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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

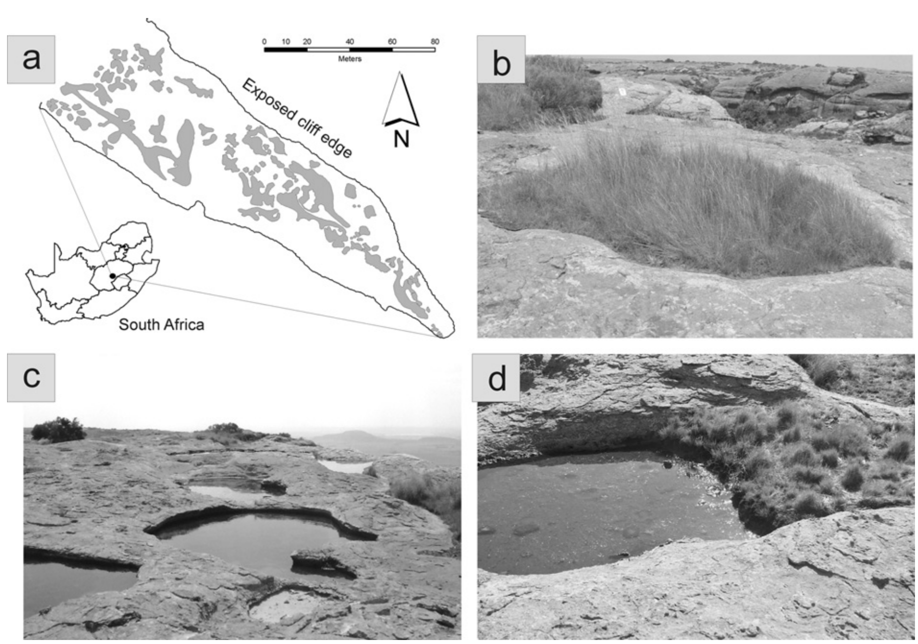

Fig. 1. The 66 geological basins on the a) Korannaberg rock shelf in South Africa which contain typical examples of b) terrestrial, c) aquatic and d) mixed-state habitats.