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Intrinsic and extrinsic drivers of succession: Effects of habitat age and season on an aquatic insect community

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Abstract

1. Classical studies of succession, largely dominated by plant community studies, focus on intrinsic drivers of change in community composition, such as interspecific competition and changes to the abiotic environment. They often do not consider extrinsic drivers of colonization, such as seasonal phenology, that can affect community change.
2. We investigated both intrinsic and extrinsic drivers of succession for dipteran communities that occupy ephemeral pools, such as those in artificial containers. By initiating communities at different times in the season and following them over time, we compared the relative importance of intrinsic (i.e., habitat age) vs. extrinsic (i.e., seasonal phenology) drivers of succession.
3. We placed water-filled artificial containers in a deciduous forest with 20 containers initiated in each of three months. Containers were sampled weekly to assess community composition. Repeated-measures mixed-effects analysis of community correspondence analysis (CA) scores enabled us to partition intrinsic and extrinsic effects on succession. Covariates of temperature and precipitation were also tested.
4. Community trajectories (as defined by CA) differed significantly with habitat age and season, indicating that both intrinsic and extrinsic effects influence succession patterns. Comparisons of AICcs showed that habitat age was more important than season for species composition. Temperature and precipitation did not explain composition changes beyond those explained by habitat age and season.
5. Quantification of relative strengths of intrinsic and extrinsic effects on succession in dipteran and other ephemeral communities enables us to disentangle processes that must be understood for predicting changes in community composition.

Keywords

Animal succession; aquatic insects; community composition; Diptera; mosquito; seasonality

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Introduction

The phenomenon of ecological succession has been a central theme of ecology beginning with early work on terrestrial plant systems (Cowles 1899). Because the concept of succession originates from the study of plant communities, it is unsurprising that early definitions of succession were botanocentric (Cowles 1901, Gleason 1917, Cooper 1926, Connell & Slatyer 1977). Succession was originally defined as a long-term process, driven by factors intrinsic to the community such as species interactions and plant-mediated changes in soil (Walker & Moral 2003). Extrinsic factors such as seasonal effects on colonist pools were excluded from the classical definitions of succession, because by definition a community domain had to be >1 year (Pickett et al. 2011).

Conflicts arise when the definition of succession is broadened to incorporate other systems (Pickett et al. 2011), particularly more ephemeral systems such as those that host insect communities. The role of seasonal effects on succession in transient systems varies widely. For example, in the Plankton Ecology Group (PEG) model of the plankton dynamics in lakes, seasonal effects such as change in light levels and temperature play a key role in species turnover (Sommer 1989, Sommer et al. 1986, Weithoff 2003). On the other hand, succession of microorganisms and insects in inquiline pitcher plant communities appears to be independent of seasonal effects (Miller & terHorst 2012), as does the ontogenetic succession of ant species in the domatia of *Tachigali* trees (Fonseca & Benson 2003). Succession of insects on decomposing animal carcasses is affected by both chronological age of the community and by season (Matuszewski et al. 2010), as are freshwater insect assemblages in temperate ponds (Ruhí et al 2012). Therefore, for insect communities it may be more reasonable to consider the contributions of extrinsic seasonal effects versus intrinsic age-dependent effects on species turnover along a single continuum, with habitat age at one end of this continuum and seasonal effects at the other end. The question then arises: How can we separate and analyse effectively the relative contributions of extrinsic and intrinsic drivers of succession within the same community?

This question is ecologically important, and can be answered, for aquatic metazoan communities that inhabit natural phytotelmata (e.g., bamboo, tree holes, bromeliads, etc.) and have secondarily colonized artificial containers (e.g., tyres, cemetery vases, buckets, etc.) (reviewed by Vezzani 2007). These communities, which are dominated by detritivorous larval Diptera (reviewed by Vezzani 2007), are good systems for testing of mechanisms of species turnover because they are (1) simple, with the majority of metazoan species being detritivores, plus a few predaceous species (Kitching 2000, Srivastava et al. 2004); (2) small, discrete aquatic habitats; (3) highly replicable; and (4) composed of species with short larval lives (Kitching 2000, Srivastava et al. 2004), which consequently causes rapid community turnover that can be directly observed and manipulated. Artificial container systems have an additional advantage: they can be established at the discretion of the researcher, at any time, enabling us to separate experimentally the effects of intrinsic drivers (community age) from extrinsic drivers (time of year, or season).

Niche partitioning is a likely mechanism for succession in container communities, as both spatial and temporal niche partitioning have been documented among aquatic Diptera

(Gilbert et al. 2008). Container-dwelling fly species co-occur across seasons, but vary their oviposition responses based on the nutrient, chemical, and insect community content of containers (Wilmot et al. 1987, Walker et al. 1991, Allan & Kline 1995, Blaustein et al. 2004, Ponnusamy et al. 2010). Additionally, larval success of several species has been shown to depend on different nutrient and resource conditions (Reiskind et al. 2004, Juliano 2009), and differential response to predation pressure (Farajollahi et al. 2009, Bradshaw & Holzapfel 1983). Species-specific oviposition choice or developmental success under these different conditions in containers may drive species turnover if these intrinsic conditions change as a function of container age. We consider these effects analogous to the autogenic effects described in classical succession, and we will call them collectively habitat age effects (Age).

On the other hand, succession in container communities could also be driven by seasonal effects. Unlike most plant systems, the dispersal stage of aquatic insects is the adult, and species vary widely in their phenology (Danks 1987). Species composition of aquatic container communities may exhibit seasonal changes due to phenology, rather than due to interspecific interactions, container age, or any other factor intrinsic to the aquatic community. Because the relative abundances of the adult insects vary over the course of a year (Jackson & Paulson 2006), changes in larval communities may merely reflect these changes in adult abundances. Further, larvae in these systems may die or senesce when their habitat disappears due to freezing or drying, creating the potential for a strong phenological component to observed species turnover. We will collectively call these kinds of extrinsic effects seasonal effects (Season).

Thus, there are three hypotheses for species turnover in these systems: turnover could result from (1) Age only, (2) Season only, or (3) a combination of Age and Season. Fortunately, the simple and replicable nature of these systems provides a straightforward method for experimental testing the Age and Season hypotheses for turnover of community composition. If two sets of containers are established at different times of year and their community composition is recorded, it is possible to compare the two sets of containers within the same Season when the container communities are of different Ages, and also when communities are of the same Age but occur in different Seasons. Although Age and Season are not mutually exclusive, in the sense that both kinds of effects could contribute to the turnover of species, their relative contributions to species turnover can be experimentally separated.

Our goal in this study was to test these three hypotheses for species turnover in container communities (Age, Season, both). If the third hypothesis is supported, another goal was to estimate the relative contributions of Age and Season to community turnover. For Age, we predict that species composition will be strongly associated with container age, regardless of season. For Season, we predict that community composition will differ significantly at different seasons, regardless of container age.

Methods

Characteristics of the model system

We performed our experiment in an oak-hickory forest at Tyson Research Center, near Eureka, MO, USA (38° 31' N, 90° 33' W). At this latitude there are a number of Diptera species that naturally colonize tree holes and other containers. The most common genera present in our containers were *Aedes*, *Anopheles*, *Culex*, *Orthopodomyia*, and *Toxorhynchites* (all Culicidae), *Culicoides* (Ceratopogonidae), *Chironomus* (Chironomidae), and *Megaselia* (Phoridae) (see **Results**). The female adults of these Diptera oviposit inside containers, either on the sides just above the waterline (*Aedes*, *Orthopodomyia*, Merritt & Cummins 1984) or directly on the water surface (all other species, Merritt & Cummins 1984). Larvae of most of these species are detritivores (Hanson & Disney 2008, Paradise et al. 2008) with the exceptions of *Toxorhynchites rutilus* which is a generalist predator (Paradise et al. 2008), and *Anopheles barberi* which is capable of intraguild predation (Nannini & Juliano 1998). Aquatic larvae inhabit the container from 4 days to 4 weeks, depending upon the species and food availability (Gerberg et al. 1994, Hanson & Disney 2008), and then leave either upon pupation (*Megaselia*, Hanson & Disney 2008) or adult eclosion (all other species, Paradise et al. 2008).

The climate at the experimental site is temperate, with container communities becoming active during the spring and senescing during the fall (personal observation), and freezing in winter. The species in this system diapause as eggs (*Aedes*), larvae (*Anopheles*, *Orthopodomyia*, *Toxorhynchites*), or adults (*Culex*) (Danks 1987). Communities are often ephemeral and can be subject to disturbance, particularly if the container dries (Paradise et al. 2008). While dynamics following a drying disturbance could provide interesting insights into secondary succession in container communities, we chose to focus only on primary succession in new containers for this study. Therefore, we studied only containers between May and August that were sufficiently large to prevent drying, yielding homogeneous aquatic habitat across treatments.

Establishment and Sampling of Communities

During the summer of 2011, we established a total of 60 black plastic 19-L buckets arranged in two rows, spaced 20 m apart, along a 580 m stretch of road. We have found in previous field assessments (Murrell & Juliano 2013, personal observation) that containers of this size and colour attract most tree-hole species while deterring colonization by freshwater pond species. The buckets were established in groups of 20 on three different dates: May 20 (“Early”), June 17 (“Middle”), and July 15 (“Late”), as Diptera colonization of containers at Tyson is highest between May-September (personal observation). Individual replicates from these groups (collectively “starting dates”) were interspersed in space to homogenize effects of container location on colonization.

Each container was initially filled with 15 L water, 30 g dried senescent white oak (*Quercus alba*) leaves, and 100 mL of 50 g/L hay infusion as an inoculum. Addition of a small amount of detrital infusion is a method commonly employed in mosquito studies to initiate and to standardize microbial growth (Alto et al. 2005, Costanzo et al. 2005, Daugherty et al. 2000).

Beginning one week after containers were established, each container was sampled weekly until the end of the study on August 19. To sample for the predaceous mosquito *T. rutilus*, which has lower abundance than prey species, we quickly swept a 20.3 cm diameter, 106 µm mesh sieve through the container twice, then poured the contents of the sieve into a white pan and counted the number of *T. rutilus* larvae and pupae. We then returned *T. rutilus* to the container. To sample all other species, we placed a flat circular magnet (90-lb pull) into the container, allowed 3 minutes for the disturbed community to resettle, then quickly plunged a 6.4cm-diameter steel tube into the container and onto the magnet. The magnet then adhered tightly to the end of the tube, sealing it and enabling us to withdraw a water column sample containing both pelagic and benthic species. We recorded the volume of this sample, collected larvae, and later identified to either genus (*Chironomus* sp., *Culicoides* sp.) or species (all others) in the laboratory. These sampled larvae were not returned to the container.

Statistical Analyses

To determine whether arrival times differed among species, we conducted a survival analysis (PROC LIFEREG, SAS 9.1) on the first arrival to each container for 11 of 13 taxa (**Table 1**). The PROC LIFEREG procedure calculates and compares median arrival times of species across all containers (SAS Institute 1990). We then conducted separate survival analyses for every pairwise combination of these 11 taxa as follow-up tests. Two taxa, *Culex territans* and *Chironomus* sp., were excluded from the survival analyses because each of these only colonized a single container.

To test for Age vs. Season, we compiled community data for 13 taxa (**Table 1**) in all of the samples into two correspondence analysis axes (CAs; PROC CORRESP, SAS 9.3). CA is closely related to principle components analysis (PCA), although CA uses chi-square distances between points representing different communities rather than Euclidian distances used by PCA (Legendre & Legendre, 1998). Because we were interested in community composition, as opposed to the abundance of species, we analysed the proportion of each species that made up the communities (data columns) within each container on each sampling date (data rows), for which the CA rather than PCA is appropriate. Also, since the PCA results based on species abundances were similar to the CA axes of species proportions (data not shown), we have elected to show only CA results.

We ran a repeated-measures mixed model analyses of the CA axes, with linear or quadratic functions of two different repeated-measures variables assigned to each sample. The first repeated-measures variable quantified Age from container establishment. This enabled us to test whether composition of container communities was significantly related to age in weeks (**Fig. 1A**). The second repeated-measures variable quantified Season based upon sampling week. This enabled us to test whether community composition was significantly related to time of year (**Fig. 1B**). We analysed both CA axes simultaneously to determine whether changes in community composition summarized by each axis responded similarly to Age and Season.

In the repeated-measures mixed model, the fixed effects are given by

$$CA\text{score} = \text{Age} * CA\text{factor} + \text{Age}^2 * CA\text{factor} + \text{Season} * CA\text{factor} + \text{Season}^2 * CA\text{factor}$$

where CAfactor is a categorical variable that distinguishes the two CA axes, and * represents interaction effects and all subordinate interactions and main effects. Because no two groups shared the same combination of Age and Season, the group effect (i.e., establishment date) was confounded with the repeated-measures variables and thus was not included in the model as a fixed effect. To account for repeated measures, we included a random effect for container that assumes first-order autocorrelation between successive samples. Furthermore, we found that residual variances increased with CA scores, and therefore we weighted residual variances by the exponent of the estimated values; this down-weights residuals that are known to have high variances, because these residuals provide relatively less information (Neter et al. 1989).

We compared full and reduced models using multimodel inference (Anderson 2008). We compared the amount of variation explained by Age versus Season by reducing the model, removing either linear and quadratic effects of Age, or linear and quadratic effects of Season. We then compared the AICc values between the full model and each of these reduced models, and interpreted the largest change (AICc) as indicating which removed variable (Age or Season) contributed more to the variation observed in the full model. Analyses of the repeated-measures linear mixed model were performed using lme (library nlme) and ANOVA (library car) in the statistical package R (2012).

To determine whether temperature and precipitation may specifically affect community composition, we downloaded daily temperature and precipitation data as reported by the NOAA station in St. Louis, Missouri USA (NOAA National Climatic Data Center, 2013). From these data we calculated the mean daily temperature and cumulative precipitation for the week preceding each sampling date. We added these temperature and precipitation values as covariates to the model and compared AICc values to determine if either or both of these variables predict community composition beyond the variability explained by the two repeated-measures variables, Season and Age.

Results

Colonization times of species differed significantly from one another (survival analysis, Log-Rank Chi-square = 194.3325, df = 10, $p < 0.001$). Groupings of species closely associated with each CA axis were related to the colonization rank of each species (**Table 1**). Specifically, two of the most common late colonizers had high CA1 scores, while the earliest colonizers had low CA1 scores (**Table 1**). The more common early-mid colonizers were positively associated with CA2, with the earliest-colonizer, *M. imitatrix*, negatively associated with CA2 (**Table 1**).

Within the mixed-model analysis of the CA axes, there were significant effects of Age, Age², and Season, meaning that community composition changed significantly over time as a function of both container age and of season. The interactions of CAfactor with Age² and Season were also significant (**Table 2**). To visualize the analysis of the CAfactors (Figure

2A), we plotted the fitted curves for the CAscores from the mixed-model analysis, along with the centroid for each species averaged over all the samples (Figure 2B). The start and endpoints for all container groups were similar on both CA axes (Fig. 2A). There was a strong, linear negative-positive relationship in the three groups along CA1, showing a clear progression from the earliest colonizers (*M. imitatrix* and *C. restuans*) to late colonizers (*T. rutilus* and *O. signifera*) (Fig. 2A&B). Variation among groups was much greater along CA2, with the early group of containers showing the greatest movement along this axis and the late group very little, although all groups converged to similar endpoints by the end of sampling period (Figure 2A&B).

Relative abundances of species contributing to CA1 (Fig. 3A,C,E) and CA2 (Fig. 3B,D,F) show that these species are generally most abundant in the Early group and least abundant in the Late group, with some species (notably *C. territans*, *A. hendersoni*, and *A. japonicus*) completely absent from the Late group. However, the initial time to first arrival of these species, when present, was consistent across groups. For example, when *C. restuans* was present, it consistently colonized containers before *C. pipiens* or *A. japonicus* (Fig. 3A,C,E), and *A. triseriatus* colonized earlier than *Culicoides* sp. (Fig. 3B,D,F).

AICc for the model with both Season and Age was 1730.11. Inclusion of either temperature or precipitation increased AICc, indicating less likely models (Table 3). AICc increased to 1792.97 when Season effects were removed (AICc=+62.87), and increased even more, to 1868.62, when effects of Age were removed (AICc=+138.51). Thus, although both Season and Age are important, the model with only Age was somewhat more likely, given the data, than the model with only Season.

Discussion

Intrinsic Age Effects

If the relative abundances of species in containers were primarily a function of Season, we should expect to see similar communities among containers of different ages when season of sampling is held constant. Instead, we found that trajectories among all of our treatment groups (i.e., start dates) differed greatly from one another, both in magnitude and direction along the CA axes. Most notably, when the late group of containers was colonized, the middle-colonizing species from early and middle group containers (*A. japonicus*, *A. triseriatus*) were largely absent, and instead these late-season containers quickly progressed from dominance by *M. imitatrix* to dominance by *O. signifera* (Fig. 3E&F). Examination of the entire pattern shows that the presence and relative abundances of early and middle colonizers were reduced as containers were established later in the season. This creates a net effect of the three groups diverging in community patterns during the first 5 weeks after establishment, then converging by the last week of the study (Fig. 2A). However, the order of colonization of the species, if they were present, was consistent for containers of the same chronological age but established several weeks apart (compare Fig. 3). Thus, it is clear that intrinsic container age effects are important contributors to community composition.

Extrinsic Seasonal Effects

Our data show significant differences in community composition over time due to season when community age at sampling is held constant. This manifested primarily as reduced or absent colonization of some of the early- and middle- (CA2) colonizing species in the Middle and Late groups. For example, *C. restuans*, *Culex pipiens* and *A. japonicus* were much less common in the containers established late in the season than in those established early or mid-season (**Fig. 3**).

Although temperature and precipitation varied over the course of the experiment, neither variable contributed in an important way to the mixed model describing the change in species composition. Instead, Season was an important contributor to the model (Electronic supplement 3). This result suggests that the Season component is driven by alternative factors beyond temperature and precipitation *per se*. One possibility is that relative abundances of the adults of different species vary over season. Although we did not measure relative abundances of adults, we know that some species of mosquitoes are more common during different times of the year. For example, *C. restuans* has two peaks of abundance in June and July (Jackson and Paulson 2006), while the peak abundance of *C. pipiens* occurs slightly later (Jackson and Paulson 2006).

Another possibility for the lack of temperature and precipitation effects is that some early- and middle-colonizing species were present as adults during the late season, but avoided ovipositing in the late containers due to incompatibility between the intrinsic biotic/abiotic conditions of the containers and the change in oviposition response of the females due to extrinsic, seasonal factors. For example, *A. triseriatus* alters its oviposition preference during the year, first avoiding ovipositing in containers with high densities of conspecific larvae during early summer, but then preferentially ovipositing in these containers during late summer (Edgerly et al. 1998). Since the late containers were established at a time when *A. triseriatus* larvae were still abundant in the early and middle group containers (**Fig. 3**), it is possible that *A. triseriatus* adults were present but selectively ovipositing in containers where conspecifics were already present.

When considering Age and Season as separate descriptors of successional change, the reduced model with Age removed provided a poorer description of the data than did the alternative model with Season removed. If species turnover in the communities were primarily a function of season, then removal of Season should give the greatest loss of model fit. Thus, our results indicate that Age (intrinsic factors) is more important than Season (extrinsic factors) in explaining successional changes in mosquito communities. Nonetheless, there is a large loss of model fit (increase in AICc) with removal of Season, indicating that both Age and Season are contributing to community changes.

The results obtained in this study are similar to community dynamics in freshwater invertebrate communities, such as in man-made ponds (Lods-Crozet & Castella 2009, Ruhí et al. 2012). While pond systems are generally less ephemeral than container systems, and succession occurs over multiple years (Jeffries 2011, Ruhí et al. 2013), they are nevertheless more ephemeral than many plant communities and have diverse insect assemblages strongly associated with habitat age (Fairchild et al. 2000, Ruhí et al. 2013). The successional

trajectory, despite its occurrence over multiple years, can be affected by seasonal (extrinsic) factors (Ruhí et al. 2012). Dispersal capability seems to play a strong role in succession patterns in these systems (Van De Meutter et al 2007, Ruhí et al. 2013) and could similarly play a role in container communities, as Diptera species vary in size, development time, and fecundity (Teng and Apperson 2000). However, the greater taxonomic variety in freshwater ponds likely produces greater disparities in physical dispersal capabilities among species than in container systems, which in our study were exclusively colonized by Diptera. We hypothesize that our observed differences in colonization rank among Diptera are likely due to behavioural differences (e.g., mobility, flight performance) and seasonal abundances of adults, although this has yet to be explicitly tested.

In any temperate system insects must have adaptations to deal with seasonal habitat deterioration due to changes in temperature (winter senescence) or other climatic variables (e.g., drought). Container-dwelling Diptera in temperate North America must deal with both change in season and drying of containers, and as such have a number of physical and behavioural adaptations to survive these climatic effects (Sota & Mogi 1992, Edgerly et al. 1998, Robich & Denlinger 2005). Similarly, season has been shown to affect insect succession on carcasses in temperate climates (Matuszewski et al. 2010) and in temperate ponds (Ruhí et al. 2012), but does not strongly affect insect systems in warmer climates (Ruhí et al. 2012, Fonseca & Benson 2003). One might speculate that season may have an even greater effect in regions with more extreme climates than the temperate region used in our study. The statistical approach we have designed in this study could be used to more quantitatively assess differences in seasonal effects within similar insect systems across a latitudinal gradient.

Although the simultaneous presence of both habitat age and season have been documented in other communities (e.g., Walker & del Moral 2003), and previous studies have qualitatively assessed intrinsic and extrinsic effects on succession (Kent et al. 2007, Antoniadou et al. 2011), ours is the first study to test explicitly and quantitatively the effects of both intrinsic and extrinsic processes on species turnover within a single community type using a single statistical test. Our experimental and statistical approach to this question could be modified to test the contributions of habitat age and season in other systems, including artificial pond communities, carrion communities, and possibly sessile marine communities, as long as similar habitats can be created at different times of year. Perhaps more importantly, our experiment demonstrates that it is possible to investigate seasonal succession as an alternative hypothesis for animal species turnover, along with age-dependent, intrinsic effects that are the basis of traditional hypotheses for succession. This approach results in a more integrated understanding of the extrinsic and intrinsic processes affecting species turnover in ephemeral communities.

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Figure 1.

Diagram of the two separate repeated-measures time effects tested in the nonlinear model. In both figures, the circles represent all the replicates of a given starting date. (A) In the repeated-measures variable Age, all samples were designated by the number of weeks since the containers were established. (B) For the repeated-measures variable Season, all samples were designated according to chronological time (sampling date).

Figure 2.

(A) Mean CAscores with standard error bars, signifying colonization of Early, Middle, and Late container groups at every sampling date. Black symbols on each line indicate the first sampling date for each group; white symbols represent the last sampling date. (B) Community trajectories of CAscores for each container group over time as fit by the mixed model analysis; the lines give the fitted model. For each line, the arrow indicates the direction from early to late succession. Grey points represent the centroid for each species averaged over all the samples on the two CA axes; the size of each point is positively correlated with the colonization rank of that species (small=early colonizer, large=late colonizer).

Figure 3.

Mean proportional abundances of species over time of the major species contributing to each CA, for Early (A&B), Middle (C&D) and Late container groups (E&F). Middle and Late graphs are vertically aligned to correspond with the chronological time at which they were established in relation to the Early group (x-axes of Figures A&B). Error bars have been excluded in order to improve clarity.

Table 1

Median colonization times of species across all containers, compared with CA1 and CA2 from the correspondence analysis (Fig. 2). Letters indicate species whose colonization ranks do not significantly differ according to pairwise Wilcoxon tests from the survival analyses with a Bonferroni correction. Species strongly associated with each CA axis (partial contribution > 0.07, as determined by PROC CORRESP in SAS 9.1) are shaded in grey.

Species		Median Colonization Time (Weeks)	SE	CA 1	CA 2
<i>Megaselia imitatrix</i>	a	1.9130	0.1669	-1.2400	-1.4460
<i>Culex restuans</i>	a,b	2.9333	0.3142	-1.2577	0.9544
<i>Culex pipiens</i>	b,c	3.5157	0.2379	-0.7957	1.1192
<i>Culex territans</i> *		–	–	-1.0372	0.9162
<i>Aedes japonicus</i>	b,c	3.5429	0.2571	-0.3739	0.7757
<i>Aedes triseriatus</i>	c	4.7073	0.3390	0.2839	0.7799
<i>Anopheles barberi</i>	b,c,d	5.5000	1.1377	0.0960	-0.2833
<i>Aedes hendersoni</i>	b,c,d	5.6667	0.4944	0.1627	1.8513
<i>Orthopodomyia signifera</i>	d	6.1628	0.4261	0.8619	-0.6480
<i>Toxorhynchites rutilus</i>	d	6.2564	0.4216	1.1742	-0.3719
<i>Culicoides sp.</i>	d	6.4074	0.5237	0.5176	0.2551
<i>Aedes albopictus</i>	d	7.5455	0.9181	1.4715	-0.3848
<i>Chironomus sp.</i> *		–	–	1.1951	-1.1070

* Species was not included in survival analysis due to limited colonization (1 container)

Table 2

Repeated-measures linear mixed model testing for changes in community composition, measured by the CA scores along two CA axes, with Age (time since container deployment) and Season (time of year). The estimated autocorrelation coefficient between consecutive samples of the same container was 0.24, and to account for heteroscedasticity, the residual variances were weighted by $\exp(c \cdot \text{CA scores})$ where c was estimated in the fitting procedure as 0.67. Results are presented for type III sums of squares. Significant effects are in bold print.

Model Parameter	Df	χ^2	p
CAfactor	1	62.4418	<0.0001
Age	1	68.7061	<0.0001
Age ²	1	41.0203	<0.0001
Age $\times$ CAfactor	1	2.4803	0.1842
Age ² $\times$ CAfactor	1	3.8652	0.0493
Season	1	50.5383	<0.0001
Season $\times$ CAfactor	1	123.5169	<0.0001

Table 3

AIC values for the CA mixed models. For time components, Age² indicates the presence of both Age and Age² in the model, while Season indicates the presence of only Season (not Season²) in the model.

Model	AIC	AIC	exp(-dAIC/2)	wiAIC
Age ² + Season	1730.106	0	0.6065	0.9964
Age ² + Season + Temperature	1742.912	12.806	0.0017	0.0027
Age ² + Season + Precipitation	1745.339	15.233	0.0005	0.0008
Age ² + Season + Temperature + Precipitation	1752.603	22.497	<0.0001	<0.0001
Age ²	1792.971	62.865	<0.0001	<0.0001
Age ² + Temperature	1804.317	74.211	<0.0001	<0.0001
Age ² + Precipitation	1811.007	80.901	<0.0001	<0.0001
Age ² + Temperature + Precipitation	1821.271	91.165	<0.0001	<0.0001
Season	1868.617	138.511	<0.0001	<0.0001
Season + Precipitation	1881.189	151.083	<0.0001	<0.0001
Season + Temperature	1885.180	155.074	<0.0001	<0.0001
Season + Temperature + Precipitation	1895.706	165.600	<0.0001	<0.0001
Temperature	2033.426	303.320	<0.0001	<0.0001
Precipitation	2034.759	304.653	<0.0001	<0.0001
Temperature + Precipitation	2049.718	319.612	<0.0001	<0.0001