



An operational framework for biome boundary research with examples from South Africa



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ABSTRACT

Understanding the ecology of biome boundaries is important in both pure and applied research. Here we develop an operational framework that categorises biome boundary research into five key approaches, namely, (1) field observations, (2) correlative modelling, (3) experimentation, (4) mechanistic modelling, and (5) the phylogenetic approach. Each approach is expanded using examples drawn predominantly from biome boundary research conducted in the South African context, which is home to a wide array of biomes and a long history of such research. Nonetheless, this framework is applicable to biome boundary research across the globe. We review the weaknesses and strengths of each approach and argue that a combination of all approaches is necessary to fully understand the complex boundary dynamics of biomes through space and time.

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1. Introduction

“There is scarcely any biological task more attractive than that of determining the nature of the weapons by which plants oust each other from habitats.” (Warming, 1895)

Ecotones – the transitions between vegetation based on floristic or functional changes – have long fascinated biologists (e.g., Clements, 1916; Van Leeuwen, 1966; Weaver and Thiel, 1917). Ecotone transitions, including biome boundaries, have been studied across a range of spatial and temporal scales using a multitude of methods. Here we place these methods into an operational framework by classifying them into five general approaches, specifically (1) field observations, (2) correlative modelling (i.e., quantitative measurements of vegetation and environment), (3) experimentation, and (4) mechanistic modelling. Lastly, we include an emerging and promising avenue of biome boundary research, the (5) phylogenetic approach. Our focus is on biome boundaries, but this framework is applicable to boundary research at all hierarchies of vegetation classification. For each approach, we provide a range of examples from the biome boundary literature and discuss its strengths and weaknesses. The examples are largely restricted to studies on biome boundaries in South Africa; this is to provide tractable limits to the extensive global literature on the topic and to keep within the geographical theme of this Special Issue. Also, South Africa contains a complex array of biomes, many of which are relevant to the continent and beyond, with boundaries controlled by a variety of interacting biotic and abiotic processes. Furthermore, as a diverse array of methods is readily at hand in this Special Issue, we

have included many of these studies as examples. Despite the focus on examples from the rich history of South African research, the operational framework is globally relevant for research into biome boundaries. Ultimately we emphasise that biome boundary research requires the use of, and synergy between, all approaches.

2. Field observations

“...the emergence of strong theory in ecology appears to have changed our perspective on natural history, to the point that observation is often used to serve theory rather than test predictions and find inspiration for new ideas.” (Ricklefs, 2012, p. 432)

Observations of nature formed a cornerstone in the foundation of ecology (McIntosh, 1985). Despite the decline in the perceived importance of field observations (including natural history observations) relative to quantitative or experimental approaches to ‘science’, these nonetheless remain an integral part of exploring and rationalising biome boundaries. Observations on the natural history of biome boundaries form the biological backbone for more analytically rigorous, hypothesis-testing approaches.

South Africa has a rich literature on the descriptive ecology of biome transitions. Most of the important works were published between 1920 and 1970 as *Memoirs of the Botanical Survey of South Africa* under the auspices of the Botanical Research Institute, a division of the national department of Agriculture. Although imbued with Clementsian dogma, this

research can provide very useful insights for contemporary scholars. Not only did these pioneering plant ecologists spend far more hours in the field than is commonly the practice today – and, hence, be capable of developing superior natural history skills – but they also worked in landscapes far less transformed. Most of these studies were located in the northern and eastern parts of South Africa, most likely a consequence of the low regard for Cape botanists held by most members of the Advisory Committee that oversaw the publication of the *Memoirs*, a situation that persisted well into the 1960s (Carruthers, 2011). Many of the *Memoirs* are replete with observations (and some rudimentary data) on the transitions between savanna, grassland, thicket, and forest (Aitken and Gale, 1921; Comins, 1962; Dyer, 1937; Edwards, 1967; Killick, 1959, 1963; Story, 1952), as well as useful observations on the densification of trees in Grassland and Savanna (e.g., Aitken and Gale, 1921; Story, 1952). Further south, Phillips (1931) provides a wealth of observations on the Fynbos–Forest boundary, and Muir (1929) contributed one of the earliest and most comprehensive accounts of the role of geology and associated soils in patterning the biomes of the Cape south coastal lowlands.

Field observations are not restricted to researcher-based observations, although this is certainly important. Any source of observations may provide important new understanding of boundary drivers; observational narratives can come from anyone who has spent time in the field (e.g., farmers) or old travellers' or town records. Old archives such as newspapers may be a source of useful observations. For example, historical newspaper articles were used to track the now-extinct migrations of springbok in the Nama–Karoo (Roche, 2008); this provides some awareness of the largely unexplored role that these migrations of vast number of springboks may have played in Nama–Karoo ecology and influencing the Nama–Karoo–grassland boundary. Obtaining field observations, either directly by the biologist or indirectly through other sources, takes time and effort. In recent decades when ecology has emphasised quantitative analyses, such effort rarely provides data that have a direct avenue for publication. Yet the time taken to explore the local narratives on the topic of vegetation shifts can lead to valuable insights. A good example is a spate of fires that occurred in Nama–Karoo around the Victoria West region (Northern Cape Province) in 2012. These fires precipitated, for the first time in living memory, the establishment of a local farmer fire brigade. Two major rainfall events in the prior year – associated with cut-off lows and each exceeding the region's mean annual precipitation – resulted in a dramatic increase in grass. So much was produced that the farmers in the region started to stock cattle in a sheep-dominated region. The subsequent fires caused a substantial decline in Nama–Karoo shrub cover (e.g., Fig. 1a; du Toit et al., 2014). This observation for the Nama–Karoo–Grassland boundary may be an early indication of an incipient fire-driven biome switch in the region. This theme is explored further using field observations by du Toit et al. (2015-in this issue). Other examples of field observations are provided in Fig. 1.

The strength of field observations is that large sample sizes can be obtained over varying conditions, including rare events. However, they generally have a limited temporal and spatial scope (Fig. 2a). Often they can be used to generate hypotheses, but they usually lack the necessary evidence to provide drivers with any level of certainty, and it is very difficult to assess interactions between possible drivers (e.g., Fig. 1c, d).

3. Correlative approach

“...a successful approach is to evaluate the broad-scale environmental gradients that occur over a region and identify boundaries that occur in the relatively steep portions of those gradients. At the scale of regions, the boundaries are likely to be those of biomes or dominant life-forms, and the environmental driving functions causing those gradients are likely to have significant effects on ecosystem-level processes.” Gosz and Sharpe (1989)

The majority of ecotone and biome boundary research locally and internationally have been performed using the correlative approach, summarised as follows: vegetation (response) variables and environmental (explanatory) variables are quantified, and patterns are explored for correlations, thresholds, and interactions. Measurements can be coordinated to be sampled simultaneously (e.g., floristic composition and soil samples for a site) or can made up from an amalgamation of different data sets (e.g., aerial photographs, stocking records, and weather station data as in Wigley et al., 2010). Therefore, we divide the quantitative relationships used in the correlative approach into two broad subcategories: tightly-linked and loosely-linked.

Tightly-linked correlative data usually cover small to medium spatial and short temporal scales (Fig. 2b). Such studies typically involve intense field-work where variables are measured that cannot easily be mapped or interpolated, such as soils (in comparison to temperature or rainfall). For example, Coetsee et al. (2015-in this issue) investigated soil properties and the Fynbos–Forest boundary and found that Forest existed over a range of soil properties that included those where fynbos occurred. Thus, the occurrence of forest vegetation was unlikely to be driven by soil status, as argued by Masson and Moll (1987) using a similar approach but a smaller sample size. Cowling and Potts (2015-in this issue) examined landscape-level (e.g., geology, insolation, fire exposure) and edaphic (physical and chemical) variables sampled at sites spread across a 1200 km² in the biome-rich Kouga region of the eastern Cape Floristic Region. The quantitative analyses of the possible biome boundary determinants yielded a complex hierarchy of interacting explanatory factors. These tightly-linked correlative examples all involved single snapshot sampling events as it is usually difficult to repeatedly sample at temporal scales that can sufficiently capture changes over time. This can be a problem in dynamic systems (e.g., Veldkornet et al., 2015-in this issue).

Loosely-linked correlative studies include any in which the data sets are compared that have been collected separately, usually under different spatial and temporal scales. Such studies usually cover medium to large spatial scales and much longer temporal scales (Fig. 2c). Staver et al. investigated the transition between Forest and Savanna in sub-Saharan Africa and globally (2011a, 2011b, respectively). Using estimates – largely satellite-derived – of woody cover, fire frequencies, precipitation and, in the case of the global analysis, soils, they identified precipitation-related thresholds above and below which Forest or Savanna biomes were stable, respectively. However, between these precipitation thresholds, these two biomes were observed to be alternative states maintained by divergent responses to fire. Analyses using satellite data can be conducted over large spatial scales but are hindered by having a temporal window that can span up to four decades, depending on the instrument. Analyses of aerial photography can be used to extend

Fig. 1. A range of biome boundaries and possible drivers established from observations. (a) A recent fire-induced switch from Nama–Karoo shrubland to Grassland (see du Toit et al., 2015-in this issue, for details). (b) A geological divide, highlighted by white triangles, between Witteberg quartzites (hill crests) and shale (hill slopes) dictates the position the Grassland–Albany Subtropical Thicket boundary (RMC and AJP, personal observations). The uneven line between the two biomes is determined by the overburden of colluvial quartzite and the effects of occasional high-intensity fires that penetrate the otherwise fire-free thicket (see also Fig 1 h). (c and d) Observed shifts in boundaries highlight the need for investigation; possible causes here include changes in fire regime, stocking rate, precipitation, and increased atmospheric CO₂. (e) The sharp boundary between Albany Subtropical Thicket and Nama–Karoo corresponds with the frost-line (AJP and RMC, personal observations). (f) A frost-damaged Spekboom (*Portulacaria afra*) individual that had been transplanted into a farm yard in the frost-exposed bottomlands. (g) The sharp boundary between Albany Subtropical Thicket and Fynbos is unaffected by a fire event. (h) A patch of thicket in a Renosterveld matrix burnt during a high-intensity fire. There was no evidence of post-fire recovery of any dominant species (i.e., *Euphorbia grandidens*, *Euclea undulata*, *Schotia afra*, and *Mystroxydon aethiopicum*). Further examples of biome boundaries can be seen in Coetsee et al. (2015-in this issue, Fig. 1), Gray and Bond (2015-in this issue, Fig. 1), Poulsen and Hoffman (2015-in this issue, Supplementary Material), and Wakeling et al. (2015-in this issue, Fig. 1). Photo Credits and Copyright: (a) JCO du Toit, (c) D Edwards – courtesy of the South African National Biodiversity Institute, (d) JR Puttick, (e and f) R Duker, (g) AJ Potts, and (h) RM Cowling.

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