PREFACE

Thomas W. Schoener*, Jordi Moya-Laraño†, Jennifer Rowntree‡, Guy Woodward§

*Department of Evolution and Ecology, University of California, Davis, California, USA
†Department of Functional and Evolutionary Ecology, Estación Experimental de Zonas Áridas, EEZA-CSIC, Almeria, Spain
‡Faculty of Life Sciences, University of Manchester, Manchester, United Kingdom
§Imperial College London, Silwood Park Campus, Ascot, Berkshire, United Kingdom

The growing realisation that ecology and evolution can often operate over similar timescales (Carroll et al., 2007; Hairston et al., 2005; Schoener, 2011) has led to exciting new avenues of investigation into the links between them, including the burgeoning field of eco-evolutionary dynamics, the dynamic interplay between evolution and ecology in real time. This volume deals with the latest advances in this multidisciplinary research endeavour, including examples of major topics of current interest to both empiricists and theoreticians, as well as providing clear signposts towards the future development of the field.

The first five contributions (Chapters 1–5) consider the feedback loops between ecology and evolution, i.e., how ecological dynamics determine the selective pressures that shape trait dynamics, as well as vice versa, how trait evolution influences ecological dynamics. Of the two directions, ecology to evolution is by far the more studied to date, focusing primarily on selective pressures that affect trait evolution (Endler, 1986; MacColl, 2011). The opposite direction, which addresses how trait evolution affects ecological patterns and processes, is only now a research area that is coming into its own. At the micro-evolutionary scale, this is the field of community genetics (Antonovics, 1992; Hersch-Green et al., 2011); at the macro-evolutionary scale, this could include community phylogenetics, or how phylogenetic distances affect ecological outcomes (Webb et al., 2002). The last four papers in the volume (Chapters 6–9) deal with this part of the reciprocal eco-evolutionary loop.

Below we provide a brief overview of the current volume, highlighting for each chapter its main themes and how each contributes to the advance of eco-evolutionary research. We conclude with a discussion of the current state of the field, especially in light of the contents of this volume, and we give some thoughts about how we envision the field developing in the foreseeable future.

In the first paper, Travis et al. (2014) synthesise a large and growing body of work on the interactions that drive eco-evolutionary dynamics in the Trinidadian guppy model system, which has provided some intriguing and often counterintuitive insights into this new field. They used a multipronged empirical and theoretical approach that encompasses mathematical modelling, laboratory common-garden experiments, replicated introductions in the wild, experiments in manipulated artificial streams *in situ*, as well as altering stream productivity through canopy manipulation. They review the widespread differences in top-down ecological effects of replicated lines of guppies evolved in high- versus low-predation environments and grown at two different densities, and how these effects feed back to determine fitness among experimental groups. They also demonstrate how unexpected indirect ecological effects can arise from the eco-evolutionary feedback loop, as seen in the dampening of a trophic cascade by cycling of limiting nutrients. Finally, the authors provide an overview of ongoing research devised to understand the evolution of the low-predation phenotypes by documenting both the effects of evolutionary changes in the guppies and the strong concomitant changes they induce in the ecosystem, including the evolutionary response of competing species.

The second paper, by Hiltunen et al. (2014), focuses on another model system in which the authors have combined predictions from differential equation models of population dynamics, either with or without evolution, with sophisticated laboratory chemostat experiments on predator prey interactions (e.g. Becks et al., 2012; Yoshida et al., 2003, 2007). Here, the authors build on recent work (Hiltunen et al., 2013) by incorporating evolution within a simple food web that includes intraguild predation. They found that the dynamics of intraguild predators and prey were sensitive to genetic variation, and thus evolution in the shared prey. These dynamics are "intriguingly complex" and their outcome depends on the trade-off in prey defence between the predators. The authors suggest that with prey evolution, the dominance of each predator essentially "takes turns" as in a type of dynamics known as a "canard cycle", having a very fast transition of dynamical behaviour within a small range of a "control" parameter. This concept is apparently described here in the context of population ecology for the first time (see May and Leonard, 1975, however, for a similar kind of behaviour with Lotka–Volterra competition equations).

The third paper (Moya-Laraño et al., 2014) deals with simulations in more diverse food webs that include up to 20 species and their spatial context. The authors have extended a recent Individual-Based Model platform (Moya-Laraño et al., 2012) to enable eco-evolutionary dynamics to be simulated for multiple genetic quantitative traits in complex soil food webs. Their results suggest that highly connected webs in islands at intermediate distances, when allowing for evolution in the 20 constituent species (i.e., high genetic variation), were generally more persistent despite otherwise widespread species extinctions. They also report diverse and fast trait-evolutionary dynamics (i.e., oscillating or monotonic changes in the means of several traits across a few generations) occurring during ecological dynamics. The authors acknowledge that these initial forays into simulations of evolving food webs can, at present, only capture a small portion of the complexity of nature, but they also suggest ways in which their framework could be developed in a Feedback Research Program to help understand real systems, including the engineering of eco-evo webs for biological pest control in the future.

In the fourth paper, Smallengange and Deere (2014) show the results of a harvesting experiment on male morphs of bulb mites. Each morph has a different sexual strategy (fighters vs. scramblers), and the authors found that, contrary to traditional theoretical predictions (Tomkins and Hazel, 2007), regardless of which morph was harvested, the frequency of scramblers always increased. The authors show how this apparently unexpected result is due to an eco-evolutionary feedback and conclude that the ecological background against which evolution is studied must always be taken into account to fully understand the drivers of trait evolution. A key aspect of the novelty of their results is that to fully understand the evolution of sexual selection (not just natural selection), one has to also consider ecological feedbacks of trait evolution: Smallegange et al.'s results provide a new benchmark in studies of sexual selection, as they show how the evolution of such traits can also be tightly coupled to ecological dynamics.

In the fifth paper, Cameron et al. (2014) introduce and review an extensive body of research on soil-mite population dynamics, returning us to an experimental approach that neatly complements Travis et al. Cameron et al. demonstrate explicitly how intimately ecological and evolutionary dynamics of living systems are linked, how complex even seemingly simple systems are in reality and how difficult it is to distinguish "ecological" from "evolutionary" effects without carefully designed experiments. The body of research covered by Cameron et al. highlights how current and historic parental states and environments interact to generate and maintain phenotypic variation of life history traits (e.g. growth rate and the trade-off between age and size to maturity) and how this can influence population dynamics at intergenerational scales. The novel experimental data presented introduce a harvesting (or management) regime that is akin to that of commercial fisheries. These experiments aim to "close the eco-evolutionary loop" by determining whether the observed changes in life history traits (a delay in developmental time linked to an increase in fecundity) are caused by selection leading to increased population growth rates. They use molecular techniques to show that, in addition to drift, selection causes the reported differences, leading to a clear feedback loop. They also ask if these selective forces can change the evolutionary trajectory of a population over time, for example, by rescuing it from extinction. Crucially, Cameron et al. show that both selection and drift play a role in determining future evolutionary trajectories of populations under different environmental and harvesting conditions, and that evolution can rescue populations even if they are facing classic extinction vortices, as is the case for many global fisheries.

In the sixth paper, Melián et al. (2014) present an individual-based modelling approach in which they link phenotypic variability in predator selectivity to species diversity in food webs. Predator selectivity is modelled using two concepts from foraging theory (Schoener, 1987; Stephens and Krebs, 1986): (1) per-prey-item profitability (net energy/handling time) and (2) a type of learning, in which previous consumptions act as an agent of reinforcement predilecting future selectivity. The resulting individual-trait-based models contain two basic parameters, the speed of learning and the strength of prey selection. Approximate Bayesian computational methods are then used to uncover which model is the best predictor of trophic links in a massive food-web data set consisting of the diets of >5500 individual fishes. They conclude that the maintenance of diversity in food webs may depend on patterns of predatory behaviour and relative abundance of prey. Strongly connected predators (having a high number of prey items, as might result from high feeding rates) preferred common prey and vice versa for weakly connected predators, and the balance between them drove patterns of species diversity. The chapter offers a glimpse into eco-evolutionary dynamics: in the authors' words, "we were able to infer different types of density-dependent prey selection from individual predators for a given ecological time scale, but we were unable to estimate how such variation in prey selectivity might drive frequency dependent selection pressures . . ."

In the seventh paper, Khudr et al. (2014) bring us squarely into the field of community genetics, presenting novel data from a genetically explicit plant–herbivore system. They deconstruct levels of diversity and examine the strength of competition among pea aphid species and genotypes in a genetically variable plant–host environment. Although competition effects among herbivores sharing a host are implicit in many of the classic community genetics systems, few, if any, of these studies have examined the interactions with the degree of detail presented here. Khudr et al. measured both inter- and intra-specific competition, alone and in combination, using a model system of aphid herbivores and faba bean host plants. In addition, they dissected the intra-specific competition to distinguish competition effects within and among different clones of the same species. They found that the strength of competition increased as relatedness among aphids increased and that the effects of the aphids on each other were stronger than the influence of the plant host. However, in all scenarios tested, plant genotype influenced or mediated competitive interactions among the aphids. These findings complement those of Cameron et al., once again clearly demonstrating the complexity that can exist within even seemingly simple ecological systems. This work also highlights the intractability of understanding the ecological and evolutionary responses of species interactions if the underlying genetics of a system are not taken into account. The use of aphids, particularly clonal ones, has proved very profitable for studies of eco-evolutionary dynamics in other contexts: in a multigenerational field experiment, Turcotte et al. (2011) studied the existence and consequences of eco-evolutionary dynamics by in essence controlling for evolution: single-clone treatments (no evolution) were contrasted with multi-clone treatments (evolution, defined as a change in gene frequency, occurs when clones change frequencies).

In the eighth paper, O'Reilly-Wapstra et al. (2014) build on previous work using a semi-natural plant genetic resource: multiple common gardens of *Eucalytus* species, in this case *E. globulus*, containing replicated families and populations, originally collected from across the Australian landscape. As with Khudr et al., they examine the influence of within-species genetic diversity at multiple scales (within and among populations), across abiotic environmental gradients, on plant–herbivore and pathogen interactions. The deconstruction of genetic diversity in this case is, however, within the plants rather than the plant pests. Again, the importance of genetic diversity within plants in determining the outcome of interactions with plant pests is highlighted, as is the difficulty in predicting under what circumstances, and at what level, this is important. More specifically, O'Reilly-Wapstra et al. determine genetic correlations among the plants and the various pest species and investigate the consistency of the patterns observed. This approach enables them to explore the stability of plant–pest interactions across different environments (the common gardens) and determine if the genetic response of the plants to any of the enemies influences the response to others (i.e., could the occurrence of multiple plant pests facilitate or hinder an evolutionary response to attack?). It is particularly notable that the team found that most of the interactions between the plant genetic variation and the plant pests were independent of each other and that there was a consistency of plant genetic response across abiotic environments. However, a family-level (but not population-level) genetic correlation was observed between the plant genetic response to a fungal leaf pathogen and the response to sawfly larvae. This suggests that an evolutionary response of the plants to one of these enemies would influence and potentially drive the response to the other, but that different evolutionary forces were acting on the interactions within and among populations.

The ninth paper stays with *Eucalyptus* as a model system but looks at the impact of global change in atmospheric carbon dioxide and soil nitrogen levels on multiple congeners of *Eucalyptus*. Genung et al. (2014) take us from the micro- to the macro-evolutionary scale and ask how evolutionary history and phylogenetic relationships among species influence the contemporary responses of the plants to these abiotic factors in multi-species communities. They show that plant productivity is positively correlated with contemporary range size, but that range size is a product of evolutionary history. That is, past evolution seems to have driven current distributional ranges through increased plant fitness. Similar to the earlier contribution by Khudr et al., the authors also explore the impact of individual relatedness among competitors on the productivity of the plants under competitive conditions. They show that plant productivity of monocultures (where conspecifics compete) is reduced compared to mixtures, but only for those mixtures in which the competitors were of intermediate relatedness. This demonstrates the contingency in responses among different organisms (cf. the findings of Khudr et al.) to competition. Overall, Genung et al. (2014) demonstrate that there are complex relationships between phylogenetic similarity, productivity and the influence of environmental stressors on the focal plants.

In summary, this volume offers a timely coverage of an important emerging field at the nexus of ecology and evolution. Its chapters represent the

Finally, O'Reilly-Wapstra et al. (2014) show for two pest species (a fungal pathogen and a sawfly larva) that damage inflicted by one of the species is genetically correlated with damage inflicted by the other species; hence, a response to selection by the plant against one of the pest species will affect the population dynamics of the other, in what they call an indirect eco-evolutionary feedback loop.

While the studies presented here are still embryonic in terms of their ability to capture the entire complexity of natural systems having eco-evolutionary dynamics, they certainly represent a major leap forward with their novel ways of linking ecology and evolution more closely than before; as such, they represent some of this new research direction's first steps towards an ultimate goal of untangling and understanding Darwin's "entangled bank" of interacting species in space and time. The multidisciplinary approaches seen in this volume do, however, fairly reflect the scale of the challenge, foreshadowing the degree to which the next generation of eco-evolutionary research will need to employ a huge range of expertise—both empirical and theoretical—to predict how natural systems are likely to respond to future change.

REFERENCES

Agrawal, A.A., Johnson, M.T.J., Hastings, A.P., Maron, J.L., 2013. A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. Am. Nat. 181, S35–S45.

Antonovics, J., 1992. Toward community genetics. In: Fritz, R.S., Simms, E.L. (Eds.), Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics. University of Chicago Press, Chicago, IL, pp. 426–449.

Becks, L., Ellner, S.P., Jones, L.E., Hairston Jr., N.G., 2012. The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics. Ecol. Lett. 15, 492–501.

Cameron, T.C., Plaistow, S., Mugabo, M., Piertney, S.B., Benton, T.G., 2014. Eco-evolutionary dynamics: experiments in model system. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 171–206.

Carroll, S.P., Hendry, A.P., Reznick, D.N., Fox, C.W., 2007. Evolution on ecological timescales. Funct. Ecol. 21, 387–393.

Endler, J.A., 1986. Natural Selection in the Wild. Princeton University Press, Princeton, NJ.

Fussmann, G.F., Loreau, M., Abrams, P.A., 2007. Eco-evolutionary dynamics of communities and ecosystems. Funct. Ecol. 21, 465–477.

Genung, M.A., Schweitzer, J.A., Senior, J.K., O'Reilly-Wapstra, J.M., Chapman, S.K., Langley, J.A., Bailey, J.K., 2014. When Ranges Collide: Evolutionary History, Phylogenetic Community Interactions, Global Change Factors, and Range Size Differentially Affect Plant Productivity. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 297–350.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T., Fox, J.A., 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecol. Lett. 8, 1114–1127.

Hersch-Green, E.I., Turley, N.E., Johnson, M.T.J., 2011. Community genetics: what have we accomplished and where should we be going? Philos. Trans. R. Soc. Lond. B 366 (1569), 1453–1460.

Hiltunen, T., Jones, L.E., Ellner, S.P., Hairston Jr., N.G., 2013. Temporal dynamics of a simple community with intraguild predation: an experimental test. Ecology 94, 773–779.

Hiltunen, T., Ellner, S.T., Hooker, G., Jones, L.E., Hairston Jr., N.G., 2014. Eco-evolutionary dynamics in a three-species food web with intraguild predation: intriguingly complex. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 41–74.

Khudr, M.S., Potter, T., Rowntree, J., Preziosi, R.F., 2014. Community genetic and competition effects in a model pea aphid system. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 243–266.

MacColl, A.D.C., 2011. The ecological causes of evolution. Trends Ecol. Evol. 26, 514–522.

May, R.M., Leonard, W.J., 1975. Nonlinear aspects of competition between three species. SIAM J. Appl. Math. 29, 243–253.

Melián, C., Baldó, F., Matthews, B., Vilas, C., González-Ortegón, E., Drake, P., Williams, R.J., 2014. Individual trait variation and diversity in food webs. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 207–242.

Moya-Laraño, J., Verdeny-Vilalta, O., Rowntree, J., Melguizo-Ruiz, N., Montserrat, M., Laiolo, P., 2012. Climate change and eco-evolutionary dynamics in food webs. In: Woodward, G., Jacob, U., Ogorman, E.J. (Eds.), Advances in Ecological Research, Vol. 47: Global Change in Multispecies Systems, Pt 2. 1–80.

Moya-Laraño, J., Bilbao-Castro, J.R., Barrionuevo, G., Ruiz-Lupión, D., Casado, L.G., Montserrat, M., Melián, C., Magalhães, S., 2014. Eco-evolutionary spatial dynamics: rapid evolution and isolation explain food web persistence. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 75–144.

O'Reilly-Wapstra, J.M., Hamilton, M., Gosney, B., Whiteley, C., Bailey, J.K., Williams, D., Wardlaw, T., Vaillancourt, R.E., Potts, B.M., 2014. Genetic correlations in multi-species plant/herbivore interactions at multiple genetic scales; implications for eco-evolutionary dynamics. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 267–296.

Schoener, T.W., 1987. A brief history of optimal foraging theory. In: Kamil, A.C., Krebs, J., Pulliam, H.R. (Eds.), Foraging Behavior. Plenum Publishing Corporation, New York, NY, pp. 5–67.

Schoener, T.W., 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331, 426–429.

Smallengange, I., Deere, J.A., 2014. Eco-evolutionary interactions as a consequence of selection on a secondary sexual trait. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 145–170.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ.

Thompson, J.N., 1998. Rapid evolution as an ecological process. Trends Ecol. Evol. 13, 329–332.

Tomkins, J.L., Hazel, W., 2007. The status of the conditional evolutionarily stable strategy. Trends Ecol. Evol. 22, 522–528.

Travis, J., Reznick, D., Bassar, R.D., López-Sepulcre, A., Ferriere, R., Coulson, T., 2014. Do eco-evolutionary feedbacks help us understand nature? Answers from studies of the Trinidadian guppy. In: Moya-Laraño, J., Rowntree, J., Woodward, G. (Eds.), Advances in Ecological Research, Vol. 50: Eco-evolutionary Dynamics, pp. 1–40.

Turcotte, M.M., Reznick, D., Hare, J.D., 2011. The impact of rapid evolution on population dynamics in the wild: experimental test of eco-evolutionary dynamics. Ecol. Lett. 14, 1084–1092.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33, 475–505.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F., Hairston Jr., N.G., 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424, 303–306.

Yoshida, T., Ellner, S.P., Jones, L.E., Bohannan, B.J.M., Lenski, R.E., Hairston Jr., N.G., 2007. Cryptic population dynamics: rapid evolution masks trophic interactions. PLoS Biol. 5, 1868–1879.