Evolutionary consequences of Ecological interactions

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“Nothing in biology makes sense except in the light of Evolution.”
Theodosius Dobzhansky, 1964

“Nothing in evolutionary biology makes sense except in the light of ecology.”
Peter and Rosemary Grant, 2008

“Nothing in evolution or ecology makes sense except in the light of the other.”
F. Pelletier, D. Garant, and A. P. Hendry, 2009
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Abstract

Eco-evolutionary dynamics integrates the reciprocal interactions between ecology and evolution. These two branches of biology traditionally assume the other as static for simplicity. However, increasing evidence shows that this simplification may not always hold because ecology and evolution can operate in similar timescales. This thesis theoretically explores how the reciprocal interactions may influence ecological and evolutionary outcomes in four different eco-evolutionary contexts.

Many species of non-social animals live in groups. Aggregating in groups often has both benefits and costs that depend on group size. Thanks to the benefits of aggregation, population growth likely depends positively on population density when it is small. This phenomenon, the Allee effect, has been hypothesized to explain the evolution of aggregation behavior. I find that the Allee effect alone does not lead to the evolution when population dynamics is explicitly accounted for. Some other mechanisms, such as frequent needs for colonizing new patches or anti-aggregation, should be invoked to explain why aggregation behavior could evolve.

Phenotypic plasticity is the ability of a genotype to express distinct phenotypes when exposed to different environments. Although it is often shown to be adaptive and not costly, highly plastic organisms are rare. Past studies demonstrated some potential reasons. I test another possibility; costs may arise from sexual selection because highly plastic individuals may be less preferred as a mate. I show that, even in the absence of the direct cost of plasticity, the level of plasticity remained low at intermediate strengths of assortative mating. This pattern is robust across wide ranges of parameter values.

Ecological speciation occurs when ecologically divergent selection between environments causes reproductive isolation between diverging subpopulations. Several verbal models of ecological speciation emphasize the roles of phenotypic plasticity in promoting speciation. The complex processes involved in speciation, however, are difficult to be evaluated by verbal accounts. I quantitatively test the proposed idea in a mechanistic model of ecological speciation in the presence and absence of plasticity. I find conditions under which plasticity can promote or hinder ecological speciation. Plasticity facilitates speciation by producing a gap in the distributions of expressed phenotypes, which serves as a barrier to gene flow in an assortatively mating population.

Ecosystem ecology and evolutionary biology are the least integrated fields in ecology and evolution. Natural selection operating at the individual levels on traits governing ecosystem functions may affect ecosystem properties, which may feedback to individuals. I reviewed this idea and demonstrate the feedback loop by using a simple consumer-resource model.
List of papers

This thesis is a summary of the following papers, which will be referred to by their roman numerals.


II. **E. Nonaka**, Åke Brännström, R. Svanback. Assortative mating can limit the evolution of phenotypic plasticity. Submitted manuscript.


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Author contributions

Paper I
Etsuko Nonaka conceived the study. Etsuko Nonaka and David Sumpter further developed the idea and the modeling framework. Etsuko Nonaka wrote the computer program, implemented the simulations, performed analysis, and wrote the manuscript. Åke Brännström and Kalle Parvinen provided assistance for mathematical derivation and interpretation of results. David Sumpter, Åke Brännström and Kalle Parvinen reviewed and commented on the manuscript.

Paper II
Etsuko Nonaka, Richard Svanbäck, and Åke Brännström conceived the study, developed the model, and interpreted the results. Etsuko Nonaka wrote the computer program, implemented the simulations, performed analysis, and wrote the manuscript. Richard Svanbäck, and Åke Brännström reviewed and commented on the manuscript.

Paper III
Etsuko Nonaka, Richard Svanbäck, and Åke Brännström conceived the study, and developed the model. Etsuko Nonaka wrote the computer program, implemented the simulations, and wrote the manuscript. Etsuko Nonaka performed analysis with Xavier Thibert-Plante. Etsuko Nonaka, Xavier Thibert-Plante, and Åke Brännström interpreted the results. Richard Svanbäck, Xavier Thibert-Plante, Göran Englund, and Åke Brännström reviewed and commented on the manuscript.

Paper IV
All the authors contributed to the initiation of the study at the end of the summer course, “interactions between ecological and evolutionary processes in aquatic ecosystems,” held at the Swiss Federal Institute of Aquatic Science and Ecology (Eawag) in 2009. Etsuko Nonaka along with two coauthors developed the model and completed the modeling section in the manuscript. Etsuko Nonaka helped literature review. Blake Matthews coordinated the work and wrote the majority of the manuscript. Etsuko Nonaka wrote small sections and commented on several versions of the manuscript.
Evolutionary consequences of ecological interactions (and ecological consequences of evolutionary outcomes)

Evolution and ecology are both dynamic and complex. They are also intertwined with each other. To get a glimpse of the complexity of nature, the disciplines of evolution and ecology traditionally take a reductionist approach; ecology keeps evolution simple by assuming no evolutionary change, and evolution keeps ecology simple by assuming ecology at its equilibrium. It has proven to be a productive simplification, and both fields of science made a lot of progresses. These progresses have also revealed that the assumption of stasis may not always hold and relaxing it may give new insights into how ecology and evolution in concert generate biological diversity. This thesis explores the causes and consequences of the interactions between ecological and evolutionary processes across the levels of biological organization.

Eco-evolutionary dynamics

Introduction
Eco-evolutionary dynamics consists of two directions of interactions between ecology and (micro)evolution (Figure 1; Fussmann et al., 2007; Kokko & López-Sepulcre, 2007; Pelletier et al., 2009; Schoener, 2011; Reznick, 2013). One is that ecological processes set a selective environment for evolution, and the other is that evolutionary outcomes affect ecological processes and their patterns. When both directions are in operation either concurrently or alternately, it is also referred to as eco-evolutionary feedback (Turcotte et al., 2013; Hendry unpublished manuscript).

Evolution is about the process of “descent with modification” (Losos, 2013), and can be considered as changes in allele frequencies in a population over time (Freeman & Herron, 2007). Evolutionary biologists are interested in changes in frequencies of genotypes in populations. It has long been well recognized that ecological interactions set selective environments and determine the fitness of organisms bearing traits under selection. One of the classic examples of natural selection is industrial melanism in the peppered moths (Biston bitularia). After the onset of Industrial Revolution, the pale morph declined and the dark morph increased in frequency dramatically (from about 1 percent to up to 90 percent in some areas) in less than a century (Futuyma, 2009). It was because avian predators preyed more on the pale morph since the dark one was better camouflaged on dark bark of trees lacking pale lichen cover due to air pollution. Another example is Darwin’s medium ground finches (Geospiza fortis) on the Galápagos Islands. When a severe drought hit the islands, small seeds became scarce and many small birds did not reproduce and died. Larger-sized birds were able to survive better, and the mean beak size dramatically increased in one generation, which was maintained in subsequent generations (Grant & Grant, 2008). Ecological consequences of evolutionary changes, if any, are not necessarily of particular interest to evolutionary biologists.
Figure 1. Eco-evolutionary dynamics in this thesis. The upper arrow depicts the effect of ecological processes on driving evolutionary responses. The lower arrow depicts the effects of evolutionary outcomes on driving ecological processes. These two paths comprise eco-evolutionary interactions and can be studied separately or together. Eco-evolutionary dynamics refers to the reciprocal interactions between ecology and evolution. The eco-evolutionary feedback is a loop between ecology and evolution, where the reciprocal interactions involve components (e.g., traits) that are directly or indirectly interacting in the ecological and evolutionary processes (Hendry unpublished manuscript).

Ecology as a discipline studies the causes and consequences of interactions among organisms and among organisms and their environments (Krebs, 2008; Molles, 2009). Ecologists traditionally perceive evolution to occur in much longer timescales than ecological processes and often assume that evolutionary change does not occur in ecological timescales. From the ecological perspective, evolution is viewed as the processes in the history that may explain what is observed today (Reznick, 2013). This view is encapsulated in the title of the book by G. E. Hutchinson (1965), “The ecological theater and the evolutionary play.” By this title, he meant that the roles of actors are determined by evolution, and they perform a play on the static ecological stage. In other words, evolution tailors organisms into ecological niches, and their niches do not change in the ecological timescale. This view has prevailed since then in ecology, and the integration of evolution in ecological studies appears quite weak (Holt, 1995; 2005; Elser, 2006). For example, the majority of theoretical models of population or consumer-resource dynamics (e.g., food webs) consider demographic and interaction parameters to be constant over time or independent of phenotypic composition of the populations. The overwhelming majority of hypotheses put forward to explain population fluctuations in small rodents are ecological such as food availability, predation, and diseases
(Krebs, 2013). Slow evolutionary change relative to ecological change is a usual assumption in ecology.

**What is eco-evolutionary dynamics?**

An evolutionary biologist, Andrew Hendry, defines eco-evolutionary dynamics as “interactions between ecology and evolution that play out over contemporary time scales” (unpublished manuscript). For practical purposes, contemporary (or rapid) evolution is thought to occur over “up to about 1000 generations, but typically many fewer” (Fussmann et al., 2007). What this means is that the conventional assumption of timescale separation between ecology and evolution can break down. This realization is one of the factors that contributed to the emergence of the field of eco-evolutionary dynamics. When evolution and ecological processes occur at similar timescales, there is a potential for reciprocal interactions between ecology and evolution (Fussmann et al., 2007). In fact, evolution does not need to be “rapid”; comparable timescales are sufficient (Fussmann et al., 2007).

Interactions between ecology and evolution can also play out over evolutionary timescales. This approach is relevant when the object of study is long-term evolutionary change, such as adaptive radiation or mutation-limited evolution. In this case, the ecological timescale is much shorter so that evolution occurs at ecological stasis. Ecology and evolution do interact at the evolutionary timescale; one feeds into the other, and the other responds back. This feedback loop can repeat over the evolutionary timescale. This view of eco-evolutionary dynamics is different from Hendry’s definition presented above, but I broadly include this type for the purpose of this thesis.

In Figure 1, I describe how I categorize eco-evolutionary interactions, dynamics, and feedbacks in a nested hierarchy, which is based on current literature and my own thoughts. I identify eco-evolutionary interactions to be the broadest category and define it as either the ecology-to-evolution or evolution-to-ecology interaction path (the two green arrows). Eco-evolutionary dynamics integrates the two and is defined as the reciprocal interactions between ecology and evolution. Eco-evolutionary feedbacks are the narrowest and involve components (e.g., traits) within ecology and evolution that are directly or indirectly interacting in the two interaction paths, such that the feedback loop may repeat (Hendry unpublished manuscript).

**Three important ingredients of eco-evolutionary dynamics**

1. Ecological and evolutionary processes feed into each other

The core of eco-evolutionary dynamics is that ecology and evolution interact reciprocally. There is ample evidence that evolutionary changes can occur in ecological timescales (Carroll et al., 2007; Fussmann et al., 2007). However, rapid evolution per se is not necessary for eco-evolutionary dynamics (Fussmann et al., 2007). The interaction can be over ecological or evolutionary timescales. The eco-evolutionary loop can go around once or multiple times. For eco-evolutionary dynamics to be meaningful, the impact of a change must be large enough to cause a significant change in the other.

As I mentioned above, timescale separation is a usual assumption in ecology. I want
to point out that it is justified as a useful simplification in many circumstances. It is probably reasonable to assume that a trait value will not importantly change at ecological timescales when it is not under strong directional selection. Studies show that the direction and strength of selection fluctuate over ecological timescales (Siepielski et al., 2009), so that selection could appear less directional in total. Also, ecological processes may replace evolution. For example, pre-adapted species can migrate into a habitat (i.e., species sorting) instead of resident species evolving new traits or into new species. Investigating relative importance of ecology and evolution is an important research question in eco-evolutionary dynamics (Hairston et al., 2005; Post & Palkovacs, 2009; Ellner et al., 2011). On the other hand, if directional selection is so strong that a selective sweep occurs very rapidly or if it is reasonable to assume that an evolutionary change has insignificant effects during ecological transients for some reason, the simplification where evolutionary changes arise only at the ecological equilibrium is useful.

2. A population is composed of individuals that are ecologically heterogeneous
Genetically based variation among individuals provides the raw material for natural selection to act on, hence evolutionary change. If there is no variation in a population, there will be no evolution. Moreover, many experimental and theoretical studies demonstrated that trait variation within a population has significant and general ecological consequences in population dynamics, community structure, and species interactions (reviewed in Bolnick et al., 2011). However, except obvious differences such as gender, age, and size, it is prevalent in ecological studies of population dynamics and consumer-resource interactions to assume that conspecific individuals are ecologically equivalent (Bolnick et al., 2003). This simplification is valid only if trait variation among individuals is “rare, weak, or has a trivial effect on ecological processes” (Bolnick et al., 2003). Thus, some within-population variation is not only essential for eco-evolutionary dynamics to happen but also it is a general pattern in natural systems.

3. Ecologically dependent fitness landscape or evolvable ecological characters
These properties tie ecological and evolutionary processes together. When fitness of individuals carrying traits under selection is density- or frequency-dependent or is affected by changes in exogenous conditions, ecological changes modify the fitness landscape. For example, changes in the composition of a population may change stabilizing selection to disruptive selection, or a severe drought may move the fitness peak to a different trait value (in this case, the loop goes only once). When traits are not fixed and evolvable, ecological processes can be affected by evolutionary changes. Without this link, interactions between ecology and evolution are difficult.

A brief history of eco-evolutionary dynamics
In major branches of evolutionary biology including life history evolution, behavioral ecology, and sociobiology, ecology has played integral roles. Ecology determines the fitness of the individuals bearing traits under selection. Fitness landscapes can be dynamic owing to frequency- or density-dependent selection as populations fluctuate. This was captured elegantly by J. Maynard Smith in his seminal work in evolutionary game theory (Maynard Smith & Price, 1973; Maynard
Smith, 1982). That ecology affects evolution is one of the major principles of evolutionary theory.

The other link, from evolution to ecology, has been less well recognized, although the idea was presented many decades ago by Chitty (1967) and (Pimentel, 1961; 1968). Chitty hypothesized that vole populations he studied were polymorphic (i.e., genetically based) in reproductive efforts, and that females with high or low reproductive efforts were selected for during different phases of population dynamics (Krebs, 2013). Pimentel’s research was motivated by the observations that stability and constancy are characteristics of many natural populations. He hypothesized that coevolution between interacting species was the underlying mechanism. He proposed a “genetic feedback” hypothesis; high densities cause strong selective pressures, which in turn alter the genetic compositions (e.g., increased resistance, competitive ability) and lead to regulation of the populations of interacting species. He demonstrated this mechanism at work in housefly-parasitoid populations in clever laboratory experiments (Pimentel, 1968). In his research, ecology and evolution clearly interacted.

Pimentel’s idea was overshadowed by Hutchinson’s view of evolutionary ecology (Reznick, 2013). In his view, ecology does not interact with evolution because it occurs much faster. Instead, evolutionary ecology seeks to explain the current states from evolutionary perspectives (Krebs, 2008). Ecology operates at evolutionary stasis; niches do not evolve in ecological timescales. Hutchinson’s view has been dominant in ecology, while a few theoretical ecologists pursued Pimentel’s genetic feedback hypothesis (Travis et al., 2013).

Yoshida and his colleagues (2003) published an iconic study of eco-evolutionary dynamics in an experimental system of rotifers and green algae. Theory says that in predator-prey systems the population dynamics should show characteristic quarter-phase shift (i.e., two timeseries are shifted by a one-quarter of the cycle period). Instead, they observed anti-phase dynamics and were able to explain the pattern if they took into account possible evolutionary changes in green algae, which they confirmed with additional experiments. The algae strain carrying costly defense against predation increased in frequency as the predator density increased, while the frequency of undefended algae increased as the predator density decreased in response to the increase in the defended strain. This cycle continued several times in their experiments. The evolution of algae defense occurred at the same timescale as the population dynamics so that the pattern of population dynamics was altered by the evolution of defense. This study marks the start of the current interpretation of eco-evolutionary dynamics (Fussmann et al., 2007; Reznick, 2013). Since then, this field has been rapidly growing.

Rather than being a brand new idea, the emerging field of eco-evolutionary dynamics is an integration of existing views about how nature works for a more holistic, mechanistic understanding. It is probably fair to say this field is composed of two old wines in a new bottle; Chitty and Pimentel put them together, and Yoshida and colleagues found the bottle in the back of the shelf. The two old wines have a potential to create something better than the simple sum of the two, and the
prospects are promising.

**Eco-evolutionary dynamics and the levels of the biological organization**

One approach to abstracting a biological system is to think they are organized in a nested hierarchy from genes to phenotypes, individuals, populations, communities, ecosystems, and landscapes. These different levels usually operate at different temporal and spatial scales (Urban *et al.*, 1987), and it is conceptualized that the level below the focal level provides the mechanism and the level above provides the context for the focal level (O’Neill *et al.*, 1986; Peterson & Parker, 1998; Turner *et al.*, 2003). Interactions are more frequent and stronger within each level, but important interactions and complex feedbacks can occur between the levels (Peterson & Parker, 1998; Bailey *et al.*, 2009; Pelletier *et al.*, 2009).

The target of natural selection is the individual organism (Mayr, 1997), which is composed of traits (phenotypes), which are in turn manifestations of underlying genetics with environmental noise. The basic unit of ecological interactions is also an individual (Sutherland, 1996). Individuals with advantageous traits can better survive and reproduce to pass on their genes to the next generation, possibly changing the trait frequencies in the population. This may in turn influence the selection pressure on the traits. This process may have direct and indirect ripple effects on community structure (Palkovacs & Post, 2009; Thuiller *et al.*, 2013; Urban, 2013) and flows of energy and materials in ecosystems (Harmon *et al.*, 2009; Bassar *et al.*, 2010; Bassar *et al.*, 2012; Chislock *et al.*, 2013). Altered nutrient availability may result and favor individuals with different stoichiometric requirements (El-Sabaawi *et al.*, 2012). Spatial structure of landscapes affects movement of organisms along with their genes and flows of energy and other materials (Turner *et al.*, 2003). Spatial structure is also important for the evolution of traits involved in dispersal as well as for the spatial patterns of evolutionary outcomes (Aguilée *et al.*, 2011; Hanski, 2011; Hanski *et al.*, 2011; Aguilée *et al.*, 2013). I envision eco-evolutionary dynamics in this complex feedback web across the levels of the biological organization. This thesis considers levels from individuals to populations in Papers I, from individuals to communities in Papers II & III, and from populations to ecosystems in Paper IV.

**Methods in eco-evolutionary dynamics**

Phenotypes are what matters for ecological interactions and natural selection. In eco-evolutionary dynamics, we need to keep track of phenotypes (trait values) and their abundances over generations. Adaptive dynamics and quantitative genetics provide means to model phenotypic evolutionary changes. The method of adaptive dynamics naturally incorporates ecological models, while the quantitative genetics approach is used in conjunction with ecological models. Trait values can be characterized by one abstract number representing a continuous trait to many numbers representing a continuous trait encoded in chromosomes.

**Quantitative genetics**

Quantitative genetics is an area of population genetics that studies how quantitative traits of a population in a given environment change over generations. Quantitative traits, such as body mass or the size of beaks, are measured in terms of continuous
values, and frequency distributions of trait values tend to be normally distributed (Barton et al., 2007). Quantitative traits exhibit such properties because they are controlled by multiple genes, each segregating according to Mendel’s laws. The prevalence of the normal distribution is remarkable in two ways, both of which are extremely convenient for modeling purposes. First, the distribution can be described by only two parameters, the mean and the variance. Second, the shape implies that trait values are the sum of many independent and random effects of genetic and environmental perturbations (Barton et al., 2007). Another remarkable aspect of quantitative genetics is that, despite its name bearing “genetics,” it can be studied with almost no information about underlying genetic mechanisms.

Quantitative genetics analyses how the mean and variance of continuous traits may change over generations at the population level. How natural selection changes these properties is a rather simple process (Barton et al., 2007; Brodie, 2013). There are three necessary conditions for evolution to occur; 1) there is variation among individuals in the population, 2) traits are heritable, and 3) differential reproductive success or fitness among individuals due to the variation in the traits. Then, we keep track of a response to selection at each generation; a change in the mean and the variance of a trait value of one generation (offspring) as a result of selection in the previous (parent) generation. The offspring create a new parental generation, and this process can iterate over generations to produce evolutionary change. When multiple traits evolve together due to functional or genetic correlation, the rate and direction of evolution can be enhanced or retarded, depending on the nature of the correlation among the traits (Futuyma, 2009).

In Papers II & III, I incorporate a quantitative genetics approach adapted to the individual-based model (e.g., Doebeli et al., 2007). In Paper IV, the parameter representing additive genetic variance controls the speed of trait evolution in the ordinary differential equation model of consumer-resource dynamics (e.g., Abrams, 2006; Fox & Vasseur, 2008).

Adaptive dynamics
Adaptive dynamics is a set of mathematical techniques to study the long-term evolutionary outcomes of ecologically important continuous traits, such as body mass or the size of beaks (Metz et al., 1996; Geritz et al., 1998; Geritz et al., 2004; Brännström et al., 2013). This method can be seen as an extension of evolutionary game theory to continuous traits, and therefore characterizes the eco-evolutionary dynamics on the evolutionary timescale. To focus on ecological aspects of the evolutionary process, it ignores underlying genetics. The premises of adaptive dynamics are 1) rare mutations and 2) nearly faithful reproduction (i.e., asexual). The first premise gives rise to two important additional assumptions that greatly simplify the mathematics. The first of two is that the resident reaches its dynamical equilibrium before another mutant arises in the population. In other words, ecology proceeds much faster than evolution, hence timescale separation. It is mathematically much more difficult to deal with invasions during transient dynamics or with polymorphism, i.e., multiple coexisting phenotypes. The second is that mutants are so rare that they do not interact with each other. These assumptions make the derivation of the invasion fitness, the central measure of adaptive
dynamics, possible. From these assumptions, we can gain mathematical tractability even when elaborate ecology is included, which is the attractiveness of adaptive dynamics. Many extensions from this basic formulation have been developed in the last two decades (Brännström et al. 2013 and references therein).

The advantage of adaptive dynamics to studying eco-evolutionary dynamics is that population dynamics are explicit and fundamental to set the selective environment. This is advantageous especially when selection is frequency- or density-dependent; fitness landscapes change as abundances and frequencies of individuals with traits under selection change over time. The eco-evolutionary process proceeds by successive replacements of the resident by a successful mutant until no new mutant can invade. A potential drawback with respect to eco-evolutionary dynamics is the strict assumption of timescale separation between ecology and evolution. This boils down to an assumption that transient ecological dynamics between evolutionary events do not influence evolutionary trajectories.

Timescale separation sounds exactly opposite to rapid evolution that triggered the emergence of the field of eco-evolutionary dynamics. First of all, we need to keep in mind that eco-evolutionary dynamics does not require rapid evolution per se (Fussmann et al. 2007). Adaptive dynamics studies eco-evolutionary dynamics at the evolutionary timescales. Second, even when selection is strong so that evolution may be rapid, changes in allele frequencies in every generation may be inconsequential for changing ecological properties. Third, when evolution is rapid, the assumption of timescale separation may no longer be valid, and adaptive dynamics may not provide a good approximation. In this case, one can resort to computationally intensive, individual-based models (DeAngelis & Mooij, 2005; Grimm & Railsback, 2005). In these models, individuals are explicitly represented with unique characters. These models are much more flexible to accommodate timescale issues and many others. Adaptive dynamics is still useful for gaining insights into evolutionary optima and potential evolutionary trajectories under simplified scenarios. This usually gives useful guidance to understanding complex outcomes from individual-based models. I took this approach in Paper II and III.

**Topics in eco-evolutionary dynamics addressed in this thesis**

Many topics in ecology and evolution are currently being studied under the framework of eco-evolutionary dynamics. This thesis examined topics that can be categorized into four themes; 1) the evolution of aggregation behavior, 2) ecological speciation, 3) phenotypic plasticity, 4) evolution at the ecosystem level.

**Eco-evolutionary dynamics in the evolution of aggregation behavior: from individuals to the population (Paper I)**

Behavioral ecology lives in the interface of ecology and evolution. Behavioral ecology theory presumes that natural selection favors behavioral patterns that maximize an individual’s chance of surviving and passing its heritable materials to
future generations (Davies et al., 2012). Ecology is integral because ecology sets the stage which behaviors to be performed on and determines the optimal behavior given the ecological selection pressures (Davies et al., 2012).

One of many kinds of behaviors is group formation. Many species of non-social animals live in groups of various sizes of mostly unrelated individuals (Prokopy & Roitberg, 2001; Krause & Ruxton, 2002; Wertheim et al., 2005). Ecology is important because the benefits and costs associated with group living often depend on group size, which in turn may vary as population density changes. The benefits of group living include creating favorable environmental conditions (e.g., huddling together), increased chance of finding mates, reduced predation risk (i.e., dilution effects), and obtaining defended food that is not attainable when acting alone (Pulliam & Caraco, 1984; Stephens & Sutherland, 1999; Stephens et al., 1999; Krause & Ruxton, 2002). Living in a group may be costly because of greater competition for shared resources, higher risk of disease transmission, increased conspicuousness to predators, and so on. Many species pay costs to attracting conspecifics (e.g., pheromones), so that a tendency for active aggregation is likely to be subject to selection in these species (Wertheim, 2005). The use of aggregation pheromones is widespread in spite of the potential cost; Wertheim et al. (2005) reports more than 300 such nonsocial arthropod species. Most of benefits accrued from grouping level off as group size increases, and the costs can outweigh the benefits beyond some group size. Thus we expect that organisms to evolve group joining or aggregation behavior that optimizes the net payoff. When aggregation tendencies can evolve, how would the evolution affect and be affected by changes in population density?

When population size is small, population growth likely depends positively on population density thanks to the benefits of grouping. The positive density dependence of small populations is called the Allee effect (Allee, 1931; Stephens et al., 1999; Courchamp et al., 2008). Gregarious insects such as tree-killing bark beetles and fruit flies are good examples. It has been hypothesized that the Allee effect is one of the factors that can explain the evolution of aggregation tendency in animals (Stephens & Sutherland, 1999; Krause & Ruxton, 2002; Rohlf & Hoffmeister, 2003).

I investigated this hypothesis using an eco-evolutionary model where local Allee effects, local competition, and population dynamics are incorporated. The model uses a site-based approach (e.g., Brännström & Sumpter, 2005) to compute the probability distribution of groups of different sizes and the adaptive dynamics approach to model the evolutionary dynamics in an individual-based model of one population.

It sounds intuitive that the Allee effect should promote aggregation. However, I found that the Allee effect alone is not sufficient for active aggregation to emerge as an evolutionary stable strategy in the model. Instead, evolution favored either the strategy of randomly selecting a group or an escalation of aggregation leading to population extinction. The latter phenomenon is called evolutionary suicide (Parvinen, 2005; Ferrière et al., 2009). The mechanism behind is feedbacks from the
population to the individuals through frequency dependent selection; aggregation can enhance population growth to be positive at low density, but once the population becomes sufficiently large it tends to cause overcrowding and becomes less advantageous. A positive side of aggregation is overcoming the Allee effect, but the benefits can be offset by severer competition at high population density. This study demonstrates that factors seemingly beneficial at the individual level may not be as beneficial when the feedback from the population level is accounted for. I conclude that some other mechanisms, such as frequent needs for colonizing new patches or anti-aggregation, should be invoked to explain why aggregative behavior could evolve.

I used the method of adaptive dynamics. Hence this paper is about eco-evolutionary dynamics at the evolutionary time scale, and the prediction is about the long-term evolutionary outcomes. Ecology influences evolution at the evolutionary timescale (i.e., ecological effects manifest only when a mutation occurs), and ecological dynamics at finer scales are simplified. Thus, this approach deals with the entire eco-evolutionary loop repeated over time spanning the evolutionary time.

**Eco-evolutionary dynamics in the evolution of phenotypic plasticity: from individuals to the community (Paper II)**

Phenotypic plasticity is the ability of a genotype to express distinct phenotypes when exposed to different environments (Dewitt & Scheiner, 2004; Pigliucci, 2005; Ghalambor et al., 2007). A phenotype is a product of genes and environments (plasticity) and is the target of natural selection. It has been also accepted that plasticity is genetically based and often adaptive (Via et al., 1995).

Plasticity is ubiquitous in nature and often adaptive. Many species of plants and fish are known to modify phenotypes that better match their local environment (Miner et al., 2005; Pigliucci, 2005). Plasticity is expected to be favored over a canalized phenotype in the presence of 1) environmental heterogeneity, 2) reliable cues, 3) benefits outweighing costs, 4) a genetic basis and variation for plasticity (Scheiner, 1993; Sultan & Spencer, 2002; Berrigan & Scheiner, 2004; Auld et al., 2010; Scheiner, 2013). Also, in structured habitats (e.g., metapopulations) plasticity is often favored when there is substantial gene flow (Sultan & Spencer, 2002).

Eco-evolutionary dynamics is relevant when we consider the evolution of phenotypic plasticity. When a population faces a new environment (e.g., climate change, colonizing a new habitat), plasticity may enable its survival and persistence, so that subsequent evolution may be possible. Plasticity also can allow individuals to adapt to different habitats, so that it likely affects how species interact in the community (Miner et al., 2005). Furthermore, when the environment experienced by individuals becomes less heterogeneous because of intrinsic or extrinsic reasons, previously plastically expressed traits may become genetically canalized. Also dispersal can affect the propensity to evolve plasticity (Scheiner et al., 2012). The evolution of plasticity is likely complex, depending on the ecological context.

It has been well recognized that plasticity has a genetic basis, although the underlying genetics are not well understood (Scheiner, 1993; Windig et al., 2004;
Smith & Ritchie, 2013). Many populations are shown to harbor substantial genetic variation for plasticity (i.e., gene-by-environment variance), and thus there is some variation in the degree of plasticity for further evolution. In addition, plasticity operates at two timescales, within generation (e.g., behavioral change) and between generations (evolutionary change). These properties make eco-evolutionary dynamics a natural approach to investigating the evolution of plasticity (e.g., Scheiner, 1998; Svanbäck et al., 2009; Yamamichi et al., 2011).

I studied eco-evolutionary dynamics of plasticity in a community of evolving predators and two non-evolving prey species residing in two contrasting habitats. A familiar example may be fish in postglacial lakes, such as sticklebacks and perch, where different morphs exploit distinct resources in pelagic habitats (zooplankton) or in the littoral habitats (macro-invertebrates). The predator population sexually reproduces (in Paper I, reproduction is clonal), and phenotypically similar individuals prefer each other as mates, which is called assortative mating. Assortative mating is essential for a sexually reproducing population to diversify, in the absence of other reproductive barriers, because it reduces homogenization of genetic materials. Depending on the habitat predators choose to feed in, they express more locally adapted phenotype through plasticity. The two prey species represent two resource peaks and hence can initiate divergent selection. In this system, I examined the evolution of plasticity of a trait that is subject to both natural and sexual selection.

Phenotypic plasticity is so far shown to be often not costly. Still, we do not see many animal species that can plastically express highly adaptive phenotypes as the environment changes. Two major explanations are: 1) past natural selection selected against costly plasticity (Dewitt, 1998; van Buskirk & Steiner, 2009) and 2) costs are measureable only when the magnitude of plasticity is high (Lind & Johansson, 2009) or under stressful conditions (Dechaine et al., 2007). I found a third possibility; costs may arise from sexual selection because highly plastic individuals may be less preferred as a mate.

Even when the direct cost of plasticity was absent, the level of plasticity remained low at intermediate strengths of assortative mating. This occurred because females searching for males were from two different habitats, so that, on average, males with intermediate phenotypes were more often chosen than extreme, presumably more adapted, males. If males possess higher plasticity, their phenotypes would be deemed suitable by only one type of females, but not by both. This results in stabilizing sexual selection on the phenotype, hence sexual selection against higher plasticity. I show that assortative mating is critical for diversification in sexually reproducing populations in sympatry but can also suppress phenotypic diversification by discouraging the evolution of phenotypic plasticity.

Eco-evolutionary dynamics in ecological speciation: from individuals to the community (Paper III)

Speciation is complete when reproductive isolation (RI) between diverging subpopulations or incipient species is attained, according to the biological species concept. RI can arise from many different causes (Coyne & Orr, 2004), but when
ecologically divergent selection between environments causes the evolution of barriers to gene flow, the phenomenon is labeled as “ecological speciation” (Schluter, 2000; Rundle & Nosil, 2005; Nosil, 2012). Research in ecological speciation asks questions regarding one or more of the three main components of ecological speciation; 1) sources of divergent selection, 2) a form of RI, and 3) genetic mechanisms linking selection to RI (Rundle & Nosil, 2005; Nosil, 2012). Ecological speciation focuses on the process of speciation rather than emphasizing geographic pattern as in the common classification of modes of speciation (sympatry, parapatry, and allopatry: Dieckmann et al., 2004; Butlin et al., 2008).

Processes involved in speciation include natural selection, sexual selection, genetic drift, and migration, while ecological speciation is driven mainly by natural selection (Schluter, 2009). A lot of efforts currently focus on genomic mechanisms of divergence and RI (Feder et al., 2012; Nosil, 2012). Well-known examples of (incipient) ecological speciation include limnetic and benthic ecotypes of sticklebacks, multiple morphs of arctic char, two ecotypes of Timema stick insects on different host plants, and two ecotypes of Littorina snails residing in upper and lower shores (more examples in Nosil 2012). The pervasiveness of adaptive divergence in nature suggests that many populations may be in the progress toward ecological speciation (Shafer & Wolf, 2013).

Research in ecological speciation currently deals almost exclusively with the ecology-to-evolution path. The ecological consequences of evolution are out of the scope, although the direction toward considering the entire eco-evolutionary dynamics loop is encouraged (Nosil 2012). Speciation directly relates to biological diversity and community composition, and changes in trait frequencies in populations may alter structures and strengths of species interactions. These changes are likely to have ecological effects, which in turn may affect subsequent evolution. We showed that the food chain consisting of one consumer and two resource species splits into two when the consumer undergoes ecological speciation. Specialized consumers can disconnect parts of food webs and decouple flows of energy and materials between different parts of the ecosystem (Quevedo et al., 2009; Bartels et al., 2012).

One swipe from ecology to evolution often represents ecological speciation in the eco-evolutionary loop diagram, but it may consist of several eco-evolutionary dynamics, during which the relative importance, strengths, and direction of different ecological (competition, predation, mutualism, etc.) and evolutionary processes (selection, drift, migration, etc.) may vary until RI is completed. It may be fruitful to look closely the processes involved in the ecology-to-evolution (i.e., speciation) path for more mechanistic understanding of ecological speciation. It has been argued that speciation proceeds in a continuum of divergence, from no divergence to complete RI (Hendry, 2009; Nosil, 2012; Seehausen et al., 2014).

The speciation continuum in an eco-evolutionary framework can be illustrated by examining the hypothesis of plasticity-facilitated ecological speciation. Several conceptual models of ecological speciation emphasize the roles of plasticity in promoting speciation (West-Eberhard, 1989; Skúlason & Smith, 1995; Smith & Skúlason, 1996; West-Eberhard, 2003; Pfennig et al., 2010). When speciation is
initiated by intense intraspecific competition for resources, plasticity may allow the population to phenotypically diversify (i.e., via plasticity) and specialize on alternative resources to alleviate competition. This phenomenon is called resource polyphenism. These models stress that it is in the early stages of a speciation process prior to genetic divergence that plasticity may play a critical role by facilitating fast phenotypic divergence (West-Eberhard 2003, Pfenning et al. 2010). However, plasticity allows individuals to express flexible phenotypes. Therefore, this ability may also interfere with the early stages of the formation of reproductive barriers, especially when there is no geographic barrier (McPhee et al., 2012). In addition, if plasticity incurs a low cost (Auld et al. 2010) or the population lives in a heterogeneous environment (Svanbäck et al. 2009), adaptive plasticity likely impedes speciation, because a plastic generalist may be a better strategy. It is unclear how plausible the conceptual models may be although they are seemingly intuitive. This hypothesis involves many ecological interactions and evolutionary responses so that eco-evolutionary dynamics is an appropriate approach.

Using the same model as Paper II, I investigated this verbal hypothesis quantitatively. In the modeled system, the continuum of ecological speciation generally starts with directional selection toward a generalist feeding on both prey species (i.e., no divergence), followed by changes in population densities, disruptive selection stemming from negative-frequency dependent competition for now scarce resources, and then the evolution of higher plasticity before divergence and finally reaching RI. Furthermore, I found conditions under which plasticity can both promote and hinder ecological speciation. Speciation was much less frequent in the absence of plasticity. Essentially, plasticity helped produce a gap in the distributions of expressed phenotypes, which served as a barrier to gene flow in an assortatively mating population. When plasticity hindered speciation, the population became a plastic generalist. The suppressing effect of plasticity comes from the fact that a plastic population has more traits to respond to disruptive selection; plasticity is just another evolving trait that can respond to selection.

Plasticity is oftentimes seen as an agent for facilitating gene flow and retarding divergence. The mechanisms by which plasticity may reduce gene flow have not been much studied. Thibert-Plante and Hendry (2011) demonstrated that selection against migrants can reduce gene flow when plasticity is expressed before dispersal. I show another mechanism where plasticity aids assortative mating directly by greater phenotypic differentiation and indirectly by more adaptive habitat choice. This link between plasticity and reproductive isolation via adaptive habitat choice has not been explicitly discussed in ecological speciation literature so far.

In Papers II and III, I used an individual based simulation model. This framework is capable of concurrent ecological and evolutionary processes. Since individuals are explicitly represented, variation among individuals is also represented.

**Eco-evolutionary dynamics at the ecosystem level; the link between evolution and ecosystem ecology (Paper IV)**

Ecosystem ecology and evolutionary biology are the least integrated fields in ecology and evolution (Holt, 1995; 2005; Elser, 2006), while some significant
progress has been made recently (Harmon et al., 2009; Loeuille, 2009; Post & Palkovacs, 2009; Bassar et al., 2010; Matthews et al., 2011; Odling-Smee et al., 2013). Ecosystem ecology concerns the flux of energy and materials. It is apparent that evolutionary concepts are rarely mentioned in major ecosystem ecology textbooks, and the other way around is also true. Many ecosystem processes are driven by biological activities. Microbial decomposers break down organic matter and make nutrients available to plants. Ecosystem productivity depends on how much carbon plants can photosynthesize and incorporate into their biomass. These ecosystem processes emerge from life history and traits of organisms that are important for their survival and reproduction. If these traits are heritable and each has variation among individuals, then these traits are subject to evolution by natural selection. Hence, selection operating at the individual levels on traits governing ecosystem functions can affect ecosystem-level properties, which may feedback to individuals.

Most of previous studies on the links between evolutionary change and ecosystem properties have examined aquatic systems and, to a lesser extend, terrestrial systems (Matthews et al., 2011 and references in Table 1). The guppy (Poecilia reticulate) system in Trinidad is probably the best-studied system in this context. The guppy populations are adapted to either high or low levels of predation, and studies show that these two ecotypes differently influence standing stocks of algae, invertebrates, and detritus, primary productivity, rates of decomposition, and nutrient fluxes (Palkovacs et al., 2009; Bassar et al., 2010; Bassar et al., 2012). Similar ecosystem effects of different phenotypes have been demonstrated for the threespine stickleback (Gasterosteus aculeatus; Harmon et al., 2009), the alewife (Alosa psudoharengus; Post & Palkovacs, 2009), and Daphnia species (Chislock et al., 2013). Studies on Populus trees show that both above- and below-ground processes are affected by the genotypes of the trees. Different genotypes produce leaves that contain various leaf chemistry, which can affect the arthropod communities in the canopy and microbial communities in the soil (Whitham et al., 2006; Whitham et al., 2008).

We discuss three routes for phenotypic evolution to affect ecosystem functions. First, phenotypic evolution can affect ecosystem functions via effects on environments. Natural selection can act on traits that underlie the capacity of organisms to alter their environment (Sterner & Elser, 2002). For example, stoichiometric traits associated with resource demands in consumers can affect the recycling rate of nutrients (Klausmeier et al., 2004). Second, phenotypic evolution can affect ecosystem functions via effects on populations. It has been shown that the demographic parameters of populations are evolvable (e.g., Walsh et al., 2012), and changes in growth rates or fecundity likely change biomass flux in ecosystems (Loeuille 2009). Third, phenotypic evolution can affect ecosystem functions through changes in community structure. The evolution of traits underlying how species interact could influence ecosystem functions. The structure of food webs, hence the flux of energy and materials in ecosystems, may change as the traits governing interactions such as predation or mutualism evolve.

We demonstrated eco-evolutionary dynamics from populations to the ecosystem in a
simple consumer-resource model. The stoichiometric ratios of the resource species can evolve and influence nutrient availability and consumer biomass in the ecosystem. The ecological dynamics are different from the classic consumer resource models because of the reciprocal interactions between ecology and evolution. Nutrient availability changes as resource species evolve their stoichiometric ratios to grow more efficiently, which causes their relative abundance to fluctuate. Since the consumer utilizes resource species at different ratios as abundance changes, the amounts of nutrients excreted by the consumer change, which in turn affects nutrient availability. Modified nutrient availability may change the direction and strength of selection on the resource species. The model illustrates how selection on the ecosystem-function traits of individuals may affect the ecosystem level properties such as nutrient availability.

Concluding remarks

Eco-evolutionary dynamics is a rapidly growing field, and new research results are published one after another in major journals. Eco-evolutionary dynamics is complex and can be overwhelming even in stylized systems as in theoretical models and simple experiments. Researchers strive to figure out how common interactions between ecology and evolution are in nature. The important question here is, when is it important, and when can we safely simplify the complexity?

I think eco-evolutionary dynamics has a potential to elucidate mechanisms regarding the causes and effects that underlie ecological and evolutionary patterns. To effectively do this, clear and operational definitions of eco-evolutionary interactions, dynamics, and feedbacks are useful. Such definitions may involve how to define the entities or components of ecology and evolution that are affecting and being affected by the interactions.

I think the field would be greatly benefitted by further integration of ecological and evolutionary theories. Research interests in ecology and evolutionary biology do not greatly overlap, so that complementing each other would be fruitful for advancing eco-evolutionary research. For example, evolutionary biologists have developed theories to explain how variation is generated and maintained in natural populations, but tend to overlook how species interactions may contribute to generation and maintenance of intraspecific variation. Ecologists study coexistence and stability of species in communities, but often disregard variation within a population. Recent review points out the importance of intraspecific variation in community ecology (Bolnick et al. 2011). How is intraspecific variation maintained when species interact in a community? How does intraspecific variation stabilize communities? Gene flow and dispersal are both evolutionarily and ecologically important processes. How does gene flow influence local adaptation and how does local adaptation affect dispersal patterns and habitat choice? Eco-evolutionary research tries to see if combining the two bodies of theories can explain patterns in nature better. Keeping complexity manageable but still the system realistic would be a challenge.
Both ecology and evolution may be in operation to create the patterns we see in nature, but what is the relative importance of ecology and evolution? Phenotypes can match the local environment through species (or phenotype) sorting, an ecological process, or adaptation, an evolutionary process. Phenotypic plasticity can also help organisms match their phenotypes to their local environments. Under what conditions are some mechanisms more important than others? Gene flow and dispersal are important not only for both species (or phenotype) sorting and local adaptation, but also for the evolution of plasticity (Scheiner et al., 2012, Sultan & Spencer, 2002). When all three mechanisms can operate simultaneously, how would different phenotypes distribute themselves over a landscape? What types of spatial structure are more conducive to, say, ecological speciation? These are all very interesting questions (to me).

Critically, what are the long-term effects of short-term evolution? If eco-evolutionary dynamics is prevalent, why do species look pretty much the same as they looked hundreds of years ago? Studies report many cases of strong directional selection in a short term, but the directions of selection often fluctuate (Siepielski et al., 2009; Svanbäck & Persson, 2009). Evolutionary biologists studied what limits adaptation and rates of evolution. To what extent, can such limits be altered by evolution in ecological timescales? Futuyma (2010) argues that interbreeding will cause local adaptation to be ephemeral without complete reproductive isolation. I would argue that rapid evolution has a potential to alter the course of long-term evolution. Are there ecological conditions under which this may be more likely?

The jury is definitely still out.

Acknowledgements

I am thankful to Henrik Sjödin, Xavier Thibert-Plante, Petter Holme, and Åke Brännström for discussions and comments on this thesis summary. I also thank Andrew Hendry for sharing the manuscript of his unpublished book on eco-evolutionary dynamics. The research in this thesis was supported by Department of Ecology and Environmental Science, Department of Mathematics and Mathematical Statistics, Department of Physics at Umeå University, the Kempe Foundation, the G. S. Magnuson Foundation, and the Wallenberg Foundation. Integrated Science Lab (IceLab) provided workspace.

References


Acknowledgements

I would like to thank my supervisors Åke Brännström, Göran Englund, and Richard Svanbäck for their guidance, and Lennart Persson and David Sumpter for their comments on Paper I. I am grateful to Henrik Sjödin, Petter Holme, and Xavier Thibert-Plante for exciting and insightful discussions. Finally, many thanks to all colleagues at the Department of Ecology and Environmental Science and Integrated Science Lab at Umeå University for professional support.