Time delays drive coevolutionary dynamics in consumer-resource metapopulations

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**I. Abstract**

Time delays are ubiquitous in population biology. From gestational lags between prey consumption to reproduction in predators to the within-host replication cycles of viruses, mathematical biologists have long analyzed how such delays affect consumer-resource dynamics. Likewise, spatial structure has long fascinated biologists interested in interspecific interactions. There is thus considerable research on how each of these two processes (time-delays and spatial heterogeneity) considered separately drive community structure over ecological time scales. Similarly, the effects of spatial structure on antagonistic coevolution (e.g., between prey and predator or host and pathogen) have received increased attention among evolutionary biologists.

Yet we know very little about how time-delays interact with spatial processes to drive coevolutionary dynamics. This is surprising, because coevolution across space ultimately reflects local processes, where time delays have major effects. To address this critical gap, we use numerical modeling from empirically derived parameter values to discern how time delays interact with migration dynamics and spatial heterogeneity in key ecological variables to drive co-evolutionary dynamics. Although motivated by host-pathogen metacommunities, through non-dimentionalization we suggest that the main conclusions are broadly applicable to different consumer-resource interactions such as predator-prey systems and thus broadly applicable to consumer-resource coevolution. Our results illustrate the central role time delays can play in altering the magnitude of coevolutionary fluctuations and arms-race dynamics. We discuss some implications of our analyses for coevolutionary theory more broadly, including as it applies to the emergence of novel infectious diseases.

**II. Introduction**

Species evolve, adapting to consistently changing environment and competing within their group and interacting with other species [1]. In ecology, interaction between species includes prey and predators. This interaction may affect each other by making prey and predator evolve in response to each other; prey will develop defense abilities to better escape from predators and predators develop their attack ability to better hunt prey. These adaptations are inherited by their offspring, and the same process would be repeated over generations. In evolutionary biology, this interaction is called an “Arms Race,” which is a competition between co-evolving species where their genes exhibit escalating adaptations and counter-adaptations against each other. “Arms races” are a special kind of coevolution.

Broadly, coevolution between prey and predator is driven by biotic factors and abiotic factors. Biotic factors are the factors that are caused by living organisms, whereas abiotic factors are the factors that are caused by non-living organisms. Biotic factors, for instance, include encounters, migration, mutations, etc. Encounters account for things like prey killed by predator; migration accounts for prey/predator immigration/emigration; mutations account for genetic changes happening during prey/predator reproduction. Note that under local coevolutionary selection, coevolution between two species can occur within a single local community, and thus migration isn’t considered. However, studies conducted in the last few decades demonstrate that most coevolution occurs not in single local communities but in broader regions. The “Geographic Mosaic of Coevolution” theory holds that “coevolution is inherently geographically structured or coevolution between two species can progress along very different trajectories in different places, causing trait differences to evolve among different populations of the same species” [2]. The main instance of abiotic factors includes the spatial arrangements of communities.

Yet there’s one more important factor that needs to be considered to develop the coevolutionary prey-predator model: time delay [3-5]. It is obvious that there are time delays in interactions between prey and predator because, for instance, predators can’t give birth to their babies right after eating prey nor prey can convert nutrition they absorbed right away into its offspring. To demonstrate the importance of taking the time delay into account, imagine the time delay doesn’t exist. Then predators will eat prey and turn it into their babies immediately. This condition can imply that in the absence of the time delay in the interaction between prey and predator can result in the prey population going extinct. Therefore, the time delay is a crucial factor in the prey-predator model which structures coevolution and drives the dynamics and stability of prey and predator populations.

“We can see evidence of ongoing coevolution by studying the same interaction in multiple places. Each group of species interacting in a local community is a potential mini-coevolutionary experiment. Each local population of those species is often genetically distinct from other populations of the same species” [6]. We do a such called mini-coevolutionary experiment in this project and prove the existence of coevolution in our spatial prey-predator coevolution models by showing that there is a change in allele frequencies or fitness, such as fecundity or survival of offspring. Furthermore, we incorporate time-delays into these models and show how time delays drive coevolutionary dynamics in consumer-resource metapopulations, how time delays impact the change in prey/predator population over time, and how species reshape each other across space within the “arms race.”

**III. Methods**

Our project uses R as a main programming language. To explore the effect of the time delay, we numerically integrate our prey-predator evolutionary model with time delays using the *dde* package, and compare it to the baseline, non-time delayed model, using the *deSolve* package in R. The *dde* package has the *ylag* function, which we use to incorporate time delays into our model, and the *dopri* function, which we use to integrate our delay differential equations.

Among various numeric models built, one of the cores is the change in the resource population:

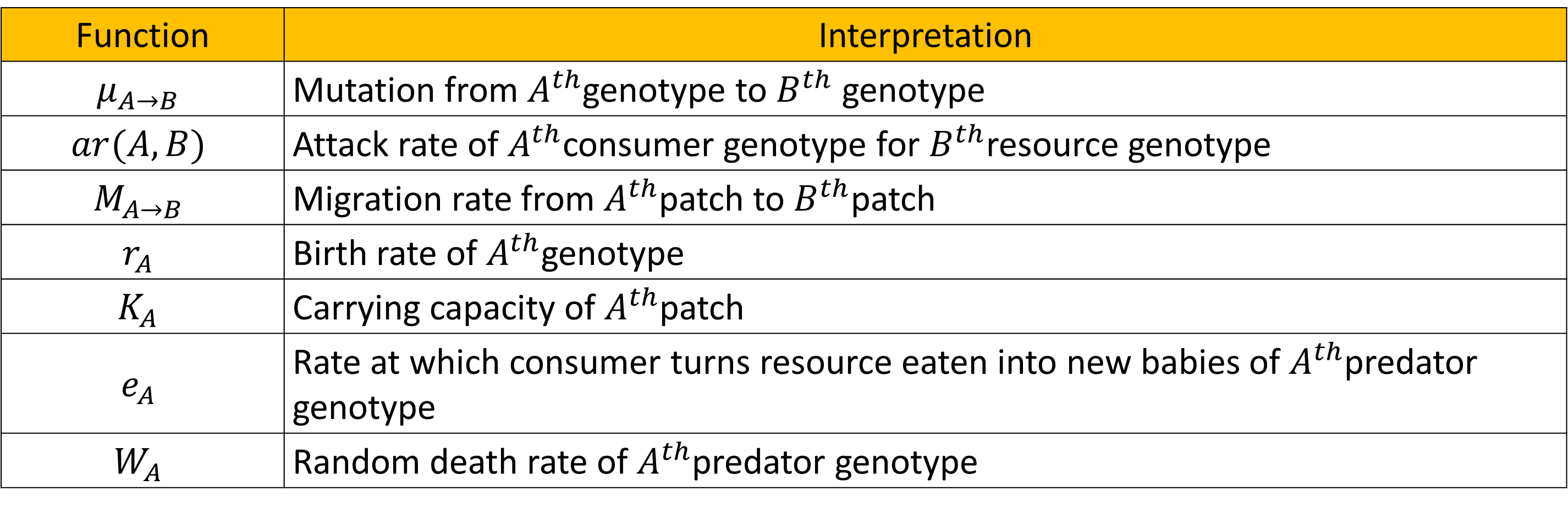
**Equation1**:

Here, the independent variable is *t* or time, the dependent variable is *R* or the resource population, and *i* indicates the prey genotype (i.e. prey genotype) and *k* indicates the patch type (i.e. patch). Another core equation is the change in the consumer population:

**Equation2**:

Here, the independent variable is *t* or time, the dependent variable is *C* or the consumer population, and *i* indicates the predator genotype (i.e. predator genotype) and *k* indicates the patch type (i.e. patch). Refer to the below tables for other parameters and functions used in Eqn. (1) and (2).A black and yellow rectangle with text

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Each Eqn. (1) and (2) largely consists of 3 parts: encounters, migrations, and mutations. “Encounters” part accounts for the number of prey/predators, the effect of predation, the number of new kids born, random death rate of predator, etc. “Migrations” part largely consists of 2 parts: the target prey/predator genotype migrating into the target patch or migrating out of the target patch. “Mutations” part also largely consists of 2 parts: some prey/predator genotypes mutating into the target prey/predator genotype or the target prey/predator genotype mutating into the other non-target genotypes.

**IV. Results**

For simplicity, we will show the impact of time delays on coevolutionary dynamics in consumer-resource metapopulations using the model with 2 prey genotypes, 2 predator genotypes, and 2 patches, which will be explained by comparing 2 different cases of it (i.e. case with time-delay and the other case without time-delay). For comparison, every condition will be set the same for both cases such as initial value for both resource and consumer population is 0.5, the phenotype matching model is used for the attack rate function (i.e. ), etc. Refer to the methods section or our codes for more details.

**A. When time delay is very small ()**

A collage of graphs

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**B. When time delay is very large ()**

A collage of graphs

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Again, this model involves 2 prey genotypes, 2 predator genotypes, and 2 patches and therefore produces total population (i.e. ) where represents the resource population of the 1st prey genotype in the 1st patch type and other populations can be interpreted in the same manner.

We can see the existence of coevolution in our spatial prey-predator coevolution model from these graphs since there is a change in allele frequencies or fitness. In other words, there is a change in the population of a specific genotype in a specific species. For example, in the graph of in terms of time, we can clearly see that is changing over time within its species and therefore we say is evolving.

Compare the resource graphs in case A and B. They have the same shape – resource population increases between the time interval from 0 seconds to 20 seconds and afterwards it increases/decreases by a very small amount that it looks like a constant graph. This is exactly what we expected to see since Eqn. (1) doesn’t involve time delays and therefore the resource graph shouldn’t change depending on time delays. On the contrary, compare the consumer graphs in case A and B. We can clearly see the difference between their shapes – the graphs in case A change more dynamically than the graphs in case B which almost look like constant graphs. This is because a very small time-delay in case A leads to a very fast reflection of the change in consumer population onto graph, whereas a very large time-delay in case B leads to a very slow reflection of the change in consumer population onto graph. This is exactly what we expected to see since Eqn. (2) involves time delays and therefore the consumer graph should change depending on time delays. The results from our basic model, thus, prove that time delays drive coevolutionary dynamics in consumer-resource metapopulations.

**V. Discussion**

This project can be further researched by overcoming some limitations that we encountered. For example, a combination of parameter values that doesn’t let the resource and consumer population become negative needs to be found. Depending on parameter values, the resource or consumer population gets integrated into negative numbers in some time interval, which shouldn’t happen since the population value must always be positive or 0. Therefore, there’s a need to find a combination of parameter values that prevents a such case from happening and to produce more accurate results. Moreover, the minimum time delay value that we could use while not interrupting the integration was 0.4. Thus, a combination of parameter values that lets us set the time delay value closer to 0 is also encouraged to be found.

In conclusion, we demonstrated the need to incorporate time-delays into spatial prey-predator coevolution models using numerical modeling. Although motivated by host-pathogen metacommunities, through non-dimentionalization we suggest that the main conclusions are broadly applicable to different consumer-resource interactions such as predator-prey systems and thus broadly applicable to consumer-resource coevolution.

**References**

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