show that the proximity to discontinuities in body mass aggregations (“distance-to-edge”) of more vs. less fit individuals within vulnerable and unthreatened populations differs. Specifically, regression analysis between the scaled mass index, a proxy of animal fitness, and distance-to-edge reveals negative and positive relationships for vulnerable and unthreatened species, respectively. That is, fitness is higher close to discontinuities in vulnerable populations and toward the center of body mass aggregation groups in unthreatened populations. Our results demonstrate the suitability of the discontinuity framework for scrutinizing non-random patterns of environmental impact in populations. Further exploration of the usefulness of this method across other ecosystems and organism groups is warranted.

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1. Introduction

Holling (1992) hypothesized that the discontinuous organization of ecological systems is mirrored in the size structure of animal communities. He posited that behavioral, life-history and morphological attributes of animals adapt to discontinuous environmental patterns because these patterns reflect opportunities for food, shelter and other resources. Indeed, Holling (1992) found a correlation between breaks in distributions of animal body mass, an integrative variable allometric with many physiological and ecological attributes (Peters, 1983), and discontinuities in structures and processes in the boreal forests of Canada. He interpreted aggregations of species (or modes) along body mass distributions as scales at which resources and structure are

available to organisms that have evolved to exploit resources at these specific scales but not at other scales (Fig. 1). In contrast, gaps (discontinuities or troughs) in the distribution (Fig. 1) reflect the transition between structuring processes, and thus scaling regimes (i.e. scale breaks). At these transitions there is limited ecological structure or resource pattern with which animals can interact, or there is great variance and instability in the structures or patterns.

Holling's discontinuity hypothesis has significant support (Allen et al., 2014; Nash et al., 2014a). It has been also expanded theoretically, and empirical analyses have shown that the location of species within body mass aggregations is non-random with regard to several ecological phenomena (Fig. 1). Increased temporal and spatial variability at transitions between scales has been associated with nomadism (Allen and Saunders, 2002, 2006), species invasions and extinctions (Allen et al., 1999; Allen, 2006), and population dynamics (Wardwell and Allen, 2009). Nomadism is often found in ecosystems that exhibit high variability in resource abundance in time and space, so nomadism

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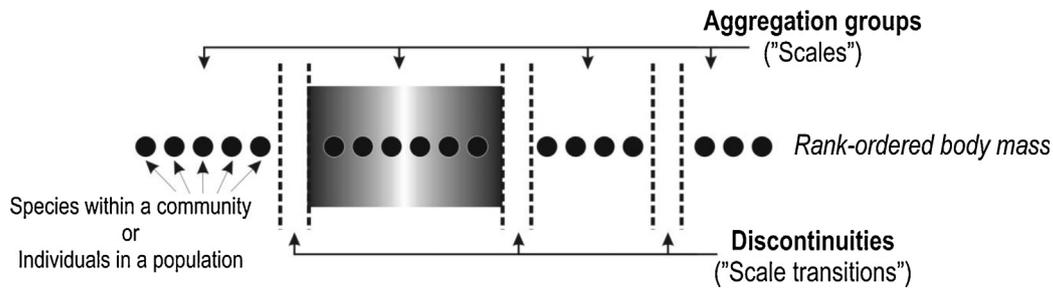


Fig. 1. Conceptual overview of the discontinuity approach. Species (individual dots) within a community are rank-ordered (from low to high) with respect to body mass (log-transformed). Discontinuities or gaps (vertical dotted bars) are identified statistically and separate species into aggregation groups of species with similar body sizes. These aggregation groups putatively mirror scale-specific structure and processes in ecosystems, while the discontinuities reflect transition zones or “scale breaks”. The figure shows that the original community based approach can be extended to population-level analysis. The shaded area in the second body mass aggregation reflects zones of higher ecological variability (edges; gray areas) and stability (center; white areas).

reflects spatial processes, whereby movement is required to locate resources in the landscape. In the absence of such spatial processes, greater resource variability can induce higher population fluctuations, enhance the effects of competition and in turn increase the extinction risk of organisms (May, 1973; Pimm, 1991).

The propensity of declining species to have body masses proximate to discontinuities suggests that transition zones between scaling regimes ultimately decreases the ecological fitness for some species (Allen and Holling, 2008, 2010), but such a relationship has not been empirically tested. In this study, we test this proposition using fish species in streams of the Iberian Peninsula (southwestern Europe). We use the discontinuity framework in a population context, focusing on individuals within a population (as in Fig. 1) rather than the more usual approach of species within a community. A population focus is useful and appropriate for species with indeterminate growth, such as fish (Nash et al., 2014b). We assess fitness of individuals in fish populations and relate individual fitness to the position of these individuals in body mass aggregations. We assess fitness in both vulnerable and unthreatened fish species, in streams with contrasting degrees of human impact. We first test if the size distribution of individuals within a species is discontinuous, and where present we determine the location of discontinuities in body mass aggregations. We then determine if measures of fitness (and therefore, potentially, survival) are non-randomly distributed in terms of the body mass distributions. We conduct these tests for different species, and within species across streams with differing levels of perturbation.

The fitness of individuals relevant for understanding population viability is influenced by many ecological attributes, for instance, foraging and reproductive success, competition, predation, and the ability to cope with environmental pressures. Because the measurement of all these fitness components is prohibitive in field studies, ecologists have used proxies of body condition, based on estimates of the nutritional state, to provide a snapshot of an animal's fitness (Stevenson and Woods, 2006; Peig and Green, 2010). These fitness proxies are relatively simple and based on determining the relationship of body mass and length of individuals in a population using a variety of techniques (Jakob et al., 1996). We use the recently proposed scaled mass index (Peig and Green, 2009), which consistently outperforms most indices of body condition (fitness) so far used in the literature (Peig and Green, 2010).

2. Methods

2.1. Study systems

We use two preliminary analyses to show the usefulness of our approach. Each analysis is based on a paired design. We compare

two species populations in two sites and determine their extinction risk through the Red List status of the International Union for Conservation of Nature (<http://www.iucnredlist.org/>) and the scientific literature.

Our first analysis compared the chub, *Squalius cephalus*, an unthreatened, tolerant species with stable populations across the Iberian Peninsula (Maceda-Veiga and de Sostoa, 2011), and the Mediterranean barbel, *Barbus meridionalis*, a declining species of conservation concern in Spain (Vila-Gispert and Moreno-Amich, 2001). Populations were sampled in the Daró stream, situated in a heavily used agricultural watershed, and the Tordera stream, sampled in a forested section of its catchment in the Catalanian province of Girona (northeastern Spain). Agricultural impacts on the Daró stream present a significant environmental stress to the barbel because this species requires oxygen-saturated waters and is very sensitive to pollution and physical changes in habitat (Vila-Gispert and Moreno-Amich, 2001).

In the second analysis, we compared common carp, *Cyprinus carpio*, an invasive species in the Iberian Peninsula that thrives under a range of environmental conditions (Angeler et al., 2002), and the European eel, *Anguilla anguilla*, a species with high extinction risk (Feunteun, 2002), in the regulated Muga stream and the unregulated Fulvià stream (Girona, Catalonia, Spain). Stream regulation and associated impacts comprise a significant environmental stress to the diadromous eel (Feunteun, 2002), a species that completes its life cycle through migration between European inland waters and the Sargasso Sea (northwestern Atlantic Ocean).

2.2. Sampling and analyses

Fish populations were sampled along Daró, Fluvià, Muga and Tordera streams. These water courses are typical of many small rivers in the Mediterranean region of the Iberian Peninsula, which increases the potential generality of our findings. Fish sampling was conducted during spring 1995 in the three first streams and spring 2003 in Tordera stream. Spring sampling was chosen because of the combination of high temperatures and high fish activity patterns, that should increase the probability of detecting inter- or intra-specific effects within local fish assemblages (Godinho et al., 1997). To avoid sampling bias, and thus provide comparable data, field work was carried out by the same research team, which has collected fish in several surveys of the same study area (e.g. Vila-Gispert and Moreno-Amich, 2001). Thus, methods followed standard and consistent sampling protocols following Catalanian legislation (Department of Environment Catalonia, 2014). Moreover, both 1995 and 2003 were hydrologically average years for the study area (Ministry of Environment Spain, 2013). Indeed, fish populations have generally remained stable since 1995 (Vila-Gispert and Moreno-Amich, 2001; Benejam et al., 2008), consequently making data from both years (i.e. 1995 and 2003)

comparable. Fish were collected from all mesohabitats present in the study streams (runs, riffles and pools) and thus a representative sample of fish assemblages was obtained.

At all sampling sites ($n = 16$, four sites per stream), electrofishing surveys employed the following procedure: stretches of 100 m were blocked off with barrier nets and electrofishing was performed from the downstream to the upstream net following a zigzagging direction (30–40 min per site). Electrofishing was conducted by three people on foot using a generator-powered unit (ERREKA model SEINA, 200–350 V, 2–3 A) along with dip nets (1.5 m long pole, 30 cm diameter net, 10 mm mesh size). After each sampling, all fish caught were immediately immersed in an innocuous solution of anesthetic (tricaine, MS-222 at 0.1 g L^{-1}), identified to the species level, measured (standard length, $\pm 1 \text{ mm}$) and weighed (total weight, $\pm 0.1 \text{ g}$). Fish were kept in a tank and supplied with oxygen (two 'Aera' aerators, portable battery pump) until full recovery before releasing them. All field procedures complied with animal use and care regulations of Europe, Catalonia and the specific license for scientific field research in the study streams. Fish collection was performed and supervised by trained personnel (i.e. the holder of the license, A. Vila-Gispert). Consequently, field procedures did not cause any adverse effects on the aquatic wildlife of the study streams and all fish recovered fully from the anesthetic.

To test the proposition that body mass distributions are distributed discontinuously, we conducted discontinuity analyses separately for each fish population. We used Bayesian Classification and Regression Tree analysis (BCART; Chipman et al., 1998), a recommended method for identifying discontinuities (Stow et al., 2007), to determine aggregation groups of individuals and the structure of gaps based on rank-ordered and log-transformed body mass values.

Two additional steps for estimating population fitness followed the discontinuity analysis. First, we calculated distance-to-edge as a measure of an individuals' proximity (in log body mass) to the edge of its body-mass aggregation (Wardwell and Allen, 2009).

Those individuals directly on the edge of an aggregation have a distance-to-edge of zero. For individuals in the interior of aggregations, the distance was measured to the closest edge. Second, we estimated an index of body condition as a surrogate of fitness. We calculated the recently proposed scaled mass index (Peig and Green, 2009), an indicator of the relative size of energy reserves and other body components that consistently outperforms most indices of body condition so far used in the literature (Peig and Green, 2010). To calculate this index mass and length were ln-transformed and standardized major axis regression in R 2.15.3 (lmodel2 package; Legendre, 2008) was used to calculate the slope (b_{SMA}) of the best-fit line. Next, the scaled mass index was calculated for individuals in each fish population with:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{\text{SMA}}} \quad (1)$$

where M_i and L_i are the body mass and length of individual i respectively, and L_0 is the arithmetic mean value for the sample.

We posited that the proximity of individuals to discontinuities affects individual fitness, and that this relationship provides insight into the relative population viability and mechanisms responsible for discontinuities in body mass distributions. We tested this proposition using simple linear regression analysis (lm function in R) using distance-to-edge (independent variable) and the scaled mass index (dependent variable) in the analyses.

3. Results

3.1. Chub–barbel comparison

Discontinuity analyses clearly showed the size distribution for both the chub and barbel to be discontinuous, and have distinct gaps and aggregations, but the observed distributions were population specific (Fig. 2). The relationship between fitness of individuals and their position in body mass aggregation groups

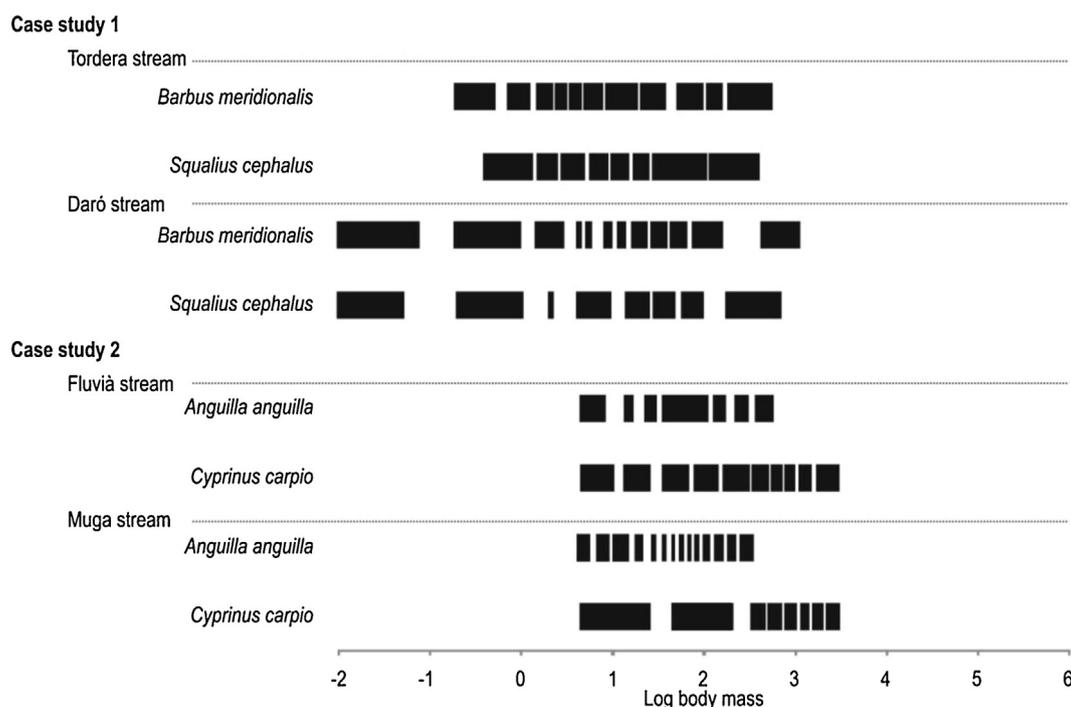


Fig. 2. Results from two case studies, showing patterns of body mass aggregation (black squares) and gap (white spaces between squares) structure of unthreatened (*Cyprinus carpio*, *Squalius cephalus*) and vulnerable (*Barbus meridionalis*, *Anguilla anguilla*) fish populations in streams with different human impact.

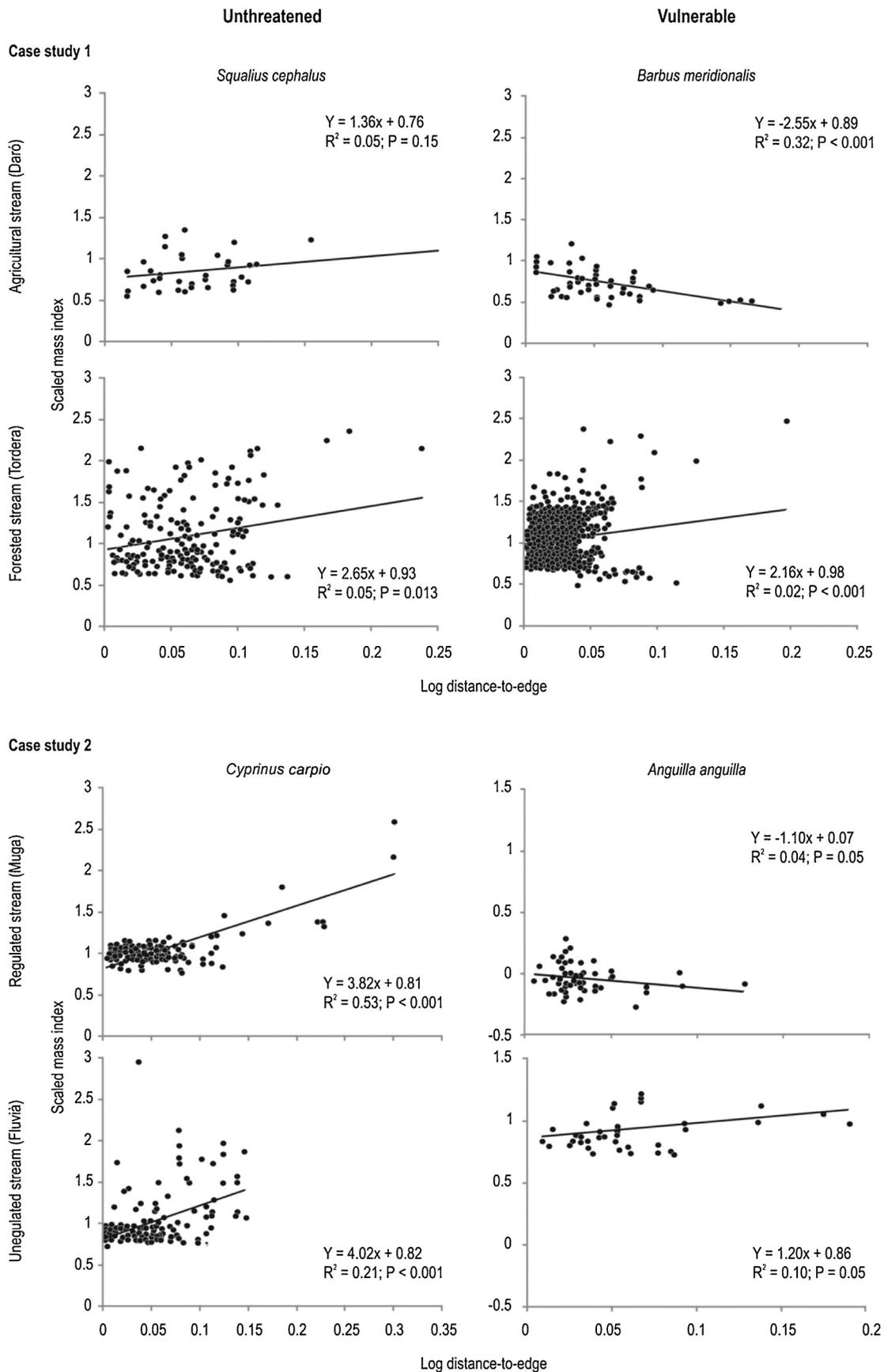


Fig. 3. Regression analyses showing relationships between a metric of body condition (log squared mass index) and the distance to the closest edge of individuals in aggregation groups identified through discontinuity analyses in the populations. The results show two case studies comparing vulnerable and unthreatened species in streams with and without agricultural (upper four panels; case study 1) and geomorphological (lower four panels; case study 2) impact. Note that individuals with distance-to-edge values of zero were not included in the regression (see [Wardwell and Allen, 2009](#)).

differed between vulnerable and threatened fish population, but the amount of variance explained and the statistical significance of regression models varied among populations (Fig. 3). The unthreatened chub showed a positive relationship between the scaled mass index and distance-to-edge but the regression was significant only for the forested stream (Fig. 3). A significant positive slope was also observed for the barbel in the forested stream section, but in the agricultural stream the slope was significantly negative (Fig. 3). Despite these findings, the scaled mass index was similar across populations (Table 1).

3.2. Carp–eel comparison

Discontinuity analysis showed that the size distributions for these species were also discontinuous, and the observed distributions were population-specific (Fig. 2). Regression revealed similar variability in terms of statistical significance and variance in the relationship of our fitness metric and distance to body size aggregation edge. Common carp, the invasive species, showed a significant positive relationship between the scaled mass index and distance-to-edge (Fig. 3). This pattern was also observed for the European eel in the unregulated stream (Fig. 3). However, in the regulated stream the eel showed a significantly negative regression slope (Fig. 3). Comparison of fitness based on the scaled mass index alone was inconclusive because of similar values observed between populations in the impact and reference streams (Table 1).

4. Discussion

Several ecological phenomena, including species extinctions, are non-random with regard to the position of animals in body mass aggregation groups, with for instance species with a higher extinction risk being located close to discontinuities (Allen et al., 1999; Allen and Holling, 2008). We tested if fitness of individuals in fish populations in streams shows similar patterns. Our results not only showed deterministic patterns of fitness of individuals in body mass aggregation groups of fish, but also that these patterns differed between impacted and near-pristine streams.

Evidence is compelling that discontinuous body mass distributions reflect discontinuous structures, in terms of resource distribution and availability in the environment (Holling, 1992; Nash et al., 2014a). That is, discontinuities reflect zones where either no resources are available or where the distribution of these resources is highly variable in space and time (Allen and Holling, 2008). This suggests that the tradeoffs in life-history attributes of organisms may be ill-suited for exploiting resources, resulting in absences of individuals or species with body sizes that place them in these zones. Previous research has shown that threatened species that face an extinction risk are more likely to have average body masses that place them at, or near to, discontinuities (Allen et al., 1999). Our results provide further evidence, but for individuals within populations and from a physiological perspective. Fitness of individuals of fish populations in near-pristine streams was lower close to discontinuities, suggesting suboptimal exploitation of resources by these individuals, but likely also stronger effects of biological interactions (competition, predation).

While the fitness patterns observed for fish populations in near-pristine streams are consistent with discontinuity theory, it was surprising that the patterns for threatened fish species in impacted streams (e.g. the barbel and eel) were opposite of expectations; that is, decreasing fitness of individuals toward the center of body mass aggregation groups. Increasing distance from edges in body mass aggregations has been interpreted as increasing ecological stability (Allen and Holling, 2010), meaning that resources are more abundant and/or more stable, facilitating their exploitation. That the sensitive species in the impacted streams have individuals with lowest fitness in the center of aggregation groups may reflect agricultural practices and hydrogeomorphological alterations. These two forms of stress impact stream ecosystems worldwide (Tilman et al., 2001; Sabater and Tockner, 2010), affecting populations that are sensitive to environmental stress. Specifically, our results suggest that the sensitivity of individuals in populations to environmental stress is non-random, manifested in the disproportionate reduction of fitness of individuals in the center of aggregation groups that are thought to reflect zones of ecological stability for populations and communities. Our results suggest that environmental stress impacts the eco-evolutionary life-history tradeoffs of the sensitive species, whereby stress alters the availability of suitable habitat conditions. Environmental stress disrupts ecological niches of sensitive species and creates novel environmental conditions to which their life-history tradeoffs are maladapted. Our results show patterns of fitness in fish body mass aggregations but further research is needed to assess how these patterns affect survival and mortality rates in populations.

An assessment of fitness, and its statistical accuracy, depends on the choice of body condition indexes (Stevenson and Woods, 2006; Peig and Green, 2010) or regression method used (Cade et al., 2008). To demonstrate our approach, we used the scaled mass index, an indicator of the relative size of energy reserves and other body components, which has been shown to satisfy biological precepts concerning mass-length relationships and to control successfully for variation in body size among individuals of different sexes and age classes (Peig and Green, 2009). This index has been thoroughly validated and shown to outperform most metrics that unreliably predict an individual's body condition (Peig and Green, 2010). We are therefore confident that our results are not compromised by the choice of metric to infer fitness. We also point out a potential problem with our approach when using some fitness measures. Distance-to-edge is calculated on body mass, similarly many fitness values are derived from calculating ratios between size and mass (e.g. Fulton's, Quételet's or body mass index), which would lead to spurious correlation in the regression analyses (Brett, 2004; Arnold and Green, 2007). The scaled mass index is based on estimated, not observed, body masses. It has fundamentally different ecological properties than body mass (Peig and Green, 2009), suggesting that the problem of spurious correlation is minimized when using our approach.

The suitability of using the scaled mass index and the discontinuity framework for inferring population viability was generally supported by both analyses in this study. We acknowledge that we could assess fitness only in one population classified as either unthreatened or vulnerable and in one stream that was either impacted or least-impacted. Ideally, sampling of multiple

Table 1

Scaled mass index values (g) for unthreatened and vulnerable fish species in impacted and reference streams. Shown are the mean \pm standard deviations from all individuals in the populations (*n*).

	<i>Squalius cephalus</i>	<i>Barbus meridionalis</i>	<i>Cyprinus carpio</i>	<i>Anguilla anguilla</i>
Impacted stream	17.19 \pm 7.39 (<i>n</i> =74)	11.89 \pm 2.36 (<i>n</i> =227)	11.10 \pm 2.22 (<i>n</i> =174)	10.33 \pm 1.41 (<i>n</i> =257)
Reference stream	12.39 \pm 2.71 (<i>n</i> =228)	11.13 \pm 2.00 (<i>n</i> =853)	11.24 \pm 2.25 (<i>n</i> =241)	10.77 \pm 1.72 (<i>n</i> =68)

streams within impact category and multiple populations with different vulnerability patterns within these categories would have strengthened inference. However, such a comparison was not possible due to different fish community structures and the limited availability of least-impacted reference streams in our study area. Despite these limitations, which also include relatively weak regression models in terms of variance explained, both case studies revealed ecological patterns that were consistent with our hypothesis and the underlying theory. Our results demonstrate the suitability of the discontinuity framework for scrutinizing non-random patterns of environmental impact in populations. More research is warranted to scrutinize fitness patterns across communities and ecosystems.

Author contributions

DGA and CRA conceived and wrote the paper. AVG and DA carried out field work and contributed to the writing. DGA analyzed the data.

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