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The genomic basis of eco-evolutionary dynamics

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Abstract:

Recent recognition that ecological and evolutionary processes can operate on similar time scales has led to a rapid increase in theoretical and empirical studies on eco-evolutionary dynamics. Progress in the fields of evolutionary biology, genomics, and ecology is greatly enhancing our understanding of rapid adaptive processes, the predictability of adaptation and the genetics of ecologically important traits. However, progress in these fields has proceeded largely independently of one another. In an attempt to better integrate these fields the center for 'Adaptation to a Changing Environment' organized a conference entitled 'The genomic basis of eco-evolutionary change' and brought together experts in ecological genomics and eco-evolutionary dynamics. In this review, we use the work of the invited speakers to summarize eco-evolutionary dynamics and discuss how they are relevant for

understanding and predicting responses to contemporary environmental change. Then we show how recent advances in genomics are contributing to our understanding of eco-evolutionary dynamics. Finally, we highlight the gaps in our understanding of eco-evolutionary dynamics, and recommend future avenues of research in eco-evolutionary dynamics.

Ecology and evolution are undeniably connected (Figure 1). Ecological factors, such as species interactions and environmental variation, can drive evolutionary change in genetically-determined phenotypic characters, enabling organisms to adapt to their environment (Darwin 1859). In turn, evolutionary change can modify the way species interact with their environment, competitors and predators influencing ecological dynamics (Levins 1968). Despite their obvious connection, the fields of ecology and evolution have proceeded largely independently of one another. This is partly due to the common belief that ecological and evolutionary processes operate on different time scales: that evolution is too slow to influence contemporary ecological dynamics, which we now know is not always true (see Hairston *et al.* 2005; Schoener 2011; Thompson 1998). Evolution can be fast – within a few generations – and can influence ecological dynamics (Thompson 1998). In turn, ecological dynamics can feedback to alter evolutionary processes, completing an 'eco-evolutionary'

feedback loop (e.g. Turcotte *et al.* 2013). These reciprocal interactions between ecological and evolutionary processes over short (contemporary) time-scales are broadly defined as eco-evolutionary dynamics (Hendry 2016; Pelletier *et al.* 2009; Post & Palkovacs 2009; Schoener 2011). Although eco-evolutionary dynamics have been the focus of theoretical investigation for decades (Schoener 2011), they are now increasingly the subjects of empirical study. As a result the focus of this growing field has changed; the question is no longer do eco-evolutionary dynamics exist, but how common are they, how important are they and can we predict them (Hendry 2016; Hersch-Green *et al.* 2011). Addressing these issues requires, in part, a greater capacity to track evolutionary change in the field and to improve our understanding of the rate and predictability of adaptation. To this end, the rapidly growing field of genomics promises to be extremely useful. In an attempt to better integrate the fields of ecology, evolution and genomics the center for 'Adaptation to a Changing Environment' (ACE) from ETH Zürich organized a conference entitled 'The genomic basis of eco-evolutionary change', at the Conference Center CSF Monte Verità in Ascona, Switzerland from the 5-9th of June 2016. The goal of the conference was to highlight recent developments in ecological genomics and eco-evolutionary dynamics and promote greater interactions between researchers in these fields. The conference involved a mix of talks by invited speakers and ACE members, followed by small group discussions focusing on key questions in eco-evolutionary dynamics. In the evenings poster sessions were held where all other participants and ACE PhD students could showcase their research. Participants presenting posters also highlighted their research in one-minute speed talks at the beginning of the conference.

Eco-evolutionary dynamics

One important goal for many ecologists and evolutionary biologists is improving predictions about how organisms will respond to environmental change. This remains a challenging task (Urban *et al.* 2016), but better predictions can be made using: i) a detailed understanding of ecological and evolutionary responses to environmental change (Hoffmann & Sgro 2011), ii)

models that consider more realistic parameters (Débarre *et al.* 2015) and iii) a better understanding of the repeatability of eco-evolutionary dynamics (Hendry 2013). In the next sections, we consider each of these in turn.

i) detailed understanding of ecological and evolutionary responses to environmental change

Andrew Hendry presented the example of evolutionary change in beak size and shape in Darwin's Finches in response to variability in rainfall (Figure 1a) and described an eco-evolutionary framework that focuses on identifying interactions between different levels of ecology and evolution: genomes, phenotypes, populations, communities and ecosystems (Hendry 2016). Previous work on Darwin's finches has established that periods of drought in the Galapagos can, via changes in the plant communities and therefore seed food availability, drive the evolution of beak morphology in finches and alter population growth rates for species with different beak morphologies (Boag & Grant 1981; Grant & Grant 1995). In his talk Andrew presented new work showing variation among islands in the responses of different finch species to selection, as well as the results of ongoing work exploring how the evolution of finch beaks might influence plant community structure. Recent genomic work has demonstrated that beak size and shape is controlled by a large effect locus (Lamichhaney *et al.* 2015), providing insight into the genetic architecture of these eco-evolutionary dynamics. The body of work in this system is ongoing and Andrew emphasized that they are still missing information on how evolution is shaping community structure and higher order ecosystem processes.

An interesting example of rapid evolution in response to human-induced environmental change was discussed by Ole Seehausen. He described how human induced lake eutrophication was responsible for reduced reproductive isolation between species of whitefish, resulting in 'reverse speciation' and a reduction in species and functional diversity within the freshwater lake fish community (Vonlanthen *et al.* 2012). The altered environment changed population dynamics and reduced species-level genetic variance in the lakes, this

loss of genetic diversity contributed to a loss of functional diversity in the lake community (Figure 1b). Ole also discussed the implications of whitefish trait evolution for fish productivity: evolution in gill-raker number in response to eutrophication is tightly correlated with lower fishery yield (Alexander *et al.* 2017). This work clearly demonstrates how eco-evolutionary dynamics can have important impacts on fisheries and their management.

Although periods of environmental change offer excellent opportunities for exploring eco-evolutionary dynamics, we can also gain insight into eco-evolutionary processes by simply studying existing adaptive variation in key phenotypes shaped by spatial variation in the environment. Patrik Nosil described work demonstrating how camouflage in the colour polymorphic *Timema* species (walking sticks) can drive variation in local predation pressure on other arthropods species (Figure 1d) (Farkas *et al.* 2013). The colour morphs are genetically determined and experienced differential survival on different host plants (Comeault *et al.* 2016; Comeault *et al.* 2015). Using reciprocal transplants, Patrik and colleagues linked variation in colour matching between the walking sticks and host plant to the insect's population growth on different host plants (Farkas *et al.* 2013). In addition, maladaptation of walking sticks to their host plants was shown to attract more bird predators, which altered arthropod species richness and abundance, and reduced herbivore pressure on the associated host plants (Farkas *et al.* 2013). This observation demonstrates how adaptive variation in a phenotype with a genetic basis can alter population dynamics of other species in the community and can potentially alter selection pressures on a host plant (Figure 1d).

The influence of ecology on evolution (eco-evo) is well established, but fewer studies have explored how contemporary evolution leads to ecological change (evo-eco). A powerful approach to reveal these dynamics is to capitalize on laboratory manipulations of organisms with short generation times (e.g. microorganisms), and run multiple parallel experiments, with and without evolution. Nelson Hairston used this setup to show that in a predator-prey

system it is possible to obtain different population dynamics in the presence or absence of evolution, i.e. with or without genetic variation (Yoshida *et al.* 2007). When cultures were initiated with a single algal genotype, rotifer and algal densities oscillated in classical predator-prey cycles (Yoshida *et al.* 2003). However, when cultures were initiated by multiple algal genotypes, only the rotifer density oscillated while the prey density remained nearly constant. This pattern was explained by contrasting population dynamics of defended and undefended prey genotypes that counterbalanced each other, resulting in a fairly stable prey density over time (Fussmann *et al.* 2003). The ecological dynamics of this system could therefore not be understood without knowledge of the evolutionary processes involved.

Another evo-eco example was presented by Jonathan Levine, one of the initiators of ACE, who presented the results of greenhouse experiments exploring the influence of evolution on colonization success by *Arabidopsis thaliana* (Williams *et al.* 2016). To test for an effect of evolution, some populations were allowed to set seed and thus evolve whilst colonizing new patches, whereas others were restarted in each generation using seeds from the starting population to exclude evolution. The results showed that evolving populations can spread faster than non-evolving populations in continuous landscapes, but much faster (up to 3x) across the most fragmented landscapes (Williams *et al.* 2016).

These studies show that ecological change can drive evolution and they also confirm the important role of evolution in shaping ecological dynamics (at least in the lab-based systems highlighted). Despite such advances, there are still few examples of how eco-evolutionary dynamics shape the higher-levels of community structure and ecosystem-level processes. Some notable exceptions include classic studies that demonstrate how fish traits can drive zooplankton community structure, primary-producer biomass and nutrient cycling, or how genetic variation in leaf chemistry can affect soil decomposition and microbial community composition in forests (reviewed in Hendry 2016; Post & Palkovacs 2009). Rarer still, are examples of complete feedback loops between ecological and evolutionary

processes. One notable example was presented by Martin Turcotte, an ACE fellow, whose work has demonstrated how population density of clonal aphids can influence the outcome and rate of evolution, and subsequently impact population growth rates (Turcotte *et al.* 2013). Eco-evolutionary feedbacks have also been shown in the context of more complex population structure. For example, variation at a genetic locus associated with dispersal ability (physiological phenotype) in the Glanville fritillary butterfly is associated with colonization-extinction (population) dynamics of a well-studied metapopulation (Hanski 2011). Accounting for the complex spatial structure of natural populations is critical to better understanding and predicting the eco-evolutionary dynamics of wild species.

ii) incorporating more realistic parameters in predictive models

A direct approach to improving predictions for species' responses to environmental change involves extending existing models to include more ecologically and evolutionarily realistic scenarios. Fréderic Guillaume provided an overview of how genetic architecture can impact the rate and direction of responses to environmental change and how population subdivision can influence the response to selection in heterogeneous environments (Débarre *et al.* 2015). He also presented ongoing modeling work to forecast changes in the distribution of alpine plants under climate change using an eco-evolutionary simulation framework (Guillaume & Rougemont 2006).

Understanding the factors that might influence evolution on timescales relevant for ecological change is also critical (Carroll *et al.* 2007), and one factor; the role of sex, was discussed by Hanna Kokko. She highlighted the diversity of sexual systems in nature (Aanen *et al.* 2016), and discussed possible drivers of spatial variation in reproductive strategies and how such variation can shape the evolutionary dynamics of populations (e.g. Tilquin & Kokko 2016). The influence of spatial variation in reproductive strategies on evolution was also considered by Yvonne Willi. She discussed the causes of range-wide variation in the genotypes, phenotypes and population dynamics of North American *Arabidopsis lyrata* and

described how at broad spatial scales selfing was more common in range edge populations during postglacial expansion and colonization (Griffin & Willi 2014). Spatial variation in selection driven by changes in population density (e.g. during distributional change or invasion) is a clear case where feedbacks between eco-evolutionary dynamics are expected to be highly relevant. Understanding interactions between ecological and evolutionary processes in the context of a spatially varying environment is important to develop more ecologically realistic models (Hanski 2011; Kokko *et al.* 2017).

iii) conducting experiments to test the repeatability of eco-evolutionary dynamics.
Another way to improve predictions for eco-evolutionary dynamics is to test parallel evolution experimentally in the lab, asking the question: how repeatable are eco-evolutionary dynamics? Lutz Becks discussed empirical work done in collaboration with Nelson Hairston that addressed this question (Figure 1c, Becks *et al.* 2012). The study investigated predator (rotifer) – prey (algae) dynamics: rotifer predation selects for an increase in algal prey defense (clumping), this increase in prey defense in turn reduces predator density and predation pressure, which in turn increases prey density and competition. Defended prey have reduced competitive ability and thus they experience reduced fitness, and as a result the proportion of vulnerable prey increases with a subsequent increase in predator density and predation pressure – and the cycle continues. Prey defense involved expression changes in many genes, but most interestingly in a subsequent cycle when the same defense phenotype evolved again different genes were differentially expressed. Phenotypic parallelism in consecutive cycles was not driven by parallel genetic changes.

The absence of repeatability in evolution at the genetic level, observed in Lutz's work raises many interesting questions about the stochasticity of evolutionary processes and how past selection may influence future responses. Investigating how evolutionary history and the rate of environmental change influences ongoing adaptation was the focus of Ben Kerr's talk. He presented work on *Escherichia coli* populations experiencing different rates of

environmental change (varying antibiotic concentration in the environment over time) and showed that evolving under gradual environmental change can provide greater opportunities to explore different mutational pathways for antibiotic resistance, resulting in higher long-term population growth rates (Lindsey *et al.* 2013). In contrast, when change was sudden many mutational pathways to resistance were inaccessible. This work is important because it emphasizes how the repeatability and rate of evolution at the genetic level is contingent both on the rate of ongoing environmental change, but also on the selection pressures that populations or species have previously experienced.

Genetics and genomics of ecologically relevant traits

Advances in DNA sequencing have revolutionized many fields in biology and invited talks at the ACE conference clearly demonstrated that this 'genomics' revolution has also begun to contribute a great deal to understanding eco-evolutionary dynamics. Here we highlight three important advances that the genomics era has enabled: i) knowledge of the genes and genetic architecture of adaptive traits in natural populations, ii) greater capacity to track genotypes and allele frequencies in natural populations through time, and iii) a better understanding of the role of adaptive and non-adaptive processes in shaping genetic variation, adaptive divergence and speciation.

i) knowledge of the genes and genetic architecture of adaptive traits in natural populations

A real advantage of the genomics era has been the ability to link phenotype to genotype and identify the underlying genetic architecture of key ecological traits in natural populations. The invited talks provided examples of how to do this in a diverse range of taxa and across multiple scales; from microbes to long lived trees, and from chemostats to landscapes. The talks demonstrated how researchers can identify the genetic architecture (Chaves *et al.* 2016; Comeault *et al.* 2014), the genes (Becks *et al.* 2012; Goldman-Huertas *et al.* 2015; Whiteman *et al.* 2012) and even causal mutations (Prasad *et al.* 2012) of ecologically relevant traits in both model and non-model taxa. Talks provided an overview of the different

approaches used to link phenotypes to genotypes and demonstrated how information at different genomic resolutions (from genomic islands to causal mutations) provides insight into evolutionary ecology.

Linking phenotypes and genotypes in the field has enabled researchers to study adaptive evolution in natural populations and in a broader range of non-model taxa, for example Victoria Sork's work on the ecological genomics of long-lived oak trees. She provided a comprehensive introduction to several approaches that enable researchers to link climatic variation with genetic and epigenetic variation in natural populations across a landscape (Sork *et al.* 2013). This can help to identify genomic regions or candidate genes that might underlie adaptation, even in long lived non-model species (e.g. Gugger *et al.* 2016). Another example of linking genotype to phenotype in non-model systems came from Patrik Nosil and colleagues' work on *Timema* walking stick insects, highlighted earlier. Ecological and evolutionary processes can clearly interact across a landscape to influence patterns of gene flow and genetic variation, and these processes can be readily studied using population samples and high throuput sequencing in a diverse range of study systems.

Another useful approach to linking phenotype and genotype, adopted by Tom Mitchell-Olds and Noah Whiteman, is to develop 'ecological' model systems in taxa closely related to traditional genetic model species like *Arabidopsis* and *Drosophila*. Using close relatives of model organisms has enabled researchers to leverage the wealth of genomic data and state-of-the-art experimental techniques, like transgenics and gene editing, with knowledge of phenotypes and ecological interactions to study adaptation in ecologically relevant traits and natural populations. Noah Whiteman presented work using newly developed genomic resources for *Scaptomyza* flies that demonstrated how the flies' leaf mining lifestyle evolved recently from a saprophagous ancestor, and which genes and

genomic changes accompanied this ecological transition (Goldman-Huertas *et al.* 2015; Whiteman *et al.* 2012).

The power of studying a close relative of a genetic model species was also demonstrated in Tom Mitchell-Olds' talk. For many evolutionary geneticists working with non-model species, identifying the candidate genes or genetic regions underlying ecologically relevant traits is realistically the upper limit of their research program. In most cases researchers do not know the causal mutation, only a SNP variant nearby, and even if they can identify the likely mutation, they often do not know the phenotypic or fitness effects of this mutation. This is where Tom's work is distinct. In an extensive body of work (see Prasad *et al.* 2012) the authors showed that a quantitative trait locus (QTL) for insect resistance in *Boechera stricta* conferred a fitness advantage in the field and identified genotype-by-environment interactions. Using transgenic *Arabidopsis* plants and natural variation in *B. stricta* they could also demonstrate that different gene variants conferred resistance against different enemies.

ii) greater capacity to track genotypes and allele frequencies in natural populations through time

The genomics era provides us with a greater capacity to track changes in genotype and allele frequencies through time and thus effectively observe evolutionary change and its influence on ecological parameters. Genomic data collected across longer temporal scales is extremely valuable for the study of eco-evolutionary dynamics, a point made by Daniel Wegmann in his talk, where he described new methods for inferring key population genetic parameters using such data. He introduced a method to infer heterozygosity from low coverage sequence data, which is often all we can get from ancient or degraded DNA samples (Kousathanas *et al.* 2016). This method will be valuable for utilizing museum specimens and detecting adaptive changes over longer time periods. He also described a new method to accurately infer population size with locus specific selection coefficients from temporal allele frequency data (Ferrer-Admetlla *et al.* 2016). On the other hand, genomic samples collected over shorter time periods are also important for detecting rapid adaption

and can reveal cryptic population dynamics that can be missed if the genotypic composition of a population is not considered (Kinnison *et al.* 2015; Yoshida *et al.* 2007). Nelson Hairston demonstrated how important the genotypic composition of the population is to species interactions and community dynamics. For example, genetic differences in fish can influence the phenotypic composition of the population, which in turn can influence the selection pressure on, and gene frequencies of, interacting heterospecifics (i.e. prey, competitors) leading to changes in communities and ecosystems (Kinnison *et al.* 2015).

iii) better understanding of the role of adaptive and non-adaptive processes in shaping genetic variation, adaptive divergence and speciation.

Within the eco-evolutionary framework we naturally focus on adaptive evolution and the interaction between ecology and genetic variation. However, non-adaptive processes, such as drift and constraints related to genetic architecture or genome organization, also have a pervasive role in shaping genetic variation and can influence a species' response to selection. The impact of drift and the importance of genetic covariation between multiple traits was shown by Yvonne Willi during her talk on *A. lyrata* populations. Yvonne's work demonstrates how drift has contributed to reduced genetic variation for ecologically relevant traits in edge populations (Paccard *et al.* 2016) and increased mutational load in small populations (Willi 2013). These findings have important implications for species facing the demands of a changing environment. Drift impacts not only the standing genetic variation, but also can alter the covariation of multiple traits, that is the G-matrix, and a population's response to selection (Paccard *et al.* 2016). Yvonne's talk, as well as those of others, nicely introduced the audience to the polygenic nature of adaptive traits and highlighted quantitative genetic concepts that are integral to understanding adaptive evolution in nature.

Synthesis and future directions

The conference bought together people working in eco-evolutionary dynamics and evolutionary genomics, providing a great opportunity for each group to hear about recent progress, but also ongoing challenges, in each field. During the conference it became clear that these two fields are still very distinct, and only one talk covered both eco-evolutionary dynamics and genomics (Becks *et al.* 2012). Nevertheless, the conference definitely helped to bridge the gap between the two fields. One ecologist commented "I now know what F_{ST} and GWAS are" and one geneticist stated "I now understand what Ecologists mean when they talk about ecological dynamics and I can see how these interact with evolutionary processes". In this section we first emphasise why genomics is useful for understanding eco-evolutionary dynamics, we then highlight some key problems in ecology and evolution that could be tackled more effectively by incorporating eco-evolutionary dynamics and finally identify clear gaps in our knowledge about eco-evolutionary dynamics and possible directions for future research in this field.

How can genomics increase our understanding of eco-evolutionary feedbacks?

Genomics can help understand eco-evolutionary dynamics in at least two important ways: 1) revealing the evolutionary processes that underlie puzzling ecological patterns and 2) by improving our ability to predict eco-evolutionary dynamics.

1) Genomics provides unprecedented opportunities to identify the genetic basis of traits and observe changes in allele frequencies though time to reveal cryptic evolutionary dynamics. Talks at the conference demonstrated how knowledge of the evolutionary processes can explain unexpected population dynamics of interacting species (e.g. Kinnison *et al.* 2015; Yoshida *et al.* 2007). Observations at the phenotypic level can conceal processes at the genetic level, and these cryptic evolutionary processes may be quite widespread and influence eco-evolutionary dynamics. In countergradient variation, for example, genetic and environmental influences work in opposite directions, as their effects cancel each other out

no change in the phenotype is observed despite a strong environmental gradient (Conover *et al.* 2009). In another example in Soay sheep, based on phenotypic-fitness covariance we predict that the proportion of dark coat coloured sheep should be increasing, but at the population level researchers observe the opposite (Gratten *et al.* 2008). Genetic and genomic analysis revealed that the coat colour gene was genetically linked to another loci that had antagonistic effects on fitness, as a result heterozygote dark sheep were fitter than their phenotypically indistinguishable homozygote dark sheep (Gratten *et al.* 2008). These examples illustrate that evolutionary adaptation is not always apparent simply by observing the phenotype, and without genetic and genomic information we may make incorrect inferences of the role of evolution in eco-evolutionary dynamics. Combing genomics, with common garden experiments and population sampling at appropriate spatial and temporal scales, can reveal cryptic evolutionary dynamics that may underlie eco-evolutionary dynamics.

2) Genomics research also helps us to predict responses to selection and evolutionary dynamics by: i) elucidating the genetic architecture and loci underlying ecologically important traits, ii) providing insights into the processes that maintain adaptive genetic variation in populations and iii) providing information on the repeatability of evolution at the genetic level. To date, only a handful of studies have identified the genetic change central to eco-evolutionary dynamics (e.g. Becks *et al.* 2012), and more work is needed before we can make any generalizations about the genomics of eco-evolutionary dynamics. It is likely that many traits involved in eco-evolutionary dynamics will have complex polygenic genetic architectures (Rockman 2011; Travisano & Shaw 2013). As such, future work should aim to use genomics to better understand the evolution of truly quantitative traits, identify loci of small effect, and also consider how genetic constraints (i.e. genetic linkage, epistasis and pleiotropy) can influence the evolution of phenotypic traits (Kokko *et al.* 2017).

What lies ahead in the field of eco-evolutionary dynamics?

As eco-evolutionary dynamics are the reciprocal interactions between ecological and evolutionary processes over contemporary timescales, they are likely to be important in systems experiencing rapid environmental change, such as species expanding their range and local communities adapting to invasive species (Box 1). Such systems provide natural experiments in which the direct effect of environmental change on eco-evolutionary dynamics can be observed. To better understand and predict the outcomes of these different scenarios, it is clear that we need to understand the feedback and interactions between ecology and evolution and not just consider each discipline separately. This is a challenging task, but genomics provides the tools to understand evolutionary dynamics beyond what can be understood when only considering interactions at the phenotypic level. If genomic resources exist for the focal species then the task is a little easier, but this is not essential as evidenced by the talks at the conference. In non-model species using population-based sampling it is possible to examine genetic variation across the genome and address many evolutionary questions relevant to eco-evolutionary dynamics.

In addition to incorporating genomics, there are several key areas of the eco-evolutionary framework that require additional experimental work. There is good evidence that ecological change can drive evolution (eco-evo). However, there are fewer examples, especially in the field, that demonstrate how evolution can drive ecological dynamics (evo-eco) and fewer still that demonstrate a complete feedback loop between ecology and evolution. Future work should focus on identifying feedback loops and understanding their complexity, particularly in natural systems, in order to better understanding the general importance of eco-evolutionary dynamics. Finally, it is less well understood how eco-evolutionary dynamics shape the higher-levels of community structure and ecosystem-level processes (Hendry 2016). Although there is evidence that adaptive divergence in species traits (e.g. predator avoidance) can drive community assembly and ecosystem functioning in semi-natural mesocosms (Bassar *et al.* 2010) or lakes (Post *et al.* 2008), these studies are

still restricted to relatively few systems. The impact of eco-evolutionary dynamics in nature on ecosystem-level processes is still far from clear and worthy of focused research in coming years. This is particularly true given the ongoing threats to biodiversity through climate change, invasive species, habitat destruction and pollution (to name but a few). Generally, given that ecology and evolution are so intimately linked, much greater integration between ecologists, evolutionary biologists and geneticists is needed to tackle the challenging field of eco-evolutionary dynamics, but also more generally to advance our understanding of how organisms will respond to changing environments in the future.

BOX 1. Eco-evolutionary dynamics and environmental change: three case-studies

1) How do ecological and evolutionary processes interact during range expansion?

Range expansions, either by invasions of introduced species or driven by climate change, are characterised by complex interactions between ecological and evolutionary processes (Chuang & Peterson 2016). For example, selection initially plays a key role during range expansions by favouring traits related to increased dispersal ability and often reduced fecundity, but as populations become established in new areas then selection can switch to favour reduced dispersal and increased fecundity (Hill *et al.* 2011; Williams *et al.* 2016). In addition to such evolutionary trade-offs, neutral evolutionary processes (particularly the interaction between genetic drift and mutations) can interact with demographic changes to produce patterns similar to that produced by adaptive evolution alone (Excoffier *et al.* 2009). Finally, colonising species will also interact with new organisms to which they must also adapt, in addition to the previously described selection pressures. Range expansions therefore offer an opportunity to explore how evolutionary processes can affect local ecological dynamics, as well as how species will respond to the new species interactions they encounter (see below).

2) How will local communities adapt to the spread of invasive species?

The spread of species across the globe by human introductions has been frequently associated with rapid evolution of the invasive species both in response to local climatic conditions and new species interactions (see Moran & Alexander 2014). In addition, adaptation of invasive species to the local environment can also drive evolutionary (and ecological change) in local native species (Benzemer *et al.* 2014; Lau 2006). For example, native plants have adapted to maintain fitness in the presence of invasive species, despite the subsequent invasion of an associated herbivore offsetting this advantage under field conditions (Lau 2006). Similarly, native insects (both herbivores and pollinators) have adapted to invasive hosts, and this has also altered interactions between native insects and native host plants (reviewed in Benzemer *et al.* 2014). However, despite increasing evidence for evolutionary change in individual invasive and native species, there are also potentially interesting, and relatively unexplored, ecological and evolutionary consequences for entire communities (Benzemer *et al.* 2014). The community-scale impact of recent invasions is therefore likely to be a fruitful system for future eco-evolutionary research.

3) How will populations respond to rapid environmental change?

The successful response of a population to environmental change is contingent on multiple different factors, which have been explored in a range of theoretical models (e.g. Chevin & Lande 2011). Both ecological factors, such as the rate of environmental change, and evolutionary factors, such as genetic variation and mutation rates, are critical in determining whether a population can persist and adapt to a rapid change in the environment. For example, in microbial populations slower rates of environmental change allow for a greater range of evolutionary paths to resistance to be explored (Lindsey *et al.* 2013). Another example using experimental evolution of yeast populations exposed to increasing salt stress also highlighted the role of initial population size in the likelihood of adaptation and probability of extinction (Bell & Gonzalez 2009). In addition to understanding the rates of evolutionary change possible in populations, it may be critical to consider phenotypic

plasticity in key traits, which may enhance the response of populations to environmental change (e.g. Chevin & Lande 2011). More empirical research is necessary to test the ecological and evolutionary factors that are theoretically predicted to affect responses of populations to environmental change.

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Figure 1. The eco-evolutionary framework attempts to understand the reciprocal interactions between evolutionary (blue) and ecological (green) processes on contemporary timescales. Although these two fields are connected, research in each has largely progressed in isolation, partly because they were often thought to happen on different timescales

(evolution was too slow to influence ecological dynamics). Recent examples of rapid evolution of genetically determined phenotypic characters has demonstrated that evolution can occur over short-timescales, and this has ignited interest into quantifying how contemporary evolution modifies ecological dynamics. Here we illustrate some examples of eco-evolutionary dynamics that were discussed by invited speakers at the ACE conference. The colours highlight the cyclical interactions between ecology and evolution. Blue highlights the aspects of the study that would traditionally have been the focus of evolutionary biologists (i.e. phenotypic trait evolution, genetic differentiation and speciation), the green those aspects traditionally the focus of ecologists (population dynamics, communities and ecosystems).

References: a) Grant and Grant 1995, Lamichhaney et al 2015, Hendry 2016, b) Vonlanthen et al 2012, c) Becks et al 2012, and d) Comeault et al 2014, Farkas et al 2013.

a) Darwin's finches

Variation in rainfall drives changes in the plant community and seed size distribution.

Variation in seed size drives changes in the optimal beak shape, which is controlled by large-effect loci. Divergence in beak shape drives reproductive isolation and genetic divergence in finches.

Mismatch between beak shape and seed availability drives finch population dynamics and plant community structure
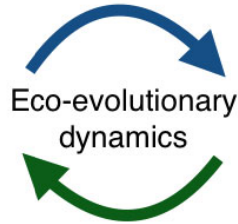
b) European Whitefish

Divergent selection on pelagic and benthic phenotypes drove reproductive isolation and adaptive radiation in lake whitefish.

Human-induced eutrophication altered the lake environment, food availability, fish recruitment and population density.

Eutrophication reduced reproductive isolation between pelagic and benthic spawners.

Erosion of species barriers lead to a loss of species and functional diversity, changing the lake's fish community.

c) Algal-rotifer

Genetic variation enables the evolution of a defended (clumped) phenotype, which is controlled by expression changes in many genes.

Defence is costly in terms of competition, thus when predation pressure is low non-defended prey increase in frequency. Differential mortality of defended and non-defended prey, not simply prey abundance, drives predator density.

During a consecutive cycle of high predation pressure, prey evolved the same defence phenotype, but gene expression changes were different, i.e. parallel phenotypic change did not involve parallel genetic change.

d) *Timema* stick insect

Camouflage on different host plants drives the evolution of two genetically determined colour morphs. Divergent selection on morphs on different host plants promotes reproductive isolation and genetic divergence.

Migration between plants results in a mismatch between colour morph and host plant. This increases localised bird predation, which in turns alters the species richness and density of other arthropods

Ecological factors drive the evolution of **phenotypic** traits, **genetic** differentiation and **speciation.**

Eco-evolutionary dynamics

Evolutionary change can alter **population dynamics**, species interactions, **communities** and **ecosystems.**