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Original article

Successional colonization of temporary streams: An experimental approach using aquatic insects

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ABSTRACT

The metacommunity concept studies the processes that structure communities on local and regional scales. This concept is useful to assess spatial variability. However, temporal patterns (e.g., ecological succession and colonization) are neglected in metacommunity studies, since such patterns require temporally extensive, and hard to execute studies. We used experimental habitats in temporary streams located within the Brazilian Cerrado to evaluate the importance of succession for the aquatic insect metacommunity. Five artificial habitats consisting of wrapped crushed rock were set transversally to the water flow in five streams. The habitats were sampled weekly to assess community composition, and replaced after sampling to identify new potential colonizers. We analyzed the accumulation of new colonizers after each week using a logistic model. We selected pairs of experimental habitats and estimated the Bray-Curtis dissimilarity index to assess the community composition trajectory during the experiment. We used the dissimilarity values in ANOVA tests, identifying the importance of time and space for the community. The number of new taxa stabilized in the third week, and we estimated a weekly increase of 1.61 new taxa in the community after stabilization. The overall pattern was a small change on community composition, but one stream had a higher weekly turnover. Our results showed a relevant influence of time in the initial communities of aquatic insects of temporary streams. However, we must observe the temporal pattern in a spatial context, once different streams have different successional history regarding number of taxa and community turnover. We highlight the importance of aerial dispersal and movement to seek oviposition sites as an important factor in determining colonization patterns.

1. Introduction

The study of colonization processes and patterns has been gaining prominence within the field of community ecology in recent decades (Vellend, 2010). Historically, colonization has been reported as the main determinant of community succession, with species showing a tradeoff between traits that favor dispersal and persistence (Herben and Goldberg, 2014; Ricklefs, 1987). Species with high dispersal ability can colonize recently created or remote habitats, causing species occupancy to become a dynamic process in biological communities (Hanski and Ovaskainen, 2000). Dispersal is important for community structure in ephemeral habitats, as it determines the initial species to settle. The ability of the species to migrate and colonize new sites is key for community organization in ephemeral habitats because the species in their communities hardly reach stability in their population dynamics (Altermatt and Ebert, 2010; Travis and Dytham, 1999).

Dispersal also leads to joint population dynamics and functionally connected communities across different sites. The relationship between communities linked by dispersal have been studied based on the metacommunity framework (Heino et al., 2015; Leibold et al., 2004). The main goal of the metacommunity theory is to explain the relative importance of dispersal and the

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interaction between the organisms and the environment in creating and maintaining communities (Winegardner et al., 2012). Dispersal among communities tends to increase the number of species (or higher taxa) and interactions (e.g., competition, predation and habitat selection), and to reduce local diversity (Caley and Schluter, 1997; He et al., 2005). When ephemeral habitats are considered in the context of the metacommunity theory, the balance between a fast colonization and competition for limited space would drive local diversity. Therefore, ecological succession in ephemeral habitats would be highly dependent on dispersal among communities, in contrast with a more stable environment, where successional patterns are largely related with local biological interactions (Murrell et al., 2014).

Despite the metacommunity concept has advanced our understanding of how spatial dynamics and local interactions structure communities, such advances are recent and more empirical evidence is required (Logue et al., 2011; Winegardner et al., 2012). Temporary streams can be used as controlled sites to assess successional patterns arising from early colonization. The aquatic insects inhabiting temporary streams are a good metacommunity model to use in successional studies, provided that transient habitat availability selects for the occurrence of species with faster dispersal across the spatial range of the metacommunity and those that develop within the timeframe when water is available. These unique attributes (ephemeral habitat availability and dispersal dependence) make temporary streams and the associated aquatic insect communities good tools to test the metacommunity concept, particularly as regards to successional patterns and processes.

The succession of insects in freshwater assemblages is affected by the age of the habitat and by other extrinsic factors such colonization and season (Ruhí et al., 2012). However, the relative contribution of extrinsic effects versus age-dependence effects on species variation is unclear, with few studies about this theme. If age-dependence is the most important factor, the metacommunity will show a largest species turnover along the temporal continuum. On the other hand, if extrinsic factors are more relevant, the highest species turnover will be observed between sites and the decay of community similarity in a spatial gradient. Thus we elaborated five hypotheses regarding the aquatic insect community dynamics in temporary streams: (1) the number of new taxa accumulated in the local community will decrease over time after colonization begins; (2) taxa turnover is a result of community aging; (3) the established communities will be different from the communities observed in recently colonized habitats; (4) community turnover will be constant with the passage of time; (5) the spatial component is important for community structure because stream colonization depends on dispersal.

The objective of this study was to test the five hypotheses above. We also evaluated the effect of time on community structure at each stream, and predicted a decrease community similarity over time. We also predicted the occurrence of different successional history for each local community due to differences in their pools of colonizers.

We evaluated our hypotheses in five streams in the Cerrado biome, which dry naturally once a year. We used an innovative study design that applies elements of the state-space concept. A state-space design depicts if the dynamics of a variable of interest (in our study the composition of the aquatic insect community) are related to their previous state (Pedersen et al., 2011). Other elements may be added to the design to discern other important factors, such as environment and space. We designed a study in which we were able to isolate each phase of community development in temporary streams, during a period in which the aquatic insect communities were expected to stabilize (Landeiro et al., 2010).

2. Material and methods

2.1. Study area and experiment design

The five temporary streams are located near Niquelandia, GO, Brazil (14°10′24″S, 48°21′47″W). The area has a semi-humid tropical climate, with rainy season from October to April, and a dry season from May to September. Small streams in this region dry during the dry season, and flood once again in the mid rainy season. Despite these small streams flood intermittently, there are two large, permanent rivers in the region, Maranhão and Das Almas that provide a pool of stream colonizers. The nearest permanent river to the studied streams is the Das Almas River (1.4–4 km from the experimental sites). Annual water temperatures are on average 24 °C (daily values ranged 23–27 °C; INMET, 2015) with pH ranging from 7.2 to 8.9. The closed tree canopy in the riparian zone prevents much of the sunlight from reaching the ground and water surface.

A total of five artificial habitats were placed transversal to the water flow and at least one meter from each other in each stream (25 experimental units) in the early rainy season of 2008. The artificial habitat consisted of nylon net bags filled with one kilogram of crushed rock (5 mm mesh size). We have chosen this kind of experimental unit because submerged rock is a representative habitat in Cerrado streams (Bispo and Oliveira, 2007). The sampling begun one week after the deployment of the artificial substrates. We collected one experimental unit per stream per week. The experiment lasted five weeks (35 days). At the time of collection, experimental units were stored in a plastic bottle with alcohol to prevent the loss of specimens.

The experimental units collected each week were replaced by new experimental units deployed at the same location. These new experimental units remained in the stream for only one week and were removed in the next sampling date (Fig. 1a). This procedure was carried out to detect variation in potential colonizers at different times as it allows a new colonizer to occupy the habitat without a pre-established community, relaxing the influence of biological interactions. Therefore, we used 45 experimental units in the study, 25 placed at the beginning of the experiment and 20 deployed to replace the sampling units collected each week. We counted and identified specimens of the orders Ephemeroptera and Diptera to the family level, because many of these specimens are fragile and became damaged after collection. Specimens in the orders Plecoptera, Trichoptera, Odonata, Heteroptera, Megaloptera and Coleoptera were identified to the genus level.

2.2. Statistical analyses

We tested the five hypotheses using two different procedures, because the hypotheses were related to different community parameters. For the first hypothesis we adjusted a logistic function for taxon accumulation in each week. This model had the advantage of identifying informative parameters in the succession event, such as the initial and established number of taxa in the community. The model is described by the following equation:

$$S_W = E\Big/\Big[1 + (E - I)/I \times e^{-a \times w}\Big],$$

where S_W is the number of taxa in week w, E is the number of taxa established in the end of succession, I is the number of taxa in the beginning of the experiment and a is the rate of changes in number of taxa through time. After estimating the parameter, we used the F ratio to validate the model. We also compared the number of taxa in each week and stream by means of a two-way ANOVA. In these analyses we considered only the experimental units placed at the