# Priority effects and species sorting in a long paleoecological record of repeated community assembly through time

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*Abstract.* We studied the relative roles of environmental species sorting and priority effects in the assembly of ecological communities on long time scales, by analyzing community turnover of water fleas (*Daphnia*) in response to strong and recurrent environmental change in a fluctuating tropical lake. During the past 1800 years, Lake Naivasha (Kenya) repeatedly fluctuated between a small saline pond habitat during lowstands and a large freshwater lake habitat during highstands. Starting from a paleoecological reconstruction, we estimated the role of priority effects in *Daphnia* community assembly across 16 of these habitat turnovers and compared this with the response of the community to reconstructed changes in three environmental variables important for species sorting.

Our results indicate that the best predictor of *Daphnia* community composition during highstands was the community composition just prior to the transition from lowstands to highstands. This reflects a long-lasting priority effect of late lowstand communities on highstand communities, arising when remnant lowstand populations fill newly available ecological space in the rapidly expanding lake habitat. Species sorting and priority effects had a comparable but relatively small influence on community composition during the lowstands. Moreover, these priority effects decayed rapidly with time as *Daphnia* communities responded to environmental change, in contrast with the highstand communities where priority effects lasted for several decades.

*Key words: community assembly;* Daphnia *spp.; Lake Naivasha, Kenya; mass effect; metacommunity; niche; paleoecology; priority effect; propagule pressure; restoration ecology; storage effect.*

## Introduction

A fundamental goal of community ecology is to understand the processes that influence species distributions, how they operate, and how deterministic they are. Many different mechanisms have been proposed, with a special focus during the last decade on the relative roles of local and regional processes (Leibold et al. 2004). The species-sorting paradigm of metacommunity ecology, in particular, focuses on the local interaction between differences in patch quality (environmental heterogeneity) and dispersal into the patch. When dispersal is not limiting, environmental sorting of species according to their respective ecological traits is expected to be maximal; as a result, there is a perfect match between the occurrence of a species and the environment. As a consequence, species sorting with nonlimiting dispersal rates is generally viewed as a highly deterministic process (Cottenie and De Meester 2004). The general importance of species sorting is illustrated by a meta-analysis

of 158 studies (Cottenie 2005), which showed that the majority of the analyzed ecological communities were affected primarily by species sorting. Deviations from expectations under species sorting are variously attributed to dispersal limitation, excessive dispersal (mass effects), colonization–extinction dynamics, or neutral processes (Leibold et al. 2004, Cottenie 2005). However, one other deterministic process that may interact with community assembly is the priority effect. Priority effects occur when a species attains higher relative abundances in a local community because it arrived first (Lockwood et al. 1997). Local residents exert a priority effect because they preempt niche space at the expense of later immigrants, even those that may be intrinsically better competitors (Begon et al. 2006, Louette and De Meester 2007).

Demonstration of priority effects has often focused on spatial occupancy at the individual level in sessile or territorial organisms, such as trees or coral reef fishes (Shulman et al. 1983, Hubbell and Foster 1986). However, priority effects can also be considered at the community level in a defined locality (sensu Leibold et al. 2004). Individuals that colonize empty habitat space and reproduce locally, fill with their progeny the
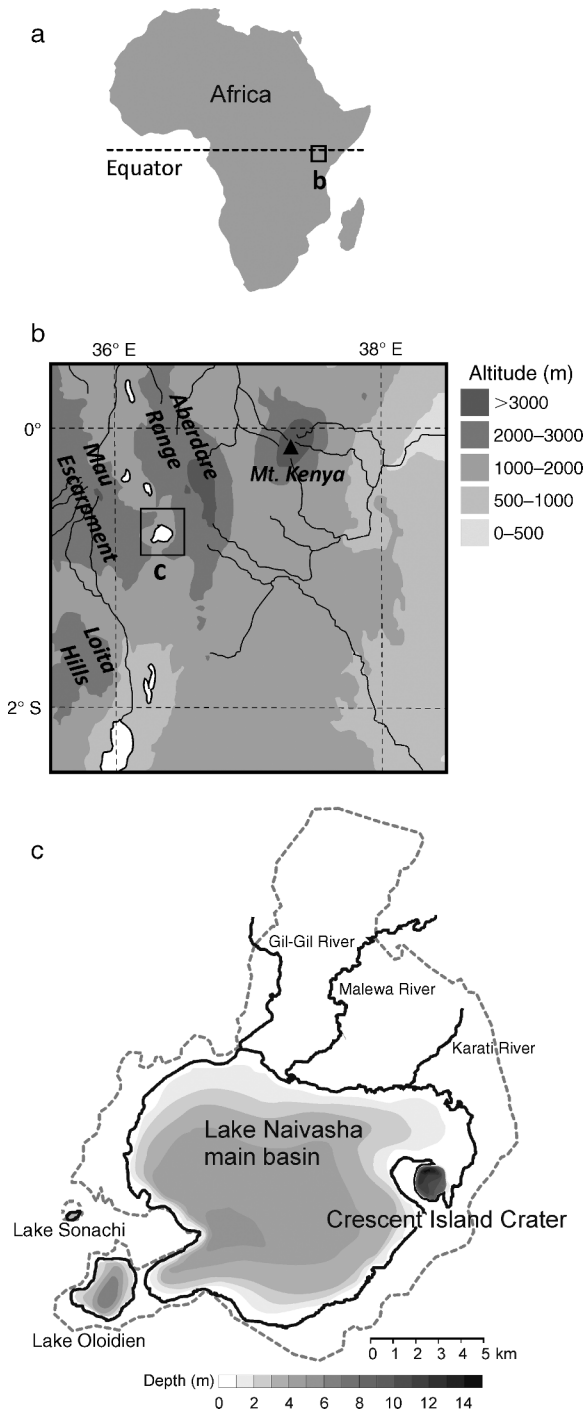
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FIG. 1. The location of Lake Naivasha in Africa and the Eastern Rift Valley, showing its catchment and bathymetry. (a) Map of Africa showing the inset (labeled b). (b) Expanded inset, with altitudinal map of the Eastern Rift Valley showing the locations of the Rift Valley lakes (in white) and the main rivers (in black). Lake Naivasha, draining the Aberdare range, is enclosed within a box (labeled c). (c) Detailed bathymetric map of Lake Naivasha and its satellite basins Sonachi, Oloidien, and Crescent Island Crater. The dashed line shows the water level during the 18th century highstand mega-lake conditions (a large, deep freshwater lake of 250 km²), with a

available ecological niche space. As a result, later colonizers have reduced establishment success, because competition for resources (e.g., space, light and nutrients) increases among the individuals of the growing community. Once the habitat is at carrying capacity or has a stable population size, new arrivers are considered immigrants instead of founders.

The magnitude of a priority effect is expected to depend on (1) the number of founders, (2) the order, timing, and frequency of colonization attempts (creating propagule pressure) relative to the growth rate of the local population, (3) the difference in niche occupancy between and among founders and later immigrants, and (4) the occurrence of local genetic adaptation (Belyea and Lancaster 1999, De Meester et al. 2002, Louette and De Meester 2007, Urban and De Meester 2009). In itself, propagule pressure is strongly influenced by the relative density of each species across a region. In organisms with long-lived dormant propagule banks (seeds, resting eggs, statoblasts, and so forth), however, propagule pressure may also arise from within the system by the emergence of local dormant propagules produced during previous periods, representing dispersal and colonization in time. Due to the massive number of propagules involved (in zooplankton, annual production can easily reach $10^3$–$10^4$ propagules/m² [Cáceres 1998]), dormant propagule banks can be more important sources of immigrants than regional communities (Mergeay et al. 2007).

Although studies on priority effects have a long history in ecology, both theoretical (e.g., Connell and Slatyer 1977, Law and Morton 1993, Gerla et al. 2009, Urban and De Meester 2009) and empirical (e.g., Shulman et al. 1983, Robinson and Dickerson 1987, Louette and De Meester 2007), few empirical studies have involved time series exceeding a few years. Consequently, very little is known on the long-term impact of priority effects. Sometimes, priority effects are little more than transient lags in the species sorting within communities that occur in response to relatively rapid environmental change. In addition, little is known on the interaction between priority effects and other deterministic processes such as species sorting (Kitching 1987, Louette and De Meester 2007).

Paleoecology offers unique opportunities to study these interactions empirically, by providing long, linked time series of both the target communities and various components of their living environment. In this study, we exploit the detailed paleoecological record of Lake Naivasha, a climate-sensitive tropical lake in Kenya (Fig. 1a, b), to study the degree to which priority effects contributed to the assembly and persistence of Daphnia (water flea) communities across repeated ecological crises associated with natural, climate-driven lake-level

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maximum lake depth of ~40 m. During lowstands (when the lake was reduced to a shallow, most often saline remnant pond) water was limited to Crescent Island Crater (~1 km²).

fluctuations. Over the past 1800 years, Lake Naivasha fluctuated eight times between lowstands when the lake was reduced to a shallow, most often saline remnant pond inside a ~1 km$^2$ crater basin, and highstand "mega-lake" phases when it was a large and deep freshwater lake of 150–250 km$^2$ (Fig. 1c and Verschuren 2001). Transition periods with intermediate ecological conditions were relatively short lived, typically lasting less than a decade (Verschuren et al. 2004). As a result of these drastic and recurrent events of habitat turnover between lowstands and highstands, the process of community assembly following each ecological crisis can be reconstructed from the paleoecological archive. This replication in time, when combined with detailed reconstructions of the paleoenvironment, allows us to test specific hypotheses with regard to the relative role of species sorting and priority effects on decadal to centennial time scales.

Priority effects typically stem from differences among species or genotypes in the rate at which unoccupied niche space is colonized (Begon et al. 2006). In our study system, priority effects are expected to be strongest at the onset of a highstand, when resident populations that persisted in the small crater basin until the end of the lowstand colonized the rapidly expanding lake habitat and monopolized resources at the expense of later immigrants. In that case, highstand communities should be strongly influenced by the species composition of the lowstand community that existed just before the large new lake habitat became available for colonization. Conversely, lowstand communities are expected to be less influenced by priority effects, and relatively more by species sorting, when the habitat available to them was contracting. We specifically tested for such priority effects, and also estimated the role of environmental variation over time in determining community structure (species sorting). To distinguish persistent priority effects from temporal lags in the response of communities, we also tested to what extent priority effects persisted in time.

## METHODS

### Study system

Lake Naivasha (LN) is today a large but shallow freshwater lake (~135 km$^2$, maximum depth 5 m in 2001) situated in Kenya's Central Rift Valley (Fig. 1). Crescent Island Crater (CIC) is a small (1.9 km$^2$) and deep (15 m in 2001) crater basin submerged in the northeast sector of LN (Fig. 1c). CIC is the only part of the lake that never desiccated completely in the past 1800 years, thereby preserving an intact sediment record of the lake's environmental history. In contrast, the main lake basin desiccated completely during lowstands, as indicated by the paleoenvironmental evidence (Verschuren 2001) and oral traditions of Maasai tribesmen reporting on episodes of 19th century drought (Hemsing 1987).

We tracked the process of community assembly and change in the *Daphnia* inhabiting LN throughout its 1800-year history of eight lowstand and eight highstand phases. *Daphnia* species are pelagic filter feeders of phytoplankton and other microorganisms, and occupy a central position in most freshwater food webs (Carpenter and Kitchell 1993). Their dormant egg capsules (ephippia) are well preserved in sediment accumulating on the bottom of lakes, providing a detailed historical archive of community change over time. These dormant eggs can remain viable up to at least 100 years (Cáceres 1998), creating a storage effect that provides an extensive buffer against fluctuations in the quality of their local environment (Chesson 1983, Cáceres 1997). Although *Daphnia* species clearly vary in their ecological preferences, there is marked overlap in the fundamental niche of many species, especially with regard to feeding ecology, tolerance for elevated salinity, and antipredator responses (Brooks 1965, Lampert 1987, Benzie 2005, Colbourne et al. 2006).

### Reconstruction of Daphnia community change through time

In July 2001 two overlapping sediment cores (NC01-1S: 0–152 cm depth; NC01-D: 88–764 cm depth) were retrieved from the deepest point of CIC to construct a continuous 1800-year record of the population history of local *Daphnia* species (Fig. 2a–g), from the stratigraphy of their fossil ephippia. An earlier study on fossil *Daphnia* ephippia in four shorter sediment cores from different locations in CIC showed highly concordant patterns of community change through time over the last ~200 years (Mergeay et al. 2004). Moreover, the resulting reconstruction of 20th-century *Daphnia* population dynamics was highly congruent with patterns of zooplankton abundance in historical surveys (Lowndes 1936, Mavuti and Litterick 1981, Harper 1987, Uku and Mavuti 1994), indicating that fossil ephippia abundances in our sediment cores are a trustworthy representation of community history. Sediment chronology was established by detailed lithostratigraphic correlation to cores from the same location that had been dated directly by $^{210}$Pb and $^{14}$C (Verschuren 2001, Mergeay et al. 2004). The composite sediment core was sliced in consecutive 2-cm intervals, resulting in 383 sediment slices of ~35 cm$^3$. The temporal resolution of our analysis thus averaged 4.4 years per sampled interval, varying between about two years in the most recent, uncompacted muds and 25 years during the most extreme lowstand, when the rate of sediment accumulation was most reduced (Verschuren 2001). The sediment slices were washed and sieved through 150-µm mesh to retain *Daphnia* ephippia and the fossil remains of fish. Abundances of *Daphnia* and fish fossils were expressed as the number of remains per gram of dry sediment per year (i.e., their production flux) to correct for both changes in sedimentation rate and sediment compaction with depth. The *Daphnia* were identified to species morphologically and/or genetically (Mergeay et al. 2005, 2006b). Variation in temporal resolution between sampled intervals was not correlated
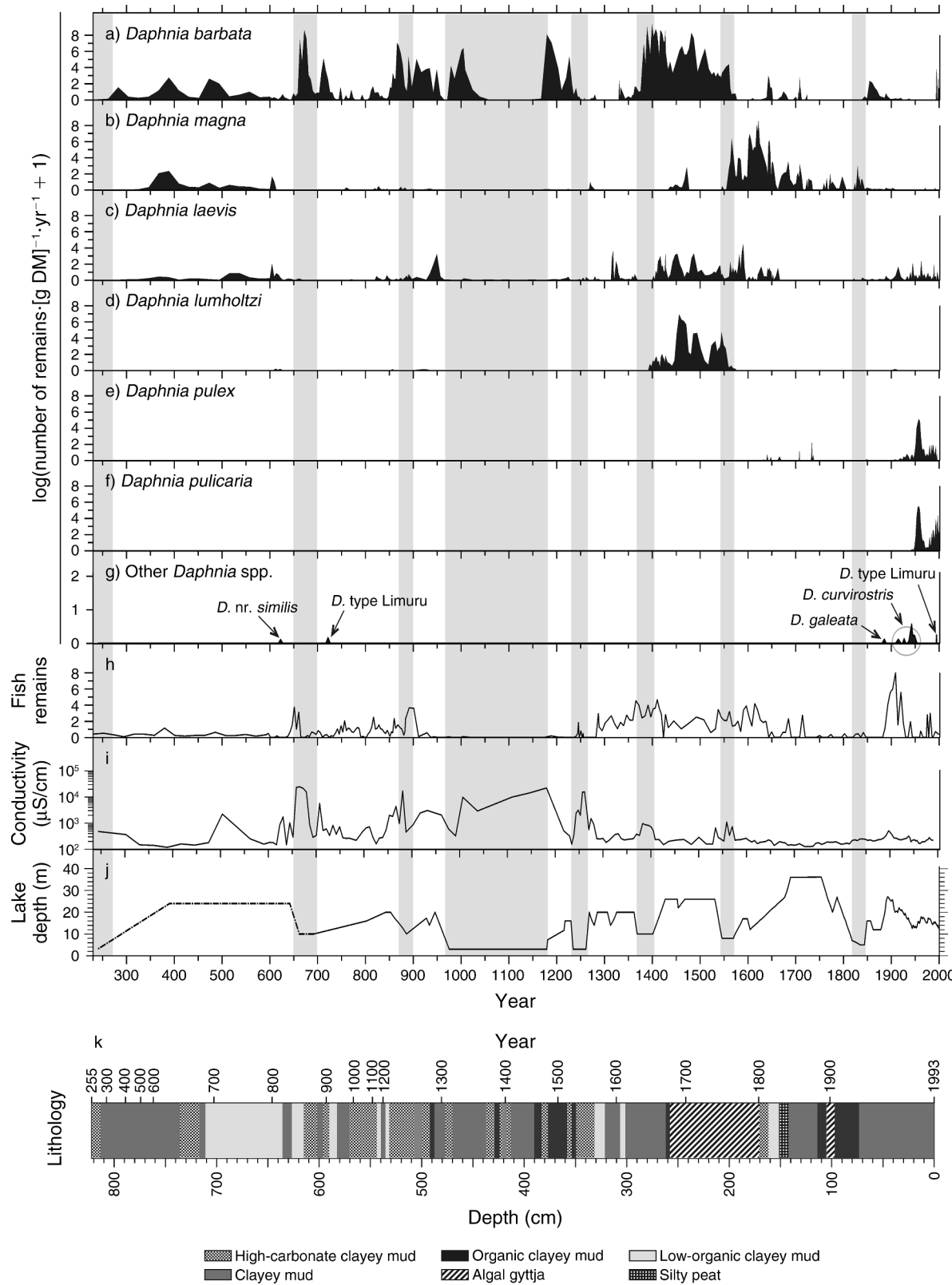
FIG. 2. (a–g) Abundance changes over time in the *Daphnia* species inhabiting Lake Naivasha over the past 1800 years (DM represents dry mass) in relation to (h) reconstructed changes in fish abundance, (i) lake water salinity (represented by the conductivity of dissolved salts), and (j) lake depth, as well as (k) the stratigraphic variation in sediment composition that allowed

with *Daphnia* species richness (Pearson product-moment correlation, $r = 0.053$, $P = 0.296$) or Shannon diversity ($r = 0.071$, $P = 0.163$). The fish fossils primarily consisted of scales and vertebrae of Cichlidae and Poeciliidae, of which the local representatives are known to be zooplanktivorous (Mavuti 1990).

### Paleoenvironmental reconstruction

Abundance changes in fossil *Daphnia* ephippia were linked to the environmental history of Lake Naivasha through reconstruction of three ecologically relevant habitat variables (Fig. 2h–j). First, we inferred lake depth from lithological characteristics reflecting the lake-bottom environment at the time of sediment deposition (see Verschuren 2001). In this fluctuating tropical water body, lake depth is a proxy for lake size and water-column mixing regime, which in turn determine oxygen distribution, nutrient dynamics, and primary production (Verschuren et al. 2000*b*). Second, we inferred the past salinity of lake water (commonly measured as conductivity, i.e., the electrical conductance of dissolved salts) from the composition of fossil diatom assemblages (Verschuren et al. 2000*a*; supplemented by unpublished data of K. R. Laird and B. F. Cumming, Queen's University, Kingston, Ontario, Canada). Third, we reconstructed relative fish density using the log ($x + 1$) abundance of fossil fish remains. This may not represent a quantitative estimate of actual fish predation, but likely provides an indication of order-of-magnitude changes in fish predation pressure. Lake depth and salinity together capture key environmental conditions that ultimately determine the physiological and ecological suitability of the local open-water (pelagic) habitat for separate *Daphnia* species (Benzie 2005). In addition, zooplanktivorous fish are important predators of *Daphnia* and often incite strong community changes (Kerfoot and Sih 1987). The combined lake depth and water conductivity data (Fig. 2i–j) define two main habitat types alternating through time. Highstand phases of relative hydrological stability were characterized by a large freshwater pelagic habitat across the main basin of LN and a full complement of nearshore and offshore bottom habitats. Lowstand phases were characterized by a lack of pelagic habitat, substantial seasonal hydrological variability, and often a critical episode of salinity increase above 1000 or even 3000 μS/cm, which is beyond what many freshwater macrophytes

and aquatic invertebrates can tolerate (Hammer 1986, Frey 1993). We demarcated lowstand phases (gray bands in Fig. 2) by the stratigraphic occurrence of high-carbonate mud or silty peat (Fig. 2k), which is most often associated with rapid change in diatom-inferred salinity (Fig. 2i).

### Priority effects

During a prominent lake-level rise, LN expands from a remnant pond inside CIC to a large freshwater lake within just a few years (Verschuren et al. 2004). Priority effects may arise when local populations that persisted in CIC until the end of the lowstand colonize this expanding lake habitat. Consider that CIC at its smallest was a pond of 1 $km^2$. With average local densities typically between 1 and 10 *Daphnia*/L (Mavuti and Litterick 1981) and an average depth of 5 m, this represents a local community of at least five billion individuals that can colonize the main basin following a lake-level rise. Resident populations thus have a massive numerical advantage compared to immigrants.

To test for the role of priority effects and the time scale of their persistence, we first performed a principal component analysis (PCA) in CANOCO 4.5 (ter Braak and Smilauer 2002) on the *Daphnia* community data set. We performed Hellinger transformation of species abundance data to standardize behavior of data across ordinations (Legendre and Gallagher 2001). We used a Horn's parallel analysis (Glorfeld 1995) to decide how many PCA axes should be retained for further interpretation. We then used regression analysis (Stat-Soft 2007) to establish to what extent the community value along each of the retained PCA axes of the last lowstand interval (Low$_{end}$) was able to predict the respective PCA score of the highstand community 10, 25, and 50 years later, as well as the reciprocal analysis of the influence of "end-of-highstand" communities (High$_{end}$) on subsequent lowstand communities. Due to issues of temporal resolution, we approximated these intervals to the closest possible value allowed by the data. For lowstands lasting <50 years, we used the last sampled interval representing that lowstand. In two cases this was the interval for the time lag of 25 years. If priority effects are only transient, i.e., representing a lagged species-sorting response to environmental change, we expected a decay over time in the predictive power of High$_{end}$ or Low$_{end}$ community values.

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delimitation of successive low- and highstand phases. Light gray bars are lake phases when aquatic habitat was likely restricted to a shallow remnant pool in Crescent Island Crater. (k) Core lithostratigraphy is plotted against a linear depth scale (lower axis); indication of sediment age at depth (upper axis) highlights variation in sediment compaction and accumulation rate down-core. *Daphnia pulex* refers to European *D. pulex* Leydig, whereas *D. pulicaria* represents a single clone of hybrid origin of the North American *D. pulicaria* complex (Mergeay et al. 2006*b*), which is often incorrectly named *D. pulex* (Mergeay et al. 2008). *D. laevis* here refers to a cryptic East African endemic lineage of the *D. laevis* Birge species complex. *D.* nr. *similis* is probably a cryptic species of the *D. similis* Claus complex, and *D.* type Limuru is an East African endemic lineage of the *D. dolichocephala* G.O. Sars complex. All other taxa are genetically similar (<5% sequence divergence at the barcoding gene *Cox1*) to counterparts from their respective type localities or regions (J. Mergeay, *unpublished data*). Years are CE (Common Era).

TABLE 1. Results of regression analyses (regression coefficients and significance values) between principal components analysis (PCA) scores of *Daphnia* species data from Lake Naivasha, Kenya, Africa.

| | | PCA1 | | PCA2 | |
|---|---|---|---|---|---|
| Predictor | Response | $r^2$ | $P$ | $r^2$ | $P$ |
| Low$_{end}$ | High$_{10}$ | 0.927 | 0.000 | 0.892 | 0.000 |
| Low$_{end}$ | High$_{25}$ | 0.626 | 0.019 | 0.800 | 0.003 |
| Low$_{end}$ | High$_{50}$ | 0.625 | 0.046 | 0.769 | 0.004 |
| High$_{end}$ | Low$_{10}$ | 0.804 | 0.006 | 0.516 | 0.069 |
| High$_{end}$ | Low$_{25}$ | 0.068 | 0.573 | 0.340 | 0.169 |
| High$_{end}$ | Low$_{50}$ | 0.003 | 0.909 | 0.327 | 0.180 |

*Notes:* The scores are determined along axes PCA1 and PCA2, with either end-of-lowstand intervals (Low$_{end}$) or end-of-highstand intervals (High$_{end}$) as predictors for highstand/lowstand intervals 10, 25, and 50 years after the transition. These results represent the degree to which highstand communities are influenced by the preceding Low$_{end}$ communities, to which lowstand communities are influenced by the preceding High$_{end}$ communities, and how this changes over time. Highstand represents a mega-lake (large, deep freshwater lake $\sim$150–250 km$^2$); during lowstands, the lake was reduced to a shallow, usually saline pond $\sim$1 km$^2$.

We then tested whether Low$_{end}$ and "highstand $q$ years later" (High$_q$) communities were more similar to each other than High$_{end}$ and "lowstand $q$ years later" (Low$_q$) communities, with the value of $q$ set to 10, 25, and 50 years. This allows us to test whether priority effects are indeed significantly stronger from lowstands to highstands (expanding lake habitat) than from highstands to lowstands (contracting lake habitat). For this we used Bray-Curtis similarity scores of $\log(x + 1)$ transformed species data (Primer 5) in a Student's $t$ test. Data were log-transformed to reduce the impact of samples with extremely high *Daphnia* abundances.

### Explanatory power of environment vs. priority effects

We then tested to what extent community structure could be explained either by priority effects (P) or by environmental variation and species sorting (E). For this we used redundancy analysis (RDA) on Hellinger-transformed species data in CANOCO 4.5 (ter Braak and Smilauer 2002) and variance partitioning (Borcard et al. 1992). We thus estimated the total explained variance, the unique contributions of environmental variation (E|P) and priority effects (P|E), and the intersection between them (P∩E). Negative values of the intersection indicate that P and E together explain the species data better than the sum of their individual effects (Legendre and Legendre 1998). To assess the role of priority effects during particular highstands and lowstands, we used as explanatory variables the PCA axis 1 and axis 2 scores of *Daphnia* species data for the last interval of the previous lowstand or highstand, respectively. The significance of each full model (including all variables) was established with 499 Monte Carlo permutations. Variance partitioning was performed separately on lowstand and highstand intervals, to establish whether lowstand and highstand communities were differently affected by environmental variation and priority effects.

### RESULTS

In total, we found 10 species of *Daphnia* in the 1800-year record of Lake Naivasha (Fig. 2a–g), among which six were frequently present ($>$10% of the 383 observations) and abundant (at least 1% of the overall fossil inventory). This species diversity amounts to all *Daphnia* taxa known from East Africa, apart from the *Daphnia obtusa* complex, which is restricted to high-mountain environments (Mergeay et al. 2005).

PCA axis 1 (PCA1) explained 40.9% of the variance in species data, compared to 27.6% for PCA2, 16.4% for PCA3, and 15.1% for PCA4. A Horn's parallel analysis indicated that eigenvalues for PCA3 and PCA4 were too low to be retained for further analyses. Regression analyses using the values of PCA1 and PCA2 to explain the corresponding PCA values 10, 25, and 50 years after a lowstand–highstand transition showed that Low$_{end}$ communities were significant predictors for ensuing highstand communities (High$_{10}$, High$_{25}$, and High$_{50}$), with $r^2$ values between 0.625 and 0.927 (Table 1). Conversely, High$_{end}$ PCA values were only strong and significant predictors of lowstand PCA values 10 years later (Low$_{10}$), but not of those 25 and 50 years later (Low$_{25}$ and Low$_{50}$; Table 1).

Bray-Curtis similarity scores between Low$_{end}$ and High$_{10}$, High$_{25}$, and High$_{50}$ communities were higher than those between High$_{end}$ and Low$_{10}$, Low$_{25}$, and Low$_{50}$ communities (Fig. 3). A $t$ test showed that these differences were significant for the last two comparisons ($t$ test for independent samples, df = 13; 10 years, $P$ = 0.211; 25 years, $P$ = 0.010; 50 years, $P$ = 0.013, respectively). This shows that, in the long run, priority effects were significantly stronger when the lake expanded and new habitat became available, than when it contracted.

The full RDA model considered three environmental explanatory variables (lake depth, salinity, log[fish remains abundance]) and two explanatory variables representing priority effects (Low$_{end}$ PCA1 and PCA2 scores for highstand periods, and High$_{end}$ PCA1 and PCA2 scores for lowstand periods). This full RDA explained 43.7% of the species variance during highstands vs. 29.2% during lowstands. Partitioning of the variance among environmental and priority-effect variables showed that purely environmental variation (E|P)

significantly explained 8.3% ($P = 0.002$) of species variance during highstands, and 9.3% ($P = 0.002$) during lowstands. However, priority effects alone ($P|E$) explained 39.5% of species variance during highstands ($P = 0.002$) vs. only 15.5% during lowstands ($P = 0.002$). The intersection between priority effects and environmental variation ($P \cap E$) was small but positive (4.4%) for lowstands and negative for highstands ($-4.1$%).

## DISCUSSION

We reconstructed the repeated reassembly of an ecological community experiencing dramatic environmental change over a time span of 1800 years. The variance in community composition explained by changes in three important habitat conditions (lake depth, salinity, fish abundance) was relatively modest, and similar for lowstand and highstand periods. The priority effect, however, was much stronger during highstands than during lowstands, and explained, especially for the highstands, a much higher portion of variance in community composition than environmental change. Moreover, priority effects at the transition from highstands to lowstands were merely transient, whereas they persisted at least for 50 years from lowstands to highstands (Table 1, Fig. 3).

The observed asymmetry in the dependence of lowstand and highstand communities on priority effects confirms that priority effects are strongest when new, unoccupied habitat is colonized (Begon et al. 2006). We propose that each time the remnant pond inside the crater expanded to a large lake, the resident local community could colonize this vast, empty habitat and preempt resources at the expense of less abundant regional immigrants (Mergeay et al. 2007). Although community composition during highstands was significantly influenced by environmental variation ($E|P = 8.3$%), it was much more influenced by the specific history of community assembly during the preceding lowstand ($P|E = 39.5$%), and thus by priority effects.

The eventual outcome of the interplay between species sorting and priority effects operating in our study system is that priority effects interfere with species sorting when local residents colonize and saturate an empty habitat before other species arrive from elsewhere. Persistence of these priority effects results in an apparently weak response of species to major environmental variation. The three environmental gradients we reconstructed are most certainly an incomplete representation of the *Daphnia* habitat. They are nevertheless key variables in the environmental regulation of African freshwater zooplankton, and the magnitude of reconstructed local variation in at least two of them (lake depth/size and salinity) covers the full gradient of habitat conditions occupied by African *Daphnia* species (Frey 1993, Benzie 2005, Mergeay et al. 2006a). Priority effects were still apparent 50 years after the environmental turnover, which represents >500 generations in *Daphnia*, including one sexual generation per year. Therefore, our
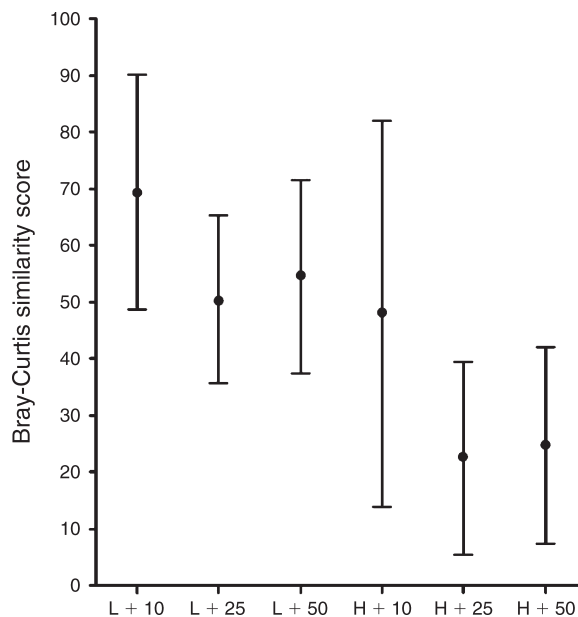


FIG. 3. Bray-Curtis similarity scores (mean and 95% confidence intervals) between Low$_{end}$ (end of the lowstand interval) and highstand communities 10 years later (L + 10), 25 years later (L + 25), Low$_{end}$ and 50 years later (L + 50), and between High$_{end}$ (end of the highstand interval) and lowstand communities 10 years later (H + 10), 25 years later (H + 25), and 50 years later (H + 50).

results underscore the importance of past (historical) habitat and community dynamics on community composition on relatively long time scales.

### Interaction between priority effects and the storage effect

We showed that locally established communities can exert a persistent priority effect over immigrants, which in *Daphnia* disperse both in space (via wind, waterfowl, and other causes) and in time (via long-viable propagules in the local dormant egg bank). At first glance, our results seem to indicate that this priority effect acts against the storage effect (Chesson 1983, Cáceres 1997). The storage effect is the positive average growth of populations with strong temporal variation in recruitment success, achieved through overlapping generations (Chesson 1983), such as dormant propagules (seeds, dormant eggs, statoblasts, and others). In temporally variable environments, the storage effect allows dynamic coexistence of species that cannot stably coexist (Chesson 1986). The strong priority effect we observed suggests that during a lowstand to highstand transition, recruitment from the vast dormant egg bank of the main LN lake basin was numerically modest compared to the influx of animals from expanding resident CIC populations. This may be related to the fact that the lowstands lasted for several decades at least, and sometimes much longer (25–210 years; Fig. 2). Although dormant eggs can remain viable for decades (Cáceres 1998), the probability that they may be exposed to favorable

hatching conditions declines with time. In a paleogenetic study on *Daphnia barbata* from Lake Naivasha, Mergeay et al. (2007) showed that successful recolonization after ~50 years of absence happened through local recruitment from the dormant egg bank and not through immigration from elsewhere, but that nevertheless the number of hatchlings establishing this new population was very low. So whereas recruitment from the dormant egg bank must certainly have been possible after most lowstands studied here, the resident CIC community expanding into the main basin of LN typically had a very strong numerical advantage. On the other hand, the priority effect exerted by an expanding resident population may be strongly enhanced by the storage effect that is created by their own production of a new, large buffer of dormant propagules. We therefore propose that the numerical advantage of the expanding resident community during the initial phase of colonization is consolidated by the dormant propagule bank they produce, and this may have extended the impact of their priority effect in time, as observed in our data.

### Local temporal vs. regional spatial priority effects

In a metacommunity context, the historical or temporal component of community variation can also be transposed to a regional component of spatial community variation, since the probability of a certain species exerting a priority effect in a new habitat is a function of different parameters. First, it depends on the relative frequency of the focal species in the regional species pool, and second, on differences in dispersal ability among species. Combined, they determine the probability that a focal species will colonize the habitat first. Third, it is affected by the overall degree of dispersal limitation of the community, determining the scope for local population growth of the first colonist before other species arrive in the habitat. Therefore, priority effects may cause strong spatial autocorrelation in the distribution of species among communities, and cause spatial patterns in the regional distribution of species that are typically interpreted as the outcome of mass effects (Cottenie 2005). The mechanisms involved in priority effects and mass effects, however, are completely different, as mass effects rely on strong immigration to compensate for negative local population growth (Leibold et al. 2004).

### Perspective

Our study emphasizes the importance of priority effects in community assembly, and the need to integrate historical components of community and environmental variation in order to understand the processes determining the present-day composition of biological communities (Ricklefs 1987, Willis and Birks 2006). Studying these temporal processes in metacommunity ecology on sufficiently long time scales, however, remains a major challenge. We suggest that combining paleoecological and metacommunity approaches may be a productive method to engage in a truly comprehensive analysis of the processes regulating ecological communities. In an applied perspective, priority effects may strongly impact the response of communities to strong environmental change and thus influence community assembly in novel or heavily disturbed habitats. Conversely, priority effects could be exploited in ecological restoration projects, by selectively inducing a long-lasting priority effect of target species to buffer against successful establishment of unwanted immigrant (exotic) species. More research is needed, however, on how such manipulation of priority effects can successfully be achieved in a restoration ecology context.

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