

Modeling coregonid fish diversification along a vertical gradient in water temperature

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Goal

To develop an adaptive dynamics model for understanding the ecological diversification of coregonid fish along an environmental gradient in depth and water temperature.

Background and motivation

Ecology of speciation

The theory of adaptive speciation and radiation suggests that macro-evolutionary phenomena of diversification are ultimately the outcome of micro-evolutionary processes driven by natural selection (Orr & Smith 1998; Coyne & Orr 2004; Dieckmann et al. 2004). Hence, phenotypic and ecological diversity are likely to imply divergent or disruptive natural selection arising from differential resource use, competitive intraspecific interaction, and ecological opportunity. Competitive interactions involving the exploitation of different resources or habitats, between individuals and populations within the same geographical area, are thus of major importance for understanding the origin of biological diversity. In addition, the geographical conditions underlying speciation processes have long been the focus of debate. However, mechanisms of ecologically based sympatric, parapatric, and allopatric speciation appear to be similar, with disruptive or divergent natural selection as the driving force of diversification and the evolution of reproductive isolation as a consequence of selection on traits between environments (Schluter 1996, 2000). The process of ecologically based speciation of sexual populations within the same geographical area does not only necessitate the emergence of reproductive isolation during diversification, but also requires the ability of the incipient species to coexist stably (Coyne & Orr 2004; Gavrilets 2004). Hence, it is often the same ecological conditions that produce disruptive natural selection, cause adaptive speciation through the gradual evolution of reproductive isolation, and enable the coexistence of closely related species in sympatry.

Speciation models

The theory of adaptive dynamics (Dieckmann & Law 1996; Geritz et al. 1998) is recognized by many as ‘the’ mathematical tool for the study of adaptive evolution. It lies at the basis of theoretical models investigating ecology-based processes of evolutionary diversification (Doebeli & Dieckmann 2005). For one-dimensional traits slowly mutating in small steps, the theory states that the frequency-dependent selection of an asexually reproducing population proceeds in the direction of a local fitness gradient until an evolutionarily ‘singular’ strategy is reached, where selection pressures cease. The singular strategy is either evolutionarily stable, implying an evolutionary outcome

with a single morph, or an ‘evolutionary branching’ point, leading to the evolutionary divergence of two morphs. In most existing models of sympatric adaptive speciation (Dieckmann et al. 2004), ecological specialization through resource partitioning is the key driver of diversification. Besides models assuming discrete or patchy environments (Meszena et al. 1997; Day 2000), models have been developed for describing the evolution of reproductive isolation along continuous environmental gradients in asexual (Mizera & Meszena 2003) as well as sexual populations (Doebeli & Dieckmann 2003).

One conclusion from advances in adaptive speciation theory is that sympatric and/or parapatric speciation is theoretically plausible and may thus be a common process in nature. However, theoretical speciation models are not easily evaluated in terms of ecological plausibility and may lack ecological realism in their assumptions about system properties. Empirically motivated and data-based speciation models including ecologically derived quantitative assumptions are therefore needed for evaluating the importance of these processes in nature. One of the best model systems for studying adaptive diversification are northern freshwater fish occupying postglacial environments, in which several taxa have generated species and ecological diversity in a manner consistent with the theory of adaptive speciation (Schluter 1996, 2000). There is increasing evidence that ecological opportunity in species-poor postglacial lakes in combination with high intraspecific competition within the ancestral population promotes adaptive divergence in fishes (e.g., Hudson et al. 2007). Biotic and abiotic environmental factors in these systems are potential causes of diversification. Their characteristics determine the strength of selection acting on phenotypic evolution and thus ultimately determine the potential for speciation.

Study system

In the deep oligotrophic postglacial Lake Stechlin in Germany, two planktivorous coregonid fish species co-occur within the pelagic area: common vendace, *Coregonus albula* (L.), and endemic dwarf-sized Fontane cisco, *Coregonus fontanae* (Schulz & Freyhof). The two species are easily distinguished by their differential spawning times and exhibit distinct morphological characteristics (Schulz & Freyhof 2003). The sympatric evolution of this species pair has been suggested based on mtDNA and microsatellite analyses (Schulz et al. 2006). Both species perform regular diel vertical migrations, but differ in their average night-time population depths, with Fontane cisco being found a few meters deeper in the water column than vendace throughout the year (Helland et al. 2007; Mehner et al. 2007). This difference in depth distribution is associated with a difference in mean experienced water temperature, which declines continuously with depth (Mehner et al. 2005). Despite the depth segregation, diet compositions of the species are rather similar, with a clear dominance of planktonic food (Helland et al. 2008). Hence, exploitative competition between the two species can be assumed to be high, whereas mechanisms reducing competition (and thus potentially driving divergence) are unrelated to diet. One mechanism promoting ecological divergence between the species is a difference in temperature-specific metabolic costs (Ohlberger et al. 2008), which directly influences the competitive abilities of the two populations. Also the temperature preferences of the two species differ according to their slight vertical segregation. These thermal preferences further correspond to temperatures of minimal net costs of swimming, highlighting temperature as the pre-

dominant environmental factor shaping the divergence between the species (Ohlberger et al., submitted).

Lake Stechlin features typical characteristics of newly colonized postglacial systems: intraspecific competition for food resources is high due to the low productivity of the lake, and ecological opportunity is high due to the weak interspecific competition with planktivores from other taxa and due to the low risk of predation by higher trophic levels. This setting offers the unique opportunity to investigate whether these system characteristics, in conjunction with adaptation in the metabolic temperature optimum, allow for ecological diversification and eventual parapatric/sympatric speciation along the environmental gradient given by water temperature. If proven plausible, this would add new insights into the theory of adaptive speciation, support the prevalence of speciation along environmental gradients in natural systems, and highlight the importance of temperature in shaping processes of ecological and evolutionary diversification.

Research questions

The main question for this study is whether a lake's temperature-depth gradient is prone to induce the adaptive speciation of fish populations in sympatry/parapatry through microhabitat adaptation and segregation along the gradient.

In particular, I will address the following two research questions:

- Are the ecological mechanisms associated with the metabolic temperature optimum, treated as the single adaptive trait in the evolutionary model, sufficient to induce evolutionary branching of the ancestral population along the temperature-depth gradient?
- Does evolutionary branching occur under the assumptions and parameter estimates inferred from observational and experimental data?

Two further research questions will be addressed if time allows:

- Is size structure necessary for evolutionary branching to occur, or is a second adaptive trait needed (such as size at maturation or a trait determining maintenance costs)?
- Does evolutionary branching occur in an extended model of sexual populations under the assumption of assortatively mating individuals?

Methods and work plan

Based on the observational and experimental knowledge about the Lake Stechlin coregonids, we will design a model for their evolutionary diversification along the lake's temperature-depth gradient. First, we will specify the basic equations to describe the system (see below) and implement these into the simulation software. After this implementation, and based on a preliminary estimation of parameter values, the model will be analyzed numerically using adaptive dynamics techniques and direct numerical simulations. Finally, a sensitivity analysis will deepen our understanding of the model's behavior and enable its refinement as needed. For simulation and analysis, we will use the MATLAB computing environment. We will begin with a fairly simple model and gradually increase its complexity as time allows. Specifically, we will start with a single adaptive trait and asexual reproduction with mutation. If necessary and

possible, we will include size structure and/or extend the model to sexual reproduction with recombination and assortative mating.

Model description

The starting point for our simple initial model is a hypothetical ancestral population with a potential for divergence in the quantitative adaptive trait given by its metabolic temperature optimum T_i . For the evolutionary dynamics, we assume asexual reproduction, a low mutation probability μ , and a small standard deviation σ of mutation steps, so that evolution follows the canonical equation of adaptive dynamics (Dieckmann & Law 1996) in conjunction with fitness-based conditions for evolutionary branching (Geritz et al. 1998), as specified in detail below. The population dynamics are deterministic and structured with regard to depth x , with $0 < x < x_{\max}$. The foraging rate $r_i(x)$ of a morph i is assumed to drop with temperature $T(x)$ on both sides around T_i . Exploitative competition for a single unstructured resource, considered as the predominant cause of competition in our system, is logistic and occurs at each depth. The rate density at which resources become available is given by a depth-dependent carrying capacity density $K(x)$. Since temperature, food density, and light intensity continuously decrease with depth $K(x)$ and prey catchability $c(x)$ decline monotonically with depth. Gain in the biomass density $B_i(x)$ of morph i at depth x , which includes fecundity, is proportional to prey catchability, foraging rate, and the logistic competition factor. Biomass loss, which includes mortality, arises from maintenance costs $m(T)$, which monotonically decrease with temperature. Therefore, the per capita growth rates $f_i(x)$, in terms of biomass, are given by the difference between per capita resource intake rates and per capita maintenance costs. We further assume the rapid redistribution of individuals along the depth gradient following foraging dynamics, which can be chosen gradually between being random and optimal by varying a parameter α . Individuals keep adjusting their depth according to their per capita growth rate. We further define the number of morphs n , the morph index i , with $i = 1, \dots, n$ for residents and $i = 0$ for a rare mutant, and the average biomass b_i of an individual of morph i . For the evolutionary dynamics we define the invasion fitness of a morph f_i , its first derivative (or selection gradient) g_i , and its second derivative h_i . Derivatives of the invasion fitness are taken with respect to the mutant trait value and are evaluated at the trait value of the corresponding resident.

Basic equations

Biomass of morph i : $B_i = \int_0^{x_{\max}} B_i(x) dx$.

Invasion fitness of morph i : $B_i^{-1} \int_0^{x_{\max}} f_i(x) B_i(x) dx$.

Resource intake rate density of all morphs competing at depth x : $I(x) = c(x) \sum_{i=1}^n r_i(x) B_i(x)$.

Per capita growth rate of morph i at depth x : $c(x) r_i(x) [1 - I(x) / K(x)] - m(T(x))$.

Foraging dynamics (fastest timescale)

$B_i(x) = B_i f_i^\alpha(x) / \int_0^{x_{\max}} f_i^\alpha(x') dx'$.

Population dynamics (fast timescale)

$\frac{d}{dt} B_i = f_i B_i$.

Gradual evolutionary dynamics (slow timescale)

$\frac{d}{dt} T_i = \frac{1}{2} \mu \sigma^2 \frac{B_i}{b_i} g_i$.

Evolutionary branching dynamics (slowest timescale)

If $h_i > 0$ and $|g_i| < \frac{1}{2}\sigma h_i$, then $n \rightarrow n+1$, $T_n \rightarrow T_i + \sigma \operatorname{sgn} g_i$, $B_n \rightarrow \frac{1}{2}B_i$, and $B_i \rightarrow \frac{1}{2}B_i$.

Relevance and link to EEP's research plan

This project aims at enhancing the understanding of ecological diversification and speciation along an environmental gradient by frequency-dependent disruptive natural selection arising from competitive intraspecific interaction and ecological opportunity. It therefore intends to provide new insights into causes of adaptive diversification within a contiguous spatial area and may advance the understanding of impacts of environmental change on ecosystems in dependence on their evolutionary history and ecological characteristics. The proposed research plan combines aspects of the *Evolving Biodiversity* and *Adaptive Dynamics Theory* research projects of the EEP. It further bridges between theoretical and empirical as well as biological and mathematical approaches by integrating experimental and observational knowledge into the described modeling approach.

Expected output and publications

This work will be included in my Ph.D. thesis and is intended for publication as a co-authored research article in an international scientific journal.

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