

SECTION 4

Community Ecology

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Evolutionary community ecology of Odonata

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Overview

Ecological dynamics among the constituent species in a community shape evolutionary processes, and the outcomes of these evolutionary processes in turn feed back to affect ecological dynamics. Determining the feedback between ecology and evolution is therefore paramount for understanding how communities are structured. Considerable progress has been made in developing this kind of research program, with studies of odonates serving as a centerpiece. This chapter highlights how the integration of ecological and evolutionary processes have provided insight into how communities containing odonates are structured. First it presents a conceptual framework from which the interactions between ecology and evolution emerge as key elements structuring communities. It then reviews the types of interactions in which odonates engage as members of complex food webs. Next it reviews the multitude of studies that capture the dynamics of natural and sexual selection in odonate communities. Lastly, it examines how adaptation has shaped the demographic features allowing species to both persist in and alter food webs, and how adaptation may contribute to species range shifts generating uniquely structured communities and novel evolutionary dynamics. At the end, it highlights future directions and key knowledge gaps. Overall, the chapter contends that odonates are an exemplar group that has provided much information about how ecology and evolution combine to structure communities.

14.1 Introduction

Ecological communities are complex networks of species interactions. There are two major facets to this complexity: interactions among species within a trophic level, and interactions among species between trophic levels, all of which occurs amidst a backdrop of abiotic factors. Much of the structure of communities results from how the constituent species exploit different ecological opportunities within and among trophic levels (McPeck 2017b). For example, a typical temperate lake might have at least one piscivorous fish species that consumes numerous other smaller fish species in the littoral zone. In turn, those smaller fish consume odonates and other invertebrates, which, in their turn, consume an array of other invertebrates that graze on a dazzling number of primary producers.

How do these pieces fit together to structure a community? The answer lies in understanding how evolutionary and ecological processes combine to structure communities—evolutionary community ecology.

The immediate ecological dynamics among the constituent species in a community shape evolutionary processes, and the outcomes of these processes can in turn feed back to affect ecological dynamics—this reciprocity unfolds over both micro- and macro-evolutionary timescales. On a micro-evolutionary timescale, natural and sexual selection, along with gene flow, mutation, and drift, can shape trait evolution that allows populations to contend with the ecological milieu in which they are engaged with. Short-term ecological effects of species interactions, such as competition and predator–prey interactions, can shift species

abundances and affect the strength of species interactions and consequently the evolutionary pressures they exert and experience (Travis et al., 2013; McPeck 2017a). Rapid evolution also frequently occurs on a timescale commensurate with ecological processes generating eco-evolutionary feedback (Hendry 2017). On longer timescales, such as the past several decades, climate change has resulted in shifts in species distributions, which has altered community composition and generated novel ecological and evolutionary community dynamics (Hanski 2012).

On a macro-evolutionary timescale, speciation, extinction, and range shifts also reshuffle species compositions across broader geographic scales. Because speciation events can be driven by both ecological and non-ecological mechanisms (Rundell and Price 2009; Wellenreuther and Sánchez-Guillén 2016), these events can have ramifications (see Chapter 15) for how the resulting communities are structured via deterministic niche or stochastic neutral-based processes (McPeck 2008a; Mittelbach and Schemske 2015). Over millennial timescales and longer, phylogeographic studies have revealed the signature of climate upheaval on the assembly dynamics of communities (Turgeon et al., 2005). Likewise, shifts into different community types over both these timescales (because of adaptive evolution in response to ecological interactions) has also generated considerable changes in community structure (McPeck and Brown 2000; McPeck 2008a; Start 2018). The structure of communities is therefore not static, and its dynamic nature is a consequence of the combination of ecological and evolutionary processes.

This chapter provides an overview of evolutionary community ecology in odonates and focuses on how certain micro- and macro-evolutionary processes structure odonate assemblages and their relations with larger communities. First, it reviews the types of interactions in which odonates are involved, during both larval and adult stages, as a backdrop to understanding their eco-evolutionary dynamics. Second, it reviews studies of natural and sexual selection in odonates. Third, it examines the consequences of trait evolution for community structure and how local adaptation may influence some of the ecological processes that regulate population growth and the ability for species to persist in communities. Finally, it reviews briefly how adaptation may contribute to species range shifts, generating unique ecological communities and novel evolutionary dynamics.

14.2 Interactions in odonates

As either top- or mid-level consumers, odonates occupy several trophic positions and engage in diverse interactions within both aquatic and terrestrial food webs (see Chapter 16). Their complex life cycle and marked ontogenetic shifts in body size means that their trophic position, as well as the types and strengths of interactions in which they engage, often change considerably through ontogeny (Knight et al., 2005; Crumrine et al., 2008).

14.2.1 Predation—odonates as prey

Odonate larvae are consumed by numerous invertebrate and vertebrate predators (Corbet 1999), and adult odonates can be consumed by other odonates and birds (Kennedy 1950; McPeck 2008b; Kuchta and Svensson 2014). The contribution of odonates as a resource subsidy to terrestrial ecosystems is also potentially vast (Popova et al., 2017). Given the disproportionate amount of time that odonates spend in the larval stage, larval mortality via predation is a critical interaction structuring odonate communities (Crumrine et al., 2008). Why certain predators establish and dominate a particular system is likely shaped in part by hydrological period, at least for lentic systems where the bulk of work has been conducted (Wellborn et al., 1996; Johansson and Brodin 2003; Stoks and McPeck 2006) (Figure 14.1). For example, odonate species with fast growth rates such as many *Lestes*, or migratory species such as *Pantala flavescens*, can be dominant, top consumers in ephemeral water bodies. When water persists for longer, dragonflies like *Aeshna* and *Anax* become top predators. In more permanent water bodies, fish dominate (McPeck 1998) and dragonflies occupy the same trophic position as damselflies. These different top predator regimes determine which odonate assemblages then develop (Wellborn et al., 1996; McPeck 1998; Start 2018).

Larval mortality via predation has an important regulating effect on odonate populations (Wellborn et al., 1996) and some demographic models suggest that it has the highest contribution to population growth (McPeck and Peckarsky 1998). Mortality rates are frequently density-dependent (McPeck 1998; Siepielski et al., 2010) and often vary by species under the same predator regime (McPeck 1998; Bried and Siepielski 2019). Larval mortality due to intraguild predation and cannibalism is also common and often

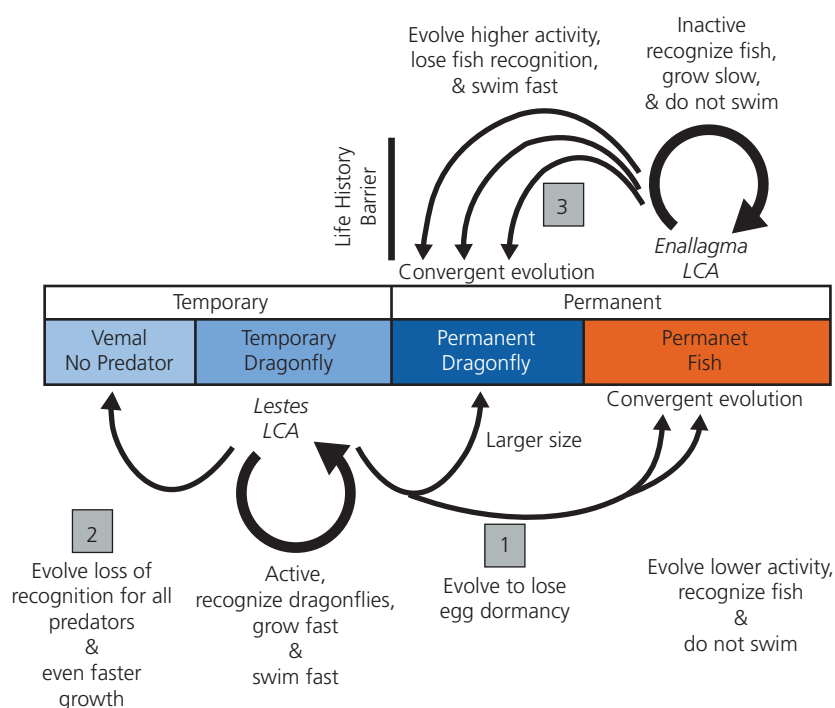


Figure 14.1 Conceptual diagram illustrating how changes in hydroperiod affect top predator regimes and the adaptive diversification and structure of *Enallagma* and *Lestes* damselfly assemblages.

"*Enallagma* LCA" and "*Lestes* LCA" refer to the habitats in which the Last Common Ancestor of each genus was hypothesized to have lived. The numbered arrows between the different habitat types denote the order of hypothesized habitat shifts, and text associated with each arrow identifies the major phenotypic changes that occurred with each habitat shift. The thick circular arrows next to the LCAs symbolizes that most diversification apparently occurred in the ancestral habitat. Figure and figure legend adapted from Stoks and McPeck 2006.

density-dependent amongst odonates (McPeck and Crowley 1987; Van Buskirk 1989; Crumrine et al., 2008; Sniegula et al., 2019). Experimental studies have also shown that non-consumptive mortality associated with the threat of predators is widespread (Stoks 2001; McCauley et al., 2011; Siepielski et al., 2014). The causes of non-consumptive mortality may stem from stress responses, depressed condition because of reduced feeding rates, or increased vulnerability to pathogens (Stoks 2001; McCauley et al., 2011). Like consumptive mortality, the effects of non-consumptive mortality likely promulgate throughout food webs to affect odonate prey assemblages and ecosystem processes (Peckarsky et al., 2008).

14.2.2 Predation—odonates as predators

As both larvae and adults, odonates can serve as top predators and intermediate consumers of a diverse

array of prey (Corbet 1999; Kaunisto et al., 2020), with the number of possible prey species available to them being quite vast (Thorp and Covich 2009). Although odonate feeding morphology is quite varied and often species-specific (Needham et al., 2000; Westfall and May 2006), these differences do not seem to translate to foraging specialization as most odonates are generalists (Thompson 1978; Corbet 1999; Kaunisto et al., 2020). Thus, despite an astounding diversity of prey there seem to be few realized opportunities for specialization (McPeck 2017b).

Studies have suggested various effects of odonates on the regulation of both aquatic and terrestrial prey communities, including negligible (Kaunisto et al., 2020), density-dependent (Thorp and Cothran 1984), and trait-based effects (Start and Gilbert 2017, 2019). Thorp and Cothran (1984) found that aquatic prey community richness and prey evenness were greatest at intermediate and highest dragonfly densities,

respectively. Start and Gilbert (2017) found that more active dragonflies preferentially consumed *Daphnia*, which resulted in copepods becoming the dominant zooplankton taxa. Such shifts in zooplankton has consequences for primary production through trophic cascades (Start and Gilbert 2017; Ousterhout et al., 2018). The effects of intraspecific trait variation, such as odonate activity rates shaping prey communities, may be stronger than interspecific differences, highlighting the role of intraspecific variation shaping communities (Start and Gilbert 2017, 2019). In terrestrial systems, odonate predation can strongly influence spatial and temporal habitat quality for butterfly assemblages (Sang and Teder 2011) and it is likely to for other terrestrial prey assemblages (Kaunisto et al., 2020).

14.2.3 Competition

Interference and exploitative inter- and intraspecific competition are common among odonates (see Chapter 15). Numerous experimental studies show that increasing larval densities reduces growth rates (Johnson et al., 1985; Van Buskirk 1987; Anholt 1990; McPeck 1998; Siepielski et al., 2010). Growth rates are a key vital odonate rate and fitness component since they determine the duration of time that larvae are exposed to their predators, and undergo metamorphosis. Importantly, growth rates are affected by prey limitation, implying a role for exploitative competition (Anholt 1990; McPeck 1998) as well as interference competition (McPeck and Crowley 1987). Finally, the threat of intraguild predation and cannibalism can also generate a stress response that can reduce growth rates up to 50% (McPeck et al., 2001).

Competition among adults is best known in the context of reproductive interference and territoriality (see Section 14.2.5 and Chapter 15). Indeed, non-reproductive competition among adult odonates remains largely undescribed but likely occurs and interacts with reproductive competition. For example, because male territory competition is energetically costly (Plaistow and Siva-Jothy 1996; Suhonen et al., 2008), it may be that successful competition in resource-limited environments depends on resource acquisition. Moreover, because female fecundity can be resource-limited (Richardson and Baker 1997), resource competition may disproportionately affect female fitness and population growth rates. Non-reproductive competition may be particularly important if species are poorly adapted, or in resource-limited environments, which could increase the fitness

costs of competitive interactions (Siepielski et al., 2018a). Clearly, more research in this area is needed.

14.2.4 Parasitism

Larval and adult odonates are frequently attacked by ecto- and endoparasites (Forbes and Robb 2008). In adults, parasitism can affect overall condition and reduce survival, mating success, and fecundity (Forbes and Robb 2008; Gómez-Llano et al., 2020). Although parasitism may affect population growth and species persistence, the role of density (McPeck 2008b) or frequency dependence (Willink and Svensson 2017) in the fitness costs of parasitism, as well as parasitism on population regulation, remain unclear. We also have little understanding of the contributions of co-infection among different parasites, and how such coinfection may scale among individuals, populations, and species (Bolnick et al., 2020). Comparative studies have found species specificity in mite susceptibility (Mlynarek et al., 2015a,b; LoScerbo et al., 2020), which can be partially explained by biotic factors, such as host range size and phenology (Mlynarek et al., 2015b), and abiotic factors, such as pH (LoScerbo et al., 2020). Species range shifts and habitat preferences altering these later facets may therefore have important consequences for odonate exposure and susceptibility to parasites.

14.2.5 Reproductive interactions

Although the adult life stage is short for most odonates, adults are subject to predation, parasitism, competition, dispersal, and (unlike larvae) strong pressure to reproduce. Therefore, interactions that lead to successful reproduction are paramount to maintaining species in a community. Competition for mating territories and to secure females (i.e. scramble competition) is common among odonates and may be energetically costly (Suhonen et al., 2008). For example, a single territorial competition event between *Calopteryx splendens* males can decrease up to 50% of fat reserves (Plaistow and Siva-Jothy 1996). Because fat reserves are size-dependent (Plaistow and Siva-Jothy 1996), smaller species and individuals may be unable to acquire and defend high-quality territories, reducing reproductive success.

Successful reproduction can also be affected by other interspecific interactions. For example, an experimental study with *Ischnura elegans* showed that parasitized males were poor competitors that experienced a 50%

reduction in mating success (Gómez-Llano et al., 2020). Moreover, abiotic conditions can also affect species interactions mediating reproductive success (Moore et al., 2019; Svensson et al., 2020). Male *Pachydiplax longipennis* have ornamental wing pigmentation that can improve flight performance and territory acquisition in cold temperatures but decrease it in warm environments. This thermally driven wing pigmentation influencing mating has led to more melanized wings in colder environments and less melanized wings in warm environments (Moore et al., 2019). Wing melanization can also affect interspecific recognition and increase aggression among competitor species, as seen in *Hetaerina*, which may affect species assemblage by preventing coexistence (Anderson and Grether 2010, see also Chapter 15).

14.3 Natural and sexual selection in communities

Interactions between odonates and their predators, competitors, parasites, and potential mates are often shaped by intraspecific phenotypic variation. The fitness consequences of these interactions frequently generate natural and sexual selection. Indeed, adaptive evolution in response to selection imposed by local environmental conditions is a critical step in establishing a species in a community.

14.3.1 Selection in larvae

Experimental studies of selection during the larval stage have focused on how survival is shaped by phenotypic variation. Fish predation has repeatedly been shown to select for less active damselflies (Strobbe et al., 2011; Swaegers et al., 2017; Ousterhout et al., 2018) (Figure 14.1). Selection operates in this way because damselflies cannot swim fast enough to evade fish (McPeck 2000; Stoks and De Block 2000), and swimming attracts fish predators (Baker et al., 1999). Therefore, reducing activity helps damselflies avoid detection (Strobbe et al., 2011). This stereotypical pattern may explain the limited ecological diversification of some damselflies like *Enallagma*. If the only option is to reduce activity, then there is only a single adaptive peak and species are limited to that region of trait space (e.g. McPeck 2017a,b). However, negative frequency-dependent survival among species from fish predation may vary among damselfly populations, indicating that some species may locally adapt to avoid predation (Bried and Siepielski 2019).

Where fish are absent, dragonflies such as *Anax* and *Aeshna* become top predators (McPeck 1998). Unlike fish predation, selection by dragonflies favors more active, faster damselflies (Swaegers et al., 2017) and dragonflies (Start 2018), which is mediated by both morphological (i.e. lamella surface; McPeck 1998) as well as physiological processes (i.e. arginine kinase; Strobbe et al., 2010) fueling escape. Studies of selection on *Leucorrhinia* larvae, especially morphological defenses like spine length, are another compelling example of contrasting patterns of selection by fish and dragonfly predators (Mikolajewski et al., 2006; Johansson and Mikolajewski 2008). Despite selection again being stereotypical, there are many paths to the realized fitness for a set of phenotypes (Strobbe et al., 2009; Mikolajewski et al., 2010; Strobbe et al., 2011; Delnat et al., 2017; Swaegers et al., 2017). Strobbe and colleagues (2009) argued that selection on performance-based phenotypes like faster swimming speed is driven by a combination of underlying traits (e.g. morphological, physiological; see also Mikolajewski and Johansson 2004; Mikolajewski et al., 2006). Such trait compensation may be common, as being suboptimal for one trait can be made up by exaggeration of other traits, as seen in selection on boldness in *Ischnura pumilio* (Figure 14.2). A better understanding of trait multidimensionality and constraints is necessary to understand how selection allows species to persist in food webs.

Most studies investigating selection examine only a single target species. Yet, multiple species typically occur in a given system and we have little understanding how selection might change as species richness changes (Eisen et al., 2020). For example, Strobbe and colleagues (2011) examined selection imposed by fish when two species of *Enallagma* were present. They found that selection on activity was only detectable in the most active species, even though fish imposed considerable mortality on both species (see also Strobbe et al., 2009; Swaegers et al., 2017). These studies suggest the selection that any one community member experiences may be shaped by the distribution of phenotypes and absolute fitness of other community members.

Although much is known about selection imposed via predation, little is known about the phenotypes that shape larval (or adult) direct or indirect competition in response to resources, or what phenotypes may mediate apparent competition (Holt and Lawton 1994). However, carryover effects from selection driven by predation are known to affect the strength of competition. Siepielski and colleagues (2020) found that

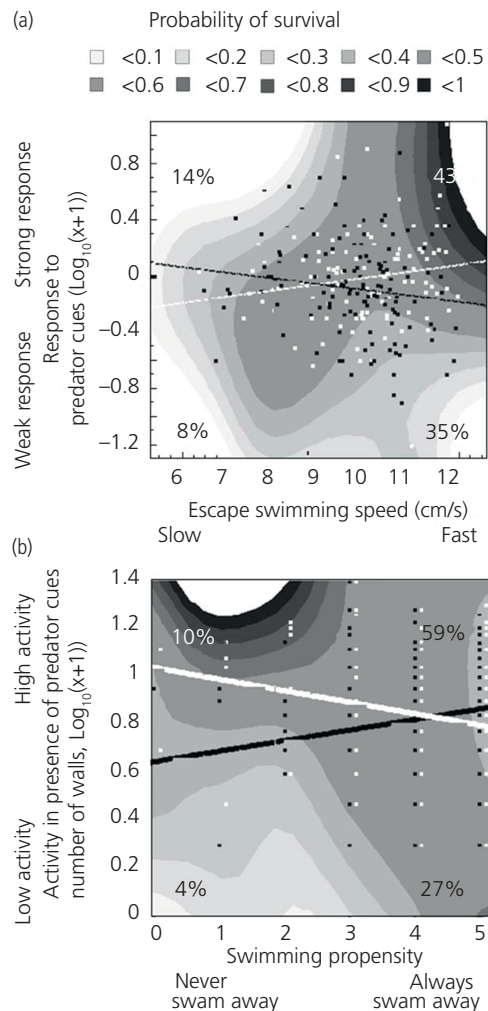


Figure 14.2 An example of natural selection on activity and behavioral traits mediating predation risk. The surface plots show how pairwise combinations of antipredator traits determine the probability of survival of *Ischnura pumilio* damselfly larvae in the presence of dragonfly predators: (a) escape swimming speed and response to predator cues; and (b) swimming propensity and activity in the presence of predator cues. Darker colors represent trait combinations with a higher probability of survival. White (black) dots represent the observed values of the survivors (non-survivors). Single dots may represent multiple observations. Percentages of larvae in each quartile are shown. The white (black) dotted lines are the fitted regression lines of the survivors (non-survivors); lines in (b) are significant. Figure and figure legend (with modification) reproduced from Delnat et al., 2017.

intraspecific competition decreased as fish densities among lakes increased. This likely occurred because higher fish densities generate stronger selection for reduced activity (Ousterhout et al., 2018), thereby

resulting in a carryover effect that, independent of predator driven reductions in density, reduced the intensity of intraspecific competition. Because traits mediating one interaction frequently shape other interactions, such carryover effects are likely common in nature. However, more work is needed to understand how selection directly affects competitive interactions in odonate assemblages.

14.3.2 Selection in adults

Adults exist in an entirely different environment than larvae, with new predators, parasites, and competitors, while also facing the added challenge of reproduction. Natural and sexual selection can generate disparate outcomes that result in tradeoffs between selective forces and may potentially limit the capacity of a given species to persist. Importantly, sexual selection can lead to character displacement and species recognition that would reduce interspecific aggression and facilitate competitor coexistence (Gómez-Llano et al., 2021).

Natural selection, especially imposed by bird predation, has been thoroughly studied for some odonate taxa. In *Calopteryx splendens* and *Lestes sponsa*, selection by birds acts on wing morphology to increase evasive flight (Kuchta and Svensson 2014; Outomuro and Johansson 2015; Outomuro et al., 2016). Predator-driven selection can also act on secondary sexual traits. For example, bird predation was higher for *C. splendens* with smaller wing patches (Kuchta and Svensson 2014), but lower for *C. virgo* with larger wing patches (Svensson and Friberg 2007). Interestingly, Svensson and Friberg (2007) found no significant selection by bird predation in wing patch length in *C. splendens*, suggesting strong context-dependent selection.

Sexual selection has been widely studied in odonates. The strength and direction of sexual selection in male body size is often highly influenced by social environments, with female density and the difference between male and female body size as key drivers (Gosden and Svensson 2008; Steele et al., 2011). Body size is an important factor determining mating success because the fit between male and female reproductive structures are correlated with body size (McPeck et al., 2009; Siepielski et al., 2018b). In territorial damselflies, but not dragonflies, there is often consistent selection for larger male body size because larger males are better at acquiring and defending mating territories (Serrano-Meneses et al., 2008).

Sexual selection on secondary sexual characters, such as body and wing pigmentation, has been studied in both damselflies and dragonflies (Moore 1990; Grether 1996). Moore (1990) partitioned sexual selection in male–male competition and female choice in the dragonfly *Libelula luctuosa* and found both forms of selection contribute to larger wing color patches (Moore 1990). Wing pigmentation is considered an honest signal because it is correlated with immuno-competence (Rantala et al., 2000), fighting ability (Grether 1996), condition (Castanos et al., 2017), and fat reserves (Koskimäki et al., 2004). However, selection for wing pigmentation can be affected by the presence of heterospecifics. *Calopteryx splendens* females prefer conspecifics with larger wing patches, but in the presence of *C. virgo* (with larger wing patches), females prefer smaller wing patches to avoid heterospecific matings (Verzijden and Svensson 2016). Thus, studies of sexual selection are not divorced from heterospecific interactions and may reflect how individuals and species contend with their local environment.

Parasites can also impose strong selection pressures on adults. Ectoparasitic mites reduce flight ability (Nagel et al., 2010) and parasitized individuals are less able to acquire resources (Morrill et al., 2013), compete for mates (Gomez-Llano et al., 2020), and escape predators (Nagel et al., 2010). Increased parasitism may also increase immunocompetence (Córdoba-Aguilar 2002), which is directly linked to survival and mating success (Contreras-Garduño et al., 2007). Moreover, recent work has suggested that parasitism may mediate sexually selected traits, with greater impacts on males than females (Gómez-Llano et al., 2020). Pre-copulatory sexual selection acts against parasitized individuals by reducing overall condition and the ability to compete for mates (Nagel et al., 2010; Gómez-Llano et al., 2020), while postcopulatory sexual selection can act against parasite load due to a tradeoff between immune response and egg production (Siva-Jothy et al., 1998, but see Córdoba-Aguilar et al., 2012). Importantly, if sexual selection is stronger on males than females because population growth is more directly linked to female fitness, species can adapt with limited demographic costs of selection.

Studies of selection across life stages are rare but may yield interesting insights. For example, high body condition in adult *Pachydiplax longipennis* can enhance ornament development (i.e. wing coloration) in late-instar larvae (Moore and Martin 2018). Because wing coloration is correlated with competition for mating

territories, and hence fitness (Moore and Martin 2016), positive feedbacks between larval and adult body condition can enhance adult fitness. However, high body condition larvae that develop wing coloration sooner than other conspecifics have reduced survival in the presence of a predator, thereby suggesting a tradeoff between life stages (Moore and Martin 2018).

14.4 Eco-evolutionary effects in communities

Section 14.3 reviewed selection as a process. This section highlights some of the evolutionary consequences of selection in communities. Adaptive evolutionary responses to selection are common and occur among populations at local scales (i.e. local adaptation) and among species at macro-evolutionary scales (i.e. during speciation). The ecological consequences of adaptive evolution in odonates have effects on interactions both within and between trophic levels. In addition, adaptive evolution to the abiotic environment further shapes food web interactions. Therefore, how fast species can adapt to the biotic and abiotic environment can determine if two species can coexist. All of these facets combine to establish how adaptive evolution allows odonate species to persist in complex food webs, as well as enter new communities during range expansions.

14.4.1 Adaptation to biotic interactions

Given the central role of predation in regulating populations, it is unsurprising that it is also a major driver of adaptive evolution. Differences in predator regimes have repeatedly generated parallel adaptive differences in phenotypic traits that mediate predator–prey interactions (Johansson and Mikolajewski 2008). Phylogenetic reconstructions indicate that micro-evolutionary driven habitat shifts between fish and dragonfly lakes have occurred independently several times in both damselfly (Brown et al., 2000; McPeck 2000; Turgeon et al., 2005; Stoks and McPeck 2006; Siepielski and Beaulieu 2017) and dragonfly clades (Mikolajewski and Johansson 2004; Mikolajewski et al., 2006; Johansson and Mikolajewski 2008; Start 2018). Such adaptive shifts could have arisen during ecological speciation events to fill ecological niches, or post-speciation. Critically, traits mediating predator–prey interactions are often heritable (Swaegers et al., 2017). Why some lineages show repeated patterns of ecological diversification in

response to varying predator regimes, but other groups (i.e. *Ischnura* species) do not, is an unresolved question.

The consequences of selection and adaptation to different predators are promulgated throughout the food web (Start and Gilbert 2017; Start 2018; Siepielski et al., 2020). Start (2018) showed that among temperate dragonfly assemblages in North America, macro-evolutionary transitions from living in ponds with fish to fishless ponds has repeatedly and independently resulted in fishless pond species being more active—a pattern mirroring *Enallagma* damselflies (McPeck and Brown 2000). Such adaptive evolution has in turn reduced prey abundance and shifted prey community composition, thereby generating stronger trophic cascades (Start and Gilbert 2017; Ousterhout et al. 2018) (Figure 14.3) that affect ecosystem functioning (Start and Gilbert 2017). Such cascading effects of predator consumption can also occur across aquatic-terrestrial system boundaries to affect ecosystem processes. Knight and colleagues (2005) showed that consumption of larval dragonflies by fish reduced adult dragonfly abundances—a key consumer of plant pollinators near ponds. As a result, plants near ponds with fish were less pollen limited and had higher pollinator visitation rates. Recent work extended this idea to consider how consumption by dragonflies could affect selection on floral traits by plant pollinators. Because dragonflies are often active pursuit predators, Benoit and Caruso (2021) hypothesized that they would strengthen pollinator-mediated selection by weakening plant–pollinator interactions. However, their experiments did not find that high dragonfly abundance strengthened selection on floral traits. Exploring how adaptation and selection in one life stage may affect selection by community members in other life stages, and thus link eco-evo dynamics between aquatic and terrestrial ecosystem boundaries, is an exciting prospect.

At a finer spatial scale, local adaptation to predators may affect consumer–resource interactions via trade-offs between competitive ability and predator avoidance. For example, higher densities of fish results in greater mortality in *Enallagma signatum*, which can increase the strength of selection on traits that mediate predation risk (Ousterhout et al., 2018). Moreover, Siepielski and colleagues (2020) demonstrated that higher fish densities among lakes correlated with increased handling times and reduced activity levels and attack rates. As a result, the strength of density dependence in damselfly growth rates, a measure of intraspecific competition, decreased with increased fish densities (Siepielski et al., 2020). Thus, local

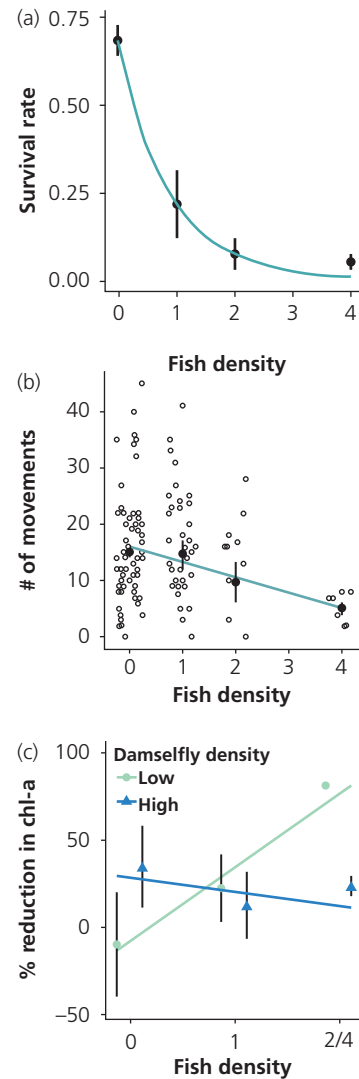


Figure 14.3 An example of how natural selection by fish predators on damselflies shapes the strength of a trophic cascade.

As fish density increased (a) damselfly survivorship declined exponentially, with (b) selection for reduced activity being most apparent at the highest fish density. These surviving damselflies likely foraged less, freeing herbivores from predation, which in turn greatly reduced primary production (c). This selection driven trait-mediated indirect effect was only apparent at low damselfly densities because the consumptive effect of damselflies at high density overwhelmed the effects of past selection. In (c), the values were jittered horizontally; the error bar for the low damselfly density 2/4 fish density treatment are smaller than the point denoting the mean, and therefore obscured. In all panels, large points shown are mean $\pm$ SE, and in panel (b), small grey points are individual damselfly observations. Figure and figure legend (with modification) reproduced from Ousterhout et al., 2018.

adaptation to fish has cascading effects that regulate damselfly competition and interactions with their prey.

The effects of competition are also directly shaped by local adaptation. Siepielski and colleagues (2016) found that the strength of intraspecific competition for *Enallagma carunculatum* was highest in their local ponds and declined as maladaptation increased. The effects of local adaptation were often greater than the ecological effects of doubling damselfly densities. These results show how eco-evolutionary dynamics can affect demographic processes that regulate population abundances (Siepielski et al., 2016; McPeck 2017b), and suggest that either the strength of density-dependent competition depends on the extent of local adaptation, or the extent of local adaptation is shaped by the strength of competition.

Odonates have multiple adaptations to defend themselves from parasites. Parasite resistance and tolerance can be achieved by behavioral (Baker and Smith 1997) and immunological responses, such as the phenoloxidase (PO) cascade (González-Santoyo and Córdoba-Aguilar 2012) and nitric oxide (Contreras-Garduño et al., 2007). Experimental work has also shown that larval damselfly grooming behaviors that remove mites may increase predation by fish (Baker and Smith 1997), which suggests a potential trade-off between defensive strategies toward parasites and predators. Local adaptation to parasites has been demonstrated in *Ischnura elegans*, as males increased their resistance to infection and reduced the negative effects of parasites through sexual selection (Gómez-Llano et al., 2020).

14.4.2 Adaptation during range expansion

Adaptive processes often differ among populations at the periphery and core of species distributions because population sizes along the periphery are often relatively low, which allows stochastic processes to dominate (Swaegers et al., 2013). For example, *Coenagrion scitulum* have higher larval growth rates and adults with more developed flight muscles in peripheral populations compared to core populations (Swaegers et al., 2013). The authors suggest that genotypes that maintain univoltinism are selected for in peripheral populations due, in part, to the relatively low population sizes in these regions (Therry et al., 2013). In contrast, other range shifting species show increased voltinism at range limits, perhaps because of selection

for larger body sizes to facilitate survival under harsher conditions at range fronts (Fitt et al., 2019).

Range expansions can also result in changes in species composition and novel selection pressures that influence community structure (Fitt and Lancaster 2017). Moreover, range expansions followed by local adaptation can alter interspecific interactions. For example, the process of range expansion and adaptation to new environmental conditions can alter interspecific competition, as warming temperatures for range shifting species, relative to resident competitors, can also reshape life history tradeoffs underpinning coexistence (Lancaster et al., 2017). More research on the ability for species to locally adapt in response to altered species interactions that arise during range expansion is sorely needed (Lancaster et al., 2017), especially on understanding the genetic underpinnings (Dudaniec et al., 2018).

14.5 Future directions and conclusion

This chapter highlights many questions that remain regarding how ecological and evolutionary processes involving odonates combine to structure biological communities. Box 14.1 outlines several questions and directions that would add much to our understanding of the evolutionary community ecology of odonates.

As one of the oldest insect groups, odonates have been community members for around 200 million years (Kohli et al., 2020). While there are no fossil records of interactions between odonates and their community members, it is likely that contemporary food webs give a glimpse of past food webs (Fraser et al., 2020). Few other taxonomic groups might cover the diverse range of species interactions across aquatic and terrestrial systems that odonates do. They serve as predators, competitors, prey, and hosts to parasites in terrestrial and aquatic food webs. Increasingly well-resolved phylogenies (Waller and Svensson 2017) allow us to better understand odonate shared evolutionary history and patterns of trait evolution that may underlie the assembly and persistence of odonate species in the communities in which they are embedded. Along with contemporary studies of species interactions, natural and sexual selection, and adaptive evolution, odonates are an exemplar group where we have learned, and can continue to learn, much about how ecological and evolutionary processes combine to structure communities.

Box 14.1 Priority questions and directions in odonate evolutionary community ecology

- How important are ongoing, rapid eco–evo dynamics in structuring odonate assemblages? Odonates vary considerably in their generation times, which may provide an opportunity to ask how differences in rates of evolution may have differential effects in structuring communities.
- Although there exist studies of co-evolution in the context of male–female reproductive structures (Córdoba-Aguilar 2005; Brennan and Prum 2015), reproductive character displacement (Grether et al., 2013), and parasitism (Forbes et al., 2002), little is known about how co-evolution may arise in the context of resource competition or between odonates and their prey. Studies demonstrating ongoing reciprocal selection and adaptive evolutionary responses are completely lacking.
- How does non-reproductive competition among adult odonates occur and interact with reproductive competition? Similarly, aside from body size, what traits mediate competitive interactions within and among species?
- What are the contributions of co-infection among different parasites, and how does such co-infection scale among individuals, populations, and species? What are the contributions of parasitism during the larval stage on ecological and evolutionary dynamics?
- A better understanding of traits constraining selection and species persistence in food webs is needed. How do trait multi-dimensionality and genetic constraints influence how selection allows species to persist in food webs? Why do some lineages such as *Enallagma*, *Lestes*, and *Leucorhinia* diversify ecologically in response to selection imposed by top predators, but others, such as *Ischnura*, seemingly do not?
- A better understanding of how and what feedback arises between species interactions, selection, and adaptive evolution between larval and adult life stages, and the aquatic and terrestrial habitats in which these occur, endures. Studies integrating across the life cycle will be critical in identifying and studying these linkages (Gómez-Llano et al., 2021).
- A better understanding of local adaptation in response to altered species interactions during range expansion is vital.

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