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Quantifying historical changes in habitat availability for endangered species: use of pixel- and object-based remote sensing

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Summary

1. Establishing medium- to long-term trends in habitat availability for endangered species is important for determining the causes of historical population declines and for designing effective management plans. For some animal species, relative habitat availability can be estimated using time series of aerial photographs, but the limited information in old black-and-white images makes it challenging to estimate accurately at large spatial scales.

2. Australia's most endangered snake, the broad-headed snake *Hoplocephalus bungaroides*, requires unshaded, exfoliated sandstone rocks for shelter. Using digitized aerial photographs of four sites from 1941 and 1971, and a Quickbird satellite image from 2006, we estimated the trend in habitat availability for a well-studied population of *H. bungaroides* in New South Wales. We did this using both traditional, pixel-based classifications and a more recently developed object-based approach.

3. Both classification methods revealed substantial, monotonic decreases (by 24–77%) in the percentage cover of bare rock from 1941 to 2006 at all sites, with concomitant (although non-monotonic) net increases in percentage tree-canopy cover of 3–70%. The cover of herbaceous and low-shrub vegetation appeared variable and was poorly resolved in the classifications.

4. Both classification methods yielded adequate (> 70%) accuracy for most images, but the object-based classifications were consistently more accurate than the pixel-based classifications and performed better when analysing images (from 1971) with comparatively low resolution.

5. *Synthesis and applications.* Our study indicates that habitat availability for broad-headed snakes has decreased considerably over 65 years due to increased shading from vegetation, and that object-based image analysis is a promising tool for assessing habitat trends using historical photographs. Multiple studies have reported woody-vegetation increases over multi-decadal time-scales in Australia and elsewhere, but few have tied these trends to habitat availability for animal species of concern. The phenomenon we document may therefore be quite widespread, and advances in remote sensing (including applications and refinements of the methods presented here) will be invaluable for revealing these trends and designing ameliorative management strategies. Management plans to conserve broad-headed snakes and similarly threatened species should include either controlled burns or regular targeted removal of vegetation, preferably after a rigorous comparison of the relative economic and biological costs and benefits of each.

Key-words: Aboriginal firestick forming bush encroachment, conservation GIS, eucalypt forests, fire ecology, long-term vegetation dynamics, object-based image analysis, population extinction, reptile conservation biology, thermal biology

Introduction

Although deforestation is probably the greatest threat to biodiversity globally, woody vegetation cover has actually been increasing in many places during recent history (Van Auken 2000; Asner *et al.* 2004). These trends have been especially pronounced in savannas (Roques, O'Connor & Watkinson 2001) and some temperate woodlands (Nowacki & Abrams 2008), where they might threaten animal and plant populations adapted to open habitats (Ballinger & Watts

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1995; Coppedge *et al.* 2001; Nowacki & Abrams 2008). Understanding multi-decadal trends in vegetation cover is therefore important for designing management strategies, such as controlled burning, to protect open-adapted species of conservation concern.

Several methods can be used to assess trends in vegetation cover, depending on the temporal and spatial scales of interest, including analysis of historical records and maps (Fensham 2008; Hall *et al.* 2002), organic deposits (Witt, Luly & Fairfax 2006), tree rings (Lunt 2002), and remotely sensed imagery (Bowman, Walsh & Milne 2001). Historical aerial and satellite imagery are a particularly useful source of information about environmental change over the past 70 years (during which time anthropogenic impacts have intensified dramatically), because they allow estimation of multiple important habitat parameters at multiple scales. Time series of images have been used convincingly to quantify increases (Bowman, Walsh & Milne 2001; Sharp & Whittaker 2003; Fensham, Fairfax & Archer 2005), decreases (Goetze, Horsch & Porembski 2006; Arce-Nazario 2007), and relative stability (Sharp & Bowman 2004) of vegetation density. They have also been used to track the population dynamics of individual tree species (Bowman & Dingle 2006) or congeneric assemblages (Lahav-Ginott, Kadmon & Gersani 2001). Far fewer studies have attempted to link multi-decadal vegetation changes with changes in habitat availability for animal populations (but see e.g. Snodgrass 1997; Erwin, Sanders & Prosser 2004), although in theory it should be possible to establish such linkages in a reliable way.

Land cover in aerial photographs can be assessed using a variety of manual/visual techniques (Fensham & Fairfax 2002), but these methods can be prohibitively time-consuming at landscape scales. By contrast, semi-automated analysis can allow rapid assessments of very large areas. One difficulty associated with semi-automated analysis of historical photographs, however, is that these images contain limited information – typically a single, panchromatic spectral band. Traditional methods of analysing such images assume that pixels in the same land-cover class are spectrally similar. This method is sub-optimal for several reasons. Even in relatively simple landscapes, individual land-cover classes (e.g. ‘forest’) may comprise a broad range of pixel spectral values, which may overlap with the ranges of other land-cover classes. Moreover, pixel-based approaches are in some respects ill-suited to modelling real landscapes, since they cannot accommodate multiple, hierarchical scales of biological organization (Townshend *et al.* 2000; Burnett & Blaschke 2003).

Recently, however, object-based remote-sensing approaches have emerged as an alternative to pixel-based classification (Benz *et al.* 2004; Blaschke, Lang & Hay 2008). Object-based image analysis avoids some of the pitfalls of pixel-based approaches by moving beyond the individual pixel to utilize contextual information about the properties of other objects in the image (Benz *et al.* 2004). While object-based approaches are increasingly used within the remote sensing community to model landscape dynamics (e.g. Mitri & Gitas 2002; Laliberte *et al.* 2004), there remain few applications within the ecology and conservation biology literatures (but see Luscier *et al.* 2006; Gergel *et al.* 2007; Weisberg, Lingua & Pillai 2007).

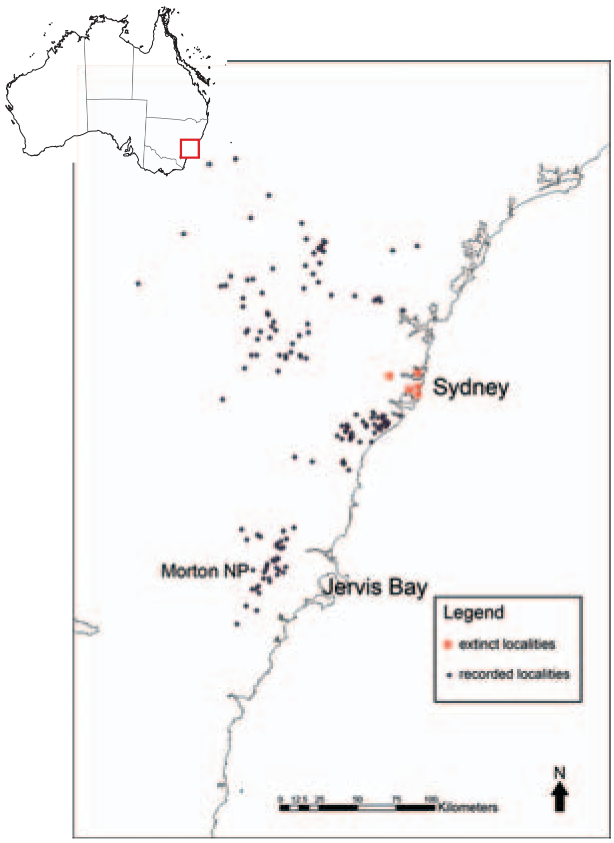

Fig. 1. Maps showing location of study sites and historical and contemporary records of *H. bungaroides* (from the New South Wales National Parks and Wildlife Service Wildlife Atlas, verified by the *H. bungaroides* recovery team).

We have two objectives in this study. The first is to answer a specific applied question about 65-year trends in habitat availability for Australia’s most endangered snake, the broad-headed snake *Hoplocephalus bungaroides* Wagler. Although little is known about the past abundance or distribution of *H. bungaroides*, there are specimen records from areas around Sydney that are now urbanized, as well as from national parks north of Sydney where the species is now extinct or very rare (Fig. 1; Newell & Goldingay 2005). This species currently consists of small populations within 200 km of Sydney, where individuals spend up to 9 months of the year sheltering under exfoliated rocks on sandstone plateaus (Webb & Shine 1997, 1998a,b). For thermal-physiological reasons, *H. bungaroides* is restricted to the small subset of all available rocks that receive direct sunlight in the afternoon, and therefore are warm during the evening foraging hours (Webb & Shine 1998b; Pringle, Webb & Shine 2003). Moreover, when overhanging vegetation is experimentally removed from above otherwise suitable rocks, those rocks are colonized by *H. bungaroides* and its lizard prey (Webb, Shine & Pringle 2005).

On the basis of these findings, we have hypothesized (Pringle, Webb & Shine 2003; Webb, Shine & Pringle 2005; Webb & Shine 2008) that if woody vegetation density has been increasing in this part of Australia, as has been documented or hypothesized for many other parts of Australia (Bowman, Walsh & Milne 2001; Flannery 1994; Banfai & Bowman 2005) and the world (e.g. Laliberte *et al.* 2004; Nowacki & Abrams 2008), then broad-headed snake populations are likely to have declined as a result. This study tests the first half of this hypothesis: that vegetation cover has increased between 1941, the date of the earliest available aerial photographs, and 2006.

Our second objective is to explore the use of object-based remote sensing for answering questions about medium-term changes in habitat structure at landscape scales. We used both the object-based platform Definiens (formerly eCognition; Definiens AG, Munich, Germany) and the pixel-based platform ENVI (ITT Visual Information Solutions, Boulder, CO, USA). Our goal here is not to establish the superiority of either approach, but rather to assess strengths and weaknesses of both in dealing with the data and application at hand.

Material and methods

STUDY AREA AND DATA ACQUISITION

The study area comprises portions of Morton National Park, approximately 160 km south of Sydney, NSW, Australia. The park is dominated by evergreen eucalypt forest and heath: *Eucalyptus gummifera*, *E. agglomerata*, and *Syncarpia glommulifera* are common canopy trees; smaller woody species include *Acacia* and *Banksia* spp. A series of sandstone plateaus of ~400 m elevation traverse the park from south to north. We chose this region because one of us (J.K.W.) has conducted a mark–recapture study of *H. bungaroides* on two plateaus in this park since 1992. Within the park, we selected four plateaus for analysis: the two for which we have data on snake population dynamics (Yalwal and Monkey Gum) and two others (Ettrema and Pioneer), selected haphazardly based on the availability of a time series of uninterrupted imagery covering large extents of the plateaus.

We obtained panchromatic, black-and-white aerial photographs of the study plateaus from the 1940s and 1970s from the Archive of Aerial Photography at Geoscience Australia (Symonston, ACT, Australia; http://www.ga.gov.au). Three of the four plateaus were covered by photographs taken in July 1941 at a scale of 1 : 14 550 (Yalwal Flight Path, Runs 16–20). The fourth plateau (Monkey Gum) was covered by photographs taken in March 1944 at a scale of 1 : 23 270 (Tianjara Flight Path, Runs 1–3). All four plateaus were covered by photographs taken in May 1971 at a scale of 1 : 79 540. All historical images were scanned as TIFF files at 1200 dpi by United Photo & Graphic Services (Blackburn, Victoria, Australia; http://www.unitedphoto.com.au/). For all sites, we obtained pan-sharpened Quickbird satellite images (DigitalGlobe, Longmont, CO, USA) from August 2006. These images contained four spectral bands (red, green, blue, and near-infrared) at a resolution of 0·6 m.

Wildfires burned parts of Morton National Park in 1939, 1968, 1978, 1983, and 2001–2002 (Webb & Shine 2008). Therefore, our imagery was taken either 2 years (1941), 3 years (1971), or 5 years (1944 and 2006) after the last major fire.

DATA PRE-PROCESSING

We orthorectified the historical aerial photographs using the Space Radar Terrain Mission (SRTM) digital elevation model in conjunction with the recent imagery as a base image, using Imagine 8·7 (ERDAS, Inc., Norcross, GA, USA). Following orthorectification, adjacent images from the same year were mosaicked and resampled to 0·6-m resolution using ENVI 4·4 (ITT Visual Information Solutions, Boulder, CO, USA). Although it is generally preferable to resample to lower (as opposed to higher) resolutions when possible, resampling to higher resolution is not uncommon (e.g. Iverson & Risser 1987; Sader & Winne 1992; Rao *et al.* 2006; Jahjah *et al.* 2007); in our case, it enabled us to avoid discarding important information from the higher-resolution 1941 and 2006 images.

Because we were interested in vegetation changes on the plateau tops, we isolated each plateau by tracing its contour and then masking all outlying pixels. The resulting images comprised topographically homogeneous areas of 2–3·7 km^2. Finally, for the 2006 QuickBird images, we generated a normalized difference vegetation index (NDVI) band to enhance vegetation differentiation; thus, all analyses of these images were based on five spectral bands. Importantly, we did not attempt to overlay images to determine land-cover transitions at particular points in the landscape. Rather, we classified each image separately, determined the coverage of each land-cover class, and then compared these numbers across years.

IMAGE ANALYSIS

Based on first-hand knowledge of the sites and visual interpretation of the images, we defined three land-cover categories for all analyses: bare rock (exposed sandstone), herbs and shrubs ≤ 2 m tall (hereafter, ‘shrubs’), and canopy trees > 2 m tall. This relatively simple scheme is appropriate for several reasons. First, our principal goal was tracking habitat availability for snakes that shelter under bare exfoliated rocks, and the extent of bare rock (not covered by *any* vegetation) is therefore the most important variable. Secondly, both trees and shrubs are hierarchically contained within the general category ‘vegetation,’ meaning that we can collapse these two categories for a more simple comparison of vegetated vs. un-vegetated area (Congalton 1991; see Results). Thirdly, relatively little information is contained in panchromatic images, making it difficult to make fine distinctions among vegetation types. In the historical panchromatic images, bare sandstone rock stood out as particularly light in shade. Trees were distinguished by their shapes and were typically dark in shade. Shrubs were more amorphous in shape and typically intermediate in shade (Supporting Information, Figs S1–S4). In the 2006 satellite imagery, multiple spectral bands made it easier to distinguish among the three land-cover types. Although some shadows were present in most of the images, they were often difficult or impossible to distinguish from tree canopies, especially in the older images. We therefore did not attempt to classify shadows separately; this decision is unlikely to have biased our qualitative results, since shadows constituted a small fraction of the total pixels under consideration.

PIXEL-BASED APPROACH

By visually interpreting the photographs according to the criteria above, we delineated 15 ‘training sites’ for each of the three land-cover types. We tried to ensure that the individual training sites were as homogeneous as possible, but that they collectively encompassed a large range of the spectral values in each land-cover type.

We conducted supervised pixel-based analyses using ENVI 4·4. Maximum Likelihood classifiers are widely used in remote-sensing studies of land-cover change, but ENVI's Maximum Likelihood algorithm is based on covariance among image bands and cannot be applied to images with < 2 spectral bands. We therefore classified historical photos using ENVI's Minimum Distance algorithm, which is based on image brightness. However, when applied to the more complex multispectral QuickBird satellite images, Minimum Distance consistently failed to produce accurate classifications (Table S1, Supporting Information). Therefore, we also applied the Maximum Likelihood classifier to these images; for simplicity, we only report the more accurate outputs obtained using this method.

OBJECT-BASED APPROACH

Object-based analyses were performed using Definiens Professional 5·0. We began by applying a multi-resolution segmentation approach to each image. The segmentation process is a bottom-up region-merging technique, which starts at the pixel level and successively merges adjacent pixels based on their similarity, according to user-defined parameters of scale, colour, and shape; this process creates a series of relatively homogeneous 'primitive objects' that are used for classifying images (Baatz & Schape 2000; see also Benz *et al.* 2004 for descriptions of the fundamentals of object-based image analysis). We applied the segmentation process at three hierarchical spatial levels. The first level targeted characteristics of the exposed rock outcrops at our study sites, with representative scale, colour, and shape parameter values determined by trial and error. The second and third levels targeted shrubs and forest-canopy vegetation, respectively.

Our classification scheme used a combination of two classifiers embedded in Definiens, 'nearest neighbour' and 'fuzzy.' With the nearest-neighbour classifier, the user selects primitive objects that are representative of each land-cover class, which is conceptually similar to selecting training sites for our pixel-based classifications. The classifier then calculates distances in the features space between object means and sample means using a distance-decay function. This classifier also calculates distances for selected statistical properties and contextual information (i.e. the properties of adjacent objects). The fuzzy classifier (a 'soft' classifier) employs fuzzy-logic theory by utilizing user-defined membership functions, based on assessment of the statistical characteristics and contextual information of each land-cover class.

The statistical properties used for the classifications differed for the panchromatic and multispectral images. For the multispectral QuickBird images, we used the NDVI band to increase separability of the shrub and forest-canopy land-cover classes. Thus, the forest-canopy segmentation level utilized the NDVI band and was classified based on mean NDVI values. We classified the shrubs using the nearest-neighbour classifier for several statistical measures: standard deviation and 'maximum pixel value' for the NDVI band, 'minimum pixel value' for the red band, and 'ratio' for the near-infrared and green bands (see Definiens Professional 5 User Guide, http://www. definiens.com, for definitions). We used the same statistical measures in the nearest-neighbour classifier for the forest class, and we implemented a hierarchical classification by including objects that had been classified as forest at the forest-canopy segmentation level. The bare rocks were classified based on the fuzzy membership for 'brightness.'

The aerial photographs required different classifier memberships because they consisted of only one spectral band; therefore, we emphasized textural information to maximize the contrast among the pixels. We defined the shrub and forest-canopy land-cover classes using mean GLCM (grey-level co-occurrence matrix) texture at all angle options in Definiens, as well as the 'mean difference to neighbours,' 'mean,' and 'minimum pixel value' measures. Exposed sandstone was clearly distinguishable from surrounding vegetation in the aerial photographs (Figs S1–S4, Supporting Information), and therefore, we needed only the 'brightness' measure to classify the sandstone class.

GROUND TRUTHING AND ACCURACY ASSESSMENT

We were able to access two of the four plateaus (Yalwal and Monkey Gum) for ground truthing. The other two plateaus (Ettrema and Pioneer) are inaccessible. On the plateaus that we could reach, we drove along the plateau, stopping periodically to perform walking surveys during which we recorded Global Positioning System (GPS) points in homogeneous patches (≥ 2-m diameter) of bare rock, low vegetation, or closed-canopy forest. We used both a Trimble Recon GPS attached to a Trimble Pro XT receiver and a Sokkia GSR2650 LB to collect points; after differential correction, the Trimble unit was accurate to ≤ 1 m, while the Sokkia unit was accurate to ≤ 20 cm. We also used a Garmin GPS 10 attached to an Ipaq handheld computer running ESRI ArcPad. This GPS combination yielded accuracy of ≤ 2 m and enabled us to visualize our position on the images while in the field.

These GPS points formed the basis of our accuracy assessments for the 2006 QuickBird images of Yalwal and Monkey Gum plateaus: for each plateau, we overlaid 100 GPS points (distinct from the areas used to train the classifier) on the completed classifications, and we assessed the correspondence of the classified land-cover assignments with the known, ground-truthed land-cover categories. From this information, we computed raw percentage accuracy and the Kappa coefficient (Congalton 1991). It is obviously impossible to ground-truth historical images, and thus, we used the same sets of points for each image in conjunction with visual photo-interpretation, based on our familiarity with the sites in question, to define an accuracy matrix. For the inaccessible Ettrema and Pioneer plateaus, we first generated 100 points in a stratified-random pattern (to ensure adequate representation of all land-cover classes) and visually interpreted their land-cover category for each year. We then overlaid these points on the completed classifications, excluding a small minority of randomly generated points that fell in areas where we were not confident in our assessments. We then quantified the correspondence of the land-use-category assignments as above.

Error matrices were generated for both classification methods. We compared reference-collection data (including GPS and visual interpretation) with classified imagery. From these matrices, we derived producers and users accuracies as well as a kappa statistic. Complete error matrices (Congalton 1991) for each classification appear in the Supporting Information, Table S1. We considered any classification with accuracy > 70% to be an adequate basis for drawing conclusions about actual trends in land cover.

Results

PIXEL-BASED APPROACH

We provide a sub-sample of raw and classified images in Fig. 2. According to the pixel-based classifications, coverage of bare sandstone decreased over 65 years (Fig. 3), while total vegetation cover increased over the same interval (Table 1). All four sites exhibited monotonic decreases in the percentage cover of bare rock, ranging from 40–54% (mean 49%).

While the percentage of pixels classified as forest was at all sites greater (by 8–70%, mean 30%) in 2006 than in 1941/1944,

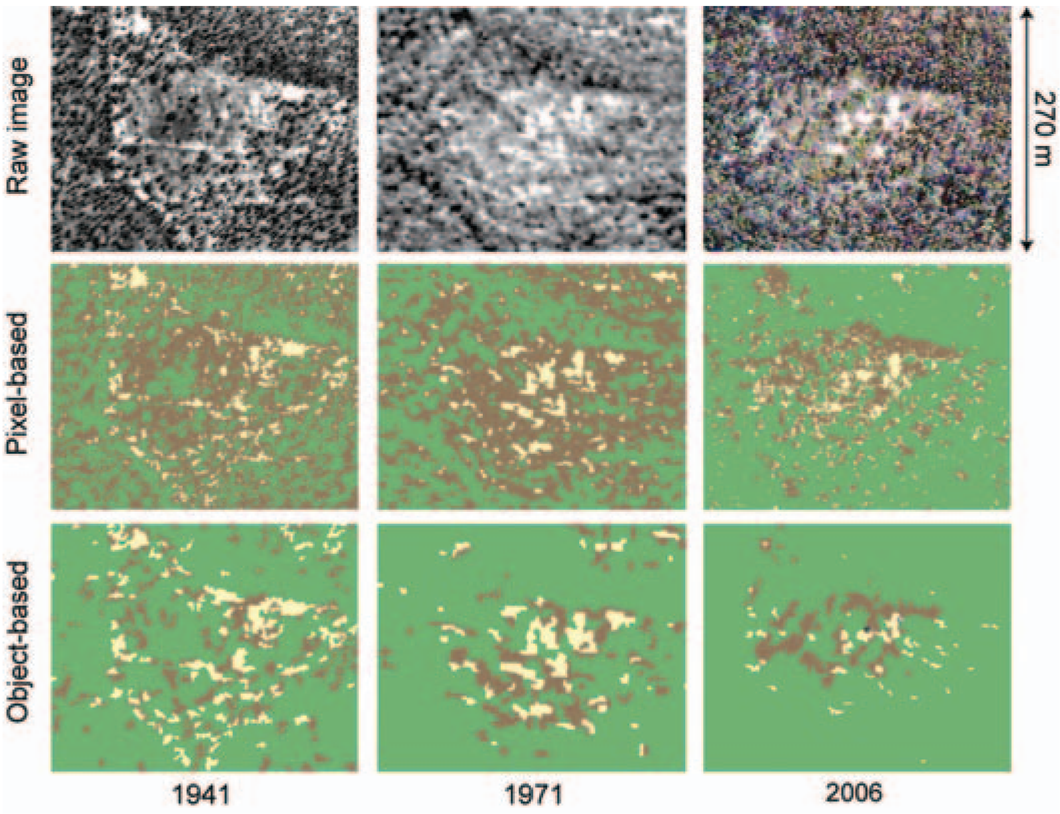

Fig. 2. A representative region of the Yalwal plateau, with corresponding pixel- and object-based classifications. Areas coloured cream represent bare rock; brown represents shrubs and low vegetation; green represents forest canopy.

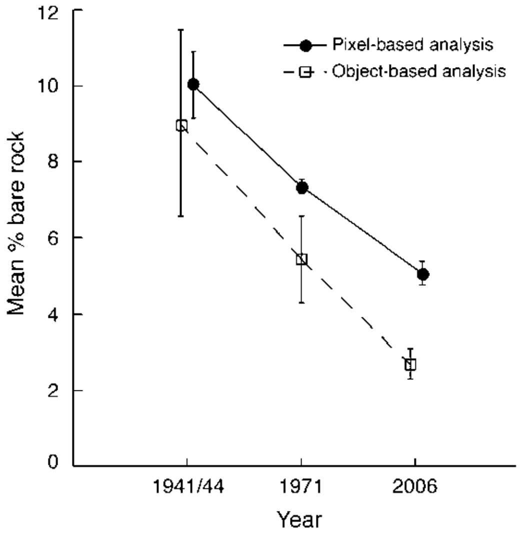

Fig. 3. Temporal dynamics in the mean percentage coverage of bare rock across all four study plateaus. Error bars represent ± 1 standard error.

the increase was not monotonic: the images from 1971 appeared to have lower levels of canopy cover than those from 1941/1944. However, this result may be a by-product of low accuracy of the 1971 classifications (Table 1), which in turn stemmed from an inability to discriminate between the forest and shrub vegetation types. Bare rock was classified with very high accuracy in all years (Supporting Information, Table S1), but the relative accuracies of the two vegetation classes varied considerably and were unacceptably low for the 1971 imagery, which had the lowest resolution and contrast of all of the images. The low contrast resulted in the over-classification of shrubs (which had intermediate brightness) relative to forest (Supporting Information, Table S1). However, combining the forest and shrub classes (i.e. simply comparing bare vs. vegetated pixels) yielded overall accuracies of 86–96% for all images (Table 1, right-most column).

OBJECT-BASED APPROACH

The overall trends revealed by the object-based analyses were qualitatively similar to those of the pixel-based analyses, namely a general increase in vegetation cover at the expense of bare rock. That said, the two classification types differed in both appearance (Fig. 2) and quantitative output (Fig. 3; compare Tables 1 and 2).

The overall coverage of bare sandstone decreased dramatically from 1941 to 2006 at three of the four sites (range 73–77%, mean 75%). However, the percentage cover of bare rock at one site, Monkey Gum, changed relatively little, decreasing 24% from 2·9% in 1944 to 2·2% in 2006 (Table 2). Percentage forest cover at all sites was greater in 2006 than in 1941/1944 (by an average of 10%), but the magnitude of this net increase varied considerably among sites (3–15%), and the temporal trend was not monotonic. Temporal dynamics in the coverage of shrub vegetation were likewise variable and inconsistent across sites (Table 2).

Table 1. Results of pixel-based analyses

Site	Year	Classifier	Bare rock % cover	Bare rock Area (km^2)	Shrubs/low vegetation % cover	Shrubs/low vegetation Area (km^2)	Forest canopy % cover	Forest canopy Area (km^2)	Overall accuracy	Kappa	Accuracy, 2 cover classes
Ya	1941	Min. Dist.	12·6	0·47	40·3	1·50	47·1	1·75	0·74	0·56	0·96
Ya	1971	Min. Dist.	7·6	0·27	51·5	1·87	41·0	1·48	*0·49*	*0·29*	0·96
Ya	2006	Max. Like.	5·8	0·21	14·1	0·51	80·1	2·90	0·87	0·75	0·95
Et	1941	Min. Dist.	9·2	0·19	36·4	0·74	54·4	1·10	0·89	0·80	0·94
Et	1971	Min. Dist.	7·2	0·15	42·1	0·85	50·7	1·03	*0·50*	*0·18*	0·88
Et	2006	Max. Like.	4·3	0·09	33·6	0·68	62·1	1·26	0·71	0·47	0·95
Pi	1941	Min. Dist.	8·5	0·30	33·0	1·18	58·5	2·09	0·76	0·58	0·87
Pi	1971	Min. Dist.	6·9	0·25	40·3	1·89	52·8	1·89	*0·56*	*0·29*	0·95
Pi	2006	Max. Like.	5·1	0·18	31·5	1·11	63·4	2·24	0·76	0·56	0·96
Mg	1944	Min. Dist.	9·7	0·33	22·9	0·79	67·3	2·32	0·70	0·40	0·86
Mg	1971	Min. Dist.	7·7	0·26	39·0	1·34	53·3	1·83	*0·57*	*0·30*	0·93
Mg	2006	Max. Like.	5·1	0·18	8·4	0·29	86·4	2·97	0·79	0·64	0·87

Site codes: Ya, Yalwal; Et, Ettrema, Pi, Pioneer; Mg, Monkey Gum.
Min. Dist., Minimum Distance; Max. Like., Maximum Likelihood.

Table 2. Results of object-based analyses

Site	Year	Bare rock % cover	Bare rock Area (km^2)	Shrubs/low vegetation % cover	Shrubs/low vegetation Area (km)	Forest canopy % cover	Forest canopy Area (km^2)	Overall accuracy	Kappa	Accuracy, 2 cover classes
Ya	1941	14·5	0·55	11·1	0·42	74·4	2·82	0·89	0·77	0·92
Ya	1971	7·9	0·29	11·9	0·44	80·1	2·94	0·93	0·84	0·99
Ya	2006	3·8	0·15	10·7	0·42	85·5	3·36	0·87	0·73	0·95
Et	1941	9·7	0·20	10·0	0·20	80·3	1·64	0·85	0·69	0·93
Et	1971	5·8	0·12	5·8	0·12	88·4	1·81	0·89	0·71	0·97
Et	2006	2·6	0·05	14·9	0·30	82·4	1·68	0·82	0·56	0·97
Pi	1941	9·2	0·33	10·5	0·38	80·3	2·88	0·85	0·71	0·89
Pi	1971	5·6	0·20	15·5	0·56	78·9	2·83	0·82	0·58	0·98
Pi	2006	2·1	0·08	6·6	0·24	91·3	3·27	0·81	0·48	0·96
Mg	1944	2·9	0·10	9·0	0·31	88·2	3·05	0·80	0·47	0·95
Mg	1971	2·4	0·08	4·1	0·14	93·6	3·24	0·81	0·37	0·98
Mg	2006	2·2	0·08	3·2	0·11	94·6	3·27	0·77	0·59	0·91

Site codes: Ya, Yalwal; Et, Ettrema; Pi, Pioneer; Mg, Monkey Gum.

The accuracy of the object-based analyses was consistently high and superior to that of the pixel-based analyses, and it varied little across years (Table 2). However, this method had shortcomings: while bare-rock and forest-canopy accuracy points were consistently classified correctly (mean accuracy 85 ± 4% SE and 96 ± 1% SE, respectively), only 42 ± 5% SE of the shrub-vegetation accuracy points were classified correctly on average (Supporting Information, Table S1). Again, however, lumping the two vegetation classes produced overall accuracies ranging from 89–99% (Table 2, right-most column).

Discussion

The amount of exposed bare rock, a limiting habitat requirement for endangered broad-headed snakes and other fauna (Pringle, Webb & Shine 2003; Webb, Shine & Pringle 2005), decreased from 1941/1944 to 2006 due to vegetation expansion. We found a similar pattern of monotonic decrease at each of four sites using two different methods. The average percentage decrease across all sites during this period was 49% or 62%, depending on the analytical method used. Because collapsing the shrub and tree categories into a single 'vegetation' category produced images with overall accuracy ≥ 86%, this most-important result is unambiguous.

The vegetation encroachment appears to have been driven by increases in the coverage of woody canopy species, with understorey vegetation remaining relatively static, but this result should be interpreted with caution. The difficulty of distinguishing vegetation types precisely in the black-and-white historical photographs (especially those from 1971) prevents a detailed assessment of successional dynamics at these sites. From the snakes' perspective, however, the vegetation type probably does not matter: both low and high vegetation shade rocks, rendering them thermally unsuitable (Pringle, Webb & Shine 2003; Webb, Shine & Pringle 2005).

Other studies have implicated overgrowth in the decline or

Table 3. Potential sources of error in our analyses and their consequences

Source of error	Explanation and potential consequence
Data pre-processing	
Sampling error	Four sites (12·7 km^2) may not be representative of Morton National Park (1046 km^2).
Orthorectification and resampling	Error is intrinsic to the process of rectifying images, although it is unlikely to bias our results.
Classification	
Subjective selection of training sites	Potential subconscious bias in selecting areas representative of each land-cover class; ultimately reflected in quality of the classification, as determined by accuracy assessment.
Differing image sources and quality	Aerial photos and satellite image have different spectral properties and scales; affects the ability to differentiate land-cover classes.
Uneven image quality	Quality and contrast varied *within* some of our aerial photographs, leading to uneven classifications.
Different image dates, times of day, angles	Temporal variation in plant phenology, reflectance, shadow, etc. may affect the accuracy with which user and the software are able to assign pixels/objects to categories.
Classification error	Pixels classified incorrectly; consequences captured by accuracy assessment.
Accuracy assessment	
Visual photographic interpretation	Subjective process with no concrete basis for determining accuracy, especially for old panchromatic photographs.
Instrument error in ground-truth points	GPS locations erroneous by up to 2 m; potential spatial mismatch when applied to images.

extirpation of snake populations. Fitch (1999), in a long-term study from Kansas, USA, noted declines of several species as shrubs invaded an old field, while Jäggi & Baur (1999) suggested that forest regeneration may have caused or hastened the local extinction of *Vipera aspis* in Switzerland's Jura Mountains. Another European viperid, *V. ursinii*, is threatened in central Italy by the encroachment of *Pinus mugo* in high-alpine pastures (Filippi & Luiselli 2004). The widespread reports of woody encroachment in old fields, savannas, and some temperate forests might therefore threaten populations of snakes and other ectotherms worldwide.

In our study, object-based image analysis in Definiens proved consistently more accurate than pixel-based analysis in ENVI for both panchromatic and multispectral imagery. Both types of imagery exhibited considerable spectral overlap among land-cover classes. In the 1940s and 1970s images, some pixels that appeared to be canopy trees had approximately the same brightness values as pixels that unambiguously represented low shrubs, while pixels at the apices of tree canopies were sometimes as bright as bare-rock pixels. This lack of segregation among land-cover classes confounded the pixel-based analyses, whereas the object-based analyses, which utilized the spatial and spectral relationships among image features, were more successful. While it is probable that applying more complex and time-consuming techniques could further boost the accuracy of our pixel-based classifications, object-based approaches seem like an attractive option for accurately classifying images with limited spectral information.

Both classification methods, however, failed to resolve the shrub-vegetation class, with the pixel-based analyses tending to overestimate its extent (relative to forest) and the object-based approaches tending to underestimate it (relative to both forest and bare rock: Supporting Information, Table S1). We attribute this both to the aforementioned spectral ambiguity of many 'vegetation' pixels and to the uneven vertical profile of the shrub class, which in turn stemmed from the biological breadth of this category. We used the term shrub for any low-profile vegetation, since profile was one of the few attributes that we could readily discern in older images, but in reality this corresponded to a broad range of species, from herbs to woody shrubs ≤ 2 m tall. This may be an unavoidable difficulty of using historical panchromatic photographs to classify > 1 vegetation type at a large scale in a moderately diverse temperate forest. Savannas, with their pronounced tree–grass discontinuities, may be easier to resolve (e.g. Fensham, Fairfax & Archer 2005; Bowman, Boggs & Prior 2008; Lehmann *et al.* 2008).

As suggested above, multiple sources of error can compromise the precision of studies such as ours (Table 3). In this study, some sources of error were unavoidable: error is intrinsic to comparisons of images taken at different scales, dates, and times of day, and by different sensors (Fensham & Fairfax 2002), and image quality varied within and among the images we used. Various digital enhancements combat some of these problems, but enhancements carry their own risks of introducing artefact. We reduced error by limiting the complexity of our analysis to the minimum needed to answer the conservation question of interest: since we were most interested in the amount of shade on the ground, we did not attempt to make fine discriminations among vegetation types, and we used the simple metric of percentage cover in each year rather than attempting to overlay the images and determine land-cover transitions at particular points. Ultimately, the qualitative trends in overall vegetation cover at these sites are clear, although the precision of our estimates was undoubtedly affected by some of the sources of error discussed here.

We do not know the mechanisms underlying the patterns of vegetation increase that we have documented. Fire suppression is an obvious candidate, although the effects of fire on historical patterns of woody vegetation change are complex (Bowman 1998). In some parts of Australia, such as eucalypt savannas in the Northern Territory (Bowman, Walsh & Milne 2001), the cessation of traditional Aboriginal landscape-burning practices has helped drive expansions of woody vegetation. Studies elsewhere, such as tropical sandstone-plateau woodlands in the Northern Territory (Sharp & Bowman 2004) and mixed woodlands in inland Queensland (Fensham 2008), have found scant evidence for fire-driven vegetation shifts.

Prior to European settlement, our sites were inhabited by Aboriginal people from the Wandandian tribe, who regularly burned plateaus to facilitate travel and promote growth of grasses for grazing wallabies (Sneddon 1988). Since the early 20th century, fires (including those ignited by lightning) have been actively suppressed in the south coast of New South Wales (Jurskis, Bridges & de Mar 2003; Cheney 2005). These policies have prompted a shift from patchy, low-intensity burns to extensive, high-intensity conflagrations (Jurskis, Bridges & de Mar 2003). It is possible, therefore, that our time series captures the tail end of a successional shift that followed fire exclusion and the conversion of relatively open woodland to closed-canopy forest.

While we cannot confidently attribute our results to changing fire regimes, we do not believe that our results can be attributed entirely to the timing of fires relative to when the images were taken. All images were taken within 5 years of the most recent fire, and the 1971 images, which in several cases exhibited the greatest apparent vegetation cover (Table 2), were taken just 3 years after the high-intensity 1968 fire (compared with 2- and 5-year intervals for the 1941 and 1944 images, respectively). Although considerable changes in vegetation structure, such as the relative cover of woody and herbaceous species, can occur rapidly after a fire, we suspect that most areas suitable for vegetation would have experienced at least herbaceous regrowth within 2 years. Thus, while our assessments of relative tree and shrub cover may have been sensitive to fire timing, our assessment of bare rock – the crucial habitat parameter – is likely robust. We can even more confidently rule out rainfall patterns as an explanation. Some studies documenting woody expansion in Australia have suggested that increasing rainfall over the latter half of the 20th century may have contributed to increased vegetation cover (Bowman, Walsh & Milne 2001; Fensham, Fairfax & Archer 2005), but average annual rainfall at the Australian Bureau of Meteorology in Nowra (20 km from Morton National Park) decreased between 1951 and 2000 (statistics available at http://www.bom.gov.au/).

The decrease in extent of bare rock over the past 65 years has almost certainly caused a decrease in retreat-site availability for *H. bungaroides* (a limiting resource: Pringle, Webb & Shine 2003; Webb, Shine & Pringle 2005). This absolute decrease may effectively be more severe, since the small-eyed snake *Cryptophis nigrescens* is an intraguild predator (Webb, Pringle & Shine 2009) with nearly identical retreat-site preferences (Webb, Pringle & Shine 2004). We have suggested (Pringle, Webb & Shine 2003; Webb, Shine & Pringle 2005) that reintroducing regular, patchy, low-intensity burns might be optimal for biodiversity maintenance in this system. Although broad-headed snakes shelter in tree hollows during the fire-prone summer months, wildfire does not affect their apparent survival – in contrast to the common *C. nigrescens*, which suffered a 48% population decrease in the 8 months after the 2001–2002 fire (Webb & Shine 2008). Thus, fire may facilitate the persistence of *H. bungaroides* both directly by increasing the availability of thermally suitable microhabitat, and indirectly by controlling the population of its intraguild predator and competitor, *C. nigrescens*.

However, burning strategies are contentious (e.g. Parr & Andersen 2006) and expensive to implement properly. It is also possible that renewed burning might harm populations whose biology is less well known than that of *H. bungaroides*, or that the crucial cliff-edge sandstone habitat has entered a new steady state that low-intensity burns cannot reconfigure. An alternative approach would be the regular, chainsaw-assisted removal of overhanging vegetation from westerly escarpments; this might be a functionally equivalent, yet comparatively low-impact, alternative to fire. To choose among these alternatives, we would ideally need at least two things, namely: (i) knowledge of the mechanism underlying the vegetation increase documented here, and whether it is reversible on westerly escarpments, and (ii) an evaluation of the likely economic and biological costs of controlled burning. One attractive management strategy would be to begin clearing overhanging westerly vegetation immediately, followed by a controlled-burning programme if the necessary experiments and impact assessments prescribe it.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figs S1–S4. Raw images and corresponding object-based classifications for the four plateaus analysed in our study. As in the main text, areas coloured cream represent bare rock; brown represents shrubs and low vegetation; and green represents forest canopy. Fig. S1: Yalwal Plateau; Fig. S2: Ettrema Plateau; Fig. S3: Pioneer Plateau; Fig. S4: Monkey Gum Plateau.

Table S1. Complete error matrices for all classifications

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