

Probabilistic description of vegetation ecotones using remote sensing

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ABSTRACT

Ecotone transitions between vegetation types are of interest for understanding regional diversity, ecological processes and biogeographical patterns. Ecotones are seldom represented on vector, line-based vegetation maps, which imply an instantaneous change from one vegetation type to another. We use supervised, probabilistic classification of remotely sensed (RS) imagery to investigate the location, width and character of ecotones between acid Sandstone and alkaline Limestone fynbos on the Agulhas plain at the southern tip of Africa, known for rapid speciation of plants and exceptional plant biodiversity at the global scale. The resultant probability map, together with the probability graphs developed for a few transects across the transition, are able to map and describe (1) sharp, narrow ecotones (under five meters); (2) moderate ecotones that have a distinct band of transition (over a few hundred meters); and (3) complex ecotones that include slow transitions, interdigitated boundaries and outliers. The latter class of transitions include portions where vegetation types change sharply over a few meters, but due to the interdigitated boundaries they are mapped over hundreds of meters to a kilometre at a landscape scale. In this study area, our findings suggest that the character of the Agulhas limestone-acid ecotone is probably more complex than often noted. Moderate transitions and broad mosaics are difficult to indicate in a vector vegetation map, whereas RS probabilistic classifications can output images indicating core areas, important for key species and biodiversity pattern, and transitional zones, important for ecosystem processes and perhaps plant evolution, which distinction is important for conservation planning.

1. Introduction

Ecotones, or vegetation transitions, have long been the focus of scientific study due to their effects on both beta and gamma diversity and thus local and landscape level diversity and pattern (Whittaker, 1960). More recently, interest has arisen from the recognition of the role of ecotones in driving genetic diversity, gene flow and speciation, as well as ecosystem processes, including population and metapopulation dynamics, provision of diverse resources, modification of flows of material across the landscape, movement corridors, and being responsive to changes in climate (Hou et al., 2017; Hufkens et al., 2009; Kark et al., 2007; Risser, 1993; Rouget et al., 2003; Strayer et al., 2003a). This has reached the extent where some authors (e.g. Fagan et al. (2003)) state that “habitat boundaries profoundly influence the structure and function of landscapes”.

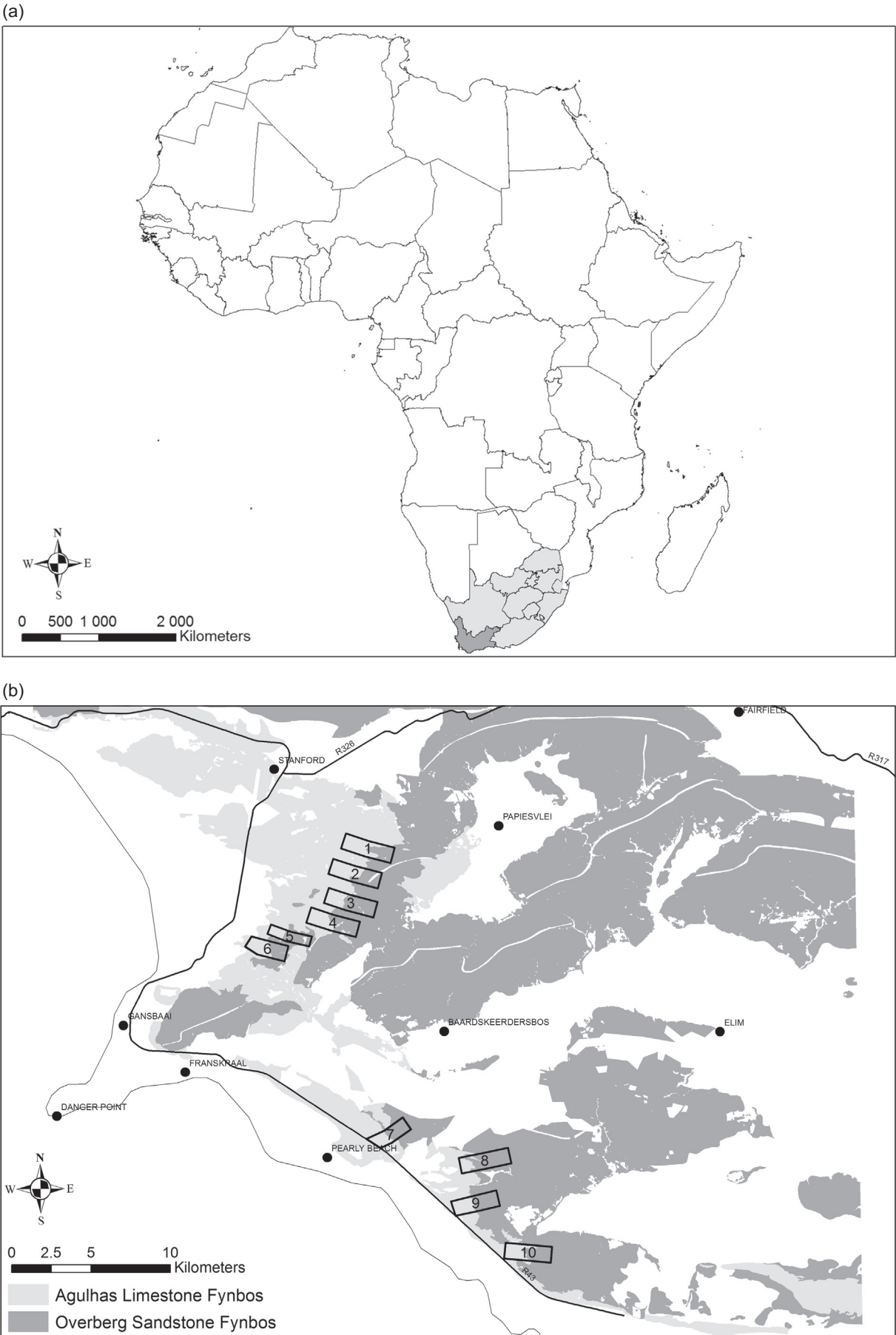
On both paper maps and GIS databases, ecotones are most frequently mapped as single lines regardless of their actual extent on the

ground, or whether they are derived from field mapping (e.g. SANBI 2006-), expert synthesis (Dinerstein et al., 2017), or statistical analysis of gridded databases (Linder et al., 2012). However, the breadth and strength of different ecotones on the ground vary dramatically according to a number of factors (Williams, 1996), meaning that single lines are often neither accurate nor appropriate.

Both gridded or extrapolated point-locality species data can provide continuous variables as inputs to various measures of the placement, strength and breadth of ecotones, and have been developed to distinguish sharp ecotones from gradual transitions and map the approximate area across which the transition occurs (e.g. Williams et al., 1999; see also Hufkens et al., 2009, for a comprehensive review). However, for most parts of the world, continuous data derived from ground-based botanical (or zoological) surveys is seldom available over large spatial extents due to constraints of time, money, and the physical and safety challenges involved (Buchanan et al., 2009). Moreover, global and regional gridded biodiversity databases are generally only available at

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Fig. 1. (a) Study area location (black dot) within the Western Cape Province (dark grey) of South Africa (light grey). (b) Location of 10 transects (numbered black rectangles) showing the acidic Overberg sandstone (mountain) fynbos (dark grey, Vegetation Map of South Africa) and alkaline Agulhas limestone (lowland) fynbos (light grey). Local towns are shown as black dots and roads as the black line.

coarse scales (e.g. South African National Biodiversity Institute's (SANBI) Integrated Biodiversity Information System (SIBIS) at a quarter-degree (<http://newposa.sanbi.org>). However, data derived from remote sensing (RS) holds much potential to provide finer scale (down to a few meters and sometimes sub-meter) and data that are continuous, both in space and time, for maps of vegetation types and ecotonal areas between them. This is based on the spectral signatures that can be recognised from individual, or combinations, of plant communities. RS has been extensively shown to be useful for vegetation or land cover/class mapping (Xie et al., 2008).

A large number of ecotone types have been studied using RS; these include examples across a large number of biome and land-use boundaries: taiga-tundra (Ranson et al., 2011); tundra-woodline; Alpine-subalpine (Resler et al., 2004); forest-woodland; forest-savanna, all reviewed by Hufkens et al. (2009) wildland-agriculture or -urban interfaces (Feng et al., 2015); forest-farmland transitions (Hou and Walz, 2014); urban-wildland econets (Hou et al., 2017) and elevational gradients (see Gallardo-Cruz et al., 2009). Ecotone studies use a range of sensors, from passive MODIS (Ranson et al., 2011; Ali et al., 2013), Landsat, Sentinel, SPOT (Radoux et al., 2016), RapidEye and aerial photography (Martin et al., 2007; Resler et al., 2004) to active airborne laser scanner (Hou and Walz, 2014) and Lidar (Guo et al., 2017). For ecotone classification, studies use various subsets of electromagnetic energy (sensor bands) as well as vegetation indices developed from the bands (Hou and Walz, 2014), and then apply various classification approaches, from manual mapping off of aerial photographs (Martin et al., 2007), to object- and rule-based classification (Hou and Walz, 2014). Hard classifiers include agglomerative, divisive/partitioning, moving window, and rate of change approaches (see Fagan et al., 2003).

Remote sensing is often used in vegetation research to help develop maps of different land use and land cover that can be further used to develop vegetation maps (e.g. South African National Biodiversity Institute, 2012). Here we test the use of fuzzy probabilistic classifiers to assign graded (fuzzy) membership to remote sensing imagery pixels, to map the location, extent (Strayer et al., 2003b), and character of ecotones at a landscape level on the Agulhas Plain at the extreme southern tip of South Africa. Field data were obtained from fine-scale vegetation maps (Euston-Brown, 1999; South African National Biodiversity Institute, 2012) and applied to imagery obtained from NASA/USGS, which we pre-processed. We use these data to produce a supervised, probabilistic classification of alkaline Agulhas limestone fynbos and acidic Overberg sandstone fynbos (Cowling et al., 1988), showing the extent of each vegetation type as well as the nature of the ecotone between these two vegetation types. We look at the vegetation ecotone across this alkaline-acid transition as it has provided opportunity for genetic exchange and rapid divergence of subspecies and species (Thwaites et al., 1988), resulting in high beta diversity as well as local endemism.

2. Materials and methods

2.1. Study areas

The Cape Region of southwestern South Africa has remarkable patchworks of vegetation types, each supporting exceptional plant species diversity, localised endemism (Cowling et al., 2009; Olson et al., 2001) and high beta diversity between vegetation types. The Agulhas Plain at the southern tip of this region (coordinates top-left: 24° 26' 51"S, 19° 15' 05"E; bottom-right: 34° 52' 08"S 19° 14' 57"E), is a botanically rich area with more than 1700 species (Thwaites et al., 1988).

There are 85 local endemics, in part driven by speciation across the ecotone between the alkaline-neutral sands, acid sands and acid loams (Cowling et al., 1988; Oliver and Oliver, 2002; Thwaites et al., 1988). For example, *Erica plukenetii* has different subspecies on both acidic sandstone and alkaline limestone, such as *subsp. plukenetii* (sandstone), *subsp. lineata* (limestone), *subsp. breviflora* (sandstone) and *subsp. brendensis* (limestone) (Oliver and Oliver, 2002). Similarly, *Erica regia* *subsp. regia* grows on acidic sandstone, whereas the *subsp. mariae* [*mariae*] grows on limestone (Oliver and Oliver, 2002). For the purposes of this paper we are specifically interested in studying the ecotones between Agulhas limestone fynbos (hereafter referred to as limestone), which is restricted to alkaline soils, and Overberg sandstone fynbos (hereafter referred to as sandstone), which is restricted to acid soils (Cowling et al., 1988) (see Fig. 1), names follow the South African National Biodiversity Institute (South African National Biodiversity Institute, 2012). Indicator species of limestone fynbos are *Protea obtusifolia*, *Leucadendron meridianum*, and *Leucospermum truncatum*, while indicator species of sandstone fynbos are *P. compacta* (sister species to *P. obtusifolia*), *Leucadendron xanthoconus* or *L. eucalyptifolium* (Rebello et al., 2006). The latter situation is sometimes complicated by the observation that quite shallow sands overlaying limestone can alter the species present. While structurally similar, limestone fynbos largely lacks graminoids and ericaceous fynbos elements.

Mean annual rainfall ranges from 450 mm in the east, to 540 mm in the west and 650 mm in the northern hills (South African Weather Service). Most (65% and 75%) of the annual precipitation occurs during the winter months of May–October, which is characteristic of a Mediterranean-type climate. The topography is flat to undulating with some small peaks, and rises from sea level to 772 m a.s.l. (Stellenbosch University, Digital Elevation Model).

2.2. Remote sensing approach

Our approach to classifying remotely sensed imagery was to start with a set of decisions on which satellite-borne sensor to use, the time of year, pre-processing of the sensor data in parallel with planning and collection of training and verification, or accuracy, data. The imagery was then classified with the training data (for supervised classifications), and the accuracy of the output then evaluated using the verification data.

2.3. Field data and accuracy assessment

Training and verification polygons were captured off of the Vegetation Map of South Africa (2012 beta version, (South African National Biodiversity Institute, 2012)) and checked against the field map used as input to this national standard (Euston-Brown, 1999). The total of 144 polygons were split roughly 70/30 split (sensu Lillesand et al., 2008) to yield mutually exclusive, independent training (100) and verification (44) polygons (Table 1). Some field work was

Table 1
Numbers of training and verification polygons captured for Overberg sandstone and Agulhas limestone fynbos.

	Training data	Verification data
	Number of polygons	Number of polygons
Overberg Sandstone Fynbos	53	23
Agulhas Limestone Fynbos	47	21
Total	100	44

conducted around transects four and five to check results that classified some areas as mosaics of limestone and sandstone, while the Vegetation Map of South Africa had mapped these as limestone. An observer familiar with the local floral species and indicator species of the different vegetation types participated in the field trip.

2.4. Satellite data and pre-processing

Landsat 8 Operational Land Imager (OLI) sensor imagery (30 m pixel size, downloaded from EarthExplorer, <https://earthexplorer.usgs.gov/>) were obtained for September 2017 for a recent representation of the growing season and of the field work conducted in November 2017. Unfortunately imagery for November 2017 was too cloudy for analyses. Land transformation, such as newly ploughed fields, that are not represented on the National Land Cover raster were manually digitised and excluded from the analysis of the 2017 imagery. Imagery was atmospheric corrected (Richter and Schlöpfer, 2014) using IDL's ATCOR.

Areas transformed by human infrastructure, ploughed lands and dense stands of invasive alien plants were removed using the 2013–2014 National Land Cover raster (NGI, 2015), as were fire scars of the previous two years (2015–2016), as well as non-target vegetation types, such as narrow bands of Western Coastal Shale Band Vegetation, Cape Lowland Freshwater Wetlands and Southern Coastal Forest.

2.5. Classification of RS data

Band statistics for images were checked for normality (band correlations and ellipsoidal relationships), as well as class separability using two common separability tests, namely the Jeffries Matusita test (Nussbaum et al., 2006) and Transformed Divergence (TD) separability measure using ERDAS Imagine software (Hexagon Geospatial 2014). Band correlations generally fit the patterns, except for band five which consistently did not show any ellipsoidal pattern. Separability of sandstone and limestone across all bands was moderate at TD of 1.67.

2.6. Classifications

Traditional hard classifiers map feature space into binary classes whereas fuzzy classifiers assign graded (fuzzy) membership to pixels. Probabilistic soft classifiers provide a probability distribution over a set of classes, where each pixel is assigned a strength of membership value for each class being mapped. We applied a Bayesian-based Class Probability algorithm in ArcMap 10.4 (ESRI, Redlands, California).

To illustrate the nature of the change of classified probabilities (class membership) from sandstone to limestone, ten transects were drawn across various parts of the transition. Transects were located using the Vegetation Map of South Africa (South African National Biodiversity Institute, 2012) so that for each 3 km transect, approximately 1.5 km stretched across sandstone and another 1.5 km across adjacent limestone. We attempted to locate these transects along parts of the transition that had not been heavily impacted by land-use transformation and across as much of the study area as possible. However, as can be seen in Fig. 1, we were restricted in our choice of locations for transects by the limited extent of natural vegetation along the ecotone boundary. Transects were 1 km wide (Fig. 1). Vegetation class probabilities were binned over the 1 km width every 30 m along the 3 km length and the mean and variance of the vegetation class probabilities were calculated.

2.7. Accuracy assessment

Standard tests of agreement between classification outputs and the verification data were conducted (R package caret, Kuhn 2008) including overall accuracy (percentage correctly classified), Kappa, sensitivity, which is the ratio of true positives to all positives (i.e. true

Table 2

Accuracy assessment of Bayesian probability classifiers of sandstone and limestone from Landsat 8 imagery.

Image	2017
Overall accuracy	95.5
Kappa	91
Sensitivity	93
Specificity	98

positives + false positives or commissions) and specificity, which is the ratio of true negatives to the sum of true negatives and commissions.

3. Results

The probability map of vegetation type shows that there are generally high probabilities of sandstone in the east, in areas indicated to be sandstone in the Vegetation Map of South Africa, and high probabilities of limestone generally in the west, in areas mapped as limestone in the Vegetation Map of South Africa. This is confirmed by accuracy statements (accuracies and kappa values of over 90% with similarly high sensitivities and specificities, Table 2, Fig. 2).

The probability map suggests that the transition between sandstone and limestone is narrow and sharp in some areas (see extended areas where groups of solid red pixels are replaced by groups of solid blue pixels, Fig. 2). More often this transition is slower and broader, taking place over a number of pixels (grey areas between the red sandstone and blue limestone, Fig. 2). Complex transitions with convoluted boundaries and outlier patches are also seen, where outlier patches of sandstone occur into the limestone. Some of these sandstone outliers are mapped in the Vegetation Map of South Africa.

The graphs of vegetation class probability values over the transects provide a second means of representing and interpreting the output of the classification, and again three patterns are seen: sharp, slow, and complex. Transect two shows a sharp transition from sandstone to limestone (Fig. 3 b) where the graph line representing sandstone probabilities shows high sandstone values in the east (right of the graph) that decrease with a steep slope towards the west (left of the graph). Over the same geographical space, the graph line representing limestone probabilities starts off with low values in the east and then shows a steep increase in probabilities as the limestone replaces the sandstone rapidly over a short distance. The rapid switch from high probabilities of sandstone to high probabilities of limestone over a short distance on the graph is interpreted as a sharp ecotone with rapid transition of vegetation types.

A slow or gradual transition is seen in transect nine and ten (Fig. 3i and j), where high probabilities of limestone in the west (left of the graph) drop to medium values over a stretch of a few hundred meters. Sandstone probabilities increase over the same geographical space, from low values in the west to high values in the east. This can be interpreted as a distinct ecotone over specific area between limestone in the west and sandstone in the east.

Transect four (Fig. 3d) is an example of a complex transition where probabilities of sandstone and limestone oscillate over the middle section of the transect.

The probability map also reflects important detail of limestone in lower lying areas within the main body of sandstone, generally along valleys (Fig. 2). In a few cases linear groups of pixels are classified with a high probability of limestone while the Vegetation Map of South Africa maps the area as sandstone, which may be due to spectral confusion along highly reflective roads and fire breaks.

4. Discussion

Traditional line (polygon) maps can only provide an indication of

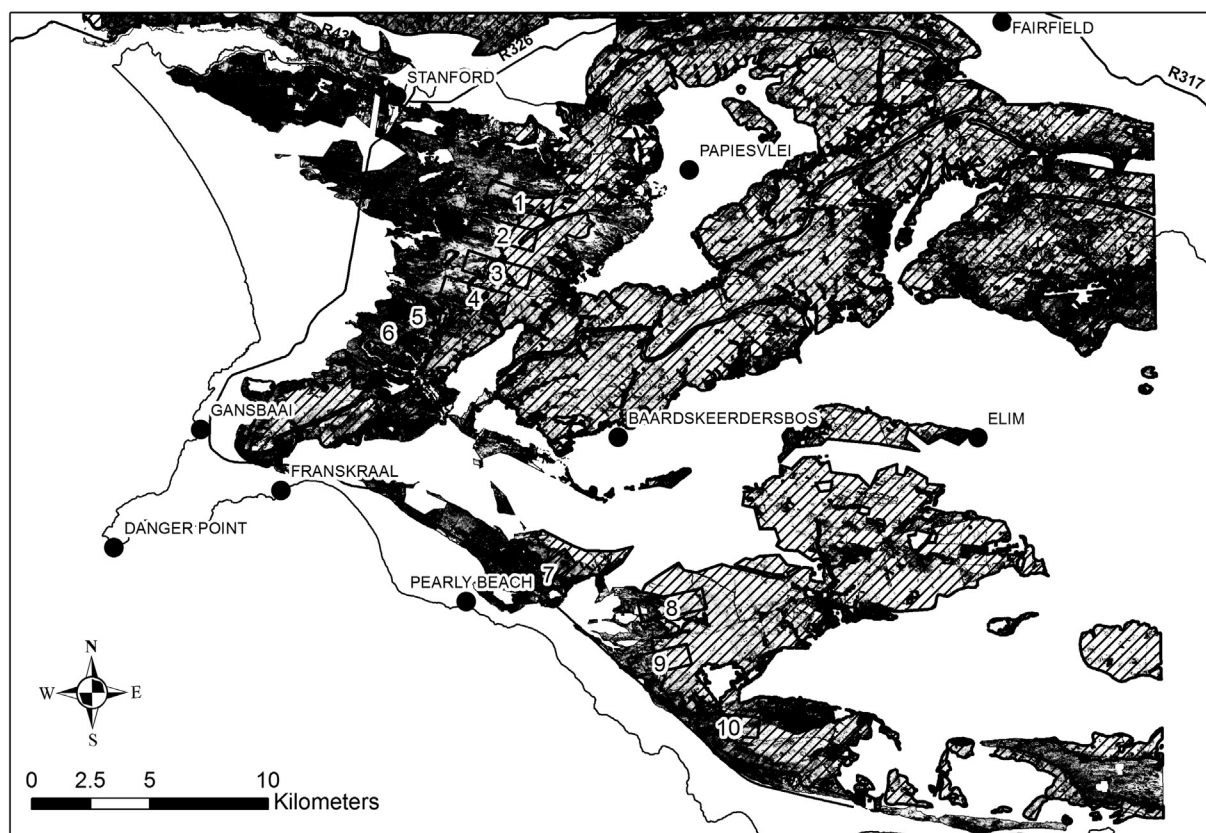


Fig. 2. Probability values for Overberg sandstone fynbos (white) and Agulhas limestone fynbos (black) with the Vegetation Map of South Africa extent of the Overberg sandstone fynbos in horizontal hashing.

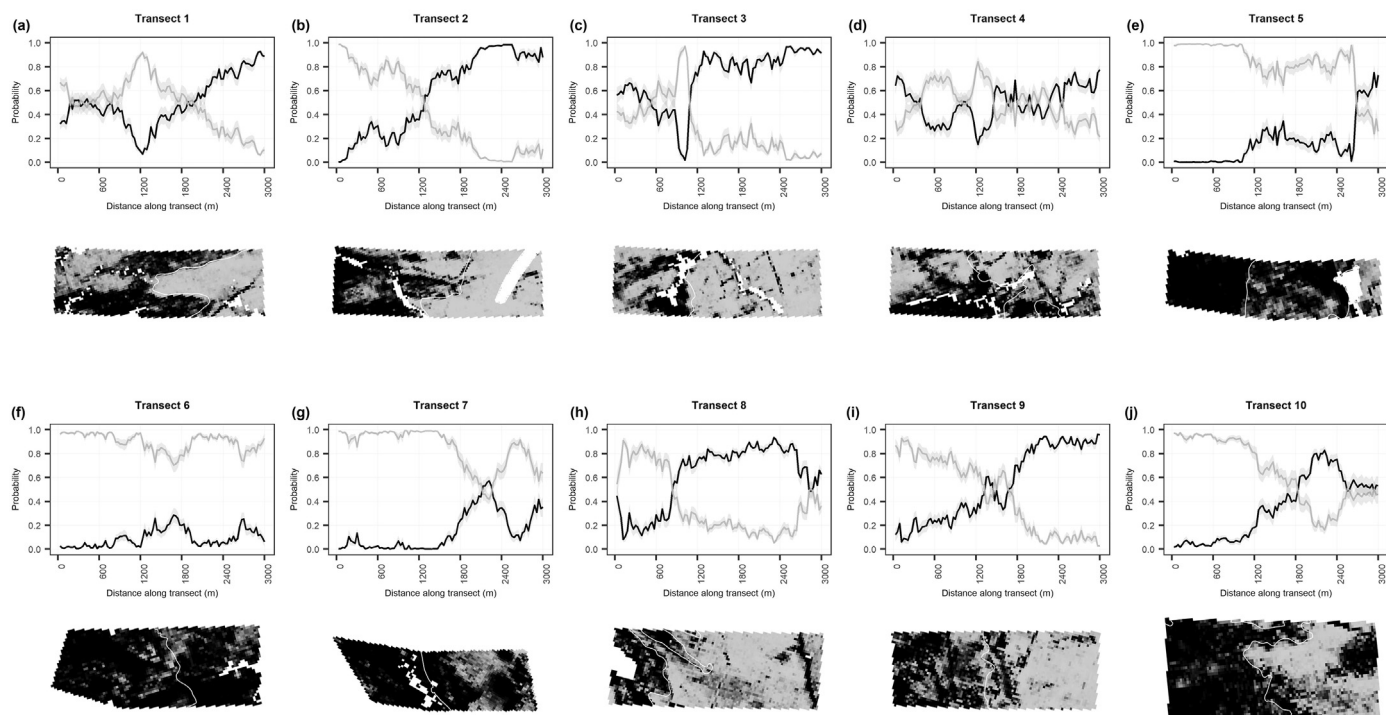


Fig. 3. Graphs (above) and maps (below) of probability values for Overberg sandstone fynbos (grey) and Agulhas limestone fynbos (black) over transects 3000 m in length generally running east (right) to west (left). For the graphs values are binned at 30 m intervals over the 3000 m length of a transect. The Vegetation Map of South Africa extent of the Overberg sandstone fynbos is represented by white lines on the maps.

the location where one vegetation type is replaced by a neighbouring vegetation. However they provide limited or no information on the distance (or width) over which transitions take place, or the heterogeneity within vegetation types (e.g. Duff et al., 2014). The proposed methodology of mapping vegetation probability works well to provide information on ecotone location, width and character. The probability map, together with the probability graphs developed for a few transects across the transition, are able to map and describe (1) abrupt, sharp transitions that take place over a very short distance; (2) moderate transitions that have a distinct band of transition; and (3) complex transitions that include slow transitions, interdigitated boundaries and outliers. In this study area, findings suggested that the character of the Agulhas limestone-acid ecotone is probably more complex than often noted. Interestingly, different portions along the length of the ecotone show different patterns. Only two transects (Fig. 3b and e) show support of a very rapid, abrupt transition from one vegetation type to the other, such as described by field botanists who comment that within three paces one can step from the sandstone into the limestone (Euston-Brown, 1999; Oliver, pers. comm.).

Slightly broader ecotones are seen in cases with well-defined bands of mixing of limestone and sandstone on the probability graph (Fig. 3i and j) where limestone soils and associated dominance by limestone species is seen on higher plateaus between sandstone peaks. It has been noted that shallow layers of neutral or acid sands can alter the composition of species from limestone vegetation to sandstone vegetation (Rebello et al., 2006).

Complex ecotones are where patches of one vegetation type are located deep into the neighbouring vegetation type (Fig. 2), or with convoluted (interdigitated) boundaries and mosaics (mixed transitions). Outlying patches of sandstone quite far into blocks of predominantly limestone vegetation is a known feature in the area (Euston-Brown, 1999) and some are mapped by the Vegetation Map of South Africa. These and more are highlighted by the probability map, which also indicates how distinct the patches are from surrounding vegetation (darker hues represent higher vegetation class probabilities of sandstone in red and limestone in blue). Outlier patches of sandstone fynbos probably occur on the “potholes” of acid (Clovelly and Constantia) soils leached out of the surrounding limestone (Bredasdorp coastal plain); these potholes are reported to have abrupt edges (Rebello et al., 2006). An example of the reverse is seen in transect four (Fig. 3d, see the eastern corner) where a patch of limestone occurs deep into the eastern portion of the transect predominantly defined as sandstone. The limestone vegetation occurs where there is a flatter slope at lower altitude than the surrounding higher altitude, steeper sandstone vegetation. Transect four highlights the utility of probability maps that can accommodate fine-scale heterogeneity of landscapes and associated changes in dominance of vegetation. The same transect (Fig. 3d) also shows an interdigitated boundary in the centre of the transect. Interdigitated acid-alkaline boundaries might also be caused by leaching along the roots of deep-rooted perennial limestone shrubs, which yields fingers of leached acid soils into the alkaline patches (Rebello et al., 2006). Such boundaries may well show sharp transitions at the scale of a metre with a narrow, simple ecotone width at a fine (or local) scale of a few meters, but on the probability graph, binned at 100 m, mixed vegetation probabilities are seen, suggesting a wider, more complex ecotone at a coarser (or landscape) scale.

The range of ecotones highlighted by the probability map can be explained by the complex interplays between alkaline and acid soils in the study area, as described above. In addition, acid proteoid species are intolerant of alkaline soils (Newton et al., 1991). Proteoid species that have adapted to alkaline soils are probably tolerant of acid soils, but are outcompeted by acid-soil specialists (Newton et al., 1991). These combined factors can be expected to yield the variety of ecotones highlighted by the probability classification produced in this study.

For the development of spatially explicit conservation plans targeted to impact decision-making (Killeen and Solo, 2008; Pressey et al.,

2003; Rouget et al., 2003), maps of ecotones are needed to (1) clearly define the extent of biodiversity features such as vegetation or community types, (2) represent transition areas, which have been proposed as ensuring the persistence of biodiversity features (Cowling et al., 2003; Klein et al., 2009) and (3) map ecotonal areas, which may serve as ecosystem processes (Klein et al., 2009; Rouget et al., 2006). Generally ecotone maps for input into conservation plans are developed as buffers of vegetation boundaries (Lagabriele et al., 2009; Rouget et al., 2003) or as the boundary-line between binary classifications of remotely sensed images (Mochizuki et al., 2015; Tapia et al., 2014). The limits of traditional polygon vegetation maps, which represent vegetation as discrete elements with sharp boundaries, and the limitations of the use thereof in conservation plans was recognised as early as 1993 by Scott and colleagues (Scott et al., 1993). The proposed methodology of mapping vegetation probability works well to provide information on ecotone location, width and character. It provides a conceptually similar approach to Lingxue and colleagues (Lingxue et al., 2015) without the need to first generate land use/land cover maps. It follows the spirit of Duff and colleagues (Duff et al., 2014) who developed fuzzy community types based on point species data, where each grid cell in the study area can hold information for more than one unit (vegetation class or community type) as well indicate the probability of the occurrence of each unit in that grid cell. We use a similar probabilistic classification approach with remotely sensed data as input, which are readily available over large areas and updated frequently, as input. These probabilistic or fuzzy approaches allow for visualisations of “core” areas of vegetation types as well as transitional areas. These can be turned into binary classification by selecting the vegetation type with the maximum probability value, by maximising the sum of sensitivity and specificity (Liu et al., 2013), or by a user defined cut-off, in each pixel. The latter could be turned into vector data. Consequently probabilistic classifications of remotely sensed data can provide vegetation class information input to conservation plans as continuous gridded data of vegetation probability; gridded binary data of the vegetation class with the maximum probability, or vector binary data.

Challenges to the approach come from bright features that can confuse the classifier. These include natural bright features such as the Soetansberg's ridge of white ferricrete stone (Thwaites et al., 1988) and unvegetated patches revealing the underlying light-coloured soils in lowland areas in the south of the image. Areas that have possibly been degraded by activities not defined by the transformation classes used in the National Land Cover, together with roads and fire breaks also cause small areas of spectral confusion.

Future work could look at using a moving window to assign core or ecotone status to each central grid pixel (Lingxue et al., 2015) to produce a more consolidated map. Application of these methods over a temporal sequence of years could help determine whether the ecotone is constant over time, or dynamic with time, and determine relevant environmental drivers, such as fire events.

5. Conclusions

Ecotones, or vegetation transitions, are important for pattern (beta and gamma diversity, (Whittaker, 1960)) and function (genetic diversity, metapopulation dynamics, movement corridors (Risser, 1993)). Environmental managers map vegetation types and associated ecotones in order to identify ‘what occurs where’ (inventory function), and to guide and inform environmental and conservation management actions, such as identification of appropriate types and intensity of land use (zonation); recognise rare and endangered features for special protection; and ensure representation of various “types” in protected area networks. In order to achieve these mapping goals for environmental management, methods are required to locate boundaries, and characterise the breadth and strength of different ecotones. This will facilitate the identification of core areas required for representation goals, and ecotones for related functions.

In the light of these mapping goals, this study demonstrates the use of fuzzy probability classifiers on readily available remotely sensed data to identify and map the location, width and character of ecotones through the production of graphs and maps of vegetation, where pixels can display the probability of neighbouring vegetation types. This obviates the need for the choice of a single, most dominant vegetation type, which sometimes leads to the oversimplification of the true situation in the field. These methods are able to capture sharp boundaries, or abrupt ecotones, which are seen on probability graphs where probability lines of two neighbouring vegetation types cross with steep slopes, i.e. where high probabilities of one vegetation rapidly drop to low values and are replaced over a short geographic distance by high probabilities of the neighbouring vegetation type. The associated probability map shows a saturated colour (high probability of one vegetation) being replaced by a saturated colour (high probability of the second vegetation). Gradual, broader ecotones are seen on probability maps as areas of pale colours (low probabilities) as well as interspersions of pixels with saturated colours of the two vegetation types (i.e. mosaics of strongly classified pixels with high vegetation probabilities). Associated probability graphs have vegetation probability lines that do not cross with steep slopes. Distinct ecotones are represented on probability graphs where high probabilities of one vegetation type drop to medium levels, and medium levels of probabilities of the second vegetation type are seen over the same geographical space, creating a distinct band of mixing where after probabilities of the first vegetation type drop-off and probabilities of the second vegetation type increase. Probability graphs of mosaics have lines which cross repeatedly. This concept methodology could be applied to various imagery for any ecotone. It also builds on the call by Hufkens and co-workers (Hufkens et al., 2009) for the use of two-dimensional data and approaches to study ecotones.

Vector (polygon or line) vegetation maps that represent transitions between vegetation types as single lines may battle to distinguish very fine scale sharp transitions as different to convoluted abrupt boundaries and mosaic transitions. For conservation plans, vegetation maps need to be able to map core areas important for key species as well as the location and extent of ecotones for ecosystem processes. The probability maps can distinguish between core areas and ecotones.

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Conflicts of interest

None.

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