

Research



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Linking trophic cascades to changes in desert dune geomorphology using high-resolution drone data

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Vegetation cover is fundamental in the formation and maintenance of geomorphological features in dune systems. In arid Australia, increased woody shrub cover has been linked to removal of the apex predator (Dingoes, *Canis dingo*) via subsequent trophic cascades. We ask whether this increase in shrubs can be linked to altered physical characteristics of the dunes. We used drone-based remote sensing to measure shrub density and construct three-dimensional models of dune morphology. Dunes had significantly different physical characteristics either side of the ‘dingo-proof fence’, inside which dingoes are systematically eradicated and shrub density is higher over vast spatial extents. Generalized additive models revealed that dunes with increased shrub density were higher, differently shaped and more variable in height profile. We propose that low shrub density induces aeolian and sedimentary processes that result in greater surface erosion and sediment transport, whereas high shrub density promotes dune stability. We speculate that increased vegetation cover acts to push dunes towards an alternate stable state, where climatic variation no longer has a significant effect on their morphodynamic state within the bi-stable state model. Our study provides evidence that anthropogenically induced trophic cascades can indirectly lead to large-scale changes in landscape geomorphology.

1. Background

Removal of large carnivores such as big cats, wolves and sharks can have profound effects on ecosystems through trophic cascades. Trophic cascades occur when the removal of a predator indirectly influences species at lower trophic levels. When released from top-down control of an apex predator, the abundance of herbivores and smaller predators increases [1,2] that, in turn, may exert drastically different pressures on key ecosystem functions [3]. Trophic cascades can propagate from predators down to plants, and even into the physical environment if, for example, increased grazing pressure by herbivores influences other species [4], fluvial processes [5] or soil–nutrient dynamics [6].

Encroachment of woody plants into grasslands, or *shrub encroachment*, has generated much interest in ecology because it has the potential to transform the structure and functioning of ecosystems [7]. In the study area for this paper, in Australia’s Strzelecki Desert, shrub encroachment has been shown to be a key outcome of a trophic cascade driven by the removal of an apex predator, the dingo (*Canis dingo*) [6,8–11]. While there is local variance, most studies have shown that in this area, the removal of dingoes has facilitated population increases of mesopredators, namely foxes (*Vulpes vulpes*) and cats (*Felis catus*) [12]. Higher mesopredator abundances lead to lower abundances of small mammals that eat shrub seeds and seedlings [8,10,13]. Finally, relaxed predation pressure on

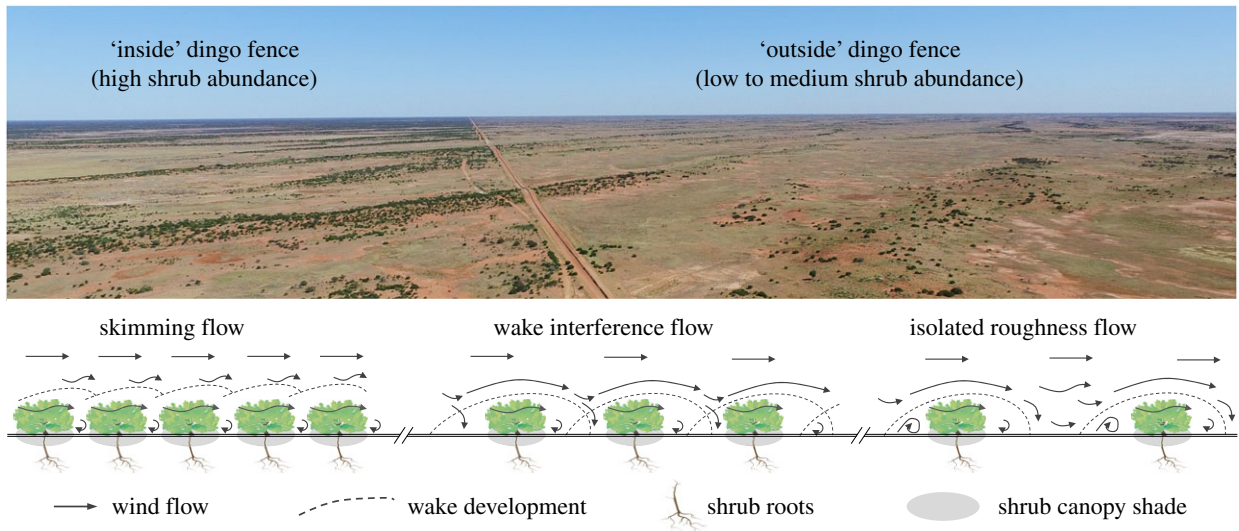


Figure 1. An aerial photo of the dingo-proof fence in the Strzelecki dune field, Australia, showing the phenomenon of increased woody shrub density where dingoes have been removed. The diagram demonstrates predicted wind flow regimes—‘isolated roughness’ and ‘wake interference’ at low to medium shrub density; ‘skimming flow’ at high shrub density (adapted from [20])—and increased root structure and canopy shade at high shrub density. (Online version in colour.)

shrub seeds and seedlings has, in turn, been linked to greater recruitment success for shrubs [10] that has led to broad-scale increases in woody vegetation cover [8].

Woody vegetation cover is a fundamental property that controls sediment transport in dryland ecosystems [14]. There are long established links between vegetation cover and dune mobility [15], and the specific composition of vegetation growth forms (non-woody grasses, forbs and herbs; woody shrubs and trees) has strong localized effects on sand deposition and erosion [16]. In our study area, the morphodynamic state of sand dunes is primarily driven by long-term climatic forcing, and they are typically very stable due to complex vegetation communities that are resistant to drought [17,18]. They are said to be mostly in a meta-stable phase within the bi-stable state model [18,19]. Under the bi-stable model, dunes can be either stable and immobile (non-active) or unstable and mobile (active). Dunes in this study area are said to be in meta-stable because they are generally non-active dunes, but climate forcing events over a certain threshold can switch them into an active state, where most notably, the dune crests become non-vegetated. Regardless of the dune’s morphodynamical state, the density of shrubs influences wind flow and sediment transport regimes [20].

Theory suggests that at greater shrub densities, wake development helps form a boundary layer in which wind flow ‘skims’ over the top of the vegetation. In this ‘skimming flow’ regime, sediment transport and erosion potential are greatly reduced [20]. At low and intermediate shrub densities, wind flow regimes are said to follow the ‘isolated roughness’ and ‘wake interference’ models [20]. These flow regimes have less wake development and do not create a strong boundary layer, so surface erosion and sediment transport potential are much greater due to increased wind flow and turbulence at the surface [20]. Sediment binding potential is much greater at higher shrub densities, both directly through the binding properties of roots and through canopy shade, which facilitate growth of ground cover-like subshrubs and forbs [17,18]. Sediment binding potential is thus limited at lower shrub densities [17,18]. Figure 1 shows these concepts visually.

Although there is a substantial literature linking vegetation composition and structure to fine-scale (centimetres to metres)

geomorphological features in coastal dunes (e.g. [21]), there is a relative scarcity for large arid dune systems. This can be attributed to lack of data and the cumbersome nature of measuring fine-scale morphological features over large, usually remote areas. The recent advancements in drone technology now enable the generation of ultra-high-resolution (centimetre scale) physical measurements of geomorphology, as well as detailed surveys of vegetation populations at comparatively large spatial scales [22,23].

In this paper, we link ecological theory to dune geomorphology by using a combination of historical and drone-based imagery on either side of Australia’s dingo-proof fence in the Strzelecki Desert. On the inside of the dingo fence, increases in shrub density have been linked to a trophic cascade triggered by the removal of dingoes, while dingo populations persist on the outside, creating two adjacent but contrasting ecological communities [8]. First, we demonstrate the differences in shrub cover on either side of the dingo fence using historical aerial photography and newly acquired drone imagery. We then used drone imagery to construct three-dimensional models of sand dune morphology which allowed us to test whether shrub encroachment leads to altered geomorphological processes on desert dunes. We theorize that the aeolian and sedimentary processes that control dune morphology have shifted into different regimes for dunes with altered shrub density. By investigating these mechanisms at very high spatial resolution, we were able to explicitly test hypotheses about underlying drivers of geomorphology in our system.

2. Data and methods

2.1. Study location

Our study area sits in the Sturt National Park region of the Strzelecki Desert in eastern central Australia (figure 2). It straddles the Queensland, New South Wales and South Australia state borders. In the early 1900s, the ‘dingo fence’ began construction, because then dingoes have been systematically eradicated through shooting and lethal baiting inside the fence. The fence was erected along the arbitrarily defined state borders, with New South Wales ‘inside’ the fence. The study area has varied

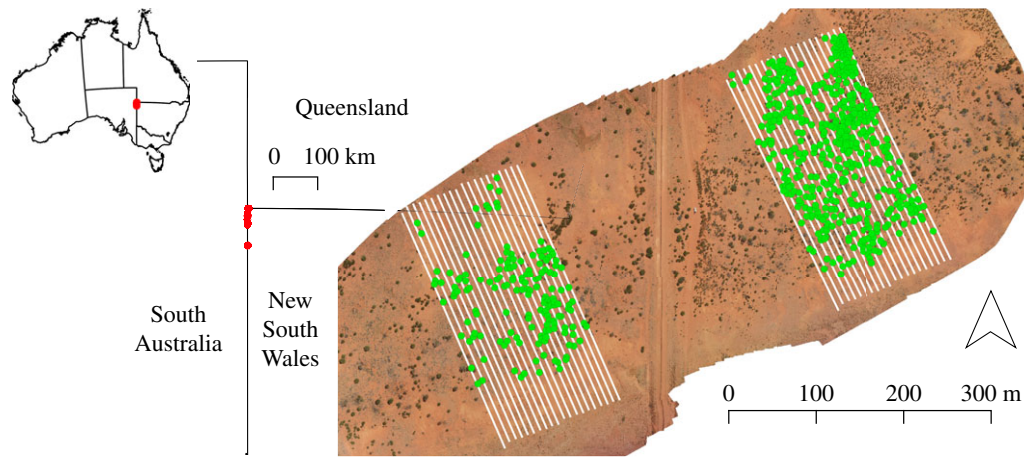


Figure 2. Study site location in the Strzelecki dune field. The red points indicate the 12 surveyed dunes along the New South Wales, Queensland and South Australia border. The image shows an example rectified orthomosaic (drone imagery) of one dune, with plot transects and shrub count (green points) overlaid. The visible line in the orthomosaic is the dingo-proof fence—New South Wales is ‘inside’ the dingo fence. (Online version in colour.)

tenure and land use history, including sheep and cattle grazing, and conservation. In 1972, the area in NSW was declared a national park, leading to cessation of all sheep and cattle grazing, though dingo control continues to the present day. In the 1970s, eradication efforts increased substantially, and new chemical control agents became more effective.

Since the dingo fence is a randomly placed geographical boundary, we can assume that prior to its construction, there were no significant anthropogenic or environmental differences between sites either side of the fence. We can also assume that after construction, our sites did not experience any significant difference in prevailing climatic conditions (e.g. wind speed/direction, rainfall) due to their proximity. Thus, a paired design was used, where each side of the fence was surveyed at each site, along the same dune. After entering the national park, we drove at least 2 km along the fence, choosing the next dune that had no visible excavation works (for dingo fence construction/maintenance) and repeated this process until 12 dunes were surveyed; 10 along the South Australia border and two along the Queensland border (figure 2). The sand dunes in this area are longitudinal tending to dendritic, are 8–10 m tall and spaced 300–500 m apart, with clearly defined dunes and flat inter-dune areas (swales) [17,18]. Both the dunes and swales are vegetated, but most of the woody vegetation occurs on the dunes.

2.2. Drone data and processing

The drone image data were collected in March 2017. The data were collected using a DJI Phantom 3 professional quadcopter. Imagery was captured for approximately 300–400 m along the same dune either side of the fence. We flew at approximately 70 m above take off height using flight lines perpendicular to the dune crest, covering at least 30–40 m into the swale on either side. Dune fields are very simple topographically, but being conservative, we still aimed for approximately 80% forward and lateral overlap. Flights took between 10 and 15 min per dune. Further details on flight patterns and animal ethics considerations can be found in [24].

The drone imagery was processed separately for each dune using the commercial software Pix4Dmapper (v. 4.19, Pix4D SA). Pix4D uses ‘structure from motion’ to generate both three-dimensional image products and orthorectified

image mosaics [23]. We generated digital surface models and orthorectified image mosaics, as well as digital terrain models (digital elevation model) that are created by removing vegetation and other non-ground features. In floristically simple environments such as dune fields, removal of non-ground features is relatively simple and accurate [22,23]. Our processed models were georeferenced with standard accuracy GPS data (± 5 – 10 m accuracy). Both remoteness (no correction stations within range) and time constraints for sampling (15–30 min per site) prevented set-up of higher accuracy GPS recording. The final image products used from Pix4D for further analysis were image orthomosaics at approximately 3 cm pixel size and digital terrain models at approximately 15 cm. Only image data that had at least five overlapping photos (per pixel) were retained. Electronic supplementary material, figure S1 shows an example series of the image processing steps, including more detail on the Pix4D methods. The slope function from GDAL (v. 2.2.2, Open Source Geospatial Foundation) was used to calculate the slope for each pixel in the digital terrain model. It does this by creating a plane from a 3×3 pixel neighbourhood for each pixel and calculating the slope in degrees.

2.3. Dune characterization

For each dune, we placed a set of 20 parallel transect lines perpendicular to the dune crest, placed approximately 5–7 m apart, each side of the dingo fence. We imposed a buffer distance of approximately 50 m either side of the fence to avoid boundary issues (see example in figure 2). Owing to the orientation of the fence and some dunes, the buffer distance meant that only eight dunes were able to be used for further analysis. Using both the orthomosaic imagery and the digital terrain model as a guide, the transect lines were placed such that they covered the full width of the dune and slightly into the swale either side. Transect lines were thus approximately the same length for each dune pair (i.e. inside/outside fence). This resulted in 316 individual transects to be treated as observations for subsequent statistical analysis.

For each dune, we counted shrubs via manual image interpretation from the orthomosaic imagery. Shrubs consist mostly of hopbush (*Dodonaea viscosa angustissima*), marpoo (*Acacia ligulata*) and occasionally mulga (*Acacia aneura*). We counted all shrubs with a crown diameter of greater than 1 m

(orthomosaics are projected, so crowns could be directly measured in GIS), so only established plants were counted to avoid confusion with seedlings and forbs. While other growth forms (grasses, herbs and forbs) are clearly visible in the drone imagery, we only counted established shrubs to avoid capturing seasonal variation in vegetation cover, as shrubs persist for many years, whereas non-woody vegetation cover and composition in the study area is highly responsive to rainfall on the short term [11,18]. The counting was performed systematically by following the transect lines and placing a point on every shrub visible within the areas defined by the transects. We then calculated shrub density for a grid of 1 m cells, using a 5 m search radius. Although we calculated shrub density in shrubs per metre square, we present in shrubs per hectare (ha) for ease of interpretability and plotting. Height (elevation from the digital terrain model), slope and shrub density were extracted along each transect. A buffer of 5 m (inside the transect area) was used to avoid the edge effects at the outer edges, and a 10 cm sampling distance was used to avoid unnecessary resampling from the 15 cm terrain model.

We then processed the sample points to calculate the dune geomorphic metrics. Height (h) was standardized for each transect by subtracting the minimum height above sea level for that transect (i.e. the beginning of the dune is approx. 0 m). This enables easier visualization and more interpretable results when calculating cross-sectional area. To be conservative, we additionally filtered out any sampling points less than 20 cm high, to ‘trim’ the transects to above the swale. This was to try to more appropriately capture the ‘width’ of the dunes and reduce the impact of the dune–swale transition zone on the geomorphic metrics. We took the remaining transect points as the width (w) of the dune and extracted the maximum height for each transect (i.e. the dune crest for each profile). We treated each transect as an observation, and thus, the morphological metrics for modelling were all per transect.

To summarize the height profile of each transect, we calculated the root-mean-square deviation in height [25], $\sqrt{(1/n) \sum_{i=1}^n (h_i - \mu_h)^2}$. Slope values (s) at such high spatial resolution tend to be locally quite variable (small rocks, logs, etc.), so we calculated two slope metrics for each transect to characterize surface roughness: (i) root-mean-square slope [25], $\sqrt{(1/n) \sum_{i=1}^n (s_i - \mu_s)^2}$, gives an indication of the absolute magnitude of slope values and (ii) the slope coefficient of variation, σ_s / μ_s , gives a standardized measure of the variation in slope values. Cross-sectional area (a) was calculated for each transect, from the standardized height values. We used two different shape metrics to describe the shape of the dunes [26]. ‘Flatness’ was calculated as the ratio of cross-sectional area to maximum height, a/h_{\max} , and ‘rectangularity’ was calculated as the ratio of cross-sectional area to the area of a rectangle with the width and height of the dune transect, a/wh_{\max} . We surmised that shape metrics based on area and width were more appropriate than compactness (based on circular area) because the dunes we studied are generally wide and flat. Electronic supplementary material, figure S2 shows a schematic diagram of the dune measurements.

2.4. Historical trends

Gordon *et al.* [8] counted shrubs from historical (1948–1999) aerial photography across our entire study area. We calculated

shrubs density on these data for dunes within approximately 2 km of each of the dunes from our surveys. This enabled us to examine the relative differences and trajectory of shrub density inside and outside the dingo fence over time for our study area. Shrub counts for 2017 were from imagery with much higher spatial resolution and may differ from the historical photography; therefore, we present the data as relative difference in shrub density inside and outside the dingo fence over time.

2.5. Statistical analysis

We performed an initial qualitative analysis to guide our choice of model specification. We produced density plots for each of the geomorphic metrics to explore how they differed either side of the dingo fence. A principle components analysis was performed on the geomorphic metrics to explore whether variation in geomorphology among dunes needed to be accounted for in our modelling, in addition to testing for the effect of our main hypotheses.

We used a modelling framework to test the two components of our hypothesis for each geomorphic metric: (i) does the dune’s morphology change either side of the dingo fence and (ii) does the dune’s morphology change specifically as a function of shrub density? Generalized additive models are a flexible framework that can incorporate random effects, nonlinear relationships and spatial autocorrelation structures. We used models of the general form as follows:

$$E(y) = X\beta_{\text{fence}} + f_{\text{shrubs}}(x) + Zb_{\text{dune}} + \varepsilon,$$

where $E(y)$ is the expectation of one of the geomorphic metrics (maximum height, height deviation, overall roughness, roughness variability, flatness or rectangularity). $X\beta_{\text{fence}}$ is the parametric part of the model for whether the observation is inside or outside the dingo fence. $f_{\text{shrubs}}(x)$ are smooth terms (thin plate regression spline) where x is the shrub density. Zb_{dune} is a (normally distributed) random intercept for each dune, because we expect dunes to vary locally and are uninterested in that variation in this analysis. Since we had many observations close together and expect some component of the data structure to be spatially dependent, we imposed a Gaussian correlation structure on the model residuals, $\varepsilon \sim N(0, \sigma^2\Delta)$, where Δ is the correlation matrix, with distances calculated using the projected eastings and northings.

All modelling and metric calculations were performed in R, using a range of base and contributed packages. We used the R package ‘mgcv’ [27] to fit the models and estimate the approximate significance of the model terms—see the code provided for more detailed parametrization (see the Data accessibility section for further details).

3. Results

3.1. Dune characterization

Shrubs were easily delineated from the high-resolution image orthomosaics (figure 2; electronic supplementary material, figure S1). The transects from the digital terrain models appeared to accurately characterize the dune cross-sections (electronic supplementary material, figure S3) and were consistent in both height and width with the descriptions and cross-section of nearby dunes given by Hesse & Simpson [17] and Hesse *et al.* [18]. Absolute accuracy is difficult to ascertain

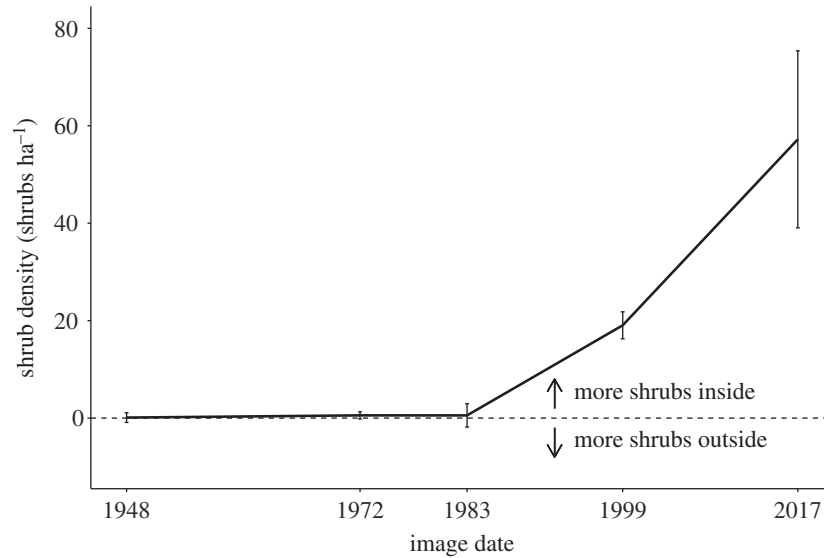


Figure 3. Long-term history of shrub density inside and outside the dingo fence. Historical data (i.e. before 2017) were obtained from Gordon *et al.* [8]. The y-axis represents the difference in shrub density between paired sites inside and outside the dingo fence. Positive values (above the dotted zero line) indicate higher density inside the dingo fence. Error bars denote 1 s.e.

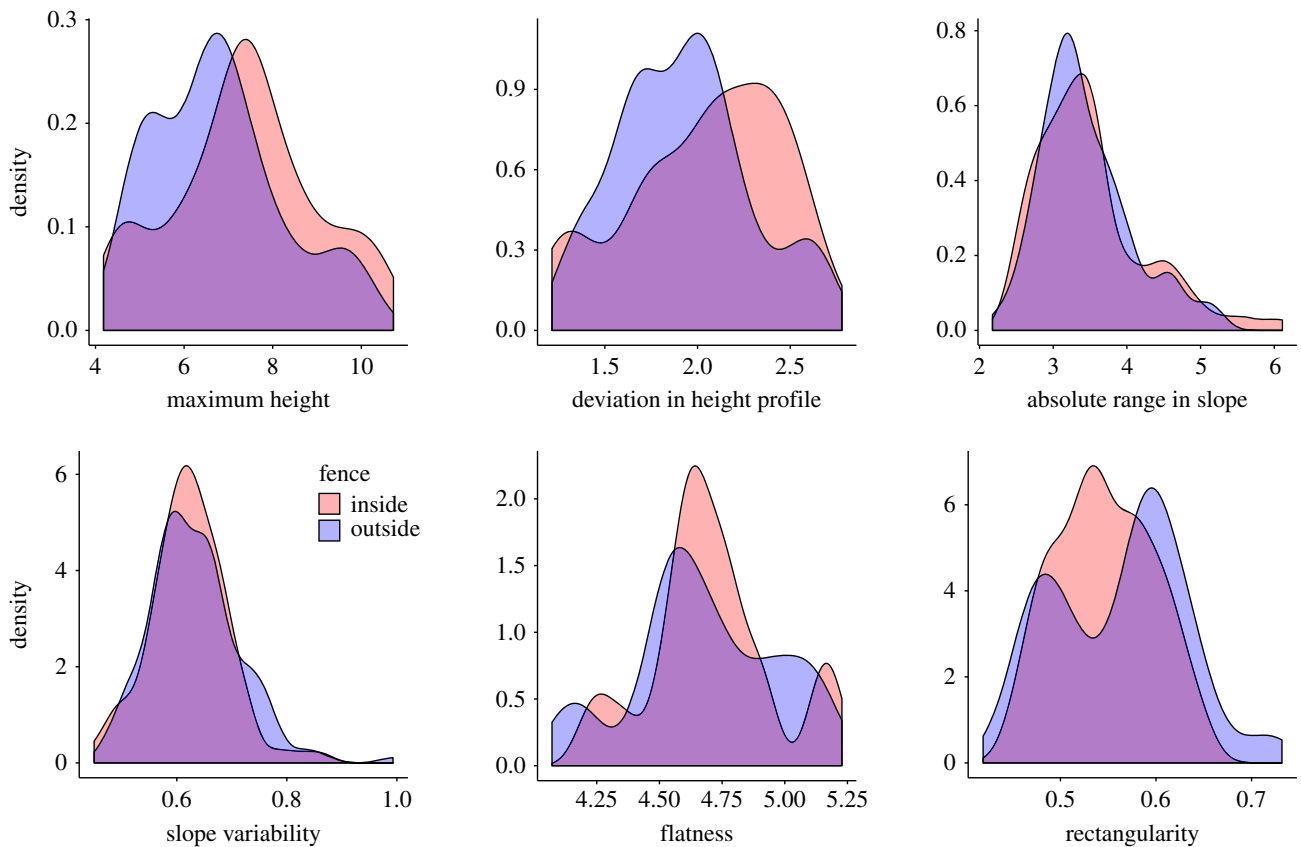


Figure 4. Kernel density estimates (smooth histogram) for geomorphology metrics of 316 cross-sections derived from high-resolution drone data over dunes surveyed in arid Australia. Metrics are plotted to compare sites inside and outside the dingo fence. (Online version in colour.)

with standard grade GPS data, but Pix4D estimates the relative positional error. Dunes typically had approximately 80–85% of images within 1 m horizontal accuracy and all images within 2 m accuracy. All dunes had 100% of images within 1 m vertical accuracy.

We know from previous research in this study area that shrub density varies significantly either side of the dingo fence [8], and our surveys confirm this result. In fact, our results suggest that the disparity in shrub density inside and outside

the dingo fence is accelerating (figure 3), though we are cautious to emphasize the acceleration due to the difference in shrub counting method. The statistical significance of this effect is not of primary interest in this paper, so we provide the analysis in electronic supplementary material, appendix A. Examining the raw data for the geomorphic metrics showed that some metrics had different mean values either side of the dingo fence, while some metrics also differed in their distribution (figure 4). The principal components analysis suggested that

Table 1. Generalized additive mixed model results for testing the effect of shrub density and the dingo fence on various geomorphological metrics of dunes. Shrubs density is a smooth term (penalized thin plate regression spline) and dingo fence is a standard categorical linear term with outside set to the contrast level. Random effects were fitted for individual dunes, and a Gaussian spatial correlation structure was imposed on model residuals. Figure 4 shows the effect of these terms on the metric predictions (easiest way to interpret smooth terms).

geomorphology metric	effect of dingo fence	effect of shrub density
	outside (treatment contrast)	inside dingo fence
maximum height (m)	lower outside $\beta_{\text{outside}} = -0.659$ ($F = 39.45, p < 0.001$)	not significant ($F = 0.31, p = 0.58$)
height deviation (m)	less deviation outside $\beta_{\text{outside}} = -0.21$ ($F = 37.65, p < 0.001$)	less deviation at higher densities ($F = 18.35, p \leq 0.001$)
slope root mean square (°)	not significant ($F = 0.31, p = 0.581$)	marginal, possibly range increases with density ($F = 3.92, p = 0.063$)
slope coefficient of variation (%)	not significant ($F = 0.08, p = 0.772$)	decreases with shrub density ($F = 8.85, p = 0.003$)
flatness (log ratio)	not significant ($F = 0.12, p = 0.735$)	marginal, possibly flatter at higher densities ($F = 2.46, p = 0.078$)
rectangularity (ratio)	more rectangular outside $\beta_{\text{outside}} = 0.025$ ($F = 18.16, p < 0.001$)	more rectangular at higher densities ($F = 4.82, p = 0.001$)

geomorphology differed substantially among dunes, as well as by their position either side of the dingo fence (electronic supplementary material, figure S4). Treating each dune as a random effect was therefore critical to elucidate trends while accounting for among-dune variation.

3.2. Statistical models

We found that several geomorphological characteristics of the dunes had significant relationships with shrub density, and for some metrics, there was a strong additional effect of position inside/outside the dingo fence (table 1). Figure 5 shows the summed effect of the smooth terms for shrub density (including the effect of fence, but removing the random effect of dune) for those geomorphic metrics that had significant results.

Dune crests were higher (by approx. 66 cm) inside the dingo fence, and although the data suggest that height also increases with shrub density, there was no statistical significance. Variability in height profile was also greater inside the dingo fence (approx. 21 cm), and the amount of variability decreased with increasing shrub density, though the effect levelled out at mid-range density values (approx. 50–100 shrubs ha^{-1}). We found no strong evidence for effect of either the dingo fence or shrub density on the absolute range in surface roughness (slope values). However, the standardized roughness values had a strong and significant negative relationship with shrub density, that is, the dunes appeared to have lower variance in slope values with increasing shrub density (approx. 7–8% from maximum to minimum density). We found no strong evidence for effects of either the dingo fence or shrub density on the flatness metric. Dunes outside the dingo fence were more rectangular, and dunes also became more rectangular with increasing shrub density, but

the effect again levelled out at mid- to high-range densities (greater than 100 shrubs ha^{-1}). Residual plots for each of the models (normal quantile–quantile, residual versus fitted values and residual histogram) did not indicate anything untoward, suggesting our choice of error distribution and spatial autocorrelation structure was reasonable.

4. Discussion

4.1. Linking ecology and geomorphology

Motivated by an apparent trophic cascade in arid Australia, the aim of this study was to investigate whether the biological consequences of the cascade could be linked to changes in the underlying geomorphology of the landscape. Our results show that there are more shrubs in the absence of dingoes (figure 3) and that dunes with more shrubs were higher, less rectangular and had more variation in their height profile than dunes with less shrubs (figures 4 and 5).

Our model results showed that these were significantly different, providing support for the idea that the proposed subsequent altering of local wind flow regimes and sediment binding potential, due to increased shrub cover, may be responsible for the observed differences in geomorphology. Taken together, these findings provide evidence that the removal of apex predators may have effects that extend to the physical structure of the landscape, and that density of woody plants might be a key factor in controlling how those effects manifest.

Dunes with low- and mid-range shrub density mostly exist in the morphodynamic state documented in the existing literature, where dune crests alternate between vegetated and bare, and occasionally switch to an active state, induced via climatic forcing [18]. When dunes become heavily vegetated

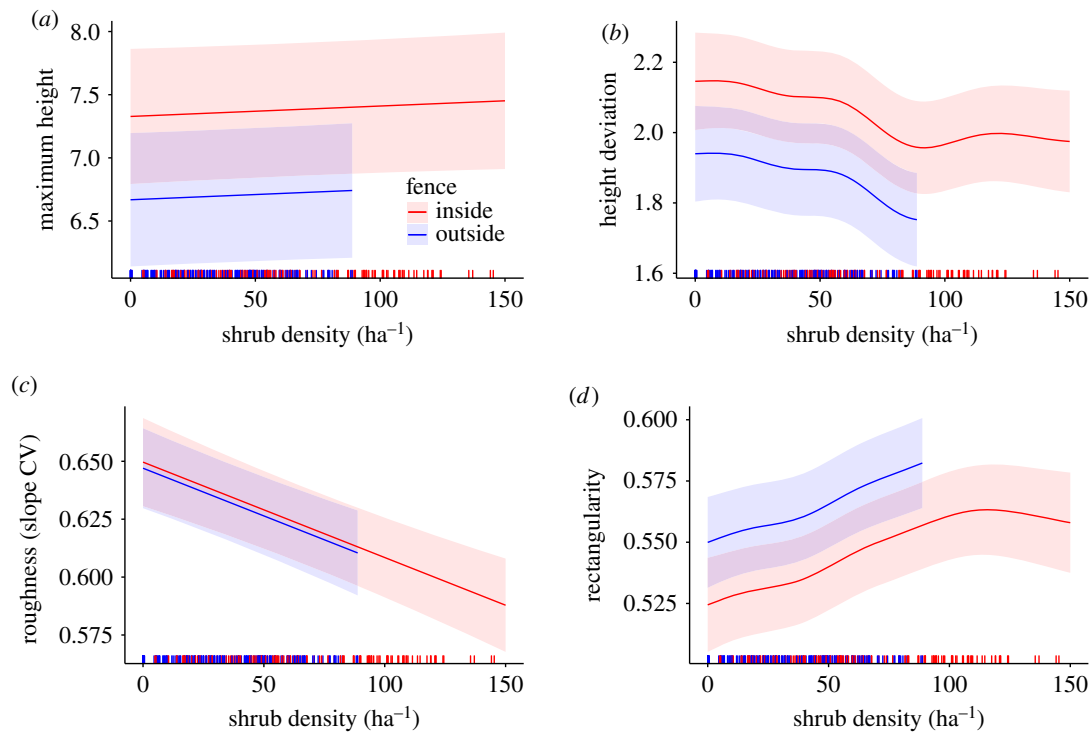


Figure 5. (a–d) Summed effects of shrub density inside and outside the dingo fence, for generalized additive models fit to dune geomorphology metrics across 316 observations derived from high-resolution drone data in arid Australia. Shrub density is a smooth term (penalized thin plate regression spline) and dingo fence is a standard categorical linear term. The random effect of dune has been removed (i.e. set to zero). The rug shows the location of shrub density values in the data, note that we do not predict the blue curve beyond the maximum shrub density observed outside the dingo fence. See table 1 for coefficients and significance results. (Online version in colour.)

by shrubs, not only do the dune crests become more permanently vegetated, but we speculate that the threshold for switching states is lifted high enough that they are pushed into alternate stable state. We note that the dunes inside the dingo fence are in the far southeastern range of the dunes described by the existing literature, and their higher than average shrub cover has not been previously explored in a purely geomorphological context [17,18].

4.1.1. Low shrub density dunes in bi-stable state

Moving up from very low to medium shrub densities, dunes transition through the isolated roughness and wake interference flow regimes [14,16]. Owing to poor wake development and increased wind flow at the soil surface, these two wind flow regimes have high surface erosion and sediment transport potential [20]. At lower shrub densities, sediment binding via roots and shade-facilitated ground cover is also limited [17,18]. Figure 1 shows this concept, linking it to the shrub encroachment phenomenon. Locally, this could explain why our results show that surface roughness decreased with increasing shrub density (figure 5c). At the broader scale, increased sediment movement potential at lower shrub densities would lead to increased sediment movement towards the dune margins (i.e. down into the swales). This increased sand movement could explain why we observed decreased variability in the dune height profiles (figure 5b) and flatter dunes (increased rectangularity, figure 5d) on low shrub density dunes.

In line with the existing literature, we characterized low shrub density dunes as existing in the meta-stable phase of a bi-stable state model [18,19]. In this case, dune crests can alternate between vegetated and bare, and occasionally switch into an active state. These changes are controlled by long-term,

stochastic interactions between wind regimes and rainfall [17,18]. Dunes at or below this shrub density limit appear to maintain this bi-stable state. Shrub density very rarely gets beyond these mid-range density levels outside the dingo fence, so we infer that the vast majority of dunes outside the dingo fence continue to be categorized in this way.

4.1.2. High shrub density leads to new stable state

Shrub density is much higher on average inside the dingo fence; in fact, a large proportion of the dune profiles, we surveyed inside the dingo fence had shrub densities far beyond the maximum values outside the fence (figure 5; electronic supplementary material, appendix A). As shrub density moves from medium to high density (greater than 50–100 shrubs ha^{-1}), the wind regime is predicted to tend towards skimming flow, in which wake and boundary layer development dramatically reduces the potential for erosion and sediment transport [20]. Binding potential due to vegetation cover is also predicted to be much higher at these densities; most of the dune crest is shaded and is stabilized by permanent root structures, which facilitates ground cover [18]. This idea can again be seen visually in figure 1. At these density levels in our data, shrub density no longer had an effect on height deviation and rectangularity (figure 5b,c).

We propose that more permanently vegetated dune crests inside the dingo fence towards an alternate stable state within the bi-stable state model [19]. This alternate state would have a much higher threshold for switching to an active state (via climatic forcing). In this state, dunes would accumulate and stabilize sediment, which could explain why they became taller and were able to maintain a more variable

height profile (figures 3 and 5*a,b*). A positive feedback loop may also activate; more shrubs may lead to more recruitment, leading to more sediment binding potential and further enhancing the skimming flow regime. We conclude that generally higher shrub densities on the inside of the dingo fence are a key underlying driver of why dunes there tend to be higher, have more variation in their height profile and be less rectangular (figures 3 and 5*a-c*). Sufficiently large climatic events (e.g. extended drought, changed wind/rain regimes), which do occur in arid Australia, have the potential to cause widespread shrub mortality and re-activate dunes, so we suggest that these dunes still fit into the bi-stable state model.

The summed model effects (figure 5) need to be interpreted in the context of temporal resolution and the sampling unit we employed. For example, we suspect that many of the dunes inside the fence have, on a whole, shifted to the more stable vegetated state—yet there were still some transects with low shrub density, which tended to be physically similar to the surrounding high shrub density dune. So, the differences attributable to the dingo fence (figures 3 and 4) are a somewhat confounded mixture of shrub density and the slew of other biological interactions associated with trophic cascades triggered by dingo removal.

4.2. Confounding factors to trophic cascade theory

We discuss our results in the context of shrub density as a mediator of aeolian and sediment transport processes, but will briefly discuss potential limitations of the trophic cascade theory that links dingo removal to shrub encroachment. The study area has a complex history of varied tenure type, including livestock grazing (sheep and cattle) and conservation, as well as varied fire regimes. Most confounded is the fact that dingo control was traditionally associated with sheep grazing; however, since 1972, our study area (within NSW) has been a national park where livestock grazing has ceased, but dingo control has continued. Mesopredator abundance has increased in areas where dingoes are rare, regardless of tenure type [12]. The associated impact of reduced small mammal abundances and resulting increased shrub seed/seedling predation has also been shown to be independent of tenure history [8,10,13]. Electronic supplementary material, table S1 gives the raw abundance data that show how these differences are maintained across tenure type. Indeed, shrub encroachment has been shown to have a stronger statistical relationship to dingo abundance than to any other historical factor [8]. Nevertheless, that dingo control and grazing types are confounded does not alter our evidence for a link between shrub encroachment and geomorphic characteristics of the dunes. This is also why our models included shrub density, rather than a direct test of dingo abundance. Although dingo abundance had a strong correlation to the geomorphic characteristics, the most compelling predictor, that we had enough data to test for, was shrub density. Future work may include richer datasets, in which more individual aspects of the trophic cascade are explicitly linked to geomorphological changes.

4.3. Limitations and further research

The main limitation of our study is the use of standard accuracy GPS for drone image correction. As mentioned in the Data and methods, remoteness and time constraints were the primary reasons for being unable to set up higher accuracy GPS control points, with only 15–30 min available at

each dune. Additionally, the dingo fence cannot be crossed, and gates are spaced too far apart to set up control points on both sides of the fence coincident to image acquisition; control point needs to be collected on the return journey, possibly days later, meaning the additional set-up time of high-accuracy GPS is even less feasible. Notwithstanding this limitation, Pix4D still estimated relative accuracy to be within 1 m for the vast majority of images, perhaps owing to the extremely simple terrain with mostly bare ground, and short flight times (less than 10–15 min). Qualitative inspection of the dune cross-sections (electronic supplementary material, figure S3) does not suggest any gross errors in relative geometric positioning, and that any error appears to be consistent across the whole acquisition. The survey is of course blind to the position of the dingo fence, so it is unlikely that there would be any systematic error biased to one side of the fence. Moreover, our characterization of the dunes was in line with existing research in our study area that characterizes the dunes [17,18], which appear to use spatial information of a similar accuracy.

An additional technical concern that we had was whether the process of removing shrubs could leave artefacts in the digital terrain model. We found no evidence of this; the terrain model algorithm in Pix4D [22] performed well (electronic supplementary material, figure S1). An advantage of structure-from-motion techniques is that visible terrain underneath canopy is incorporated into the three-dimensional models [22,23]. If shrubs were leaving a significant artefact, we would expect the roughness and height deviation metrics to show positive relationships with shrub density, not negative as our models indicated (figure 5). Moreover, the predicted effects on height are of the order of metres, well beyond what would be expected from an artefact. The dune cross-sections (electronic supplementary material, figure S3) do not have the appearance of being effected by significant artefacts either.

Future research could explicitly test our hypotheses with *in situ* experimental data. This could include measuring aeolian and sedimentary processes that are unable to be surveyed via drones, particularly sediment transport potential and sediment characteristics. Grain size distribution is likely to change with changing stabilization and wind flow regimes [14,16,18], so has the potential to impact geomorphological processes. The additional survey effort at individual dunes would also facilitate the additional time required to set up additional GPS equipment and capture enough GPS data to apply high-accuracy corrections.

Variation in both short- and long-term rainfall plays a key role in driving both shrub density and alternative state switches [19]. Rainfall and grazing pressure also drive the composition of other stabilizing vegetation [7]. More detailed quantification of floristic composition, including non-persistent and other non-woody vegetation, is possible, but several years of survey would be required to capture its variability [18]. Automated methods for counting shrubs and quantifying non-woody cover are under development (electronic supplementary material, figure S1), but are not yet validated sufficiently to be used in models to test specific hypotheses.

5. Conclusion

Our study demonstrates an approach for using drone imagery to study the biological and physical characteristics of dunes and

provides evidence of a link between ecological theory on trophic cascades and dune morphology. Our shrub counts confirmed the documented trend of increased woody shrub density inside the dingo fence [8] and show it may even be accelerating. We used fine-scale geomorphic measurements to show that dune morphology is related to vegetation cover as predicted, and we provide evidence that changes in geomorphology may be inextricably linked within a trophic cascade driven by the removal of an apex predator. Unexpectedly, our findings pointed towards increasing shrub density as driving dunes inside the dingo fence towards a new, alternate stable state. Our paper shows that removal of a keystone species has had effects that may reach right down to the underlying physical structure of the landscape, within a model that suggests future restoration (e.g. via reintroduction [28]) is plausible.

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