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Back to Africa: monitoring post-hydropower restoration to facilitate reintroduction of an extinct-in-the-wild amphibian

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Citation: Vandvik, V., I. E. Måren, H. J. Ndangalasi, J. Taplin, F. Mbago, and J. C. Lovett. 2014. Back to Africa: monitoring post-hydropower restoration to facilitate reintroduction of an extinct-in-the-wild amphibian. Ecosphere 5(8):95. http://dx.doi.org/10.1890/ES14-00093.1

Abstract. Monitoring of the ecological efficiency of different restoration and mitigation measures is important to inform decision-making but can be challenging, especially in remote and low-resource settings. Species composition of the vegetation is sensitive to environmental variation, and can thus be used in restoration assessment, but this requires statistical approaches that can accommodate multivariate responses. We use principal response curves (PRC) to assess the efficiency of post-hydropower mitigation measures installed to secure the reintroduction of an extinct-in-the-wild amphibian back into its only native habitat.

The endemic ovoviviparous Kihansi spray toad *Nectophrynoides asperginis* is only known from a wetland in the Lower Kihansi River Gorge in the Eastern Arc Mountains in Tanzania. River flow was diverted from the gorge for hydropower production in 1999, causing the spray wetland to desiccate, consequently threatening the toad and other plant and animal species dependent on the spray-zone habitat. To mitigate the toad population collapse, a sprinkler system was installed over a limited section of the original spray-zone wetlands to mimic the waterfall spray and toads were taken to the USA for ex situ breeding. The decline, extinction, ex situ breeding, and planned reintroduction of the species has driven substantial research on Kihansi spray toad biology. In contrast, the efficiency of the mitigation measures in restoring the spray-zone wetland habitat required for its successful reintroduction has not been formally evaluated.

Here, we analyze re-sampled vegetation data from the spray-zone wetland over a period of eight years by means of principal response curves to investigate if the post-hydropower mitigation measures have successfully restored the pre-hydropower ecosystem. The results show that the spray-zone vegetation is recovering. The wetland flora and especially species important to the Kihansi spray toad have increased and the restored ecosystem has stabilized, favoring the reintroduction of the Kihansi spray toad to its native habitat. However, the wetland ecosystem is not restored entirely and continued mitigation measures are needed. Continued monitoring is essential to support evidence-based restoration, and we conclude that assessment based on vegetation monitoring coupled with principal response curve analyses provides a cost-effective and efficient monitoring tool for such projects.

Key words: Eastern Arc Mountains; endemic amphibians; hydropower development; Kihansi spray toad; mitigation; *Nectophrynoides asperginis*; principal response curves; restoration assessment; Tanzania; wetland habitat.

Received 28 March 2014; revised 20 May 2014; accepted 28 May 2014; final version received 26 June 2014; **published** 11 August 2014. Corresponding Editor: R. Parmenter.

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Introduction

Enabling economic and social development whilst retaining high environmental values is central to the principle of sustainability (UN 1987), but activities under these three pillars of sustainability are often in conflict. Balancing nature conservation and development is challenging (Myers et al. 2000), especially in high diversity–high demand settings such as in Eastern Africa, and may be seen as a 'wicked problem' (Rittel and Webber 1973). Provisioning of energy from environmentally sound technologies is critical for economic development in Africa and hydropower offers a reliable way of doing this (Moss 2013). Globally, dams for irrigation, flood mitigation, and hydropower now hold nearly six times as much water in storage as occurs in free-flowing rivers (MEA 2005, Kareiva et al. 2007). Hydropower projects have typically been associated with negative biological impacts related to flooding of the reservoir impounded by the dam (Bergkamp et al. 2000). Much less attention has been paid to the immediate downstream effects of dams, such as the loss of waterfall spray-zones (but see Brassard et al. 1971, Odland et al. 1991, Björk et al. 2009).

The Lower Kihansi Hydropower Project (LKHP) in the Udzungwa Mountains in Tanzania is a model example of the application of technology to minimize environmental impact (Alam et al. 1995, NORPLAN 1995, 2001, 2002). However, although the geographic extent of the project is relatively small, it is located in a biodiversity hotspot where almost any development potentially has a substantial negative impact on biodiversity (Myers 1988, Fjeldså and Lovett 1997, Myers et al. 2000, Brooks et al. 2002, Burgess et al. 2004). The Udzungwa Mountains are exceptionally rich in species of restricted range size (Lovett and Wasser 1993, Burgess et al. 1998) and the forests in the Kihansi and Udagaji Gorges contain many Eastern Arc endemics and globally threatened plants (Lovett et al. 1997, Vollesen 2000, Cheek 2003, Burgess et al. 2004, Davis and Mvungi 2004, Rija et al. 2011) and animals (Poynton et al. 1998, Zilihona et al. 1998, Dinesen et al. 2001, Menegon et al. 2004, Cordeiro et al. 2006, Menegon 2008), including the ovoviviparous Kihansi spray toad *Nectophrynoides asperginis* (Poynton et al. 1998, Taplin et al. 1999, Channing et al. 2006). At the time of its discovery in 1996 the Kihansi spray toad occurred in a spray wetland habitat of about 4 ha maintained by spray from falls on the Kihansi River. After the LKHP's start-up of hydropower production in 1999, river flow was diverted causing the habitat to desiccate, threatening plants and animals dependent on the spray-zone habitat. Due to alarming declines in population numbers and a subsequent population crash in late 2003, variously attributed to pesticide use upstream, chytrid fungus, or safari ants (*Dorylus* sp.), the Kihansi spray toad was declared "Extinct in the Wild" by the IUCN in October 2009 (IUCN 2014). Fortunately, in 2000 a population of 499 toads was collected and transferred to the Bronx Zoo, and later also the Toledo Zoo, in the USA for ex situ breeding. Today, this constitutes the largest captive population of an "Extinct in the Wild" amphibian species in the World (Rija et al. 2010). This ex situ population constitutes the core element in the re-introduction plans, which started in August 2010 when 100 individuals were transported from the Bronx Zoo and Toledo Zoo to a transit lab in Dar es Salaam. In October 2012, the reintroduction of 2,500 toads to their native Tanzanian wetland habitat in the Kihansi Gorge took place. The reintroduction plan predicts a return of approximately 4,000 animals annually to Tanzania. Much of the research focus on saving the toad from extinction has been aimed at investigating diseases and pathology (Rija et al. 2010), pesticides and environmental toxins (Chanson et al. 2008) and biological attacks (Weldon and du Preez 2004, Weldon et al. 2004). As pointed out by Channing et al. (2006), it is ironic that the Kihansi spray toad is both Africa's most well-studied amphibian and its most endangered, yet knowledge of its only known habitat in the Kihansi catchment remains patchy, at best.

The successful reintroduction of the toad back into the gorge is contingent on the restoration and subsequent conservation the toad's wetland habitat. Towards this end, an elaborate sprinkler system was installed in 2000/2001 over a limited section of the original spray zone wetlands to mimic the original waterfall spray. Up till now, the effectiveness of this artificial misting of the reduced waterfall spray-zone habitat is still unclear (Krajick 2006). The success or failure of the sprinkler system as a mitigation measure needs to be evaluated against the ultimate restoration goal; to fulfil the habitat requirements and ecological needs of the Kihansi spray toad and to enable the long-term survival of the toad population in the gorge. Unfortunately, data on the environmental conditions in the gorge pre-diversion, or on the environmental requirements of the toad in the wild, are scant. However, there are data on the plant community composition pre-diversion (Quinn et al. 2005) and observational evidence on the toad's use of different plant species (Channing et al. 2006). In this study we therefore use plant species composition monitoring in combination with information from these two sources as a surrogate for environmental information and ask: Has the installation of the sprinkler system restored plant species composition in the former waterfall spray zone? And specifically, have plant species known to be used by the Kihansi spray toad increased, suggesting that the restored habitat will be suitable for the toads?

The restoration goal in this case is thus to optimize habitat conditions and thus species composition towards a specific target, rather than to maximize it (SER 2004). To evaluate restoration success towards this goal we used the community-based statistical approach principal response curves (PRC), which analyses the deviations over time between the species composition (or other multivariate responses) of a control treatment versus one or more experimental treatments (van den Brink and ter Braak 1997, 1998, van den Brink et al. 2003). We explicitly incorporated information on toad habitat use and pre-diversion species composition (Quinn et al. 2005, Channing et al. 2006) into the assessment by combining the PRC analyses with a species classification, following Poulin et al. (2012).

Material and Methods

Study area

The Kihansi River Gorge (Fig. 1) is situated in the Udzungwa Mountains (07°15′–08°45′ S, 35°00′–37°00′ E) which is part of an extensive upland area formed by fusion of the ancient Mozambique shield of Usagaran biotite gneiss to the south-east and Archaean granites to the north-west, followed by uplift and faulting (Rodgers and Homewood 1982). They cover about 10,000 km^2 rising from 300 m above sea level (asl) in the east to around 2,500 m asl in the west and are under direct climatic influence of the Indian Ocean (Lovett 1990). The rainfall is monomodal with a major peak in April and smaller peak in January. The average annual rainfall is 1,800 mm, the mean daily maximum and minimum temperatures are 25°C and 13°C, respectively. The vegetation changes from woodland to thicket and grassland, as rainfall drops rapidly to the rain shadow in the west (Rodgers and Homewood 1982), with much local variation. The area is largely covered in moist forest of which about 450 km^2 still remains forested.

The Kihansi River drains a catchment covering 607 km^2 of the upland plateau, of which 73% is under cultivation, 10% is grassland, 14% is moist forest, 3% is dense bush land and 0.5% is open woodland (Minja 1995). The Kihansi River Gorge is 6 km long, runs north-south, from an elevation of 300 m to 1,100 m. It contains about 90 ha of closed canopy high forest, most of which consists of mixed tree species (Lovett et al. 1997). The forest is rich in restricted range plant species with several new taxa discovered during the course of environmental monitoring for the LKHP (Lovett et al. 1997). The Kihansi River was diverted for the Lower Kihansi Hydropower Project in 1999 and flows reduced from 16.3 to 1.5–2.0 m^{3}sec^{-1}. The concrete gravity dam on the Kihansi River has a height of 25 m and a length of 200 m, the inundated area is about 26 ha when the reservoir is full and creates a reservoir with a storage volume of 1 million cubic meters. The turbines use the 850 m drop in the Kihansi Gorge and return the water to the river about 6 km downstream. It generates 180 MW, providing 13% of Tanzania's electricity.

The upper part of the gorge is bounded by a tall cliff, over which the Kihansi River fell prior to

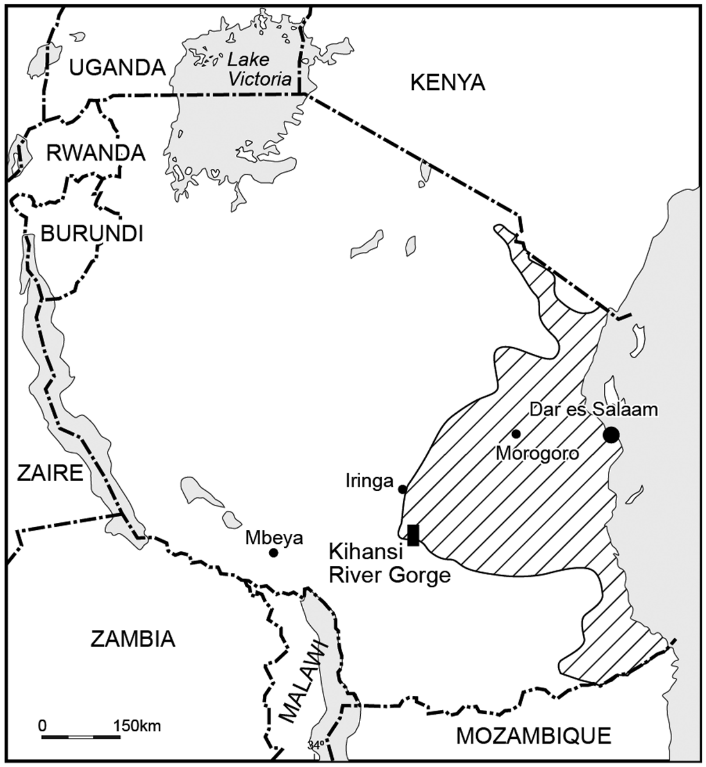

Fig. 1. Map showing the location of the study area, the Kihansi River Gorge in Tanzania, Africa. Hatched area delimitates the region of the Eastern Arc Mountains and the coastal forests of Tanzania.

the hydropower project. The Upper Spray Wetland (USW) with an area of approximately 6,090 m^2 was the largest wetland in the Kihansi Gorge (see Appendix) and the main habitat for Kihansi spray toad *Nectophrynoides asperginis* (Poynton et al. 1998, Taplin et al. 1999, Zilihona and Nummelin 2001). Prior to the hydropower project, in areas where there was constant spray, growth of the forest was retarded and vegetation was dominated by a fertile boggy herbaceous wetland sward between 5 and 30 cm tall (usually 5–10 cm), dominated by *Selaginella kraussiana* with low growing grasses in the genus *Panicum,* together with *Alchemilla kiwuensis*, *Begonia oxyloba*, *Brilliantasia madagascariensis*, *Dymaria cordata*, *Impatiens* spp., *Rumex abyssinicus*, *Streptocarpus buchananii* and the fern *Tectaria gemmifera* (Poynton et al. 1998, Quinn et al. 2005). Species like *Cyperus exaltatus* and *Basananthe hanningtoniana* were only observed in a 1998 pre-project survey (Quinn et al. 2005). The spray zone was characterized by lower and more stable temperatures and higher and more stable relative humidity, with a mean spray precipitation of 300 mm/day.

Diversion impacts and mitigation measures

During the first year following commissioning of the hydropower project in 2000, several of the spray wetlands in the Kihansi Gorge suffered severe desiccation and before emergency mitigation measures were put in place, the available habitat of the Kihansi spray toad was dramatically reduced. A system of sprinklers at USW, consisting of nozzles mounted 1–2 m above the ground to obtain a minimum input of 70 mm/day, was installed in March 2001. This was the precipitation input estimated in the center of the USW under a natural river flow of ca. 20 m^3/s. The system covers an area of approximately 2,900 m^2, and uses approximately 6.5 l/s of water obtained from the Jabali intake (a small stream located on the west bank of the Kihansi River) and a portion of the minimum bypass flow from the dam. Temperatures and relative humidity (RH) are relatively constant in the spray wetlands, under the artificial sprinklers, examples being 20°C, 95% RH (April 2001), 16°C, 90% RH (June 2001) and 15°C, 80% RH (August 2001) (Channing et al. 2006). Disturbance caused by human presence (damage to the vegetation and the soil structure) was partly mitigated by constructing stepping stone walkways in the USW in July 2001, and a total of ca. 170 m of walkways were installed in the Upper Spray Wetland.

Experimental design, sampling, and data

In the Upper Spray Wetland (USW) eight permanent blocks, each ca. 100 m^2, were established in April of 2001 (Fig. A1). Six blocks were placed in the sprinkled area while the remaining two were established in the un-sprinkled area towards the edge of the wetland as controls. In each block, 10 1-m^2 quadrats were randomly distributed, and all species within the quadrat were recorded and their percentage cover estimated. Sampling of the vegetation started in April 2001 and was repeated yearly through 2008, with the exception of 2006, yielding seven repeated measurements.

A total of 77 species in 55 genera, belonging to 28 families were recorded over the eight-year period (where the number of species per family, for families with two or more species, are shown in parenthesis); Poaceae (21), Asteraceae (11), Pteridaceae (6), Acanthaceae (6), Balsaminaceae (3), Polygonaceae (3), Urticaceae (3), Cyperaceae (2), Hypericaceae (2), Melastomataceae (2), Passifloraceae (2), Rubiaceae (2), and Zingiberaceae (2). Only 12 species were found in all years, indicating a high species turnover in the years after mitigation measures were imposed. The most frequently occurring species were *Brillantaisia madagascariensis, Microstegium vagans, Selaginella kraussiana, Polygonum salicifolia, Pilea rivularis, Drymaria cordata* and *Leersia hexandria*. Weedy species such as *Ageratum conyzoides, Alchemilla kiwuensis, Commelina bengalensis, Crassocephalum crepidioides* and *Helichrysum schimperi* were frequent right at the beginning of post-diversion mitigation in 2000 but no longer present in 2008. Specimens of each species were collected and confirmation of their identification made at the Herbarium of the Department of Botany, University of Dar es Salaam, Tanzania, and the Royal Botanic Gardens, Kew, England. Voucher specimens were also deposited at the Herbarium for future reference. The nomenclature used follows Hubbard et al. (1952 et seq.) and Exell and Launert (1970).

Numerical analyses

We tested the mitigation effect on community composition using principal response curves (PRC) (van den Brink and ter Braak 1997, 1998, van den Brink et al. 2003). PRC is a derivative of RDA (ter Braak 1994) that analyses the effect through time of one or more treatments relative to a control. It is coded as a partial RDA that allows for time-specific treatment effects (e.g., time × mitigation) while controlling for the overall temporal trend (time) and variation among experimental blocks. Thus, the hypothesis that the mitigation treatment affects the species composition of the wetland was tested by a simple PRC analysis, contrasting quadrats from sprinkled blocks with quadrats from controls. To assess variation in responses among treatment blocks the main mitigation effects over time was partialled out, and the mitigation effects in the different blocks were coded as different 'treatments'.

Treatment effects (C_{dt}) quantify the compositional difference between quadrats of treated blocks and controls at each sampling date, and temporal trends can be visualized by plotting C_{dt} against time. The species weights (b_k) can be interpreted as the affinity of the species with this diagram; species with high positive values follow the overall community response and species with high negative values respond in the opposite way. In addition to individual species scores, we also calculated and displayed mean species scores (following Poulin et al. 2012) of four ecologically important plant groups: (1) group A: species that were observed to be used by the Kihansi spray toad for different life functions (e.g., foraging habitat for adult and juvenile frogs, shelter, maintain humidity); (2) group B: species that were common in the wetlands pre-diversion; (3) group C: species classified as edge, grassland, or forest species; and finally (4) group D: ruderal species (Quinn et al. 2005, Channing et al. 2006).

Monte Carlo permutation tests were used to evaluate statistical significances. In general, permutation schemes were set up to isolate the

Table 1. Summary of RDA and PRC analyses quantifying and testing the effects of experimental blocks, time and mitigation treatments on the spray-zone vegetation composition. The variance explained by each model is given, along with *p*-values from Monte Carlo permutation tests.

Testing for effect of	Variables	Covariables	Variance	*p* (999)
Blocks	B		16.7	<0.001
Time	T		7.2	0.003
Mitigation treatment over time	M × T	B + T	5.5	<0.001
Differential successional trends among blocks	B × T	B + T	20.2	<0.001
Total variance explained	B × T		44.0	<0.001

Notes: The model for each analysis is given by the 'Variables' and 'Covariables'. Abbreviations are: B = a set of dummy variables representing the eight experimental blocks, T = set of dummy variables representing time (years), M = mitigation treatment or control. In the Monte Carlo permutation tests, the quadrate data was permuted freely across blocks within years for all tests except for the main effects of time, which were tested by permuting the data from different years freely across years within blocks. In all cases, 999 permutations were used. n = 560.

variable of interest while performing permutations at the appropriate scale. Change over time was thus tested by permuting different sampling years freely within blocks, whereas the PRC axes were tested by permuting entire time-series freely among blocks. Changes in treatment effects through time were evaluated in sequential tests where seven data subsets (one per year) were constructed and the first RDA axis in each of these tested by permuting the quadrate data freely among blocks. The overall compositional variation between years was partialled out in all PRC analyses, and permutation tests were run with 999 permutations. These analyses were performed using the software package CANOCO 4.5 (ter Braak and Šmilauer 2002), and ordination diagrams were drawn in CanoDraw 4 (ter Braak and Šmilauer 2002) and PRC diagrams in Sigma Plot version 5 (SPSS 1999).

Results

A dramatic shift in species composition occurred over the first two years after sprinkler installation, followed by a stabilization of the new post-mitigation plant community over the next six years (Tables 1 and 2, Fig. 2). This effect size was generally stronger in blocks near the waterfall (cf. Fig. 2 and Appendix: Fig. A1). The new community that assembled in the sprinkled area was characterized by increased abundances of a number of characteristic spray wetland species, as well as of species that constituted important components of the pre-diversion habitat of the Kihansi spray toad such as *Selaginella kraussiana*, *Pilea rivularis*, *Panicum hymeniochilum*, *P. parvifolium*, *Leersia hexandra* and *Impatiens* species (negative scores on PRC axis 1; Fig. 2a; see also Fig. 3, Appendix: Table A1). The estimated species responses imply a ca. 1.5 to 2.5-fold increase in the abundance of these species in treated blocks relative to in controls; (proportional change in cover = $e^{bk \times Cdt}$). In contrast, relatively few species declined in abundance in response to sprinkler installation, but these include both the characteristic spray-zone grasses *Panicum monticolum* and *P. trichocladum*, as well as widespread ruderal species, e.g., *Commelina bengalensis* and *Stephania abyssinica* (positive scores on PRC axis 1; Fig. 2a, Appendix: Table A1). The responses of the pre-defined ecological species groups show that the community shift instigated by the sprinklers led to

Table 2. Summary of the effect of the mitigation treatment on the vegetation composition over time. The variance explained by each model is given, along with the F-ratio, and *p*-values from Monte Carlo permutation tests.

	Mitigation treatment effect		
Year	Variance	F-ratio	*p* (999)
2001	11.0	9.7	<0.001
2002	20.0	19.6	<0.001
2003	11.4	10.0	<0.001
2004	8.3	7.0	<0.001
2005	10.7	9.3	<0.001
2007	10.6	9.2	<0.001
2008	14.2	12.9	<0.001
Whole time-series	6.1	38.6	<0.001

Notes: The model for the whole time-series is described under 'Mitigation treatment over time' in Table 1. The Monte Carlo permutation tests were set up so that whole time-series were permuted freely across blocks in the whole time-series analysis, and individual quadrates were permuted freely across blocks in each of the 2001–2008 analyses. In all cases, 999 permutations were used. n = 80 per year and 560 overall.

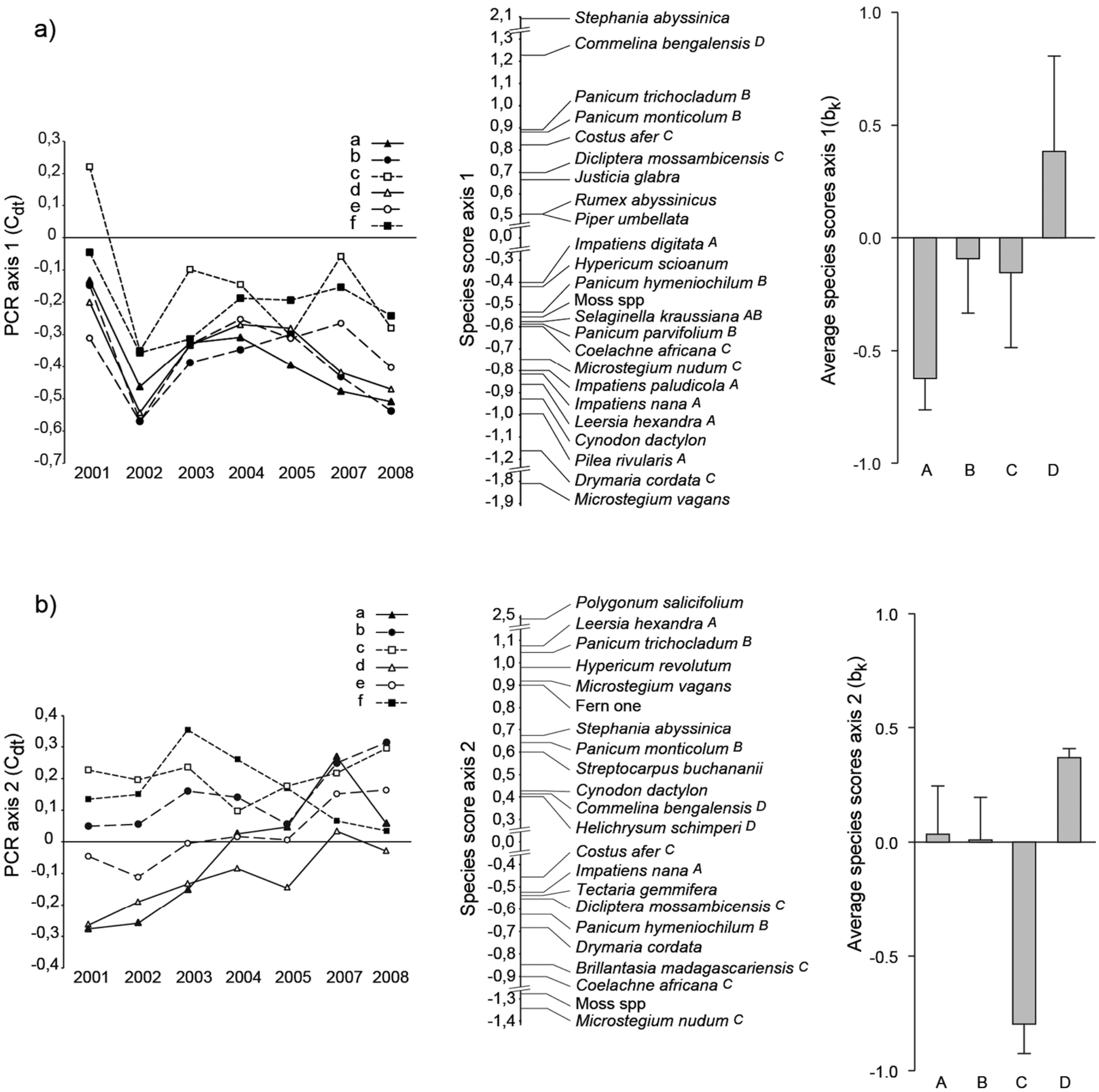

Fig. 2. Principal response curve (PRC) analyses showing the overall impact of the mitigation treatment on the spray-zone vegetation (C_{dt}), the responses of selected taxa, and the mean responses (± standard deviations) of ecologically important plant groups on (a) PRC axis 1 and (b) PRC axis 2. Letters a–f refer to the experimentally sprinkled blocks; control blocks fall on the x axis and are not shown. Species codes used in superscripts and for classifying species into groups for the bars plots on the left-hand panels: A = species used by the Kihansi spray toad (Channing et al. 2006), B = species characteristic of spray-zone wetlands (Quinn et al. 2005), C = forest and edge species, and D = ruderal species (Quinn et al. 2005). The significance of the mitigation treatment over time is given in Table 1, the treatment effects per year are given in Table 2, and individual species scores are given in Appendix: Table A1.

substantially increased average abundance of species used by the Kihansi spray toad (estimated average responses imply a ca. 1.3-fold increase, group A; Fig. 2a) paralleled by a decrease in ruderal species (ca. 0.8-fold decrease, group D; Fig. 2a). In contrast, there was no clear

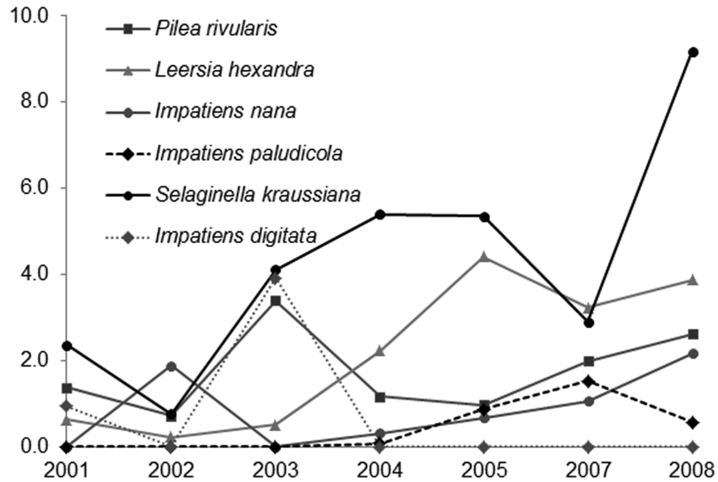

Fig. 3. Mean abundance (% cover) of plant species known to be used by the Kihansi spray toad (Channing et al. 2006) recorded in the sprinkled blocks (a–f) over seven years of vegetation monitoring after the mitigation treatment was installed in the Upper Kihansi Spray zone, Tanzania.

trend in the wetland and edge species (groups B and C; Fig. 2a).

In addition to this main shift in species composition there was also a secondary effect, where the areas closest to the waterfall (blocks a, d, and e in Fig. 2b) grew more similar to the rest of the treated area over time. This is reflected in a relative decline in species associated with grassland-, bush land- and forest margins such as *Microstegium nudum*, *Coelachne africana, Brillantasia madagascariensis*, *Drymaria cordata*, *Dicliptera mossambicensis*, *Impatiens nana* and mosses in these blocks (negative scores on PRC axis 2, implying a ca. 0.9-fold decrease, group C; Fig. 2b).

After the second year of mitigation measures, the species composition shift was relatively slower, and more affected by year-to-year and block-to-block differences. However, there is a consistent trend for the effect to be stronger in the wetter end of the gradient, as blocks a and d respond strongly, and blocks c and f respond relatively moderately to the mitigation measures.

Discussion

Restoration of the Kihansi Gorge Wetland

Our results demonstrate that it is possible to restore at least some aspects of the ecological integrity of spray-zone habitats that have been degraded by reduced water flow following hydropower dam construction. The wetland was reported to have changed rapidly after the dam was created and the waterfall diverted, but when the sprinkler system was installed, the species composition in the former waterfall spray-zone reverted equally rapidly towards a community characterized by high abundances of some characteristic wetland species (sensu Quinn et al. 2005) and, encouragingly, especially of species used by the Kihansi spray toad (Channing et al. 2006). The abundances of grassland, forest edge and ruderal species decreased markedly. The main directional compositional changes took place over the first two years after mitigation, and the species composition change later stabilized. While the wetland is not fully restored, this bodes well for the future of the toad's habitat in the Kihansi Gorge. Additionally, we saw a consistent trend for the effect of the mitigation measures to be strongest in the formerly wetter end of the gradient. As the current spray intensity (sprinkling treatment) is equal over the whole mitigation zone, this suggests greater receptivity in the vegetation blocks that were situated in lower/wetter areas, i.e., closer to the waterfall spray-zone prior to the hydropower project. The homogenization of the sprinkled wetland during the study period is expected, as the sprinkler system exposes the entire wetland to the same artificial precipitation regime, but it also suggests the wetland is relatively resilient and could change quickly in response to future adjustments in the precipitation regime. In sum, the vegetation development under the first seven years of mitigation demonstrates that it is possible to restore at least some aspects of wetland functioning by means of a sprinkling system.

In order to maintain a viable toad population under natural conditions, the habitat must provide shelter, high humidity and abundant food in the form of small insects for adult toads, and very small insects for juveniles. Adult toads feed on the top leaves of broad-leafed plants, within the grass or moss vegetation, or on wet rock faces (Channing et al. 2006). The structure of the habitat should include low growing wetland vegetation (e.g., grasses, small herbs and the spike-moss *Selaginella kraussiana*) and wet rock faces. We do, however, lack more specific data on the plant species preferences of the toads in their former natural habitat. Additionally, we do not know if a differentiated sprinkler pressure across the spray zone could have mimicked the pre-diversion spray-zone conditions better than what is presently operating in the gorge, nor do we know the consequences of spatial or temporal variation in the precipitation for the toad population. Our results show that the spray-zone vegetation is relatively resilient and the area may possibly be increased by adjusting the sprinkler system. Consequently, the mitigation measures have succeeded in restoring aspects of the wetland ecosystem that are likely to facilitate the re-introduction of the Kihansi spray toad back into its native habitat. The long-term success of any restoration programme is critically dependent on our ability to monitor and assess ecosystem responses to restoration and mitigation measures and strategies over time, as well as on our abilities to use the results to modify or continue restoration or management practices. In the case of the Kihansi spray toad we advise continued vegetation and toad population monitoring as we still need ecological information that can be used to adjust operation settings and maintenance of the sprinkler system.

Principal response curves as a tool in restoration monitoring

Comprehensive environmental monitoring can be both costly and prone to operation errors, especially in remote and low-resource settings. Plant community composition is sensitive to environmental variation, and allows low-tech and relatively cost-efficient monitoring. Efficient statistical assessment and display of the resulting multivariate monitoring data is a challenge, however, as the ecological information often resides in the species-specific responses and are lost in summary statistics such as species richness, evenness, biomass, etc. (SER 2004, Poulin et al. 2012). Principal response curves (van den Brink and ter Braak 1997, 1998, van den Brink et al. 2003) offers a rigorous statistical framework and attractive graphical opportunities for multivariate response variables in experimental settings. This makes the method well-suited for usage in restoration ecology, as exemplified by recent applications assessing the efficiency of restoration of habitats degraded by invasive species (Måren et al. 2008, Alday et al. 2013*a*, *b*), overgrazing (Pakeman et al. 2003), land-use abandonment (Vandvik 2004, Vandvik et al. 2005, Maccherini et al. 2007, Galvánek and Lepš 2009, Andersen et al. 2010), forestry (Wu et al. 2011) and mining (Alday et al. 2010). PRCs are relatively demanding in regards to study design, however, as the method is developed for before-after control-impact design experiments, but see Heegaard and Vandvik (2004), for an application in a spatial context.

The Society for Ecological Restoration International Science and Policy Working Group (SER 2004) recommend including the target natural ecosystems as references sites for restoration, and points out that this is especially important in cases where the restoration goal is not necessarily to maximize biodiversity, but rather to optimize it for a specific ecological function. Assessment of restoration success relative to a target community (rather than relative to a pre-restoration degraded state) is easily accommodated in PRC; it is merely a matter of choosing the appropriate 'control' sites included in the analysis (see Poulin et al. 2012). However, the methodological rigor of the PRC may limit its applicability. Before-after-control-impact designs may not always be achievable, for example if the target habitat no longer exists (there was only one Kihansi Gorge) or if the monitoring programme was not in place before the habitat was degraded (again, this was the case in the Kihansi Gorge). In such cases, the species classification scheme proposed by Poulin et al. (2012) offers an attractive alternative, as illustrated by our analyses of the Kihansi Gorge vegetation data. Pre-treatment data did not exist, and we were thus forced to start the time-series at the first data point available, and we did not have undegraded 'target' sites, and were thus forced to use the degraded spray-zone vegetation as our control and monitor succession away from the degraded state. But we had information on species characteristic of the pre-diversion spray zone, and of species used by the Kihansi spray toad before it went extinct in the wild. By including these data as basis of a species' classification used in conjunction with the PRC, following Poulin et al. (2012), we were able to assess the improvement of the spray toad habitat in response to the sprinkler treatment. The results suggest that the conditions for the toad have improved substantially over the course of the experiment, and also that conditions have stabilized over the last few years of monitoring.

Implications for policy

The LKHP appears on paper to be a relatively environmentally benign development project, but in spite of its small size, the project has had drastic impacts on biodiversity. Despite recognition as an IUCN Global Biodiversity Hotspot, the biodiversity of East African rainforests is currently being lost at an unprecedented rate, primarily due to increasing human-induced disturbance related to energy and food production. This begs pressing questions of what trade-offs we are willing to accept, and what mitigation measures do actually work? There are clear transferable applications of our results and methods to other areas where dam construction and river flow diversion has or will take place. The Kihansi Gorge case illustrates the trade-offs involved in converting natural capital to other uses. Tanzania has immediate needs for economic growth and poverty alleviation. The Eastern Arc Mountains and Eastern African Coastal Forests biodiversity hotspot is home to many endemic species; at least 1400 plants, 50 reptiles, 33 amphibians, 22 birds and 16 mammals, many of which are threatened by global extinction. Putting a hydropower project in the midst of such a hotspot highlights the contradictory interests of development and nature conservation. Stronger policies and institutions that can integrate biodiversity conservation into regional and national development in a truly sustainable framework are urgently needed.

Hydropower projects which include dam construction are often contested by local inhabitants and conservation agencies. The LKHP highlights the vital importance of initial comprehensive environmental baseline studies and impact assessment (EIA) for avoiding ecological disasters, as well as maintaining economic viability, of large development projects. The original EIA, conducted prior to the environmental monitoring programme, did not include field work at the base of the Kihansi Falls, the area most severely affected by this hydropower-project, although we know that such areas often contain unique or rare plant and animal species (Brassard et al. 1971, Odland et al. 1991).

The LKHP shares many features with the classic Tennessee Valley Authority's Tellico Dam Project in the USA, where the Tellico Dam construction was temporarily halted following the discovery of a new fish species, the Snail Darter (*Percina tanasi*), which was declared an endangered species under the 1973 Endangered Species Act (Murchinson 2007). The two projects differ, however, on two crucial points: (1) the Tellico project was economically and politically controversial and the discovery of the endangered fish species became a means for the opponents to stop the project (Weeler and McDonald 1986) whereas the discovery of the Kihansi spray toad had no impact on the LKHP; and (2) despite some weaknesses, the Endangered Species Act is one of the world's most powerful species preservation laws, of which Tanzania does not have an equivalent.

Alarmingly, restricted-range species tend to be the most poorly represented biodiversity targets, especially in analyses using coarse scale biodiversity surrogates. Rarity, poor taxonomy, lack of adequate data, and omission errors in conservation analyses make restricted-range species hot candidates for unrecorded extinction (Lawler et al. 2003, Nogueira et al. 2010). Amphibian declines and extinctions are global and rapid (Mendelson et al. 2006) due to habitat loss, pollution and commercial overexploitation. In particular, the conservation of amphibians is suffering from land-use changes on a global scale and ex situ programs may be the only option to prevent extinction for many species (Mendelson et al. 2006). There is a slight possibility that the Kihansi spray toad might be found elsewhere in the Eastern Arc Mountains as new species and extensions of distributions continue to be found. However, there are no rivers on the escarpment of comparable volume to the Kihansi River and no known areas where a large volume of spray maintains a habitat comparable to the Kihansi Gorge wetlands. Further, the Kihansi River Gorge was home to other endemic and severely range-restricted plants (Lovett et al. 1997, Vollesen 2000, Cheek 2003, Burgess et al. 2004, Davis and Mvungi 2004, Rija et al. 2011) and animals (Poynton et al. 1998, Zilihona et al. 1998, Dinesen et al. 2001, Menegon et al. 2004, Cordeiro et al. 2006, Menegon 2008) that have, unfortunately, received much less attention than the Kihansi spray toad. The fate of these species after the diversion and the effectiveness of the irrigation system in mitigating negative impacts remain uncertain (see Davis and Mvungi 2004) and merit further study.

Acknowledgments

The study of The Lower Kihansi Hydropower Project was partly funded by the Norwegian Development Agency (NORAD) and the World Bank. Engineers from NORPLAN A/S installed the sprinkler system. We are grateful to Siobain Finlow-Bates, Ole Vallevik, George Mosha, Walter Gomez and Boniface Mhoro for support and assistance. Financial support to finalize this publication was given by The Nile Basin Research Programme (NBRP), funded by the Norwegian Foreign Service, and the Norwegian Research Council (FRIMUF project 187487). We thank Kjell Helge Sjøstrøm for assistance with figures, and Alan Channing and an anonymous reviewer for constructive comments on a previous version of the paper.

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Supplemental Material

Appendix

This appendix contains a brief description of the sprayzone wetland habitats in the Kihansi River Gorge pre-diversion, an overview of the ecology, abundance, and response of each individual species to the mitigation treatment (Table A1), and an aerial photograph of the study site (Fig. A1).

A brief description of the five discrete areas of spray wetland habitat in the Kihansi River Gorge

Upper Spray Wetland.—This lies on the east bank of the Kihansi River at an altitude of 850 and 950 m asl. Before diversion this wetland covered an area of 70 m × 90 m. The northern part consists of rock faces. The accessible section is covered by low vegetation near the falls, such as the moss *Selaginella kraussiana* and *Panicum* grasses, and higher vegetation such as *Costus afer* further from the falls. A large rock on the eastern slope is termed 'Old Frog Rock', as spray toads were clustered there before the diversion. This is the site where the mitigation treatment sprinkling system is installed (see Fig. A1).

Lower Spray Wetland.—This is located below the USW, on the east side of the river, between 750 and 800 m asl. Before diversion it covered an area of 100 m × 70 m. It is a steep area with less uniform vegetation than the Upper Spray Wetland. A small section of the wetland is found on the west side of the river, where the Mhalala River joins the Kihansi River.

Mid-gorge Spray Wetland.—This lies on the west bank of the river at 650 m asl. It is small; 4 m × 10 m, and covered by a dense mat of tangled vegetation. The wetland is surrounded by tall forest.

Mhalala Spray Wetland.—This is the only spray wetland not along the Kihansi River. It is situated about 100 m west of the Kihansi River, at 850 m asl, and receives spray from the small Mhalala River. The wetland is small, 24 m × 10 m, and steep. The Mhalala River has a catchment of only 16.6 km^2, but under natural flow conditions the spray was augmented by spray from the Kihansi falls, particularly in the wet season.

Main Falls Spray Wetland.—This small wetland is situated at the base of the main falls, at 1000 m asl. It is mostly boulders and rock slopes, with some low vegetation. This wetland was only easily accessible after ladders and a bridge were constructed.

Table A1. The ecological characteristics (Ecology), number of occurrences (n), and principal response curve (PRC) axes 1 and 2 species scores (b_k values) of all taxa with more than 2% occurrence (35 out of 65 taxa) in the dataset. The Ecology column summarizes knowledge on whether the species is used by the Kihansi spray toad (A), was characteristic of spray-zone vegetation pre-diversion (B), is known as an edge, grassland, or forest species (C), or is known as a ruderal species (D), according to Quinn et al. (2005) and Channing et al. (2006). Species with positive PRC axis 1 and 2 scores have responses that correlate positively with the trend in the PRC diagram (in Fig. 2a and b, respectively), and vice versa.

Species	Ecology	n	PRC axis 1	PRC axis 2
Microstegium vagans		309	−1.81	0.92
Drymaria cordata	C	171	−1.16	−0.68
Pilea rivularis	A	148	−0.99	−0.20
Cynodon dactylon		37	−0.93	0.42
Leersia hexandra	A	120	−0.87	1.08
Impatiens nana	A	41	−0.81	−0.53
Impatiens paludicola	A	22	−0.80	0.29
Microstegium nudum	C	72	−0.75	−1.34
Coelachne africana	C	27	−0.60	−0.90
Panicum parvifolium	B	16	−0.59	0.23
Selaginella kraussiana	A/B	185	−0.58	0.27
Moss spp		46	−0.56	−1.28
Panicum hymeniochilum	B	15	−0.54	−0.62
Hypericum scioanum		23	−0.42	0.23
Impatiens digitata	A	28	−0.40	−0.38
Fern one		18	−0.06	0.90
Helichrysum schimperi	D	12	−0.03	0.40
Brillantasia madagascariensis	C	405	0.05	−0.85
Thelypteris dentata		37	0.06	−0.30
Panicum I	A/B	40	0.07	−0.29
Streptocarpus buchananii		72	0.10	0.60
Polygonum salicifolium		291	0.11	2.49
Tectaria gemmifera		21	0.19	−0.54
Vernonia auriculifera		12	0.24	0.03
Thunbergia alata		16	0.37	0.26
Hypericum revolutum		52	0.38	0.98
Rumex abyssinicus		13	0.51	−0.22
Piper umbellata		12	0.51	−0.27
Justicia glabra		17	0.67	−0.26
Dicliptera mossambicensis	C	13	0.70	−0.55
Costus afer	C	17	0.83	−0.46
Panicum monticolum	B	59	0.88	0.64
Panicum trichocladum	B	57	0.89	1.05
Commelina bengalensis	D	69	1.23	0.41
Stephania abyssinica		202	2.09	0.67

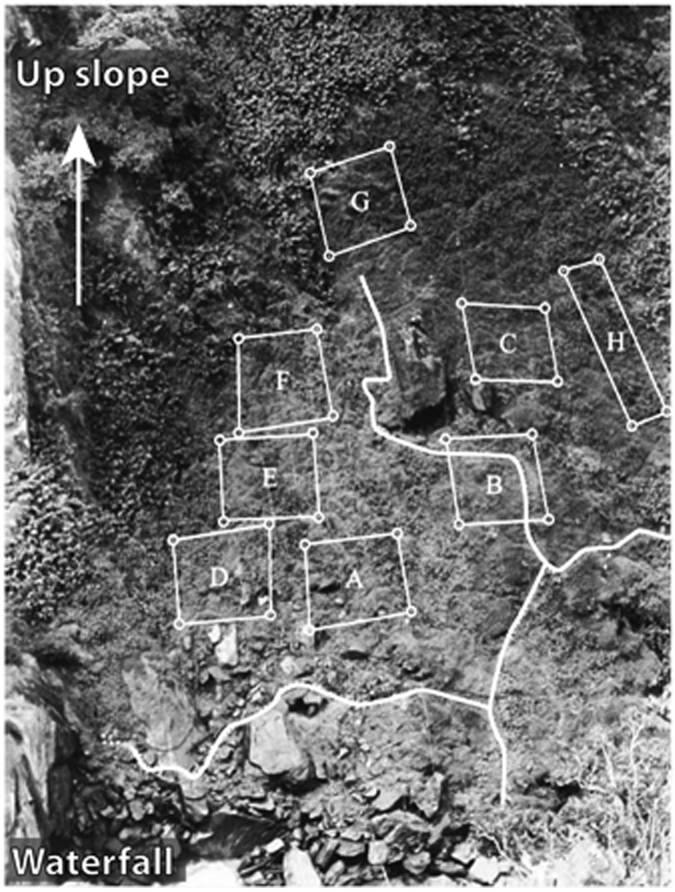

Fig. A1. Aerial photograph of the wetland at the Upper Spray Wetland in the Kihansi River Gorge with the position of the eight vegetation analysis blocks A–F and footpaths used for experimental treatments and analyses superimposed. The sprinkler system used for the mitigation treatment covers blocks A through F, whereas blocks G and H are unsprinkled controls.