The roles of density dependence, developmental asynchrony, and niche traversal costs in shaping the evolution of ontogenetic complexity

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Abstract

Most organisms undergo some degree of niche transition throughout their life cycles, which are typically accompanied by morphological, physiological, and/or behavioral changes. Ontogenetic complexity generally refers to the magnitude and abruptness of these changes. Evolutionary theory has described how various genetic properties facilitate and constrain the evolution of ontogenetic complexity, while ecological theory has described how ontogenetic dynamics shape populations and community dynamics. However, the general ecological properties that create a selective gradient for greater ontogenetic complexity have received less theoretical attention. To further our explanation of the evolution of ontogenetic complexity, here we present a general theoretical framework that considers the roles of population density, ontogenetic (a)synchrony, the breadth of competitive effects across niche space, and the costs of ontogenetic niche traversal in shaping the selective gradient for greater degrees of ontogenetic niche traversal. Mathematical analysis of this model showed that beyond a critical threshold, increasing population density monotonically increased the evolutionarily stable degree of ontogenetic niche traversal. However, this relationship was mediated by the degree of ontogenetic asynchrony and how diffuse competition was across niche space, both of which had non-monotonic effects on the evolutionarily stable degree of ontogenetic niche displacement. Density dependence is well established as a driver on life history evolution, and this framework further situates the evolution of ontogenetic complexity within the broader framework of life history evolution.

Keywords: Ontogeny, Complexity, Population ecology

Introduction

Most organisms undergo some degree of morphological, physiological, and/or behavioral shift throughout their life cycles. Ontogenetic complexity generally refers to the magnitude and abruptness of these changes, with more drastic changes indicating greater complexity. While there is debate regarding what specifically constitutes greater life cycle complexity, it is generally accepted that most organisms undergo life cycles with some degree of complexity ([1, 2]). Changes in patterns of diversification throughout natural history are often associated with principle changes in ontogenetic complexity, prompting a long interest in explaining evolutionary changes in ontogeny ([3–6]). Significant progress has been made in describing the the genetic basis of life cycle evolution ([7–11]). However, the ecological properties that generate selective pressures for greater ontogenetic complexity have received relatively less attention.

Foundational theory on the ecological drivers of life cycle evolution suggests greater ontogenetic complexity spreads individuals within a population across a broader niche ([12, 13]). Connecting this property to more general ecological theory, this greater within-population niche differentiation then decreases the strength of intraspecific competition, which can make population dynamics more stable and reduce invasibility ([14–16]). Because the strength of intraspecific competition typically increases with population density, traits that reduce niche overlap with conspecifics should be selectively favored under stronger negative density dependence. Ontogenetic niche differentiation provides a mechanism to accomplish this reduction in niche overlap, motivating the hypothesis that negative density dependence may select for the evolution greater life cycle complexity. While extensive work has established the interplay between density dependence and ontogenetic niche shifts in stage-structured populations ([17]), the role of negative density dependence in driving the evolution of greater life cycle complexity (ontogenetic niche differentiation) has not been generally synthesized.

While general ecological theory implies a role of density dependence in selecting for greater ontogenetic complexity, there are several population and organismal properties that may mediate or constrain said selective pressure. One such property is the degree of synchrony in ontogenetic progression among members of a population. If all individuals in a population progress through their life cycle in complete synchrony, individuals traversing niche space maintain their relative positions, thus reducing relief from intraspecific competition. In contrast, ontogenetic asynchrony allows individuals within a population are spread across their niche, allowing ontogenetic movement to generate meaningful niche separation and reduce intraspecific competition. The degree of (a)synchrony in ontogenetic progression among members of a population can play an important role in determining their ecological interactions, both intraspecific and interspecific ([18–20]). The degree of ontogenetic (a)synchrony also varies naturally among populations and taxa, driven by factors including the seasonality of reproduction, environmental stochasticity, and the degree of generation overlap ([21, 22]). While previous work has primarily focused on explaining how ontogenetic (a)synchrony shapes various aspects of population dynamics (e.g., demographic rates, coexistence), its role in shaping the selective landscape for life cycle complexity has received less formal theoretical attention.

In addition to intrinsic population properties, ontogenetic movement through niche space is typically accompanied by organismal costs that could oppose selection for greater ontogenetic complexity ([2]). These costs may be energetic, as developing traits that facilitate ontogenetic niche movement can be energetically expensive ([23–25]). Organisms may also be more vulnerable during ontogenetic transitions, as they can face elevated sensitivity to environmental stressors and altered predation risk as they shift ecological roles ([26–30]). Therefore, explaining the conditions under which greater ontogenetic complexity should evolve requires considering both the competitive benefits that said complexity confers as well as the costs it imposes. While these costs associated with ontogenetic niche changes have been described across a variety of systems, their inclusion in theoretical explanations of the evolution of ontogenetic complexity is somewhat more recent and less established ([2]).

To further our explanation for the evolution of ontogenetic complexity, here we develop a general theoretical framework that considers population density, ontogenetic (a)synchrony, the breadth of competitive effects across the niche, and the costs associated with ontogenetic niche movement. We describe a simple yet general evolutionary model where fitness is determined by the competitive effects experienced by individuals from conspecifics throughout their lives. Individuals can traverse some distance within a niche space throughout their life times, and the strength of intraspecific competition depends on their placement relative to the placement of conspecifics within the niche space across ontogeny. We then mathematically analyze the selection gradients produced by this model, and describe how population density, ontogenetic (a)synchrony, the costs associated with ontogenetic niche movement, and the breadth of competitive effects across the niche are expected to shape the evolution of greater ontogenetic complexity.

Model Description

We consider a population of individuals that live until some maximum lifespan T and occupy a position x in niche space at each time point t throughout their lifetimes. Change in niche position over time is described by $x(t)$, where changes in $x(t)$ correspond to morphological, physiological, and/or behavioral changes an organism undergoes throughout its life cycle. For simplicity, we consider one dimension within a more complex niche space, making $x(t) \in \mathbb{R}$. Also for simplicity and analytical tractability, we assume a linear progression at a constant rate v through niche space, such that $x(t) = x_0 + v \cdot t$. The total distance D traversed through niche space by an individual throughout their life time is then

$$D = \int_0^T \left| \frac{dx}{dt} \right| dt, \tag{1}$$

where greater values of D correspond to more extreme ontogenetic niche shifts.

Individuals that occupy more similar niche positions compete more strongly than those in more distant niche positions. The strength of competition between a focal individual $x_f(t)$ and a conspecific $x_c(t)$ is described by the competition kernel $\alpha(x_f(t), x_c(t))$. Letting σ_c^2 define how quickly competition declines with distance in niche space, the competition kernel takes the Gaussian form

$$\alpha(x_f(t), x_c(t)) = \exp\left(-\frac{(x_f(t) - x_c(t))^2}{2\sigma_c^2}\right). \tag{2}$$

Here, small σ_c^2 indicates competition rapidly declines and only very similar individuals compete strongly, while a large σ_c^2 indicates competition is more diffuse across the niche.

Individuals within the population may be at different developmental stages at a given time. Letting τ_n represent the age offset of individual n, the niche position of individual n at time t under a linear ontogeny is $x_n(t) = x_0 + v(t + \tau_n)$. Here, the degree to which age differences are spread across the population determines the degree of developmental asynchrony. Letting age differences be drawn from a normal distribution with a variance of σ_s^2, the competition kernel between the focal individual and individual n becomes

$$\alpha(x_f(t), x_n(t)) = \exp\left(-\frac{v^2(\tau_f - \tau_n)^2}{2\sigma_c^2}\right). \tag{3}$$

Here, a large σ_s^2 corresponds to a high degree of asynchrony, where individuals are spread broadly across developmental states simultaneously. This illustrates how developmental synchrony and ontogenetic rate interact. When σ_s^2 is small, age differences are similar across individuals and competition remains high regardless of ontogenetic rate v. When σ_s^2 is high, individuals differ significantly in developmental state, and a greater ontogenetic rate more effectively separates the focal individual from its competitors in niche space.

The total competitive load experienced by the focal individual from all other members of its population is then

$$C(x_f(t)) = \sum_{n \neq f}^{N} \alpha(x_f(t), x_n(t)) = \sum_{n \neq f}^{N} \exp\left(-\frac{v^2(\tau_f - \tau_n)^2}{2\sigma_c^2}\right), \tag{4}$$

and this quantity averaged over the individual's life time is

$$\bar{C} = \frac{1}{T}\int_0^T C(x_f(t))dt. \tag{5}$$

Note that under a linear trajectory, $\bar{C}$ depends on v, N, and σ_s^2 but not absolute niche position relative to x_0, since competition depends only on pairwise differences in niche position.

Transitioning to a different area in niche space requires the development of traits needed to operate within said space. This added development comes at an energetic cost, designated as λ, which reduces an individual's competitive ability. Therefore, the effective time-averaged competitive load is

$$\bar{C}_\epsilon = \bar{C} + \lambda \cdot v^2, \tag{6}$$

where λv^2 reflects the energetic cost of ontogenetic changes. That is, faster or more extreme niche traversal requires greater developmental investment, effectively increasing the competitive burden on the individual due to its weaker competitiveness. Letting c scale how strongly competition and developmental costs reduce fitness, fitness W declines exponentially with $\bar{C}_\epsilon$ such that

$$W = \exp(-c \cdot \bar{C}_\epsilon). \tag{7}$$

Methods

Analytical evaluation of the selection gradient

Because the age difference between a focal individual and a conspecific ($\tau_f - \tau_n$) does not vary over time, Equation 5 becomes

$$\bar{C} = \frac{1}{T}\int_0^T C(x_f(t))dt = \sum_{n \neq f}^{N} \exp\left(-\frac{v^2(\tau_f - \tau_n)^2}{2\sigma_c^2}\right) \tag{8}$$

That is, $\bar{C} = C$ because under a linear trajectory with fixed age differences, the pairwise niche distance between any two individuals is constant through time. To solve for $\bar{C}$ in terms of population size N, niche movement rate v, and variation in age difference σ_s^2, the sum over individuals can be replaced with the expectation over the distribution of age differences. Letting $\Delta\tau = \tau_f - \tau_n$ be drawn from a normal distribution with a variance of σ_s^2, since $\tau_n \sim \mathcal{N}(0, \sigma_s^2)$ and τ_f is fixed, $\Delta\tau \sim \mathcal{N}(0, \sigma_s^2)$. The expected competitive load from a single conspecific is then

$$\mathbb{E}\left[\exp\left(-\frac{v^2\Delta\tau^2}{2\sigma_c^2}\right)\right] = \int_{-\infty}^{\infty} \exp\left(-\frac{v^2\Delta\tau^2}{2\sigma_c^2}\right) \cdot \frac{1}{\sqrt{2\pi\sigma_s^2}} \exp\left(-\frac{\Delta\tau^2}{2\sigma_s^2}\right) d\Delta\tau \tag{9}$$

Combining exponents gives

$$-\frac{v^2\Delta\tau^2}{2\sigma_c^2} - \frac{\Delta\tau^2}{2\sigma_s^2} = -\frac{\Delta\tau^2}{2}\left(\frac{v^2}{\sigma_c^2} + \frac{1}{\sigma_s^2}\right) = -\frac{\Delta\tau^2}{2\sigma_\epsilon^2}, \tag{10}$$

where

$$\sigma_\epsilon^2 = \left(\frac{v^2}{\sigma_c^2} + \frac{1}{\sigma_s^2}\right)^{-1} = \frac{\sigma_c^2\sigma_s^2}{\sigma_s^2 v^2 + \sigma_c^2}. \tag{11}$$

The integral then evaluates to

$$\mathbb{E}\left[\exp\left(-\frac{v^2\Delta\tau^2}{2\sigma_c^2}\right)\right] = \frac{\sigma_\epsilon}{\sigma_s} = \sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}}. \tag{12}$$

Multiplying by $N - 1$ to sum over all conspecifics then gives the expected competitive load

$$\bar{C} = (N-1)\sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}}. \tag{13}$$

Equation 13 shows how population size N, niche movement rate v, and variation in age difference σ_s^2 jointly determine competitive load. When $v = 0$, $\bar{C} = N - 1$, making an individual experiences competition from all other individuals at full strength. As v increases, $\bar{C}$ decreases at a rate governed by σ_s^2. That is, greater asynchrony results in faster relief from competition. When $\sigma_s^2 \to 0$, the denominator of Equation 13 approaches σ_c^2 regardless of v, so $\bar{C} \to N - 1$ and ontogenetic niche movement provides no relief from competition. Including the cost of ontogenetic niche movement then gives the expected effective competition

$$\bar{C}_\epsilon = (N-1)\sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}} + \lambda v^2. \tag{14}$$

Substituting this expression into fitness then gives the expected fitness

$$W(v) = \exp\left(-c\left[(N-1)\sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}} + \lambda v^2\right]\right). \tag{15}$$

Since $W = \exp(-c\bar{C}_\epsilon)$ and the exponential is monotonically decreasing, maximizing W is equivalent to minimizing $\bar{C}_\epsilon$. Therefore, the selection gradient is

$$\frac{\partial W}{\partial v} = -c \cdot W \cdot \frac{\partial \bar{C}_\epsilon}{\partial v}. \tag{16}$$

Here, the sign of $\frac{\partial W}{\partial v}$ is determined by $-\frac{\partial \bar{C}_\epsilon}{\partial v}$, and the evolutionarily stable condition $\frac{\partial W}{\partial v} = 0$ reduces to $\frac{\partial \bar{C}_\epsilon}{\partial v} = 0$. Taking the derivative gives

$$\frac{\partial \bar{C}_\epsilon}{\partial v} = (N-1) \cdot \frac{\partial}{\partial v} \sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}} + 2\lambda v. \tag{17}$$

For the first term,

$$\frac{\partial}{\partial v} \sqrt{\frac{\sigma_c^2}{\sigma_s^2 v^2 + \sigma_c^2}} = -\frac{\sigma_c^2 \sigma_s^2 v}{(\sigma_s^2 v^2 + \sigma_c^2)^{3/2}}. \tag{18}$$

Therefore, the full gradient condition is

$$\frac{\partial \bar{C}_\epsilon}{\partial v} = -(N-1) \frac{\sigma_c^2 \sigma_s^2 v}{(\sigma_s^2 v^2 + \sigma_c^2)^{3/2}} + 2\lambda v = 0. \tag{19}$$

Finally, factoring out v gives

$$v \left[2\lambda - \frac{(N-1)\sigma_c^2 \sigma_s^2}{(\sigma_s^2 v^2 + \sigma_c^2)^{3/2}} \right] = 0 \tag{20}$$

The non-trivial solution is then given by solving

$$\frac{(N-1)\sigma_c^2 \sigma_s^2}{(\sigma_s^2 v^2 + \sigma_c^2)^{3/2}} = 2\lambda, \tag{21}$$

which gives

$$(\sigma_s^2 v^2 + \sigma_c^2)^{3/2} = \frac{(N-1)\sigma_c^2 \sigma_s^2}{2\lambda} \tag{22}$$

and therefore

$$v^* = \frac{1}{\sigma_s} \sqrt{\left(\frac{(N-1)\sigma_c^2 \sigma_s^2}{2\lambda} \right)^{2/3} - \sigma_c^2} \tag{23}$$

Results

Greater population density selectively favors the evolution of greater ontogenetic niche displacement

From Equation 19, setting $\frac{\partial \bar{C}_\epsilon}{\partial v} = 0$ yields two solutions. The trivial solution $v^* = 0$ corresponds to no ontogenetic niche movement, where individuals experience the full competitive pressure from all conspecifics. The non-trivial interior solution, from Equation 23, is $v^* = \frac{1}{\sigma_s} \sqrt{\left(\frac{(N-1)\sigma_c^2 \sigma_s^2}{2\lambda} \right)^{2/3} - \sigma_c^2}$, which gives the evolutionarily stable ontogenetic rate as a function of population size N, niche competition breadth σ_c^2, the degree of developmental asynchrony σ_s^2, and the cost of development λ. Recalling that ontogenetic displacement $D = vT$, the evolutionarily stable ontogenetic displacement is

$$D^* = \frac{T}{\sigma_s} \sqrt{\left(\frac{(N-1)\sigma_c^2 \sigma_s^2}{2\lambda} \right)^{2/3} - \sigma_c^2} \tag{24}$$

which increases with population density (Figure 1).

The interior solution $D^* > 0$ only exists when the expression under the square root term in Equation 24 is positive, requiring

$$\left(\frac{(N-1)\sigma_c^2\sigma_s^2}{2\lambda}\right)^{2/3} > \sigma_c^2. \tag{25}$$

Solving for N gives the critical population density

$$N^* = 1 + \frac{2\lambda}{\sigma_s^2}, \tag{26}$$

below which the only evolutionarily stable state is $D^* = 0$ (Figure 1B). Here, ontogenetic complexity is selectively disfavored and simpler life cycles are predicted to persist. Above N^*, the evolutionarily stable ontogenetic displacement D^* increases monotonically with population size N, which is shown in Figure 1 and confirmed by taking the partial derivative of v^* with respect to N:

$$\frac{\partial v^*}{\partial N} = \frac{1}{\sigma_s} \cdot \frac{1}{3}\left(\frac{(N-1)\sigma_c^2\sigma_s^2}{2\lambda}\right)^{-1/3} \cdot \frac{\sigma_c^2\sigma_s^2}{2\lambda} \cdot \frac{1}{v^*\sigma_s} > 0. \tag{27}$$

This threshold arises because at low population densities, the competitive benefit associated with niche displacement is insufficient to offset the associated costs. Likewise, at sufficiently high population densities, the relief from competition gained by ontogenetic displacement outweighs the associated developmental investment.

The role of ontogenetic asynchrony in shaping the selective landscape for greater ontogenetic niche displacement

Intuitively, niche traversal of any distance by an individual does little to release them from intraspecific competition if conspecifics undergo the same traversal in synchrony. Therefore, one could reason that selection for greater ontogenetic complexity necessitates some degree of ontogenetic asynchrony. This intuition is consistent with our model predictions. From $N^* = 1 + \frac{2\lambda}{\sigma_s^2}$ (Equation 26), it is clear that increasing the degree of asynchrony (σ_s^2) decreases N^* (Figure 2A). More specifically, as $\sigma_s^2 \to \infty$, $N^* \to 1$, meaning the range of population densities that would be experience selection for any ontogenetic niche traversal widens. In other words, it becomes easier to get any selection for ontogenetic complexity. Conversely, under the limit of perfect synchrony, $\sigma_s^2 \to 0$ and $N^* \to \infty$, meaning greater ontogenetic niche displacement is never selectively favored regardless of population density.

While ontogenetic asynchrony makes selection for increased ontogenetic complexity occur over a broader parameter space, the optimal degree of ontogenetic niche traversal (D^*) is non-monotonic and depends on population density (Figure 2). Ontogenetic asynchrony σ_s^2 enters Equation 24 in the numerator of the square root term and in the prefactor $\frac{1}{\sigma_s^2}$. Therefore, increasing asynchrony increases the term under the square root, therefore increasing the competitive relief achievable by ontogenetic niche traversal. However, the prefactor $\frac{1}{\sigma_s^2}$ decreases with increasing asynchrony; if the population is spread more evenly across the available niche, further increases in ontogenetic niche traversal (D) is less necessary to escape competition. Conversely, in a more ontogenetically synchronous population (lower σ_s^2), greater ontogenetic niche traversal is more

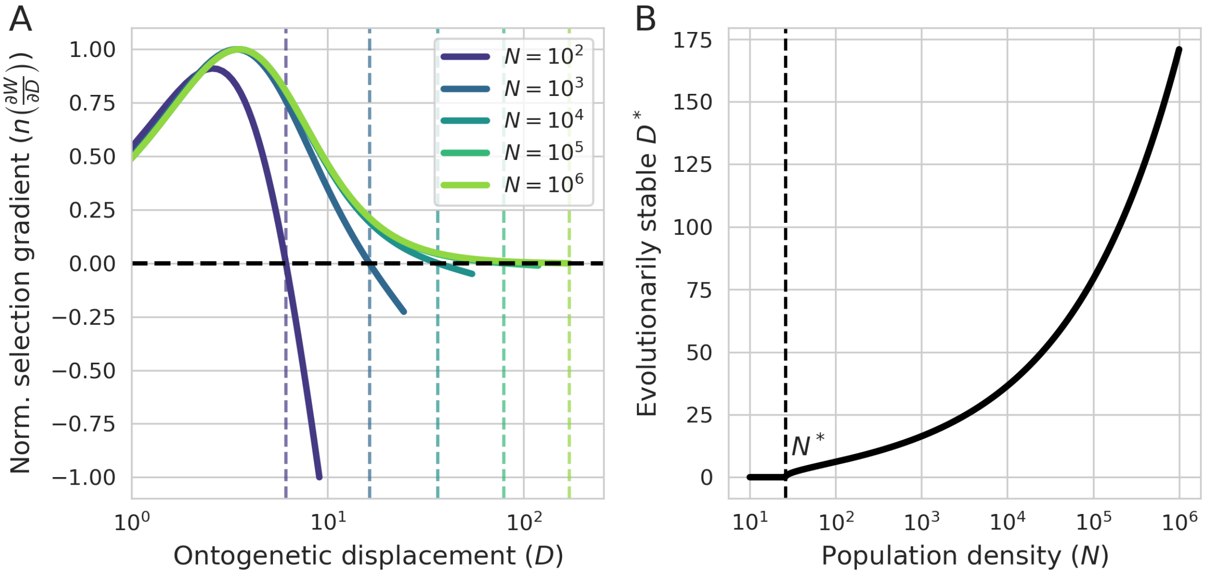

Figure 1: Increasing population density increases the evolutionarily stable ontogenetic niche displacement. A) The normalized selection gradient (Equation 16) as a function of ontogenetic niche displacement D. Different colored solid lines represent different population densities. Greater ontogenetic niche complexity is selectively favored when $\frac{\partial W}{\partial D} > 0$ and is selectively disfavored when $\frac{\partial W}{\partial D} < 0$. The evolutionarily stable degree of ontogenetic niche displacement D^* occurs where $\frac{\partial W}{\partial D} = 0$, denoted by the dashed vertical line of the corresponding color for each population density. B) The evolutionarily stable degree of ontogenetic niche displacement D^* as a function of population density N. The dashed vertical line denotes the population density N^* below which greater ontogenetic complexity is never favored. Above N^*, greater population density monotonically increases D^*.

selectively favored because less relief from competition is achieved per unit increase in niche displacement (Figure 2B).

The role of ontogenetic costs in shaping the selective landscape for greater ontogenetic niche displacement

Although alleviation from competition can selectively favor the evolution of ontogenetic complexity, costs associated with niche traversal places a limitation on when we would expect ontogenetic complexity to be favored. The niche traversal cost term λ appears only in the numerator in Equation 26, illustrating that increasing niche traversal costs increases the critical population density (N^*) at which any increase in ontogenetic complexity is favored (Figure 3A). In other words, taxa with higher costs associated with morphological, physiological, and/or behavioral changes require denser populations before ontogenetic niche displacement becomes selectively favored. Similarly, λ only appears in the denominator in Equation 24, illustrating how increasing niche traversal costs decreases the evolutionarily stable degree of ontogenetic niche displacement (D^*) (Figure 3B).

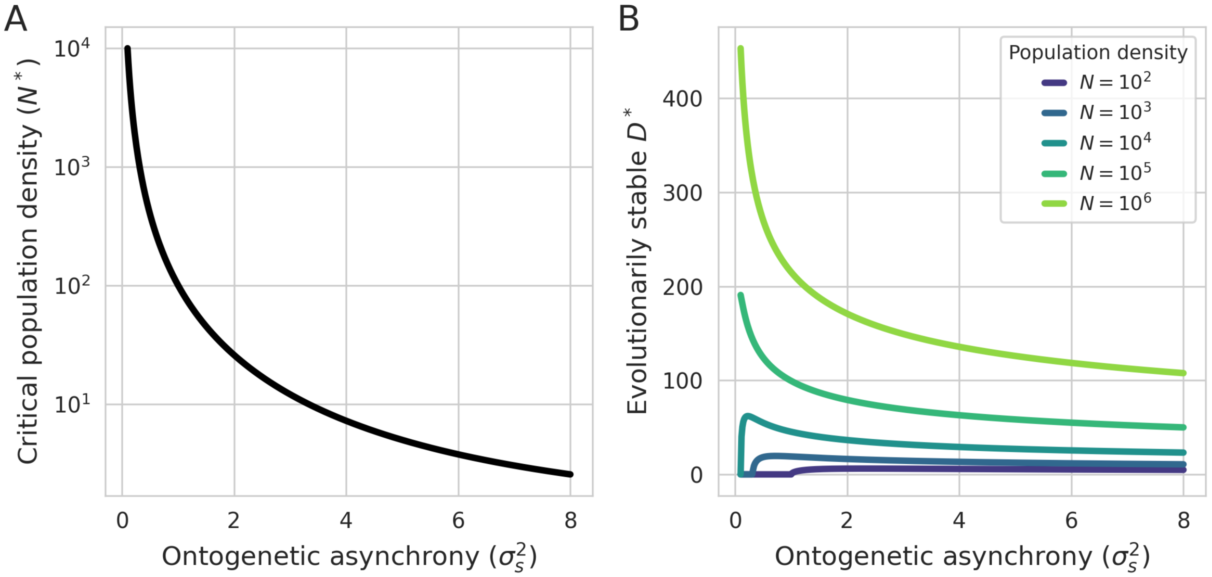

Figure 2: Ontogenetic asynchrony alters the selective landscape for greater ontogenetic niche displacement. A) The critical population density needed for any selection for greater ontogenetic niche displacement (N^*) as a function of ontogenetic asynchrony (σ_s^2) (Equation 26). B) The evolutionarily stable ontogenetic niche displacement (D^*) as a function of ontogenetic asynchrony (σ_s^2) for different population densities, which are represented by different colors (Equation 24).

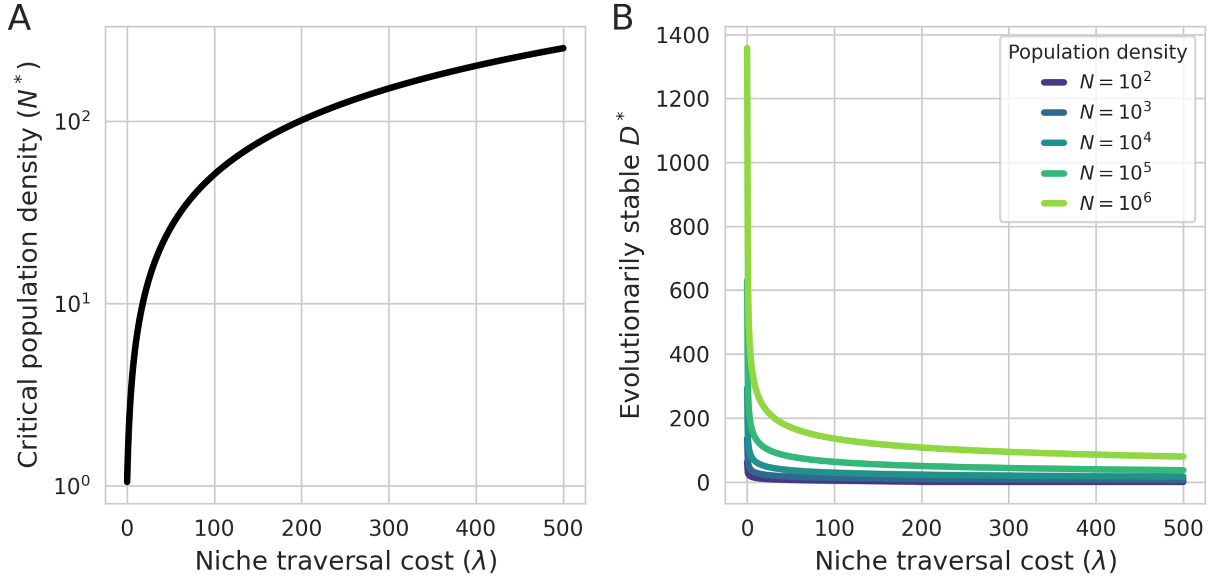

Figure 3: Costs associated with niche traversal limit the conditions under which ontogenetic complexity is selectively favored. A) The critical population density needed for any selection for greater ontogenetic niche displacement (N^*) as a function of niche traversal cost (λ) (Equation 26). B) The evolutionarily stable ontogenetic niche displacement (D^*) as a function of niche traversal cost for different population densities, which are represented by different colors (Equation 24).

The breadth of competition within a niche has non-monotonic effects on selection for greater ontogenetic niche displacement

The extent that competition declines with distance in niche space (σ_c^2) appears in both the numerator and as a subtractive term in Equation 24, producing a non-monotonic effect on the evolutionarily stable ontogenetic displacement D^*. A greater σ_c^2 increases the numerator term, reflecting that when the effects of competition span more broadly across niche positions, the benefit of moving away from conspecifics is greater. Here, at low σ_c^2, competition is more localized across niche positions and the numerator effect dominates, making D^* increase with σ_c^2. However, at high σ_c^2, competition is so diffuse that ontogenetic niche movement provides diminishing relief, making the subtractive term dominate and therefore suppressing D^* (Figure 4A).

Examining Figure 4A, it is clear that the niche competition breadth that maximizes the evolutionarily stable ontogenetic displacement varies with population density. We can describe this trend explicitly by solving $\frac{\partial D}{\partial \sigma_c^2} = 0$, which gives

$$\sigma_c^{2*} = \frac{8}{27}\left(\frac{(N-1)\sigma_s^2}{2\lambda}\right)^2. \tag{28}$$

Equation 28 shows that the the competition breadth that maximizes the evolutionarily stable ontogenetic niche displacement (σ_c^2) scales as $(N-1)^2$, meaning the evolution of greater ontogenetic complexity is maximized when competition is more diffuse across niche position in larger populations (Figure 4B). This suggests the relationship between how diffuse competition is across niche positions and the evolution of life cycle complexity is not fixed, but rather depends strongly on the ecological context in which a population exists.

Discussion

To further our theoretical explanation of the evolution of ontogenetic complexity, here we describe an ecological and evolutionary model where fitness depends on proximity to conspecifics across niche space. We analytically found that beyond a critical population density, which depends on the cost of ontogenetic niche movement and ontogenetic asynchrony (Equation 26), the evolutionarily stable degree of ontogenetic niche displacement monotonically increases with increasing population density (Equation 24, Figure 1). This relationship is mediated by how asynchronously individuals traverse niche space throughout ontogeny, which broadens the range population densities that experience any selection for greater ontogenetic niche traversal but has non-monotonic effects on the evolutionarily stable degree of ontogenetic niche traversal (Equations 24 and 26, Figure 2). More intuitively, increased costs associated with ontogenetic niche traversal monotonically increased the threshold population density that would experience any selection for greater ontogenetic niche traversal and decreased the evolutionarily stable degree of ontogenetic niche traversal (Equations 24 and 26, Figure 3). Finally, we found the breadth of competitive effects across the niche had a non-monotonic effect on selection of greater ontogenetic niche displacement, where low competitive diffusion across the niche increased the evolutionarily stable ontogenetic niche displacement but higher competitive diffusion suppressed it (Equation 24, Figure 4A). Likewise, the breadth of competitive effect that maximized the degree of evolutionarily stable ontogenetic niche displacement increased monotonically with population density (Equation 28, Figure 4B).

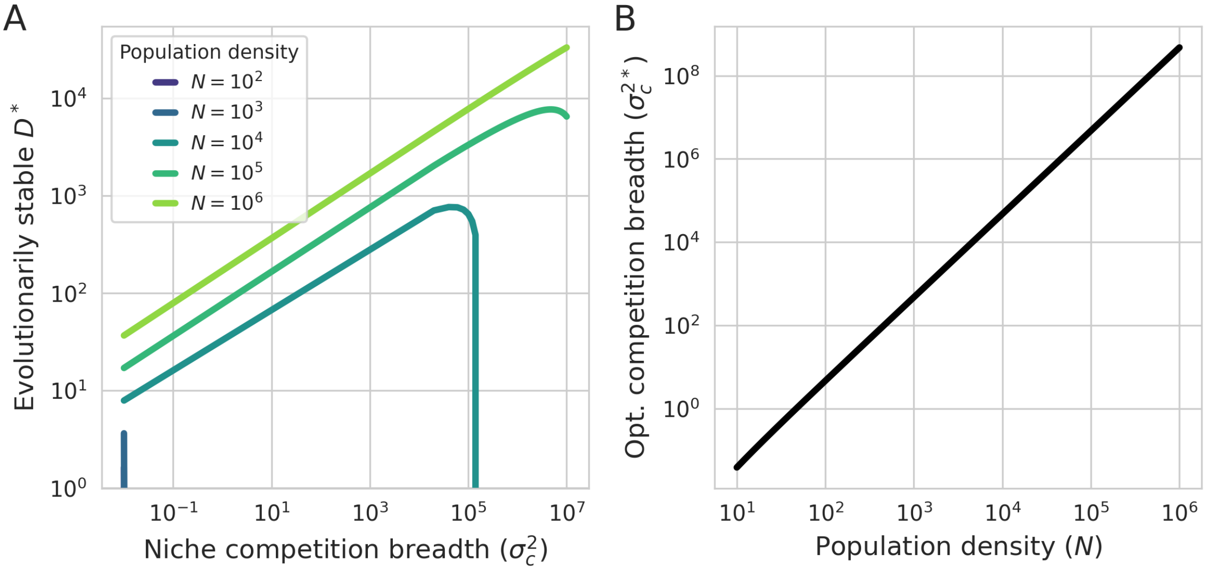

Figure 4: The breadth of niche competition within niche space has non-monotonic effects on selection for greater ontogenetic niche displacement. A) The evolutionarily stable ontogenetic displacement (D^*) as a function of the breadth of competitive effects within niche space (σ_c^2) (Equation 24). Here, each line represents a different population density. Only lines for population densities of $> 10^4$ are clearly visible due to scale. B) The breadth of competitive effects across niche space that maximizes D^* as a function of population density (Equation 28).

The model we have presented here makes several simplifying assumptions that warrant discussion. Most notably, we assume a linear progression through niche space at a constant rate v, which is shared among all members of the population. While this assumption granted analytical tractability, real ontogenetic trajectories through niche space are rarely constant and linear. Rather, they often undergo nearly discrete developmental transitions, experience periods of stasis, can have genetically heritable heterochrony, and even reverse direction in niche space throughout ontogeny ([14, 31–34]). Relaxing this assumption to allow for non-linear ontogenetic trajectories and variation in ontogenetic rates, perhaps through individual-based modeling, would likely produce rich insights and should be the subject of future work. We also modeled ontogenetic asynchrony as a fixed population-level property, rather than as a dynamic trait or consequence of ecological dynamics. In reality, the degree of ontogenetic asynchrony within a population may be shaped by selection, environmental properties, density dependence, and other ecological interactions ([35–37]). This means ontogenetic rate and asynchrony may co-evolve in ways not captured by our model. Therefore, incorporating the joint evolution of v and σ_c^2 could be a natural and important extension of this framework.

For simplicity, we also assumed fitness exponentially declines with competitive load, which grants further tractability. This assumption is somewhat standard, but including more mechanistic fitness functions that ellipticity link competitive load to features like resource acquisition, survival, and reproduction might lend different quantitative predictions ([38, 39]). However, this would come at a cost of generality, and the qualitative predictions and structure would likely remain unchanged. Finally, we only consider the effects of intraspecific competition, but real populations exist in communities where interspecific competition, predation, and mutualisms may also shape selection on ontogenetic niche displacement. Therefore, extending this framework to include interspecific interactions would allow for addressing broader questions about the potential role of community context in shaping the evolution of ontogenetic complexity. Despite these limitations, we believe this work can serve as an initial framework which can be built upon to explore more nuanced aspects of these dynamics.

Previous theoretical and conceptual work regarding the evolution of ontogenetic complexity primarily approaches the subject from two different angles. First, prior work has focused on describing how genetic properties allow for the evolution of greater ontogenetic complexity by facilitating the evolution of traits that allow for specialization in different areas of niche space across ontogeny ([4, 13, 40–42]). Second, a large body of work has focused on describing the ecological consequences of ontogenetic niche shifts, including its effects on population dynamics, invasibility, and community interactions ([12, 14, 17, 35, 43]). While these ecological perspectives describe the effects of ontogenetic niche shifting, explanations of the evolution of greater ontogenetic complexity have primarily come from a genetic perspective. Therefore, the framework we have described here complements existing work by providing an ecological description of what selectively drives the evolution of greater ontogenetic complexity.

Our findings that population density creates a selective force, albeit modified by ontogenetic asynchrony and developmental costs, for the evolution of greater ontogenetic complexity connects to the broader literature on density dependence and life history evolution ([44, 45]). Density dependence is well established as a driver of life history variation, shaping traits like age and size at maturity, reproductive investment, and dispersal ([46–48]). Therefore, our model extends this framework to the evolution of ontogenetic complexity, illustrating the same ecological force (greater intraspecific competition at high density) that shapes many other life history traits may also drive the evolution of complex life cycles. This explicitly situates the evolution of ontogenetic complexity within the broader framework of life history theory.

Data and code availability

The notebook containing code used to generate figures is available at :
https://github.com/gabe-dubose/ontogenetic_complexity_eco_evo_theory

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Conflict of interest disclosure

The author declares no conflict of interests.

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