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Original article

The dynamics of mountain rock pools – Are aquatic and terrestrial habitats alternative stable states?

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ABSTRACT

The theory of alternative stable states (ASS) proposes that ecosystems can exhibit multiple equilibria stabilised by positive feedback mechanisms. There are signs that terrestrial and aquatic habitats could exhibit ASS and we investigate this possibility in eroded basins on an isolated rock outcrop. The coverage of terrestrial and aquatic habitats on the Korannaberg Mountain in South Africa was quantified using GIS for three intervals between 1993 and 2011. Results confirmed that the proportional coverage of habitat states showed a consistent bimodal distribution over the study period, thereby supporting the ASS hypothesis. The depth of geological basins and the distance from the exposed cliff face were significantly associated with the proportion of aquatic habitat within the basins. These patterns were interpreted by hypothetical feedback mechanisms driven by basin inundation and wind erosion. Findings supported dual responses of habitat classes to basin parameters; a phenomenon often associated with ASS. Stability of aquatic and terrestrial habitats and the differential responses of these habitats to similar combinations of system parameters oppose the succession hypothesis and support the ASS hypothesis. These findings are consistent with unique diversity patterns demonstrated by previous studies and further justify the use of rock pools and vegetation patches as natural models in ecology and evolutionary biology research.

1. Introduction

The theory of alternative stable states (ASS) proposes that ecosystems can exhibit multiple equilibria stabilised by positive feedback mechanisms (Scheffer et al., 2001; Scheffer, 2009). Classic examples of this are found in both aquatic and terrestrial systems such as alternative turbid and clear water states in shallow lake systems (Ibelings et al., 2007; Scheffer, 1989) or the positive feedback between vegetation and precipitation considered important in the Sahel-Sahara (Foley et al., 2003). There is also evidence that intermittent streams and riverine wetlands represent alternative stable states enforced by substrate stabilisation by herbaceous vegetation (Heffernan, 2008). An extension of such substrate driven mechanisms would imply that terrestrial and aquatic habitat could potentially be alternative stable states. We investigate this idea with a case study based on habitat patches that occur in eroded basins on top of isolated rocky outcrops.

Biological diversity on rocky outcrops is often concentrated in discrete micro habitats (Porembski et al., 2000). These habitats are formed when patches of softer substrate weather at rates faster than the parent geology to form depressions (hereafter, referred to as basins) which, over time, may evolve into deep potholes in the surrounding bedrock. In some basins, substrate tends to accumulate allowing for colonization by terrestrial vegetation (Porembski and Barthlott, 2000) while similar depressions, where substrate is absent, can collect water after rainfall events transforming into aquatic habitats.

Due to their small size, structural simplicity and clear delineation, both terrestrial and aquatic habitat patches occurring in eroded basins are frequently used as model systems for ecological and evolutionary research (Altermatt and Edbert, 2010; De Meester et al., 2005; Krieger et al., 2003; Müller, 2007; Pajunen and Pajunen, 2003). Most studies, however, focus on either terrestrial or aquatic habitat patches and, to our knowledge, there are none that have simultaneously investigated both terrestrial and aquatic habitats and their interactions. Nonetheless, Jocque et al. (2010) speculated that sediment accumulation in aquatic rock pool habitats could, over time, facilitate colonization of the patch by terrestrial vegetation. Similarly, Vanschoenwinkel et al. (2008, 2009a)

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demonstrated the potential of wind and water erosion in removing sediment from rock pool basins, suggesting successional transitions between habitat types. This hypothesis, however, is not supported by empirical evidence.

In this study, we explore whether terrestrial and aquatic habitats in eroded basins represent two states on a successional continuum or two self-reinforcing ASS. To do this we, firstly, investigated the frequency distribution of proportional habitat types (terrestrial or aquatic) in separate basins over the 18 year duration of this study. A bimodal distribution which remains consistent over time, as predicted by ASS, would imply positive feedback mechanisms rather than a continuum between habitat types. Secondly, we explored whether the characteristics of the basins (area, depth and location on the rock shelf) affected the likelihood of either habitat type in each basin. If the two habitat classes represent ASS, we expect that deeper basins with smaller surface areas will mostly be aquatic habitats as they should be inundated for longer periods (due to low surface area-to-volume ratios), drowning any terrestrial vegetation. Additionally, marginal basins near the edge of the rock ledge would tend to be aquatic habitats as they are more susceptible to sediment mobilisation through wind and water runoff. Thirdly, we investigated whether habitat states respond uniformly to similar combinations of basin parameters. Lastly, we discussed different potential feedback mechanisms that complement the findings.

2. Methods

2.1. Study system

This study was carried out on a horizontal sandstone rock shelf on the north-western plateau of the Korannaberg Mountain (1700 m a.s.l.; 28° 51.217 S, 27° 13.85 E). The mountain represents an isolated part of the Drakensberg Range in the summer-rainfall region of the Free State Province in South Africa, but differs in that it is not basalt-capped (Irwin and Irwin, 1992). Although the mountain comprises multiple geological formations, the youngest (Clarens) formation tends to form flat-bottomed, vertical-sided basins of variable depths and surface areas. These basins tend to be polygenetic in origin and weathering processes include chemical and mechanical erosion (Grab et al., 2011). Sixty-six of these basins were surveyed in this investigation (Fig. 1a).

In basins where favourable substrate has accumulated, terrestrial Afromontane fynbos vegetation becomes established (Fig. 1b). This type of vegetation is restricted to high altitude habitats of South Africa and it is suggested by Du Preez (1992) that the fynbos is specifically restricted to sandstone outcrops on Korannaberg due to the protection from fire. Additionally, eco-hydrology has been identified as one of the drivers of the niche segregation of fynbos species from the Cape Floristic Region (Araya et al., 2011), suggesting that water balance plays a role in the structuring of these communities.

The Korannaberg rock ledge also includes discrete rock pools that intermittently hold water after rain (Fig. 1c). Variation in depth and surface area is reflected in differences in hydroperiod (average of 3–101 days) and inundation frequency which are the most important determinants of variation in aquatic communities in these habitats (Vanschoenwinkel et al., 2009b). Some of the aquatic habitats have accumulated thin sediment layers allowing hydrophytic vegetation (*Limosella grandiflora*, *Lindernia conferta*, *Isoetes traansvaalensis* and other algal species) to establish. Certain geological basins host both aquatic and terrestrial habitats simultaneously and are characterised by clearly delineated boundaries at the interface between the two habitat types (Fig. 1d).

The 36 terrestrial plant species and the 37 aquatic invertebrate species occurring in Korannaberg rock basins are listed in Tables A1 and A2 in the online Appendix.

2.2. Quantifying habitat states

We digitised the coverage of habitat types from hand-drawn maps compiled directly from field observations at a 50 cm by 50 cm grid scale in 1993 and 2004 using ArcMap 9.3 (ESRI Inc., 2008). The latter map contained greater detail of micropools, cracks and fissures but we selected only those features which occurred in both maps for our analyses. A third set of data was obtained through a field survey carried out in March 2011 which re-described the features from the first two data sets. We categorised the within-basin features into two classes: terrestrial habitat and

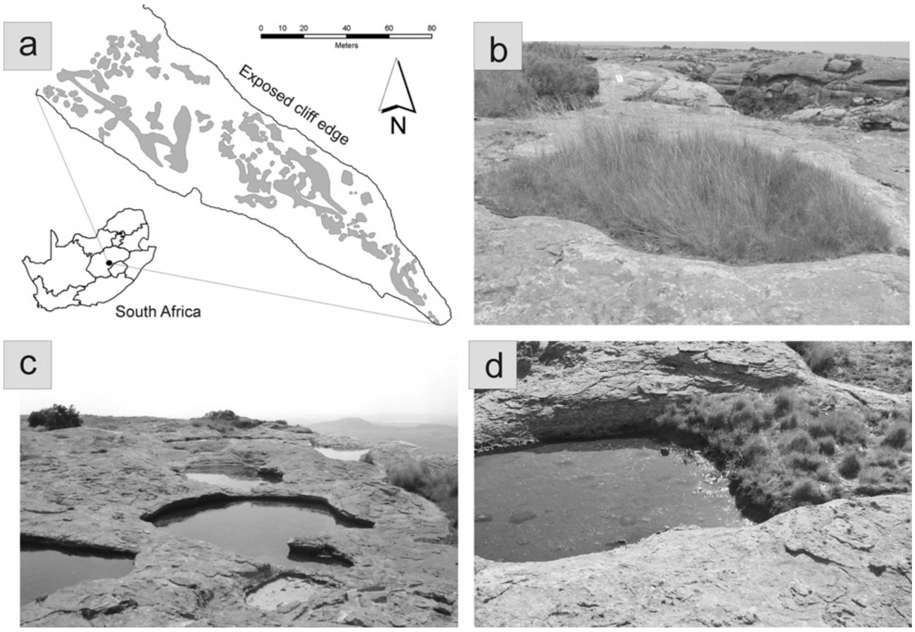

Fig. 1. The 66 geological basins on the a) Korannaberg rock shelf in South Africa which contain typical examples of b) terrestrial, c) aquatic and d) mixed-state habitats.

aquatic habitat for each of the three sample dates. Terrestrial habitats included areas covered by terrestrial vegetation, including those covered by mosses, whereas aquatic habitats were those features which could hold water for a period of time sufficiently long to sustain populations of aquatic plants and animals. Bayly (1997) found that pools shallower than 4 cm did not host aquatic species other than very resilient Oribatid mite species in a comparable system in Australia. Similar patterns were confirmed on Korannaberg (Vanschoenwinkel, unpublished data) and this can be attributed to the short-lived nature of these depressions which rarely contain water for more than 2–3 days. As a general rule, we only classified depressions with a maximum water depth greater than 4 cm as aquatic habitats.

Although the basins were flat-bottomed, they differed in that some had over-flow points or fissures through which water could escape. Basin depth (cm), therefore, was considered as the maximum potential water depth from the deepest point of the basin to the shallowest outflow point even if the edges of the basins extended beyond these levels. Depth was measured in the field to the nearest 0.5 cm. A metal rod was hammered into sediment-filled terrestrial habitats and, where sediment accumulated higher than the maximum water level (Appendix Fig. A1), minimal sediment was removed to take an accurate reading of the maximum potential water depth and prevent unnecessary disturbance to the system. Aquatic habitats were easily measured because the deepest points were observable but in sediment filled basins five random measurements were made within the basin and the largest was taken as the maximum potential water depth.

Surface areas (m^2) and minimum distances from the exposed cliff (m) of the basins were measured using GIS methodologies. The accuracy of GIS projections was tested by comparing the log-transformed surface areas of 36 basins manually measured by Vanschoenwinkel et al. (2009b) to those determined through GIS methods using a Pearson product–moment correlation test.

2.3. Data analysis

We determined the frequency distribution of proportional habitat area in each basin for each sample year. Based on the observed histograms, a continuous density estimation of habitat classes was calculated by performing a fast Fourier transformation on the discrete distributions of frequency data to provide a linear approximation of the density at each specific proportion. A Gaussian kernel was used with a rule-of-thumb default bandwidth smoothing estimator (Silverman, 1986).

A beta regression with a logit link function was performed to investigate the effect of basin parameters on habitat characteristics. Beta regression shares properties with generalized linear models but is a more suitable alternative for modelling proportional data (Cribari-Neto and Zeileis, 2010). It is, however, constrained to continuous measures in the open standard interval (0, 1), so a transformation ($(y.(n-1)+0.5)/n$; where n is the sample size) was required to account for proportional data predominated by single habitat states. The effects of log-transformed surface area, log-transformed distance from exposed cliff and basin depth on proportional aquatic habitat were tested for each of the sample years. The original beta regression model was multiplicative in that it included interaction terms but because there were neither *a priori* assumptions regarding the interaction of variables nor statistically significant interaction terms, we reduced the model to an additive one without interaction terms. Lastly, basins were divided into predominantly terrestrial (<50% aquatic habitat) and predominantly aquatic habitat (>50% aquatic habitat) and the discrete and continuous density distributions of the habitat types were determined for the variables shown to be statistically significant in the beta regression. Statistical significance was evaluated at a 5% level and all analyses were carried out in R version 2.12.2 (R Development Core Team, 2011) using the packages: *stats* (density distribution) and *betareg* (beta regression).

3. Results

The basin surface areas determined from GIS were correlated to those directly measured in the field (Pearson $r = 0.9441$, $t = 16.706$; $p < 0.001$). Bimodal frequency distributions showed that basin surface area was generally dominated by a single habitat class, either exclusively terrestrial or aquatic, and that combinations of classes were less common (Fig. 2). Furthermore, since the greatest majority of basins remained unchanged for the study period (Appendix Fig. A2), the constant bimodal frequency distribution is attributed to habitat permanence and not some other underlying cause (such as zero-sum dynamics of habitat modification and replacement).

The estimated parameters of the beta regression showed that habitat proportion was closely associated with specific basin characteristics (Table 1). The proportion of aquatic habitat was significantly associated to the depth of the basins for each sample year; aquatic habitats were more prevalent in deeper basins (1993: $z = 3.98$, $p < 0.001$; 2004: $z = 4.18$, $p < 0.001$; 2011: $z = 4.13$, $p < 0.001$). Distance from the exposed cliff edge was negatively

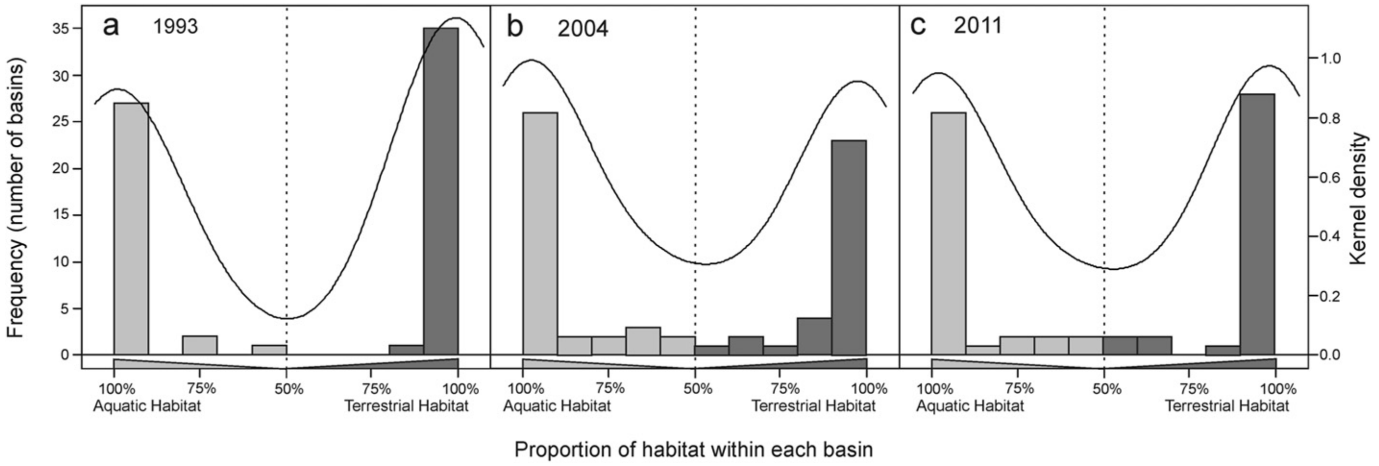

Fig. 2. The discrete frequency (bars) and continuous density (lines) distribution of the proportional surface areas of terrestrial and aquatic habitats for a) 1993, b) 2004 and c) 2011.

Table 1
The estimated parameters from a beta regression model of the relationship between the proportion of aquatic habitat and the physical characteristics of the basins on the Korannaberg rock shelf for 1993, 2004 and 2011. Significant *P*-values are shown marked with an asterisk (*).

	Estimate	Standard error	*z*-value	*P*-value
1993				
Log (Distance from edge)	−0.4229	0.2417	−1.750	0.0801
Log (Area)	−0.2247	0.1174	−1.914	0.0556
Depth	0.0556	0.0140	3.986	<<0.001*
2004				
Log (Distance from edge)	−0.4931	0.2397	−2.057	0.0397*
Log (Area)	−0.1861	0.1162	−1.602	0.1091
Depth	0.0581	0.0139	4.183	<<0.001*
2011				
Log (Distance from edge)	−0.4971	0.2397	−2.073	0.03814*
Log (Area)	−0.2007	0.1162	−1.726	0.08429
Depth	0.0573	0.0139	4.132	<<0.001*

associated to the proportion of aquatic habitat but this association was only statistically significant for the latter two sample years (1993: $z = -1.75$, $p = 0.08$; 2004: $z = -2.06$, $p = 0.039$; 2011: $z = -2.07$, $p = 0.038$). Aquatic habitat area showed signs that it might be negatively affected by basin surface area, but no statistically significant correlation was found over the study period (1993: $z = -1.91$, $p = 0.056$; 2004: $z = -1.60$, $p = 0.109$; 2011: $z = -1.73$, $p = 0.084$).

The findings of the beta regression were supported by the density distributions of the habitat types for the basin variables (Fig. 3). However, for both the distance from the cliff edge (Fig. 3a, c, d) and basin depth (Fig. 3 b, d, f), there was a large overlap of the density distributions of the two habitat types, suggesting dual relationships and multiplicity of the regression model. This implies that there is an equal probability of aquatic and terrestrial habitats occurring at certain basin variable levels.

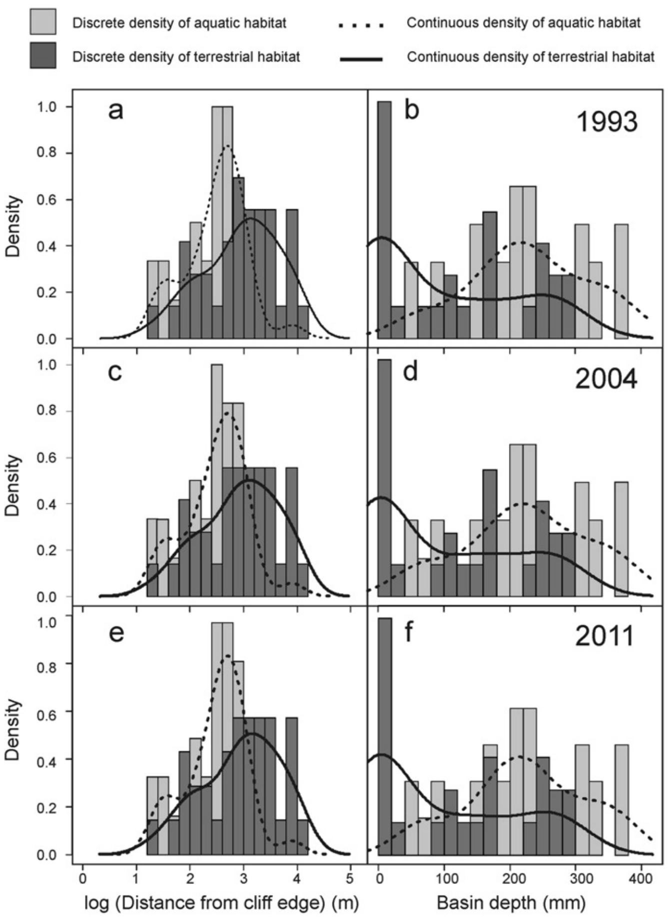

Fig. 3. The discrete and continuous density distribution of aquatic and terrestrial habitats in the 66 geological basins as a function of a, c, e) distance from the cliff edge and b, d, f) basin depth for 1993, 2004 and 2011 respectively.

4. Discussion

This study aimed to explore whether the two contrasting habitat types (aquatic and terrestrial) occurring in geological basins on the Korannaberg inselberg represent true alternative stable states, where two states are self-reinforced by positive feedback loops (Petraitis and Hoffman, 2010; Scheffer and Carpenter, 2003; Scheffer et al., 2001), or simple linear succession (succession reset by disturbance hypothesis) from one state to another as suggested by Jocque et al. (2010).

The phenomenon of hysteresis, which explains why state shifts can often not simply be reversed by returning environmental conditions to that of the previous state, lies at the forefront of understanding alternative stable states (Beisner et al., 2003). Schröder et al. (2005) listed the four characteristics of hysteresis-driven systems: (1) sharp state transitions and the absence of intermediate stages, (2) sharp spatial boundaries between states, (3) bimodal state variable frequency distribution and (4) dual response to driving parameters. Although Shcröder et al. (2005) intended for these criteria to be used as outcomes from experimental tests, our observational field patterns generally met each of these conditions. Abrupt state transitions which would have been reliable evidence of ASS (Scheffer, 2009; Scheffer and Carpenter, 2003) were not observed during this study. Despite the absence of state transitions, our findings offered little evidence of intermediate stages because the bimodality of habitat types, and the habitats types of individual basins, remained unchanged for the 18 year duration of the study. Some aquatic basins had enough sediment to be habitats for aquatic plants (hydrophytic Cyperaceae species, but not exclusively terrestrial species), but evidence that this precluded colonization by terrestrial species remains to be found. In basins where both aquatic and terrestrial habitats co-existed, the interface between the two was clearly delineated meeting the ASS assumption of sharp spatial boundaries between states. As a consequence of the absence of transitional phases, state variables displayed the consistent bimodal frequency distribution indicative of ASS (Scheffer, 2009; van Wesenbeeck et al., 2008).

Porembski et al. (2000) distinguished general types of vegetation in eroded basins and attributed these categories to basin characteristics. This also contradicts the succession hypothesis and implies deterministic causality. Our findings, on the other hand, showed that both aquatic and terrestrial habitat types were equally probable for certain ranges of basin variables. This opposes deterministic basin-driven explanations and suggests habitat bistability. Similar evidence has been considered as verification of alternative stable states in grassland, savannah and forest systems (Hirota et al., 2011; Staver et al., 2011).

Alternative stable states entail that system states configure themselves through feedback mechanisms, whereas succession requires that the structure of the system is a function of time-dependent environmental conditions and disturbance events. Our findings support the former process and we propose the following system whereby aquatic and terrestrial habitats positively reinforce themselves through feedback mechanisms. In addition, we suggest that the strength of these feedback mechanisms is determined by physical basin characteristics. Terrestrial vegetation will be unable to become established in deeper (predominantly aquatic) basins as it would be drowned by water during inundation periods. The length and variation of inundation period (hydroregime cfr. Hulsman et al., 2008; Vanschoenwinkel et al., 2009b) in aquatic habitats, would, therefore, play an important role in reinforcing these states. The low prevalence of vegetation in these ephemeral pools would mean that, during inter-inundation periods, any accumulated sediment not aggregated by plant roots could be gathered up by wind as shown possible by Vanschoenwinkel et al. (2008, 2009a). Being more exposed, basins positioned nearer to the cliff edge are more susceptible to wind erosion, hence the predominance of aquatic habitats in these basins.

In turn, shallower basins which exhibit shorter inundation periods (Vanschoenwinkel et al., 2009b) are predominantly terrestrial. The aggregation of sediment by vegetation and the reduced exposure to wind erosion, due to basins being further from the cliff edge, would positively reinforce terrestrial habitats (Braskerud, 2001). Despite the significant associations between habitat type and basin parameters, which support feedback speculations, certain basins with similar physical characteristics had different habitat types. This dual response to driving parameters could be indicative of an underlying hysteresis curve. However, since the original habitat conditions are unknown it is not possible to confirm that this dual response is due to path-dependency (Scheffer, 2009; Scheffer and Carpenter, 2003).

Considering that geological basin structure remained unaltered for the duration of this study, we suppose that, in the absence of extenuating stimuli, these states would remain unchanged indefinitely and remain stable (Ives and Carpenter, 2007). Destabilising extenuating stimuli could be in the form of disturbances to terrestrial habitats where substrate can be mobilised. Graham and Wirth (2008) showed that even slight disturbances can significantly increase the amount of sediment mobilized by the wind in a similar system in North America. Although speculative, natural disturbances could include the diggings of porcupines or baboons (which are both present on the Korannaberg rock ledge), for roots, bulbs or tubers. Sediment mobilised from disturbed terrestrial habitats could be deposited into aquatic basins through wind or water sheet erosion over the sandstone rock shelf and, if the sediment depth exceeds a certain depth threshold, terrestrial vegetation could colonize the patch. Due to the undisturbed and pristine nature of the Korannaberg rock shelf, we refrained from potentially degrading the system through manipulative experiments to test these mechanisms. Although multiple stable states can only be decisively demonstrated by experimental manipulation (Peterson, 1984; Schröder et al., 2005), our findings provide enough evidence to formulate robust inferences.

The evidence of this study supports the hypothesis that aquatic and terrestrial habitats are ASS; at least for the 18 years of this study. Zooplankton species, such as *Branchipodopsis* fairy shrimp, need as little as 7 days of inundation to reach sexual maturity and reproduce (Vanschoenwinkel et al., 2010a). Rock pools on Korannaberg may have more than 10 inundations suitable for reproduction each wet season (Vanschoenwinkel et al., 2009); meaning that 18 years is enough time for 150 generations. The long term habitat stability is consistent with the substantial levels of genetic diversity, including unique haplotypes, found in certain populations of rock pool invertebrates (Hulsman et al., 2007; Vanschoenwinkel et al., 2011) and is consistent with community differentiation among patches shown in other studies (Jocque et al., 2010; Vanschoenwinkel et al., 2007). Furthermore, long term habitat stability validates the use of long term climate data in reconstructing the inundation patterns of rock pools (Hulsman et al., 2008; Vanschoenwinkel et al., 2009b, 2010b), providing further incentives for using such basins in evolutionary research.

To conclude, aquatic and terrestrial habitats within geological basins on an inselberg demonstrated stability over an 18 year period thereby opposing the succession hypothesis at this timescale. Bimodality and differential responses to similar combinations of system parameters supported the ASS hypothesis. The long-term permanence of these systems explicates certain features of the biological communities within them, thereby justifying their extensive usage as model systems for ecological and evolutionary studies. This study opens the door for researchers to extend the usage of this model system to experimentally test alternative stable state hypotheses using empirical field data.

Author contributions

FB wrote the manuscript and did the GIS analyses. SE and BV commented extensively on earlier drafts of the manuscript. FB, SE, MK and BV carried out field surveys. MS and LB initiated and supervised the research. FB and BV designed the study and carried out the statistical analysis. The authors state that they have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2012.11.005.

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