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Original Research Article

Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals

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ABSTRACT

Ecological signs of Earth's biosphere forewarn an alarming trajectory towards a global mass-extinction. Assessing species performance and susceptibilities to decline is essential to comprehend and reverse this trend. Yet it is challenging, given difficulties associated with quantifying individual and population processes that are variable across time, space, and life-stages. We describe a new approach to estimating and comparing species performances that combines empirical data, a novel theoretical consideration of population dynamics, and modern statistics. Our approach allows for a more realistic continuous representation of individual performances along development stages while taking into account non-linearity, and natural variability as captured by spatio-temporally replicated observations. We illustrate its application in a coral meta-assemblage composed of populations of the three major reef-building taxa *Acropora*, *Pocillopora*, *Porites*. Using a unique set of highly replicated observations of individual coral dynamics under various environmental conditions, we show how taxa differ in their investment in recruitment and size-specific aptitude for growth and survival, notably through different use of clonal shrinkage, fragmentation, fission, and fusion processes. Our results reveal contrasting life-history trade-offs among taxa which, along with differing patterns of density-dependent recruitment, modulate species responses to decline. These differences in coral life history traits reflect opposing life-strategies, imply regulation at differing life-stages, and explain divergence in species trajectories. Our findings indicate a high potential for resilience in *Pocillopora* and *Porites* populations, thanks respectively to a sustained recruitment that promotes demographic elasticity through replacement of individuals, and a steady resistance to mortality which confers persistence through lingering of individuals. Resilience in *Acropora* appears more arbitrary, given high susceptibility to perturbations and dependency of recruitment on presence of established local populations. We identify management actions that can complement *Acropora*'s life history and benefit recovery of its populations following mortality events. Our regression-modelling approach to quantifying and comparing species performances in different population processes is applicable to all taxa, as illustrated even those with complex clonal life histories, and can be implemented at wide spatio-temporal and taxonomic coverage. It can promote more accurate representation of species dynamics in both descriptive and predictive modelling approaches. The semi-parametric contrast curve method we develop facilitates comparing response variables along continuous explicative metrics while accounting for multiple sources of complexity in empirical data. It should widely benefit investigations in ecology and quantitative science.

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1. Introduction

As global indicators of Earth's biosphere show inexorable signs of erosion, localized examples of successful ecosystem management attest to the potential for sustainable development (Butchart et al., 2010; Lotze et al., 2011; Barnosky et al., 2012). Yet practical opportunities for establishing conservation plans remain limited mainly due to a lack of political prioritization (Christensen et al., 1996). In this context, improving ecological understanding of the underlying drivers of species dynamics can help refine management efficiency (Mumby et al., 2014; Anthony et al., 2014; Vercelloni et al., 2014). In particular, quantitative assessments of species performance and susceptibilities are essential in allowing us to recognize where and why species fail to maintain their populations (Winemiller, 2005; McGill et al., 2006; Foden et al., 2013).

Investigations of species performances are not new. However, comprehensive performance-based approaches to population dynamics, those studies specifically designed to identify the most vulnerable stages in species lives, have been hampered by multiple limitations. These include complexity of species' life-cycles, diversity of life-strategies, variability in organism performances among observations, and a lack of advanced statistical and analytical tools (Jopp et al., 2011). Ecological investigations have especially suffered from difficulties associated with quantifying individual and population processes that are variable in nature, and comparing such empirical measurements across multiple explicative factors such as taxonomic identity, development stage, and environmental condition (Menge, 2000; McGill et al., 2006). These limitations have restricted most studies on species performances to mono-specific investigations, and inter-species comparisons to single population processes or life-stages. As a result, the prevalence of different population processes and their contributions to population maintenance remain unknown in many species groups. Therefore, a better quantitative knowledge of the mechanistic drivers of species dynamics can benefit our understanding of community trajectory, and improve our ability to identify species vulnerable to decline. For example, the importance of life-strategies, i.e. how species allocate energy to survival, growth, and reproduction, to ecological success needs to be evaluated (Winemiller, 2005; van Woesik et al., 2012; Foden et al., 2013; Rees et al., 2014). Similarly, species' abilities to resist and respond to various sources of stress and disturbance need to be quantified to improve our comprehension of ecosystem resilience (Lotze et al., 2011; Anthony et al., 2014; Mumby et al., 2014). Moreover, the importance of recruitment and individual performance across life-stages in population maintenance remains to be assessed (Caley et al., 1996; Menge, 2000). In general, our qualitative understanding of species dynamics lacks quantitative evaluation, which in turn limits our ability to achieve accurate predictions and efficient management of ecosystems.

We addressed these issues relating to ecological knowledge on the underlying drivers of species dynamics in a French Polynesian reef-building coral meta-assemblage composed of populations from the three major genera dominating tropical reefs: *Acropora*, *Pocillopora*, *Porites*. Because of their crucial role as foundation species in reef ecosystems and their high vulnerability, improving knowledge of coral dynamics can benefit both their conservation and management of marine resources in the tropics (see Box 1). The three taxa we studied exhibit different life forms that contribute differently to reef accretion and habitat structure (Veron, 2000). Their co-occurrence contributes to generating diverse refuges that are essential to host prolific reef communities (Appendix A). Yet, ecological mechanisms leading to their co-existence are not understood, particularly as recent research suggests these taxa rely on opposite life-strategies (Darling et al., 2012; Hughes et al., 2012; van Woesik et al., 2012; Riegl et al., 2013). Branching *Acropora* often grows fast, but is more susceptible to predation and disturbance. Massive *Porites* typically grows slowly yet resists diverse sources of stress. Sub-branching *Pocillopora* usually shows intermediate levels in growth and survival. Given such differences in life history traits, one expects populations from these taxa to show differing degrees of persistence on reefs and different rates of individual turnover. However, our understanding of coral life-strategies comes mainly from observations from disparate sources, as the complexity of the coral study model has limited most empirical studies of coral performance as mono-specific, restricted in time and space, or limited to single traits (see Box 1). As a result, a quantitative comparison of coral performance in different life history traits and the mechanisms supporting population maintenance had remained impossible.

Here we provide comprehensive measurements of population dynamics that are complementary to existing data on corals, resulting mostly from large-scale surveys of reef communities and short-term experiments. Based on a thorough in situ survey of populations exposed to various levels in environmental gradients and natural disturbances, we tested how individual coral performance varied as a function of size and taxonomic identity, and how populations responded to disturbance-driven alteration of communities. Our results show that taxonomic differences in coral performance are highly stage-dependent, and that each taxon relies on a different mechanism for population maintenance. We discuss the implications of the antagonistic life-strategies observed in coral protagonists for the mechanisms supporting population resilience and in the light of the community regulation literature. Our quantitative approach to life history traits and population dynamics is fully empirical and based on an analysis of species performance in different population processes as observed in nature (Hughes and Jackson, 1985; Darling et al., 2012). It differs from other methods using simulations and predictive modelling (e.g. Easterling et al., 2000; Kayal, 2011; Riegl et al., 2013; Rees et al., 2014), although more accurate demographic information obtained from real-life data can highly benefit such purpose. Our approach is applicable to any species, underpinned by modern non-linear modelling statistics, and can be implemented at differing geographical and taxonomic resolution while accounting for variability among observation units. We introduce the application of semi-parametric contrast curves in ecology, and show how their use facilitates comparing ecological responses (e.g. individual growth, species abundance) along continuous covariates (e.g. size, time, environmental stress) while accounting for natural variability and statistical complexity (e.g. non-linearity, spatio-temporally structured observations), thus promoting more accurate estimation of ecological thresholds (see Box 2). We further extend the advancement of this tool by developing a statistical method for calculating contrasts for binomial-distribution data (e.g. survival rates; Appendix B). Our study should thus benefit quantitative investigations in ecology, and the ability to build powerful data-based models in different fields of science.

2. Methods

2.1. Sampling design

We considered a French Polynesian coral meta-assemblage composed of populations from the locally most abundant species within each of the three major genera: branching *Acropora globiceps*, sub-branching *Pocillopora meandrina*, and the massive *Porites* spp. complex *P. lobata*, *P. lutea*, *P. australiensis* (Appendix A). To capture natural variability in coral performances, sympatric populations of the three taxa were surveyed through time and