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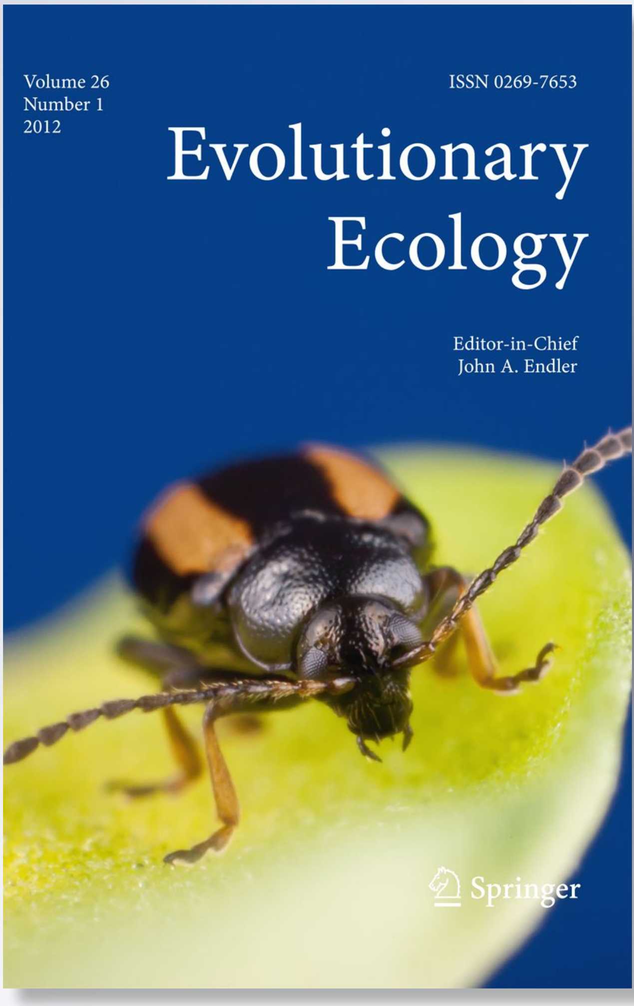

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ORIGINAL PAPER

A festschrift for Jeremy B.C. Jackson and his integration of paleobiology, ecology, evolution, and conservation biology

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Abstract This collection of papers is dedicated to the career and achievements of Dr. Jeremy B.C. Jackson, and is written by a sample of his students, post-docs, and colleagues over his career. Jackson is an influential leader in cross-disciplinary research integrating ecology and paleontology. His contributions are broad in scope, and range in topic from the ecological and evolutionary consequences of the formation of the Central American Isthmus to the long-term impacts of human activities on the oceans. Two areas of particular interest have been the evolutionary ecology of coral reef organisms and the tempo and mode of speciation in the sea. Papers in the collection examine: colonial marine animals (Buss and Rice, Lidgard et al.), marrying genes and fossils (Budd et al., Marko and Hart, Palumbi et al., Jagadeeshan and O'Dea), the geography, tempo, and mode of evolution (Bromfield and Pandolfi, Norris and Hull, Vermeij, Erwin and Tweedt), and marine ecosystem health (Sandin and Sala).

Keywords Colonial animals · Ecology · Evolution · Taxonomic turnover · Conservation biology · Panama paleontology project · Historical ecology · Paleobiology

Introduction

This collection of papers is dedicated to the career and achievements of Dr. Jeremy B.C. Jackson. The papers are written by a sample of his students, post-docs, and colleagues over

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his career, and are an exciting mix of contributions that not only bring into sharp focus the broad contributions of Jeremy's illustrious papers and career in evolutionary ecology, but also provide a taster for the exciting new developments occurring in the field.

Jackson's contributions to evolutionary ecology, though focused most on coral reefs, are manifold. They have been monumental and sustained over more than four decades. He has worked extensively on the evolutionary ecology of coral reef communities and the tempo and mode of speciation in the sea. His research ranges from the long-term impacts of human activities on the oceans to the ecological and evolutionary consequences of the gradual formation of the Isthmus of Panama. His early discoveries on coral reefs increased insight into the intensity and complexity of spatial competition, and the importance of clonal (modular) life histories. He has also carried out long term observations and experiments to assess the comparative importance of larval recruitment, competition for space and food, predation, and environmental perturbations as determinants of reef community development and succession. Perhaps his most enduring approach has been his ability to find a creative nexus in the marriage between neontology and paleontology—constructing studies at the interface and providing us all with models about the best and most rigorous way to approach such studies. Jeremy's career can be summed up by the review to his 2001 'Evolutionary Patterns' volume as '…illustrating the point that the full understanding of the whole range of evolutionary phenomena requires both neontological and paleontological study' (Bambach 2001).

Colonial marine animals

One of Jackson's most enduring legacies is his contribution to the biology, evolution, and ecology of clonal marine organisms, that included an entire edited volume devoted to the population biology and evolution of these organisms (Jackson et al. 1985), and a portion of another edited volume devoted to evolutionary patterns derived from the fossil record (Jackson et al. 2001a). In the opening paper to this special issue Buss and Rice propose an intriguing mechanism for the formation of 'colonies of colonies' of the extinct group of hemichordates, the graptolites. These 'synrhabdosomes' may have formed super-colonies in a manner similar to two genera of modern colonial rotifers.

Lidgard et al. revisit Jackson's age-old question of whether (and in what way) ecology matters to evolutionary biology. Drawing on multiple examples of zooid polymorphism in cheilostome bryozoans, they suggest that the division of labor represented by polymorphs and other structural modules within bryozoan colonies evolved (at least in part) in response to predation by small mobile epibionts. Thus, the relationship between morphological plasticity and natural selection at the zooid level not only has mediated ecological interactions among predator and prey, but has also led to the evolution of alternate phenotypes and species diversification at the macroevolutionary level. Their answer to Jackson's question is a resounding Yes!

Marrying genes and fossils

In 1986, Jackson co-founded the Panama Paleontology Project (PPP), an international group of more than 30 scientists to help unravel the timing and consequences of the rise of the Isthmus of Panama on the history of Caribbean marine ecosystems. The PPP gave Jackson the data for two major insights. He and Alan Cheetham demonstrated that speciation of bryozoans observed in the fossil record perfectly fulfils the predictions of the controversial model of "punctuated equilibrium" (reviewed in Jackson and Cheetham 1999). The work was the first to convince sceptical evolutionary biologists that stasis and punctuated speciation are real biological phenomena and the results are now included in some basic texts of evolution. One of the cornerstones of that work was the demonstration of congruence between genetic and morphological data, so that morphospecies were unambiguously distinct genetically (Jackson and Cheetham 1990). This work has inspired similar approaches in other groups, especially the *Montastraea 'annularis'* coral species complex from the Caribbean Sea (Budd and Klaus 2008; Budd and Pandolfi 2010). In the present issue, Budd and colleagues searched for patterns of cryptic species similar to the *M. 'annularis'* complex in a congeneric 'species' *Montastraea cavernosa*. In this example, genetic and morphological data were incongruent, suggesting the absence of cryptic species. Moreover, polymorphism in *M. cavernosa* is maintained in the presence of gene flow, is widespread across the geographic range of the species, and may have existed for 25 myr of geologic time, including the severe environmental perturbations of the Plio-Pleistocene.

Marko and Hart address ecological processes over evolutionary time scales through an analysis of newly developed non-equilibrium coalescent methods and their comparison with 'classic' genetic approaches, such as gene flow inferences derived from F_{st}. True to the goals of Jeremy Jackson's career, the authors take a close look at these retrospective methods that 'look backward in time to make inferences about evolutionary forces'. Marko and Hart find that variables such as variation in duration of isolation and effective population size can be more important in explaining the spatial patterns of population differentiation than gene flow. The authors then apply a non-equilibrium approach to two classic metapopulation species to assess the potential of these newer methods to distinguish among marine metapopulation models that differ with respect to the population genetic forces that have shaped patterns of differentiation (i.e., extinction, recolonization, and recurrent gene flow). Echoing Jackson's application of evolutionary and ecological studies to conservation issues, the authors discuss how these models have different implications for the design of marine protected areas.

Palumbi et al. show how analysis of the genetic diversity of Caribbean *Acropora* adds a dynamic temporal context to understanding the complex ecology of coral genetics at the species and population level. Patterns of genetic variation within and among species at four loci are used to assay the timing and nature of species divergence, intra-specific gene flow and movement of alleles among populations. Although divergent species continue to exchange genes with one another, gene flow is unidirectional and highly variable among loci. As a result, the two Caribbean *Acropora* species have remained distinct for millions of years.

Finally, Jagadeeshan & O'Dea, reporting on research completed within the context of Jackson's PPP, examine the spatial and temporal dynamics of cupuladriid bryozoan species divergences over the last 10 million years using a combined fossil and molecular approach. They examine in detail the trajectories of morphological traits in closely related species during and following divergence. The groundwork laid by the PPP over a 25 year period provides the authors with an exceptional stratigraphic and geographic framework that allows them to demonstrate that species became isolated not only across the Isthmus, but also within the southwest Caribbean during the final 2 Ma of isthmus closure. During this time of major oceanographic change, new species pairs became generally allopatric but showed little morphological divergence. Only when the isthmus finally closed and closely related species become sympatric did they demonstrate salient divergence in morphology. This pattern is consistent with allopatric speciation caused by local isolating mechanisms followed by secondary contact, and is concealed without the incorporation of the exceptional fossil record provided by the PPP.

The geography, tempo and mode of evolution

Jackson's foray into Caribbean turnover of tropical ecosystems also enabled the Panama Paleontology Project to uncover a mass extinction that wiped out more than half the species of Caribbean reef corals and one third of the mollusks 2 million years ago (Jackson and Johnson 2000). Extinction lagged 1–2 million years behind the major environmental changes associated with the closure of the Isthmus. This lag suggests a kind of threshold effect in the evolutionary response to major environmental perturbations that is highly relevant in contemplating future biological response to ongoing global warming and climate change. Bromfield and Pandolfi pick up on this theme as they explore the environmental drivers of taxonomic turnover in Neogene Indo-Pacific reef corals. Faunal turnover was studied from the central Indo-West Pacific (cIWP) region from Indonesia in the west to Fiji in the east from the early Miocene to the early Quaternary ($\sim$17 to 1.8 Ma). They found evidence for two faunal turnover events. The first from the mid-Miocene (17–14 Ma) was an increase in generic richness of reef corals associated with both large-scale sea level fluctuations and the great Mid-Miocene collision event. The later turnover event resulted in an overall lowering of coral generic diversity throughout the late Miocene and Pliocene (7–3 Ma), that was followed by a pronounced pulse of extinction at the Pliocene–Pleistocene boundary ($\sim$2.6 Ma). There were no tectonic, eustatic, climatic or oceanographic events that neatly coincide with this second episode of Neogene coral taxonomic turnover, though the onset of northern hemisphere glaciation around 2.5 Ma might explain increased extinction during this time. Interestingly, comparison of the timing and potential environmental drivers of corresponding evolutionary patterns in the cIWP with those previously documented in the Neogene and early Quaternary in the West Atlantic revealed no coincidence in timing of taxonomic turnover, so Bromfield and Pandolfi conclude that the environmental drivers of Neogene reef dynamics are regional in scale.

One of Jeremy Jackson's most passionate approaches to science was to bring together the ecological and evolutionary time scales—that not only could lessons from one be fruitfully used to interpret the other, but, more importantly, that only through their integration could a truly synthetic view of nature be found. Norris and Hull apply this approach in advancing our thinking on the nature of the origin of species. They consider three consequences of the long time frame of speciation: (1) large scale environmental variability that alters the genetic diversity, selective regime, and geographic isolation of populations; (2) the long duration of speciation means that many short-lived, young species will not be detected in both fossil and modern surveys for reasons of under-sampling, dependence upon morphology for a species concept and the time necessary to accumulate genetic differences; and (3) extinction will cause increased separation among taxonomic groups by truncating geographic ranges and reducing opportunities for cross-breeding among nascent species. They conclude with a set of research questions that provide an agenda for refining the study of speciation through the integration of genetic and morphological/paleobiological techniques.

Vermeij focuses on the geographic origins of shallow-water tropical molluscan innovations, comparing the incidence of innovation from two situations in which evolutionary innovations might arise. The first is in island-like environments from the peripheral Indo-West Pacific ocean and the other is in the highly diverse, competitively rigorous ecosystems of the inner areas of the Indo-West Pacific (IWP) marine realm. He finds an overrepresentation of novel states in the central areas of the IWP, and that molluscan innovations that are unique to island species or to species from peripheral parts of the great tropical realms are not manifest. Instead, innovations in shallow water tropical molluscs appear to be associated with large, productive, taxonomically diverse settings. He also found more innovations in the inner IWP than in the Atlantic-eastern Pacific region. Thus, warm, large, highly productive environments are more conducive to the establishment of new ecological roles and phenotypic states than are smaller, less productive, or more island-like settings. Vermeij concludes from this that diversity need not be correlated with either high productivity or evolutionary opportunity for innovation.

Erwin and Tweedt's paper is concerned with the degree to which evolutionary effects of ecosystem engineering drove the Ediacaran-Cambrian diversification event. Through both a new compilation of the timing of origination of metazoan clades and a compilation of generic diversity they evaluate the degree to which 'ecosystem engineers' might have driven chemical and physical modification of Ediacaran-Cambrian marine environments. They find that ecological feedbacks were much more important in facilitating increases of biodiversity during the Cambrian and Ordovician than they were in the pre-Ediacaran times when such feedbacks were limited to microbial trapping and binding of sediment and its geochemical effects.

Marine ecosystem health

Jeremy Jackson's latest efforts have focussed on the investigation of human historical impacts on marine ecosystems, beginning with his plenary talk at the Panama ICRS "Reefs Since Columbus" (Jackson 1997). His subsequent paper titled "Historical Overfishing and the Recent Collapse of Coastal Ecosystems" has become a seminal contribution to our understanding of the early and pervasive impacts of humans on marine environments, especially in regard to overfishing (Jackson et al. 2001b). Jackson was able to show a remarkable contrast between what was natural in the sea prior to human interactions and modern ecosystems in various phases of degradation, with all of the intermediate stages in-between. Sandin and Sala utilize a novel approach to measure impact of humans on ecosystem health by employing successional theory. Human impacts drive ecosystems toward early successional trajectories, an opposite direction to successional change toward climax communities in the absence of human disturbance. Thus, Sandin and Sala propose that indicators consistent with successional dynamics may provide a generalized framework for comparing the health of ecosystems in space and time.

To attempt to summarize Jeremy Jackson's influential, dynamic, integrative, wide-ranging and applied approach to biology is difficult at best. His current passion focuses the long-term impacts of human activities on the oceans, and he continues to publish extensively with collaborators on the ecological and evolutionary consequences of the gradual formation of the Isthmus of Panama. Regardless of whether you ascribe to all of the viewpoints Jeremy promulgates, we believe he is one of those few individuals one encounters in the scientific community that has done so much to alter our scientific perspectives, and to encourage new scientific research. We are lucky that he has chosen to concentrate his efforts on evolutionary ecology, paleontology, and conservation biology and for this it is entirely appropriate to honor him with this dedicated special issue of *Evolutionary Ecology*. His research, mentoring and extended influence in multiple scientific disciplines, government and society makes him both a public and academic scientist of the highest caliber. Go well, Jeremy.

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