esa ECOSPHERE

Understanding arid-region waterbird community dynamics during lake dry-downs

Graeme S. Cumming,[1,2,†] Dominic A. W. Henry,[1,3,4] Gregory L. Mutumi,[1,5]
and Mduduzi Ndlovu[1,6]

[1]FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701 South Africa
[2]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811 Australia
[3]Endangered Wildlife Trust, Johannesburg 1685 South Africa
[4]Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Cape Town 7701 South Africa
[5]Life and Environmental Sciences, University of California–Merced, Merced, California, USA
[6]School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela 1200 South Africa

Citation: Cumming, G. S., D. A. W. Henry, G. L. Mutumi, and M. Ndlovu. 2021. Understanding arid-region waterbird community dynamics during lake dry-downs. Ecosphere 12(8):e03668. 10.1002/ecs2.3668

Abstract. The community dynamics of organisms that exhibit multi-scale responses to habitat change are poorly understood. We quantified changes in species diversity and the functional composition of a waterbird community over two iterations of a repeated transition, the annual drying-down of arid-region Lake Ngami, Botswana. We used our data to test three theoretical predictions: simplification of the bird community over time due to a reduction in habitat area and concurrent niche loss; large fluctuations in densities of mobile, opportunistic species; and high variance in predator and prey abundance. Despite temporal variance in species accumulation, we observed no obvious simplification and distinct but consistent groupings of abundance and composition across transitional stages. There were some rapid shifts in functional composition, such as loss of deepwater foragers; winners and losers also occurred within foraging guilds. We conclude that understanding community-level trends during transitional periods will require stronger theoretical frameworks that more effectively integrate unique species traits and functional groups. For conservation managers, our study offers a cautionary tale of the importance of understanding connectivity, trajectories of change, and the potential for large fluctuations in animal communities independent of management actions during periods of ecological transition.

Key words: Africa; bird; Botswana; disturbance; drought; regime shift; resilience; wetland.

Received 8 March 2021; accepted 18 March 2021; final version received 19 May 2021. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** graeme.cumming@jcu.edu.au

INTRODUCTION

Ecology seeks to understand the distribution and abundance of organisms (Andrewartha and Birch 1954). Despite many decades of progress in ecology, fundamental challenges remain in poorly studied ecosystems and for species that exhibit complex, multi-scale responses to habitat variation. The local and regional movements of waterbirds in arid areas are particularly difficult to predict, due in part to often extreme spatiotemporal variation in landscape resources at several scales. Arid-region waterbirds have been shown to respond at regional scales to sequences of flooding and drying, with some predictability by functional group (foraging guild) in responses to the seasonal creation and loss of habitat (Roshier et al. 2002, Kingsford et al. 2010, Cumming et al. 2013), but these responses have not been widely studied. Reduction of hydrological variation reduces waterbird diversity (Kingsford et al. 2004), suggesting long-term ecological benefits of both flooding and drying, but the mechanisms that underpin waterbird community responses to drying in arid regions are poorly understood.

The general lack of detailed information on seasonal shifts in waterbird communities in arid regions means that surprisingly few datasets are available at appropriate temporal resolution to develop and test relevant hypotheses (Thomas et al. 2015). Theory that might predict community-level shifts at relevant spatial and temporal scales is also scattered across different areas within the ecological literature. Classical ecological theory focused on resource and niche availability as drivers of community composition (Hutchinson 1959, Rosenzweig 1995), with secondary consumers expected to respond more slowly to environmental change than primary consumers and species diversity increasing with sampling area (Rosenzweig and MacArthur 1963, Chesson and Warner 1981). Interactions between similar species may likewise create a predictable trajectory of community change governed by processes of competition, facilitation, and tolerance acting on and between species (Clements 1916, Connell and Slatyer 1977). These classical concepts, however, assume that the system is near to or approaching an equilibrium. By contrast, during regime shifts and transitions, theory predicts a release of nutrients, a decrease in biomass, and overall community simplification (Holling 1973, 2001), with colonization sequence and patch size influencing community stability and composition (MacArthur 1955, Terborgh et al. 1997, 2001). Shifts in the balance between within-patch production (population growth rates) and between-patch dispersal (both immigration and emigration) can create boom-and-bust dynamics during transitional periods (Stott et al. 2010). Lastly, resource pulses during transitions (e.g., exposure of nutrient-rich lake substrate) are thought to favor opportunists and weedy species that can take advantage of favorable conditions; trophic level and behavior (e.g., aggregative or not) affect the magnitude of response (Yang et al. 2008, 2010).

Based on these bodies of theory and our previous research on wetland birds (Cumming et al. 2012, 2013), we tested three related predictions that seemed to be potential candidates for generalizations about wetland birds: (1) The community should simplify over time, driven by the reduction of wetland area (and presumably, loss of niches) during dry-down; (2) we should see particular fluctuations in the densities of opportunistic, mobile species; and (3) there should be high variance in the numbers of predators and prey.

METHODS

We used standardized point counts to document waterbird community dynamics through two cycles of an annually repeating 11–12 month shift from wet to dry conditions in a large arid-region wetland, Lake Ngami. Data and supporting code are available through Dryad (Cumming and Henry 2021).

Study site

Lake Ngami is an endorheic (no outflow) seasonal lake 85 km southwest of Maun in northern Botswana at the end of the Okavango wetland system. It has a maximum known extent of 277 km^2. Water enters via the Boro and Thamalekane Rivers for 2–6 weeks in a given year. Lake Ngami was dry from roughly 1990 to 2003 (Kurugundla et al. 2018). Water entering the Okavango derives from rainfall in the Angolan highlands, and so flooding is out of synchrony with local rainfall events, making it a potentially rich oasis for mobile species during regionally dry months. Floods fill a shallow basin (mean depth 3.5 m; Kurugundla et al. 2018) littered with dead plant matter and cattle droppings, resulting in a pulse of nutrients when flooded. Flooding typically starts in July and peaks in late August. Dry-down periods last until June or July, with the lake either drying fully or being reduced to a few muddy puddles. The woodlands surrounding the lake are dry in October but become greener with local rainfall by February.

Data collection

We collected bird count data at Lake Ngami during six different sampling periods, spread at four-monthly intervals over a two-year period from October 2007 to October 2009. Each sampling period involved five days of standardized point counts at between 8 and 13 points. Points were each visited four times, at different times of day, over each 5-d counting period. The total sample size was 228 point counts. Each count used a ten-minute habituation period followed by a half-hour counting period by stationary observers, during which all birds seen within a 150 m radius in front of the observers were recorded. All counts included at least one skilled observer and mostly the same group of people. Birds were identified only by sight using high-powered binoculars. Transect boundaries were estimated using a Bushnell Yardage Pro laser range finder with a manufacturer's stated small-feature accuracy of ±91 cm (one yard) over a range of 5–183 m.

Counting locations were at least 500 m apart. Since our focus was on waterbirds, we moved counting sites perpendicular to the shoreline to stay within 5–10 m of the water's edge. This typically did not involve moving sites more than 20 m between counting periods, and some sites were not moved at all. A few sites became too close to each other to qualify as independent in February and/or June; the number of counting points thus varied between 13 and 8. Count timing was randomized by day but stratified to fall once into each of four different time slots (06:00–09:00; 09:00–12:00; 12:00–15:00; and 15:00–18:00), although in midsummer (February) we sometimes started earlier or finished later to include dawn and dusk periods. To avoid temporal autocorrelation, we did not re-count any location within two 3-h counting periods, so all counts were separated by at least 6 h. The counts thus gave four standardized samples for each point for 8–13 different points, and a minimum of 32 point counts (16 h observation time) per sampling period. All bird common names reported in this study are from the standard regional reference (Hockey et al. 2005).

Lake areas were estimated from remotely sensed data as described by Gaidet et al. (2012). According to Kurugundla et al. (2018), our study occurred during a transitional phase from a dry to a wet cycle in Lake Ngami's flow regime; thus, even after flooding, the surface area was below the maximum of 277 km^2 achieved in 2012.

Foraging guilds

We classified each bird species into one of the categories developed for the Botswana waterbird community by Cumming et al. (2012). Due to differences in observed species and analytical focus, we modified the scheme (Table 1; see species-level summary in Appendix S1). Changes included (1) placing raptors in a single group, rather than by habitat (e.g., African Fish Eagle and African Marsh Harrier now group together); (2) addition of a scavenger/opportunist category for carrion-feeding species found near water but not strictly water-associated, such as Marabou Storks, vultures, and gulls; and (3) inclusion of passerines other than the highly agile aerial foragers (i.e., swallows, swifts, bee-eaters, rollers) into a potential prey category. We also excluded a priori a few observed bird species with weak dependence on water, as being poor indicators of ecological change in wetlands and unlikely to influence raptor densities: Swainson's and Red-billed Spurfowl, Coppery-tailed Coucal, Namaqua and Burchell's Sandgrouse, Grey-headed Kingfisher, Diderick Cuckoo, Crimson-breasted Shrike, Black-headed Heron, and African Grey Hornbill.

Table 1. Guilds considered in this study.

Guild	Foraging habitat or style	Example species
1	Short vegetation/ mud/grass	Egyptian Goose, Kittlitz's Plover
2	Emergent vegetation	African Jacana, Black Crake
3	Shallow water	African Spoonbill, Cape Teal, Pied Avocet
4	In or over deep water	Reed Cormorant, Great Crested Grebe
5	Aerial feeder	Black-winged Pratincole, Collared Pratincole
6	Scavenger/opportunist	White-backed Vulture, Marabou Stork
7	Raptor	African Fish Eagle, Martial Eagle
8	Small passerine, potential prey	Laughing Dove, Cape Sparrow
9	(Excluded from functional analysis)	Brown-throated Martin, Burchell's Sandgrouse

Note: The assignment of each bird species to a guild is given in Appendix S1.

Statistical methods

The study area is generally open and all counts were undertaken on shorelines, where even fairly cryptic species were easy to observe. In addition, the counting method was standardized, analyses focus on comparisons between counts, and fluctuations in numbers of birds were very large (making it unlikely that we would miss genuine trends). Repeating the counts four times at each site also decreased the probability that species which occupied the site went undetected. It has been shown that species richness is underestimated when detection probability is not accounted for, but in our case absolute species richness was of less importance than relative species richness between sites. Our estimates of relative between-site species richness were especially robust because of our highly standardized sampling protocol. We thus did not attempt to undertake corrections for detectability.

Community-level analyses.—We first estimated Shannon–Wiener diversity, species evenness, and species richness for each time step, using vegan (Oksanen et al. 2011). We then compared patterns in species accumulation curves (SACs) across our point counts using the vegan (Oksanen et al. 2011) and sars (Matthews et al. 2019) packages in R 3.6.3 (R Core Team 2013). We avoided pseudoreplication by averaging all four counts from each individual point location for each sampling period. Initial analysis of all data together in sars indicated both that a standard log model provided an acceptable fit to the data and that when all count data were combined the SAC began to level off, indicating adequate sampling effort. We fitted an SAC to the entire bird community for each time step individually using the specaccum function in vegan, calculated coefficient values using sar_loga in sars, and compared the resulting values for the slope of the relationship and their standard errors. Species-area and species accumulation curves are not identical in the presence of environmental heterogeneity (Matthews et al. 2016) but under our sampling methodology (same sites, same areas sampled during each sampling period) reporting both would be redundant.

Foraging guild analyses.—To explore how waterbirds (guilds 1–4, 77 species) responded to lake level fluctuations, we modeled abundance of each species as a function of water level. We used ordinations to assess how count sites and foraging guilds grouped through periods of transition. We used model-based (as opposed to distance-based) multivariate methods for two primary reasons: First, model-based methods explicitly acknowledge and account for the positive mean-variance relationship inherent in many community datasets (i.e., rare species have low variation around their mean abundance while common species exhibit higher variance); and second, model-based methods allow direct and easy diagnostic checks that the data meet the assumptions of the models, ensuring the validity of our inferences (Warton et al. 2012, 2015, Hui et al. 2015). This was important since our data had a prominent positive mean-variance relationship across the pooled point count data.

To test the community- and species-level relationship between abundance and lake level, we used the manyglm function from the mvabund R package (Wang et al. 2012). This function fits a separate generalized linear model (GLM) to each species using a common set of explanatory variables, which in this case was lake level. Given the distribution of our count data, we used a negative binomial regression to ensure an adequate model fit. We used the anova.manyglm function to test both the significance of the overall effect of lake level on community abundance and species-level significance. This function takes into account correlation between species and *P* values are adjusted to control error rate across species using resampling-based methods for multiple testing. We used the boral function from the boral R package (Hui 2016) to fit a hierarchical correlated response model to assess how water level structures the waterbird assemblage in terms of both abundance and composition. The boral model is run using Bayesian Markov chain Monte Carlo (MCMC) estimation. This multivariate model also takes into consideration correlation between species that is not accounted for by model covariates (termed "residual correlation"). The residual correlation is accounted for by including latent variables alongside measured covariates in the model structure (see Appendix S2 for a full description of the model structure and details of settings used for MCMC sampling). We plotted and inspected the residuals for both multivariate analyses to confirm that the data met the model assumptions.

Our data included some extreme changes in the local population sizes of particular species. Changes in local population densities reflect the nature of the transitioning ecosystem and thus are of interest in the analysis. However, we excluded two species, Red-billed Quelea and Red-headed Quelea, from community-level analyses. We obtained estimates of up to 56,000 queleas in a single point count; their abundance is heavily influenced by regional climate and vegetation dynamics (Mundy and Jarvis 1989), and

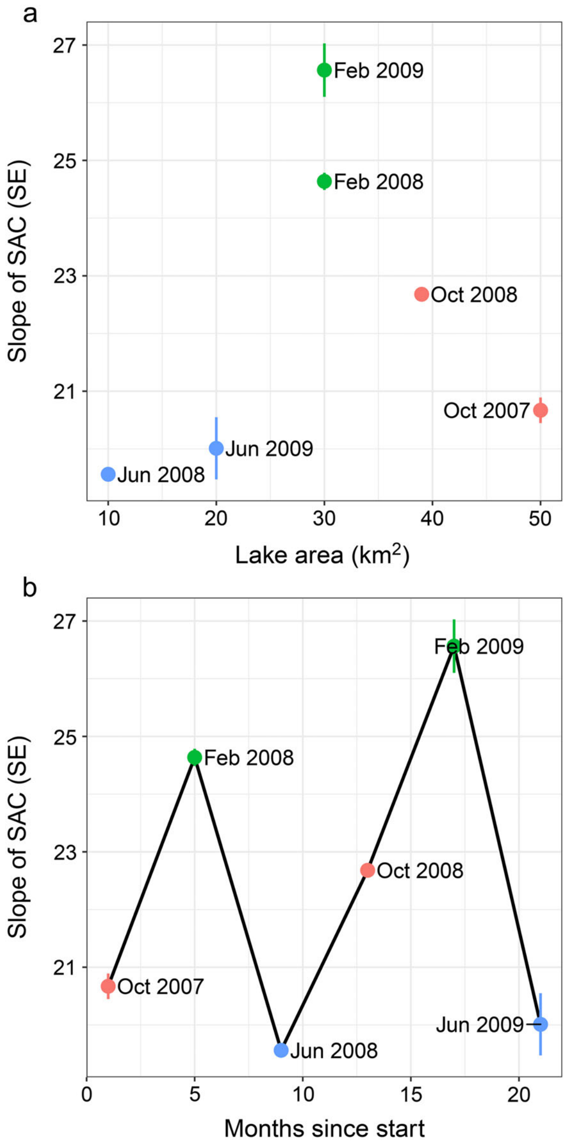

Fig. 1. Value and 95% standard error for the slope (z coefficient) of the species-area curve (SAC) for each sampling period against (a) lake area; and (b) months since start of sampling.

their inclusion would dominate other patterns in the data.

Species-level analyses.—We recorded 181 different bird species (Appendix S1). To identify species with high variance in relative abundance, we first removed species observed during only one counting period and then focused on those that either had individual abundances >2 deviations from the mean for any individual counting period or demonstrated changes in abundance that we found surprising or informative. We also calculated the maximum total number of birds of each species observed in any single point count. Fluctuations in numbers of predators and prey were clearly evident during fieldwork, but also highly idiosyncratic and not fully amenable to standard statistical approaches that average across data points; it has been previously observed by others that aggregate community measures may not show pronounced effects even when individual populations do (Holt et al. 1995). We thus adopted a more descriptive approach in the second half of the results.

RESULTS

Community-level analyses

Rather than the expected trend of a gradual decline in bird diversity per unit area as the lake dried, all three biodiversity indices increased and then decreased as the lake dried down (Appendix S3). The slopes (z coefficients) of the SACs for each survey period demonstrated clear and significant differences, with a net increase in slope between October and February and a net decrease in slope between February and June (Fig. 1). Survey-level SACs did not level off, indicating that recorded species richness was an under-estimate of the true community pattern (Appendix S4).

Foraging guild analyses

Analysis of deviance from the combined GLMs identified a significant effect of lake level on abundance ($\text{Dev} = 226.4$, $\text{df} = 56$, $P = 0.002$). There were 38 waterbird species (49% of total waterbirds) across the four foraging guilds which had significant lake level coefficients from the GLMs (i.e., standard errors of coefficients did not overlap with zero). By guild (Fig. 2), there were 11 significant coefficients from guild 1 (nine negative and two positive), one from guild 2 (positive), 22 from guild 3 (14 negative and eight positive), and four from guild 4 (all positive). Multivariate site ordination showed patterns of distinct but consistent groupings of abundance and composition at point counts across each stage of transition (i.e., sites from sampling months grouped together across years; Fig. 3). This grouping was most prominent in October

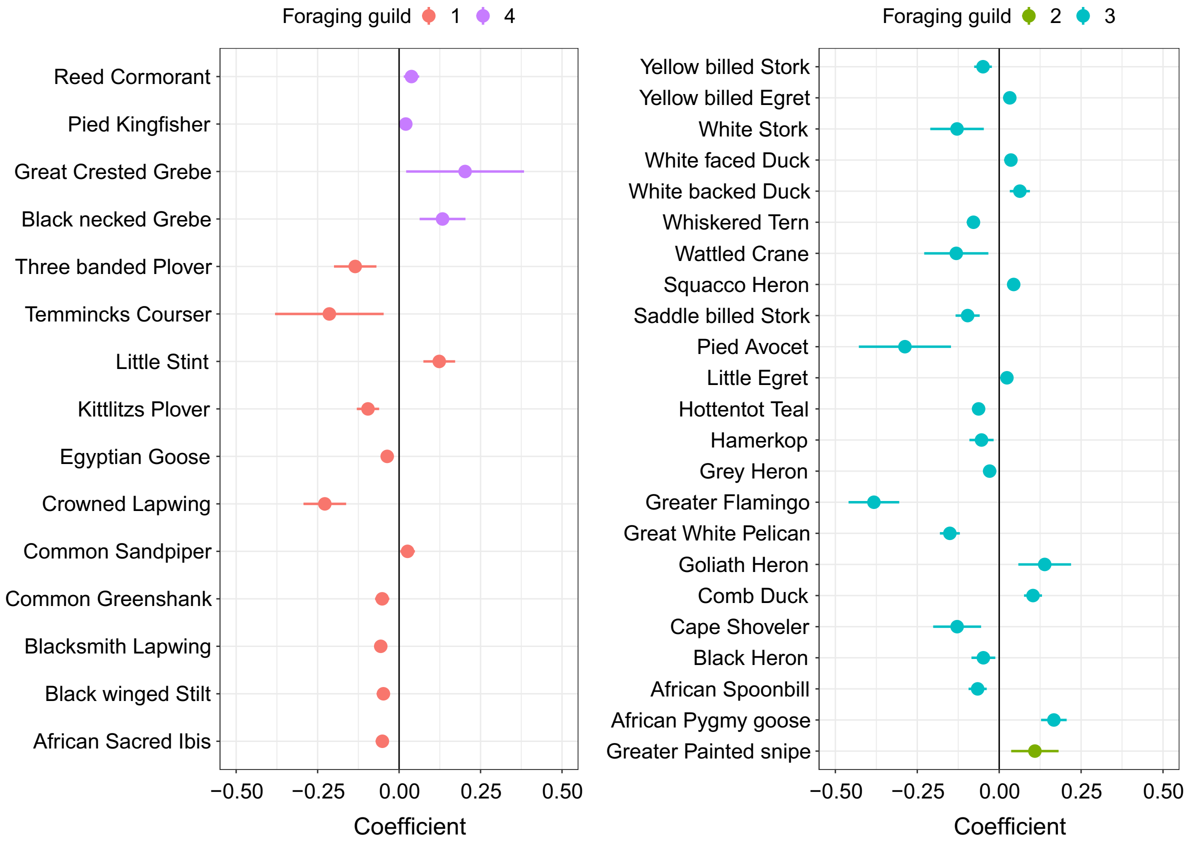

Fig. 2. Values and standard errors of significant lake level coefficients of species-level generalized linear models. Points are colored by foraging guild.

and June. The multivariate species ordination plotted by foraging guild revealed moderate grouping of foraging guilds 2 and 4, while species from guilds 1 and 3 were far more dispersed across the ordination space (Fig. 4). Diagnostic plots confirmed the absence of any pattern in the residuals.

Species-level analyses

Seventy-nine species (44% of 179 observed species) had a maximum standardized abundance of more than two deviations from the mean across all six sampling periods. Some of this variance was due to the 58 species observed during only one counting period, although many were present in relatively large numbers and across many different counts during that period. For example, during the first sampling period we observed a mean of 19 African Openbills per count, with as many as 145 in one count; but we did not see this species at Lake Ngami again. Some other notable observations with strong water dependence included Black Crake (mean abundance 0.11, only seen in sampling period 2); Black-Crowned Night Heron (0.44, period 2); Black-Necked Grebe (0.77, period 3); Great Crested Grebe (0.36, period 4); Lesser Jacana (0.2, period 5); Lesser Moorhen (2.22, period 2); and White-breasted Cormorant (0.92, period 1). These examples highlight the fluctuating nature and high variance in the bird community of Lake Ngami. Mean abundances for all species and sampling periods are given in Appendix S1.

Other species that were more consistently present at Lake Ngami also exhibited some unusually high abundances and large fluctuations in their numbers (Table 2). At a species level, the data showed both expected and unexpected trends. Lake Ngami appears to offer ideal habitat for diving and piscivorous birds during the

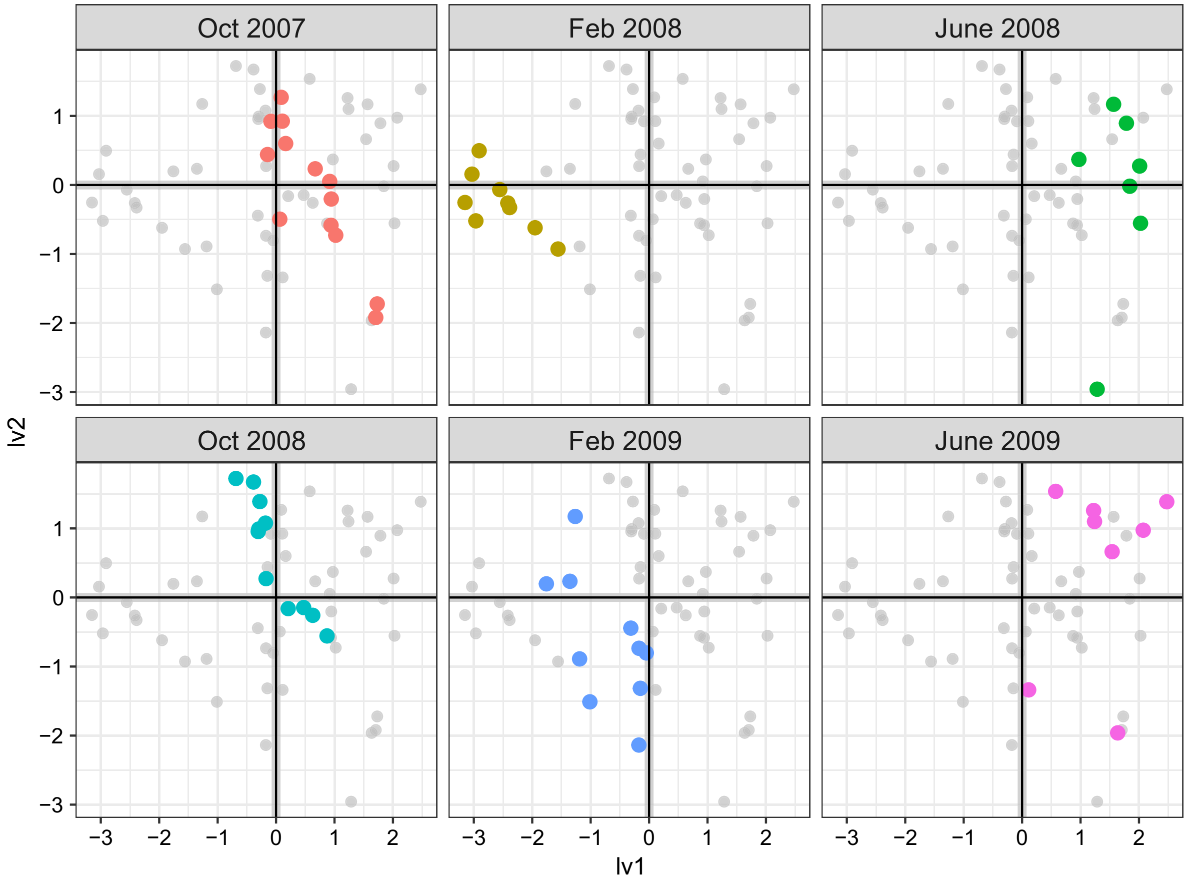

Fig. 3. Ordination of point count sites along two latent variable axes. The latent variables can be interpreted in the same way as those from typical ordination methods. Here the variables represent the main patterns of covariation among species and sites after accounting for lake level. Each panel highlights in color the sites from an associated sampling period against the sites from all periods in gray.

middle period of its dry-down, with single point counts as high as 710 Reed Cormorants in February 2008 and 152 Great White Pelicans and 95 Southern Pochards in February 2009. Similarly, emergent vegetation foragers in the middle period included up to 58 African Jacana and 58 Common Moorhen as well as an unusually large flock (for this species) of 46 White-backed Duck.

Highly mobile species using the lake area in large numbers during the middle dry-down period included Black-winged Pratincoles (highest single point count of 2000), which are insectivorous long-distance migrants that roost on grassy banks and forage over water. The abundance of these birds and the relatively high abundance of swallows, swifts, and bee-eaters during the same period (e.g., highest counts included 356 Barn Swallows; 68 Common Swifts; 39 Blue-cheeked Bee-eaters) suggested that there was a temporary boom in insect numbers as the lake dried down. The presence of large numbers of opportunistic predators such as Marabou Storks (150 in a single point count) and Yellow-billed Storks (103 in a single point count) also implied a high level of other prey items during this period, such as fish, frogs, and mollusks.

Shoreline and shallow water foragers such as Blacksmith Lapwing (277 in a single point count) and African Spoonbill (50 in a single point count) were also observed in very high numbers as the lake reached its late stages of dry-down. By the third sampling event of each successive cycle, we observed no jacanas, cormorants, Little Grebes, or White-backed Ducks. These species depend

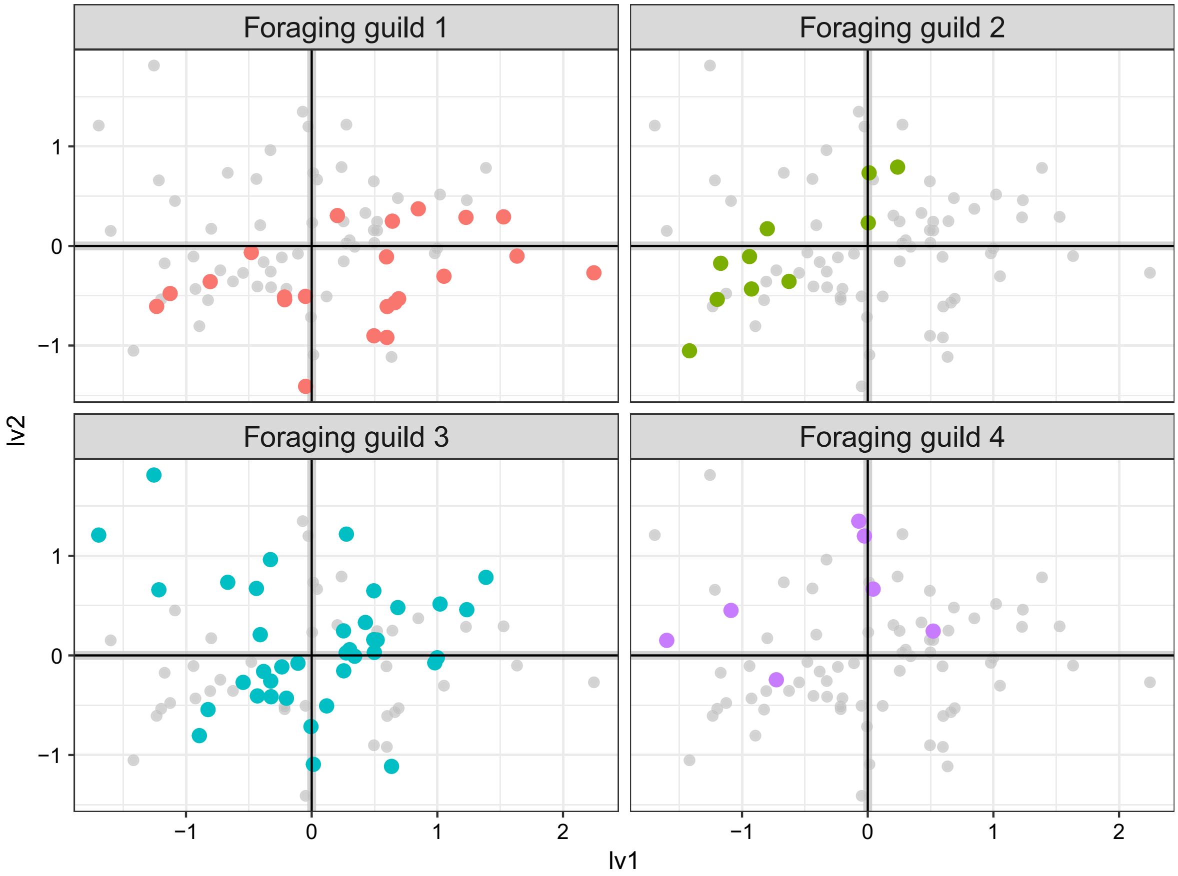

Fig. 4. Ordination of 77 waterbird species from foraging guilds 1–4 along two latent variable axes. Each panel highlights in color the species within each guild against the species from all guilds in gray.

on emergent vegetation and/or deeper water, which are lost as the lake dries.

The relative abundance of raptors is generally much lower than that of species at lower trophic levels. Numbers at Lake Ngami in June 2008 were unusually high by comparison to those typically observed at permanent wetlands in southern Africa. Outside the counting locations, we observed large groups of Peregrine Falcons, Lanner Falcons, goshawks, and flocks of Wahlberg's Eagles. The counts showed a relatively high species richness of large eagles (e.g., Brown and Black-chested Snake Eagles, Booted Eagle, African Hawk-Eagle, Long-crested Eagle, Tawny Eagle, African Fish Eagle), coinciding with abnormally high numbers of potential prey species, such as the African Mourning Dove (51 in a single count), Cape Turtle Dove (1650 in a single count), and Wattled Starling (2520 in a single count). We also captured 8 (Near Threatened) African Skimmers *Rynchops flavirostris* the week after counting; a new species record for this location.

Discussion

Our results illustrate the complexity of the community-level responses of arid-zone waterbirds. Multiple lines of evidence show that the bird community was structurally and functionally distinct through different periods of the drydown cycle. Bird diversity, bird richness, and encounter rates with new species during sampling were consistently highest during the middle period of the transition from full to dry. Thus, the species-area relationship offers a poor proxy for understanding changes in diversity in an open system where organisms can respond to environmental change at multiple scales.

Table 2. Relevant environmental and sampling data and mean abundances of a selection of species with abundance ~2 standard deviations from the mean during one or more sampling periods.

Bird species or dataset	Cat	Guild	October 2007	February 2008	June 2008	October 2008	February 2009	June 2009
Approximate lake area (km^2)			50	30	10	39	30	20
No. counting locations			13	9	7	11	10	8
Total counts (4 per location)			52	36	28	44	40	32
African Jacana	1	2	1.24	7.24	0	1.50	10.44	0
Green backed Heron	1	2	0.08	0.78	0	0	0	0
Long toed Lapwing	1	1	0	0.67	0	0	0.10	0
Reed Cormorant	1	4	10.27	64.44	0	8.57	4.53	0
Black-winged Pratincole	2	5	0	8.33	0	0	262.68	0
Marabou Stork	2	6	0	0	9.83	0	24.07	0.96
Yellow-billed Stork	2	3	0.54	2.67	1.43	1.27	16.30	0
African Mourning Dove	3	8	0.08	0.22	16.43	0	0.10	0
African Spoonbill	3	3	0.77	0	13.14	1.49	9.38	1.40
Black-winged Stilt	3	1	7.52	0.11	75.91	7.86	3.38	9.88
Blacksmith Lapwing	3	1	4.12	2.56	39.27	4.05	47.48	5.45
Great White Pelican	3	3	0.15	1.44	27.64	1.00	33.16	11.93
Long tailed Paradise Whydah	3	8	0	0	8.29	0	0.68	0
Black-chested Snake Eagle	4	7	0	0	0.71	0	0	0.63
Wahlberg's Eagle	4	7	0	0	1.43	0	0.10	0

Notes: Abundance across all counts can be recaptured by multiplying reported mean abundance by the total number of counts for that sampling period. Foraging guilds (Guild) are detailed in Table 1. Cat groups species into four categories: (1) mid-transition species that depend on emergent vegetation or require deep water and fish, as in the middle period of a dry-down; (2) highly mobile species that used the lake mid-dry-down, but were in large numbers only in the second year of sampling; (3) species that use shorelines and shallow water intensively and appear to have first increased in number after flooding, then followed the ever-shortening shoreline toward a central point as it contracted; and (4) raptors.

Changes in abundance of approximately half of the waterbird species at Lake Ngami (foraging guilds 1–4) were nonetheless significantly related to changes in lake level. This response was consistent in some foraging guilds; we expected and observed loss of the deepwater foraging guild as the water level dropped, providing a good example of a predictable, step-wise threshold response in community composition (Cumming et al. 2012). However, several other guilds showed a more varied response; for example, for shallow water feeders showing a significant response, 63% of species increased as lake levels fell and 37% increased as lake levels rose.

Species numbers on the shores of Lake Ngami showed extreme and often inconsistent fluctuations as water levels dropped, with many species either opportunistically using short-term resource pulses or vanishing during periods of scarcity. Our results did not support the hypothesis that the bird community would simplify through the transition. Instead, we saw idiosyncratic, species-specific responses to particular windows of opportunity. The largest single surprise at a community level was the extreme abundance of some species during low-water (June) sampling periods, with high concentrations of locally breeding shorebirds (e.g., Blacksmith Lapwing, which are usually territorial) and shore-using passerines (e.g., Cape Turtle Dove) and very high raptor species richness. Several mechanisms may have contributed to these dynamics. First, as the water level drops, individuals may simply follow the shoreline inwards. This could result in higher densities of shoreline birds. Second, the retreating waters deposit rich resources that may allow many animals to briefly coexist in a smaller area. Hippopotamus observed at the lake in June 2009 would also keep shoreline vegetation short and contribute to nutrient turnover. Third, by June, Lake Ngami may be unusually resource-rich at a broader (regional) scale as a wet location in a dry landscape. Lastly, due to its relative isolation and seasonality, Lake Ngami may offer some degree of predator release for ground- and shore-nesting birds (e.g., Red-billed Teal, Blacksmith Lapwing) from water mongoose, jackal, and hyena. Predation on juvenile waterfowl is considered an important influence on their breeding patterns across southern Africa (Cumming et al. 2016).

Patterns in bird abundance at Lake Ngami were different from those at similar but more permanently flooded locations during the same period (e.g., Lake Manyame and Lake Chivero in Zimbabwe; and Barberspan, in the North West Province of South Africa). Lake Ngami is also comparable to the Okavango River, north of the Okavango Swamps (Cumming et al. 2012). Each of these systems sees seasonal fluctuations in water levels and occasional large aggregations of waterbirds (Cumming et al. 2011), but none reaches the extremes of Lake Ngami.

Our findings have at least three general implications for conservation. First, increases in predator numbers may be relatively short-term where high densities of prey items can attract highly mobile predators and do not necessarily reflect local management. Recognition of the potential for boom-and-bust predator-prey dynamics is critical for effective conservation of both predators and prey; for example, short-term management of high predator densities or critical refuges through a transitional cycle may be vital for the protection of vulnerable species.

Second, a functional group perspective was useful for describing some but not all trends in our data. We expected predictable changes by foraging guild, as documented by Cumming et al. (2012) for bird communities following seasonal flooding on the Okavango River. Instead, foraging guild membership appeared less relevant than the ability of individual bird species to exploit resource pulses, suggesting that the unique traits of each species, and not just their foraging guilds, determined emergent community-level responses to ecosystem change. For example, while some small shorebirds thrived (e.g., Blacksmith Lapwing and Kittlitz's Plover), others did not (e.g., Common Ringed Plover, Common Sandpiper, Pectoral Sandpiper, Three-banded Plover). These differences were presumably due to small distinctions in prey and habitat requirements, but the success of a conservation strategy of managing shorebirds as a single guild in this context would be difficult to evaluate.

Third, if the changes described here had occurred over decades and replication in either time or space were impossible—reflecting conditions for the study of many long-duration ecological transitions—our observations would not fit conveniently with current theory. There is a genuine risk that transient fluctuations in abundance and community composition are misinterpreted as conservation successes, failures, or responses to management actions (Möllmann et al. 2011). Variance in the responses of many ecological communities to directional environmental change may obscure true long-term trends and contribute to misplaced or wasteful management responses. Regime shifts may also cause changes in connectivity and create short-term resource pulses, creating noise in ecological data (Kingsford et al. 2010, Yang et al. 2010, Cumming et al. 2013, Weber and Brown 2016).

Our analysis exposes some important gaps in ecological theory. High variability and some degree of boom-bust dynamic are to be expected in many climate change-impacted transitioning systems (e.g., forests, Lindenmayer and Taylor 2020; and coral reefs, Pratchett and Cumming 2019). Our understanding of ecological transitions is limited by the absence of theoretical frameworks that connect the drivers of change in non-equilibrium systems to the sequential responses (and the diversity of responses) of animal communities inhabiting them. If ecology and conservation are to successfully confront the challenges raised by anthropogenic change, it is vital that we develop stronger, more cohesive theory for understanding change in non-equilibrium ecological communities.

ACKNOWLEDGMENTS

We are grateful to the many people who contributed to field data collection during this study, particularly Leo Bruinzeel, David Nkosi, Innocent Magunje, Tertius Gous, and Jonathan Aronson. Many thanks are also due to David Cumming for his valuable comments on an earlier draft of this manuscript. Permission to work at Lake Ngami was granted by the Botswana Government with the assistance of the Kalahari Conservation Society. The field component of this research was funded by a USAID-sponsored Global Avian Influenza Network for Surveillance (GAINS) subcontract from the Wildlife Conservation Society to GSC, with additional contributions from the DST/NRF Centre of Excellence at the FitzPatrick Institute.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Chesson, P. L., and R. R. Warner. 1981. Variability promotes coexistence in lottery competitive systems. American Naturalist 117:923–943.

Clements, F. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, D.C., USA.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Cumming, G. S., et al. 2011. The ecology of influenza A viruses in wild birds in southern Africa. EcoHealth 8:4–13.

Cumming, G. S., D. M. Harebottle, J. Mundava, N. Otieno, and S. J. Tyler. 2016. Timing and location of reproduction in African waterfowl: an overview of >100 years of nest records. Ecology and Evolution 6:631–646.

Cumming, G. S., and D. A. W. Henry. 2021. Waterbird count data and R code for community-level analysis: Lake Ngami 2007–2009. Dryad, Dataset. https://doi.org/10.5061/dryad.w0vt4b8rd

Cumming, G. S., M. Ndlovu, G. L. Mutumi, and P. A. Hockey. 2013. Responses of an African wading bird community to resource pulses are related to foraging guild and food-web position. Freshwater Biology 58:79–87.

Cumming, G. S., M. Paxton, J. King, and H. Beuster. 2012. Foraging guild membership explains variation in waterbird responses to the hydrological regime of an arid-region flood-pulse river in Namibia. Freshwater Biology 57:1202–1213.

Gaidet, N., et al. 2012. Understanding the ecological drivers of avian influenza virus infection in wildfowl: a continental scale study across Africa. Proceedings of the Royal Society B: Biological Sciences 279:1131–1141.

Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. 2005. Roberts' birds of Southern Africa. Russell Friedman Books CC, Devon, UK.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390–405.

Holt, R., D. Debinski, J. Diffendorfer, M. Gaines, E. Martinko, G. Robinson, and G. Ward. 1995. Perspectives from an experimental study of habitat fragmentation in an agroecosystem. Pages 147–175 *in* Ecology and integrated farming systems. Wiley, New York, New York, USA.

Hui, F. K. 2016. boral–Bayesian ordination and regression analysis of multivariate abundance data in R. Methods in Ecology and Evolution 7:744–750.

Hui, F. K., S. Taskinen, S. Pledger, S. D. Foster, and D. I. Warton. 2015. Model-based approaches to unconstrained ordination. Methods in Ecology and Evolution 6:399–411.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:145–159.

Kingsford, R. T., K. Jenkins, and J. Porter. 2004. Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. Ecology 85:2478–2492.

Kingsford, R., D. Roshier, and J. Porter. 2010. Australian waterbirds–time and space travellers in dynamic desert landscapes. Marine and Freshwater Research 61:875–884.

Kurugundla, C., B. Parida, J. Buru, and B. Paya. 2018. Revisiting hydrology of Lake Ngami in Botswana. Hydrology: Current Research 7:2.

Lindenmayer, D. B., and C. Taylor. 2020. New spatial analyses of Australian wildfires highlight the need for new fire, resource, and conservation policies. Proceedings of the National Academy of Sciences USA 117:12481–12485.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536.

Matthews, T. J., K. A. Triantis, F. Rigal, M. K. Borregaard, F. Guilhaumon, and R. J. Whittaker. 2016. Island species–area relationships and species accumulation curves are not equivalent: an analysis of habitat island datasets. Global Ecology and Biogeography 25:607–618.

Matthews, T. J., K. A. Triantis, R. J. Whittaker, and F. Guilhaumon. 2019. sars: an R package for fitting, evaluating and comparing species–area relationship models. Ecography 42:1446–1455.

Möllmann, C., T. Blenckner, M. Casini, A. Gårdmark, and M. Lindegren. 2011. Beauty is in the eye of the beholder: management of Baltic cod stock requires an ecosystem approach. Marine Ecology Progress Series 431:293–297.

Mundy, P. J., and M. Jarvis. 1989. Africa's feathered locust. Baobab Books, Harare, Zimbabwe.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. vegan: Community ecology package. R package version 1.17-6. http://CRAN.R-project.org/package=vegan

Pratchett, M. S., and G. S. Cumming. 2019. Managing cross-scale dynamics in marine conservation: pest irruptions and lessons from culling of crown-of-thorns starfish (*Acanthaster* spp.). Biological Conservation 238:108211.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist 97:209–223.

Roshier, D., A. Robertson, and R. Kingsford. 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. Biological Conservation 106:399–411.

Stott, I., M. Franco, D. Carslake, S. Townley, and D. Hodgson. 2010. Boom or bust? A comparative analysis of transient population dynamics in plants. Journal of Ecology 98:302–311.

Terborgh, J., et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Terborgh, J., L. Lopez, and J. Tello. 1997. Bird communities in transition: the Lago Guri islands. Ecology 78:1494–1501.

Thomas, H. L., P. A. Hockey, and G. S. Cumming. 2015. Solving the challenges of monitoring mobile populations: insights from studies of waterbirds in southern Africa. Ostrich 86:169–178.

Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton. 2012. mvabund–an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution 3:471–474.

Warton, D. I., S. D. Foster, G. De'ath, J. Stoklosa, and P. K. Dunstan. 2015. Model-based thinking for community ecology. Plant Ecology 216:669–682.

Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution 3:89–101.

Weber, M. J., and M. L. Brown. 2016. Effects of resource pulses on nutrient availability, ecosystem productivity, and temporal variability following a stochastic disturbance in eutrophic glacial lakes. Hydrobiologia 771:165–177.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. Ecological Monographs 80:125–151.

DATA AVAILABILITY

Data are available from Dryad: https://doi.org/10.5061/dryad.w0vt4b8rd.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3668/full