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Life-history strategies constrain invertebrate community tolerance to multiple stressors: A case study in the Ebro basin

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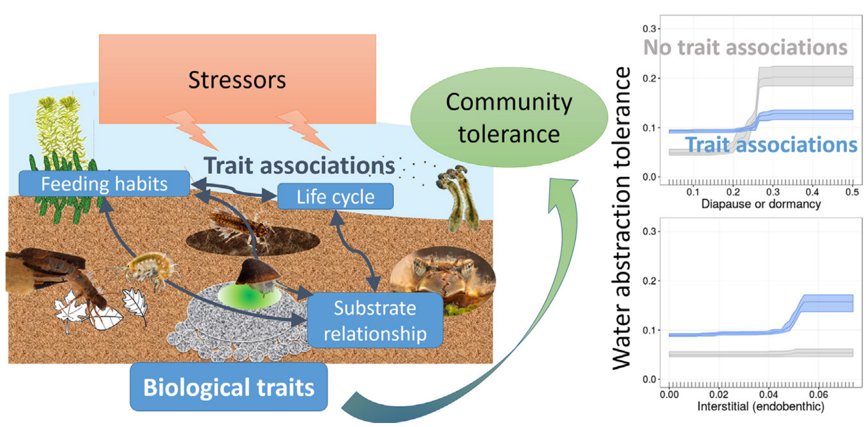
HIGHLIGHTS

- Multiple stressors are a serious threat to aquatic ecosystems and communities.
- Life-history strategies reflect adaptation to given environmental conditions.
- Predict community tolerance using trait combinations and boosted regression trees
- Obtain efficient models where trait associations affect community tolerance
- Trait combinations and association are the basis of stressor-specific tolerance.

GRAPHICAL ABSTRACT



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ABSTRACT

Context: Multiple stressors constitute a serious threat to aquatic ecosystems, particularly in the Mediterranean region where water scarcity is likely to interact with other anthropogenic stressors. Biological traits potentially allow the unravelling of the effects of multiple stressors. However, thus far, trait-based approaches have failed to fully deliver on their promise and still lack strong predictive power when multiple stressors are present.
Goal: We aimed to quantify specific community tolerances against six anthropogenic stressors and investigate the responses of the underlying macroinvertebrate biological traits and their combinations.
Methods: We built and calibrated boosted regression tree models to predict community tolerances using multiple biological traits with *a priori* hypotheses regarding their individual responses to specific stressors. We analysed the combinations of traits underlying community tolerance and the effect of trait association on this tolerance.
Results: Our results validated the following three hypotheses: (i) the community tolerance models efficiently and robustly related trait combinations to stressor intensities and, to a lesser extent, to stressors related to the presence of dams and insecticides; (ii) the effects of traits on community tolerance not only depended on trait identity but also on the trait associations emerging at the community level from the co-occurrence of different traits in species; and (iii) the community tolerances and the underlying trait combinations were specific to the different stressors.
Conclusion: This study takes a further step towards predictive tools in community ecology that consider

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combinations and associations of traits as the basis of stressor tolerance. Additionally, the community tolerance concept has potential application to help stream managers in the decision process regarding management options.

1. Introduction

Freshwater ecosystems are subjected to multiple human pressures and stressors, placing them among the most threatened ecosystems (Vörösmarty et al., 2010). Indeed, interactions between different types of stressors (related to water quality, hydromorphology and water scarcity), which are rather common in these ecosystems, can produce unexpected patterns and consequently make their management difficult (Ormerod et al., 2010). In Europe, the Water Framework Directive (European Council, 2000) aims to incite member states to reach "good ecological status" for all surface waters by 2027. However, such a goal appears complicated to attain within the desired time frame because the first River Basin Management Plans (EEA, 2012; ETC-ICM, 2012) have characterized >50% of the European rivers as being in a less than "good ecological status". The main pressures acting on rivers and streams include point and diffuse pollution (*e.g.*, increased nutrient loads that often jointly occur with fine sediment and pesticide inputs) and hydromorphological alterations (*e.g.*, water abstraction, flash floods, weirs, straightening, removal of riparian vegetation). These co-occurring stressors obviously act on communities through complex interactions, and the understanding of such interactions is one of the many challenges that remain to be addressed (Hering et al., 2010). To respond to the increasing societal demands associated with this particular challenge, the following European research projects have been initiated in the last few years: SOLUTIONS (Brack et al., 2015), MARS (Hering et al., 2015) and GLOBAQUA (Navarro-Ortega et al., 2015). In a context of climate change, water scarcity and interactions with other human stressors are key issues, especially in sensitive areas, such as those surrounding the Mediterranean Sea (Ludwig et al., 2011). As a result, the EU-funded GLOBAQUA project aims to understand how multiple human stressors, including water scarcity, interact to modify freshwater biodiversity and ecosystem functioning (Navarro-Ortega et al., 2015).

Based on the hypothesis that environmental conditions act as a template on which evolution forges specific combinations of organism attributes (Southwood, 1977; Townsend and Hildrew, 1994), species traits have been presented as a promising tool that can provide a mechanistic interpretation of the stressor effects on communities (Statzner and Bêche, 2010). Therefore, trait-based approaches (TBA) can potentially unravel the effects of multiple stressors acting simultaneously on communities (Dolédec and Statzner, 2008; Lange et al., 2014; Mondy and Usseglio-Polatera, 2013; Statzner and Bêche, 2010; Wooster et al., 2012). However, the concrete delivery of this promising objective is still to come (Statzner and Bêche, 2010). Most of the current studies using TBA have often lacked strong predictive power and have failed to adequately reflect species-environment relationships (Ings et al., 2009). Verberk et al. (2013) have argued that the following two main issues could explain why there is such failure in most current TBAs: (i) the lack of consideration of the co-occurrence of different traits (however, see Küster et al., 2008) and (ii) the need of more hypothesis-driven investigations (however, see Arce et al., 2014; Bonada et al., 2007a; Dolédec and Statzner, 2008; Pollard and Yuan, 2010). As a first issue, species sorting, one of the mechanisms occurring during community assembly, does not operate on single traits but rather on whole organisms (Townsend and Hildrew, 1994; Verberk et al., 2008a). Therefore, it makes sense that using combinations of biological traits should be the next TBA development to efficiently address the issue of multiple stressors (Verberk et al., 2013), whereas many TBA studies have used multiple individual traits in their attempts to reveal response patterns of individual traits to global pressure levels (Dolédec et al., 2006; Mondy et al., 2012), to individual stressors (Brabec et al., 2004; Rabení et al., 2005) or to stressor combinations (Dolédec and Statzner, 2008; Townsend et al., 2008). Moreover, the response of a given trait to a given stressor in a community may depend on the other traits possessed by the organisms (trait association or trait context-dependence; Verberk et al., 2013), potentially masking or blurring the expected trait responses (Resh et al., 1994; Statzner et al., 1997). As a second issue, linking trait responses to multiple stressors should rely on *a priori* hypotheses based on the mechanistic effects of each stressor on organisms (Statzner and Bêche, 2010). Life-history strategies represent detailed trait combinations that reflect adaptation to given environmental conditions, *e.g.*, general responses to disturbances (Verberk et al., 2008a). However, the number of life-history strategies to specify can rapidly grow because of the number of traits and their combinations when considering multiple stressors having different modes of action on organisms. Therefore, the definition of such life-history strategies and their adaptive value in specific environmental conditions is a challenging task (Verberk et al., 2013).

In this study, we aimed at using combinations of biological traits to predict the tolerance of invertebrate communities to specific individual stressors. We considered multiple traits and took into account trait association at the community level. We also defined *a priori* the direction (*i.e.*, increase or decrease) of trait responses according to given stressors, based on the habitat template theory (Southwood, 1977; Townsend and Hildrew, 1994) and the literature about the responses of macroinvertebrate traits to stressors (*e.g.*, Baird and van den Brink, 2007; Bonada et al., 2007b; Buendia et al., 2013; Dolédec and Statzner, 2008; Lange et al., 2014; Mondy and Usseglio-Polatera, 2013; Statzner and Bêche, 2010), while limiting the complexity of manually defining the individual life history strategies corresponding to the different stressors. More specifically, we tested (i) whether combinations of biological traits constrained the community tolerance to six stressors related to water quality, hydrology and hydromorphology (Hypothesis H1); (ii) whether the consideration of trait associations can modify the stressor tolerances (H2); and (iii) whether the community tolerances and the underlying trait combinations are stressor-specific (H3).

2. Material and methods

2.1. Study area

The Ebro River catchment, the largest in Spain, has a drainage basin of 85,550 km^2 (Sabater et al., 2009; Fig. 1) and is subjected to multiple stressors. In particular, numerous dams and channels alter the hydrological regime and sediment loads within the river catchment (Muñoz and Prat, 1989). Ground and surface water abstraction for agriculture irrigation and industrial activities have compromised water demand and quality. Additionally, pollution from nutrients and organic compounds is a concern in the middle and lower reaches of the river that worsens during low flow conditions.

2.2. Data

2.2.1. Fauna

Macroinvertebrate data recorded during the period 2006–2013 were retrieved from the water agency 'Confederación Hidrográfica del Ebro' (CHE) website (http://www.datossuperficiales.chebro.es). The initial faunistic data set comprised 414 sites, 1508 sampling events (*i.e.*, site × date) and covered 148 taxa. We removed sites without information about river identity or type. We also discarded some faunistic