Acta Oecologica 85 (2017) 116–125

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

# Thermodynamics, ecology and evolutionary biology: A bridge over troubled water or common ground?

Keith R. Skene

*Biosphere Research Institute, 5A The Den, Letham, Angus DD8 2PY, UK*

## ARTICLE INFO

*Keywords:*
Diversification
Diffusion
Ecological succession
Evolutionary replacement
Maximum entropy production principle
Systems biology

## ABSTRACT

This paper addresses a key issue confronting ecological and evolutionary biology, namely the challenge of a cohesive approach to these fields given significant differences in the concepts and foundations of their study. Yet these two areas of scientific research are paramount in terms addressing the spatial and temporal dynamics and distribution of diversity, an understanding of which is needed if we are to resolve the current crisis facing the biosphere. The importance of understanding how nature responds to change is now of essential rather than of metaphysical interest as our planet struggles with increasing anthropogenic damage. Ecology and evolutionary biology can no longer remain disjointed. While some progress has been made in terms of synthetic thinking across these areas, this has often been in terms of bridge building, where thinking in one aspect is extended over to the other side. We review these bridges and the success or otherwise of such efforts. This paper then suggests that in order to move from a descriptive to a mechanistic understanding of the biosphere, we may need to re-evaluate our approach to the studies of ecology and evolutionary biology, finding a common denominator that will enable us to address the critical issues facing us, particularly in terms of understanding what drives change, what determines tempo and how communities function. Common ground, we argue, is essential if we are to comprehend how resilience operates in the natural world and how diversification can counter increasing extinction rates. This paper suggests that thermodynamics may provide a bridge between ecology and evolutionary biology, and that this will enable us to move forward with otherwise intractable problems.

## 1. Introduction

Ecology and evolutionary biology are enduring areas of scientific research, focusing on the spatial and temporal dynamics and distribution of diversity. Both of these fields have developed rapidly over the last century and continue to do so. Originally relevant in terms of basic survival (in our earlier guise as hunter gatherers dependent on understanding seasonality of foodstuffs and migration tempo) and as explanations for why the natural world looks and functions the way that it does, these subjects now occupy a more exigent role, predicting the impact of environmental perturbation on the biosphere as a whole, in terms of ecosystem service provision, resilience and diversity. It is as important to understand the processes of species diversification in functional and morphological space and time as it is to understand the processes of species extinction. The relationship between ecology and evolutionary biology has itself evolved over the last one hundred and fifty years.

It has long been recognized that spatial variation in diversity results from the combination of both ecological and evolutionary mechanisms acting over time (MacArthur, 1972). Hutchinson (1965) described this relationship as the ecological theatre and the evolutionary play. Since then, efforts have been made to elucidate the relative importance of these mechanisms (see, for example, Terborgh and Faaborg, 1980; Graham et al., 2014; Kozak and Wiens, 2016; Suárez-Atilano et al., 2017).

Yet for all of the common ground that they occupy, ecological and evolutionary studies differ, specifically in the approaches and underpinning philosophy that scientists employ in each of these fields. Their academic foundations differ significantly, with the modern evolutionary synthesis (MES) and its conspecific concepts such as the selfish gene relying, ultimately, on a reductionist, empiricist approach, whereas ecology has more recently utilized a system theory approach, embracing emergence. This has resulted in a conceptual and experimental gulf developing between these two fields, in spite of their seeking to address questions with mutual implications.

The Modern Evolutionary Synthesis (MES) focuses on the gene as the unit of selection, and advocates a selfish gene approach, wherein fitness is measured by the success of genetic variants being expressed in successive generations. Dawkins (1982) comments that “the organism is a tool for DNA, rather than the other way around”. This molecular

*E-mail address:* krskene@biosri.org.

http://dx.doi.org/10.1016/j.actao.2017.10.010
Received 24 August 2017; Received in revised form 17 October 2017; Accepted 18 October 2017

approach has been successfully applied at individual and population levels in particular environments, but fails to find a role at ecosystem and biome levels. The extended evolutionary synthesis (EES), though by its very title acting as an extension of the MES rather than a revision, attempts to embrace some systems aspects while maintaining the core elements of the MES.

The gene-centric approach is perceived by some to have shortcomings in terms of accounting for the drive and direction in ecological succession, post-mass extinction recovery, the broader tempo of diversification over geological time and the more fundamental importance of replacement rather than displacement as the basis for the emergence of new lineages (Benton, 1996; Brusatte et al., 2008; Mahler et al., 2010; Venditti et al., 2010; Percival et al., 2017).

Many researchers recognize that ecology does impact upon evolution. It is now recognized that adaptive radiation is dependent on ecological context (Pires et al., 2015). Any understanding of post-extinction recovery must begin with ecological succession (Solé et al., 2002). Bell (2013) argues that traditional approaches of relative fitness fail to form a sufficient basis for population genetics, instead advocating the need to combine ecology, population genetics and population dynamics, embracing absolute fitness.

Evolution is also viewed by many to impact upon ecology. Recent research has shown that evolution can affect species diversity (Schreiber et al., 2011; Pantel et al., 2015), population demography (Reznick et al., 2012), ecosystem function (Bassar et al., 2012; ter Horst et al., 2014) and the outcome of species interactions (Yoshida et al., 2003; ter Horst et al., 2010). ter Horst and Zee (2016) conclude that it is impossible to understand the ecology of a community without understanding concurrent evolutionary change.

Spatial and temporal considerations dominate both fields. Function tends to feature more in ecological thinking, with the fields of ecophysiology and functional ecology becoming significant areas of recent research over the latter part of the 20th century (e.g. Calow, 1987; Keddy, 1992; Buchmann, 2002; Norling et al., 2007).

Given the differences in these two fields and the fact that an understanding of how nature responds to change is now of essential rather than of metaphysical interest as our planet struggles with increasing anthropogenic damage, there is an emerging need to unify our approach, in order to fully understand the processes of diversification, change and function within our biosphere. Ceballos et al. (2015) warn that: “Averting a dramatic decay of biodiversity and the subsequent loss of ecosystem services is still possible through intensified conservation efforts, but that window of opportunity is rapidly closing”. However, without a unified theory of evolution and ecology, it is hard to unravel the patterns and processes that generate and maintain the biotic diversity of our planet, a necessary basis for any ambition toward maintaining ecosystem services.

### 1.1. *Bridge building?*

Calls for an integrative understanding of biological processes have been made for many years in the literature, from Dobzhansky’s (1973) famous quote, “Nothing in biology makes sense except in the light of evolution”, to current, more focused statements that evolution itself only makes sense when viewed in its ecological context (e.g. Coulson et al., 2006; Saccheri and Hanski, 2006; Johnson and Stinchcombe, 2007; Metcalf and Pavard, 2007; Pelletier et al., 2007; Grant and Grant, 2008). Pelletier et al. (2009) went further by claiming that nothing in evolution or ecology makes sense except in the light of the other. However, Levin (1998) concluded that the disciplinary links between ecological studies and evolutionary biology are among the weakest in the biological sciences.

There have been recent attempts at building bridges between the two fields (see Matthews et al. (2011) for a summary). Weber et al. (2017) call for more work to develop diversification models that include a mechanistic understanding of how ecological and evolutionary processes interactively influence speciation and extinction. As early as 1976, Antonovics (1976) announced the brave new world of ecological genetics. Thuiller et al. (2013) emphasise the importance of eco-evolutionary processes in biodiversity models. Elser (2006) employed stoichiometric theory as a chemical bridge between ecosystem ecology and evolutionary biology, while Kokko and López-Sepulcre (2007) turned to ecogenetic feedback loops. Laland et al. (2008) and Matthews et al. (2014) suggested a more complicated triple bridge between evolution, development and ecology, suggesting that niche construction could provide a “useful conduit” between evolution and development. Valladares et al. (2006) focused on phenotypic plasticity as a bridge while Gonzalez et al. (2013) suggest that evolutionary rescue lies at the intersection between ecology and evolution.

Yet bridges do not unify nor do they reach all parts of the discursive landscape. Given the significant philosophical and material differences that exist (such as reduction contrasting with emergence, a single unit of selection compared with interactive levels of organization, the emphasis of form contrasting with function, the importance and significance, or otherwise, of energy and material flow), the two discourses would appear so different that bridges are unlikely to help unify the fields.

Schoener (2011, p. 426) questions whether such bridge building is valid at all, writing: “We still don't know if the evolution-ecology pathway is frequent and strong enough in nature to be broadly important”. Johnson and Stinchcombe (2007) concluded that no study has convincingly demonstrated that rapid evolution in one species affects community dynamics in the field, and stated that “The importance of bridging community ecology and evolutionary ecology has not yet been convincingly demonstrated”.

Another issue relates to the timescales of micro- and macro-evolution. Jablonski (2008) points out that attempting to study any interplay of ecological and evolutionary dynamics is problematic due to mismatches in scale and level. Research into the interactions between ecological and evolutionary dynamics has largely focused on relatively simple ecological communities and on local spatial scales (Urban et al., 2008). Difficulties relating to how the short term ecological impacts of rapid evolutionary change really inform macro-evolution as well as how the origins of species diversity relate to macro-evolutionary events are discussed by Weber et al. (2017). Fussmann et al. (2007) concluded that no study had come close to providing empirical support for eco-evolutionary community dynamics. Weber et al. (2017) counter this viewpoint, concluding that “Ignoring the role of evolution in community studies may be inappropriate in many cases”.

This paper explores the idea that pursuing common ground may be more productive than isolated bridge building. Given that ecology and evolutionary biology are focused on the one biosphere, and that this biosphere is made of the same components as the rest of the universe, subject to the same physical laws and is an open system dependent on energy mostly from our neighbouring star, then this common ground may not be so mysterious. Starting with the premise that the biosphere is merely an extension of the rest of the universe in terms of its drives, functioning and development, we examine the significance or otherwise of the laws of thermodynamics as a common ground that could unify evolutionary biology and ecological science.

We begin by summarizing the key developments in the field of thermodynamics, before examining the existent literature on thermodynamic theory relating to ecology and evolution. Next, we explore the importance of thermodynamics in each level of biosphere organization, before considering the potential of such common ground in addressing key issues in both fields.

## 2. Thermodynamics and the MEPP

Thermodynamics is the study of the energy flow, heat and movement in structures within the universe. In 1824, Carnot published his book, Réflections sur la Puissance Motrice du Feu (Carnot, 1824), in