Down the rabbit-hole: satellite-based analysis of spatiotemporal patterns in wild European rabbit burrows for better coastal dune management

Chloé Bentze 1 · Helene Burningham 2 · Emer Magee 3

Journal of Coastal Conservation (2023) 27:61
https://doi.org/10.1007/s11852-023-00992-6

ABSTRACT

Coastal dune systems in northwest Europe are facing conflicting challenges associated with climate change and human interventions in landuse and landscape management. Research over the last decade has highlighted a global stabilisation pattern in coastal dunes, fuelling long-standing debates surrounding conservation approaches. Dune erosion can be considered an important process within a naturally functioning dune system, but also a management challenge. The fossorial behaviour of burrowing mammals within coastal dunes is one driver of erosion that has long tested our perspectives on natural processes within dunes, but is understudied in coastal dune conservation and research. This is particularly the case for the wild European rabbit, a common naturalised invader of dune systems.

In this study, the spatial distribution of wild European rabbits inhabiting a coastal dune system in Ireland is explored through geospatial mapping approaches using satellite and drone imagery, supported by spatial analyses and statistics. This reproducible approach has shown that rabbit activity fluctuates at inter-annual time scales that infer aligned changes in population, and that burrows clearly cluster in fixed dune habitats on landward slopes toward the rear of the dune system.

Keywords: Coastal dunes - Rabbits - Burrowing - Remote Sensing

INTRODUCTION

Coastal dune systems and conservation management of their habitats are facing new challenges. In the past century, important losses and shifts have been reported. For instance, in Europe about 40% of their area has been lost since 1900, a third of which has occurred in the last 50 years (O'Briain 2005). Rising sea level and shifts in weather patterns increase erosion of dune margins and frequency of overwash and flooding, leading to disruption in their successional processes (Carter 1991; Jiang et al. 2012; de Winter and Ruessink 2017; Mentaschi et al. 2018; Gao et al. 2020). There is also evidence of widespread stabilisation, i.e. fixation through vegetation, globally (93% of 176 sites considered worldwide; Gao et al. 2020). This pattern of coastal dune stabilisation, or "greening", since the 1960s (Martínez et al. 2008; Jackson and Cooper 2011; Provoost et al. 2011; Gao et al. 2020) is likely driven by factors such as climate change, nitrogen deposition, and intensification of human activities (Jones et al. 2004; Arens et al. 2007; Hesp et al. 2010), which contribute to vegetation spread and dune fixation (Provoost et al. 2011; Jackson et al. 2019; Gao et al. 2020).

Coastal dune systems are important environments that provide a natural buffer against wind, tides and waves, and are hotspots of microhabitats, ecological niches and biodiverse communities (Everard et al. 2010), through high levels of environmental heterogeneity (Ranwell 1972; Carter and Wilson 1991). This diversity is also guided by the inland movement and compaction of sediments, driving their characteristic spatiotemporal gradients from embryo to fixed dunes (Carter and Wilson 1988), making them a classic example of ecological succession (Slingsby and Cook 1986). Overall, they are recognised as biodiversity hubs within national and international conservation legislation, and in Europe, many of their habitats are protected by the EU habitats directive (Everard et al. 2010; NPWS 2019).

The abiotic and biotic factors influencing coastal dune dynamics are generally well known (macro- and micro- climates, sediment supply, vegetation colonisation, grazing, among others; Carter and Wilson, 1988; Levin et al., 2006; Pye and Blott, 2020) but studies of the influence of rabbits, often found colonising dune systems, has been limited to the impact of their grazing (Ranwell 1960; Sumption and Flowerdew 1985; van Dijk 1992; Provoost et al. 2011; Herron 2014; Moulton et al. 2020). The European wild rabbit (*Oryctolagus cuniculus*) is a widespread invasive species to Ireland and much of northwest Europe, and is known to favour the grassier parts of coastal dune systems, likely because they provide attractive substrate for burrow digging, and vegetation for feeding (Rogers and Myers 1979).

However, to the best of our knowledge, coastal dune system conservation research on the direct contribution of fossorial behaviours to dune destabilisation is anecdotal. A study in 1992 analysed the geomorphic implications of rabbit burrowing in a coastal dune system in the Netherlands, and suggested that it contributed to an overall destabilisation through sand displacement and the creation of stepped slopes (Rutin 1992). Evidence that rabbit warrens increase instability and erodibility, as well as reduce plant diversity, was also found in an Australian semi-arid woodland (Eldridge and Myers 2001). The geomorphological impact of burrowing is likely to vary according to soil and vegetation type, but the looser nature of sand implies erosion associated with rabbits is greater in dune warrens. The effects of burrowing are also likely to be long-lasting (around 300 to 500 years according to Whitford and Kay (1999)), potentially owing to rabbits' site fidelity, until the extirpation of the population (Wood 1984). There are suggestions that burrowing may interfere with coastal dune system dynamics in environments where rabbits are naturalised invaders, but understanding goes no further than this, largely due to a lack of data. Despite widespread habitation within coastal dunes, there is limited knowledge of population dynamics, within-dune habitat preference and warren distribution, and impacts on biogeomorphic processes.

Rabbit population surveys are largely absent in Ireland; records exist from the Northern Ireland Rabbit Survey, and some Irish Hare surveys have also reported on rabbits, but no systematic monitoring has been undertaken. Elsewhere, rabbit population and burrow surveys used trapping and radio-tagging (Kolb 1991; Lombardi et al. 2003), georeferencing burrow locations along transects (Dellafiore et al. 2008) or simple field counts (Myers and Parker 1965; Sanchez et al. 2009). Others have relied on field data collection through hair, faecal pellet sampling, and visual observations of burrow entrances (Rogers and Myers 1979; Sanchez et al. 2009). There has been increasing interest in utilising the expanding earth observation data resource to fill gaps in environmental monitoring or deliver solutions where physical and logistical access to a site is difficult. This has already been extended to the needs for rabbit monitoring as shown by Cox et al. (2021) who report on the potential for drone-acquired thermal-sensing of rabbit activity.

In this study, we explore the potential for earth observation data in the mapping of rabbit warrens on coastal dunes. Undertaking rabbit population surveys on dune systems should be supported by field-based techniques, but the Covid-19 pandemic necessitated the exploration of alternative methods of monitoring aspects of the environment. The aim of this study is to explore possibilities for the assessment of changing rabbit populations through the mapping of rabbit warrens from remote and near- sensing imagery. The main objectives in this study are i) geospatial mapping of rabbit warren entrances across a dune system from available and relatively high resolution earth observation data, ii) evaluation of changing patterns in warren entrance density and distribution as a proxy for rabbit population dynamics, and iii) consideration of conservation management implications for coastal dune systems.

ENVIRONMENTAL SETTING

The northwest coast of Ireland is rich in coastal dune systems (Carter and Wilson 1991) that have become relatively fixed, albeit with episodes of progradation and erosion (Carter and Wilson 1991; Barrett-Mold and Burningham 2010). "Sealing" of coastal dunes has been observed elsewhere in Ireland, where response to short-term climatic change (recent reduced storminess) is thought to have encouraged stabilisation over relatively short time-frames (between 5 and 10 years; Jackson and Cooper 2011). The conservation status of many Irish dune sites protected by the EU Habitats Directive has been assessed as "inadequate" or "bad" due to human disturbance and "unsuitable" grazing practises in the last 10 years (NPWS 2019).

The Sheskinmore nature reserve in Donegal is classified as a Special Area of Conservation, under the EU Habitat Directive, comprising protected habitats including grey dunes (fixed with herbaceous vegetation), Atlantic decalcified fixed dunes, machair and humid dune slacks (Everard et al. 2010; NPWS, 2019). These habitats have international importance because of their vegetation's highly restricted range (Provoost et al. 2011). The dune system at Sheskinmore covers roughly 315 ha and comprises four main dune sectors: the rear of Tramore strand, the central estuary-margin Magheramore, the marsh-linked Sandfield, and the inner estuary Derryness Point headland (**Fig. 1**). Rabbits were introduced to Ireland in the 12th century (Hayden et al. 2001), and are thought to have inhabited the Sheskinmore area for at least 200 years, but population dynamics have not been monitored (Quigley 1991). In addition, reports have barely acknowledged their presence nor their consequences and impacts on dune habitats.

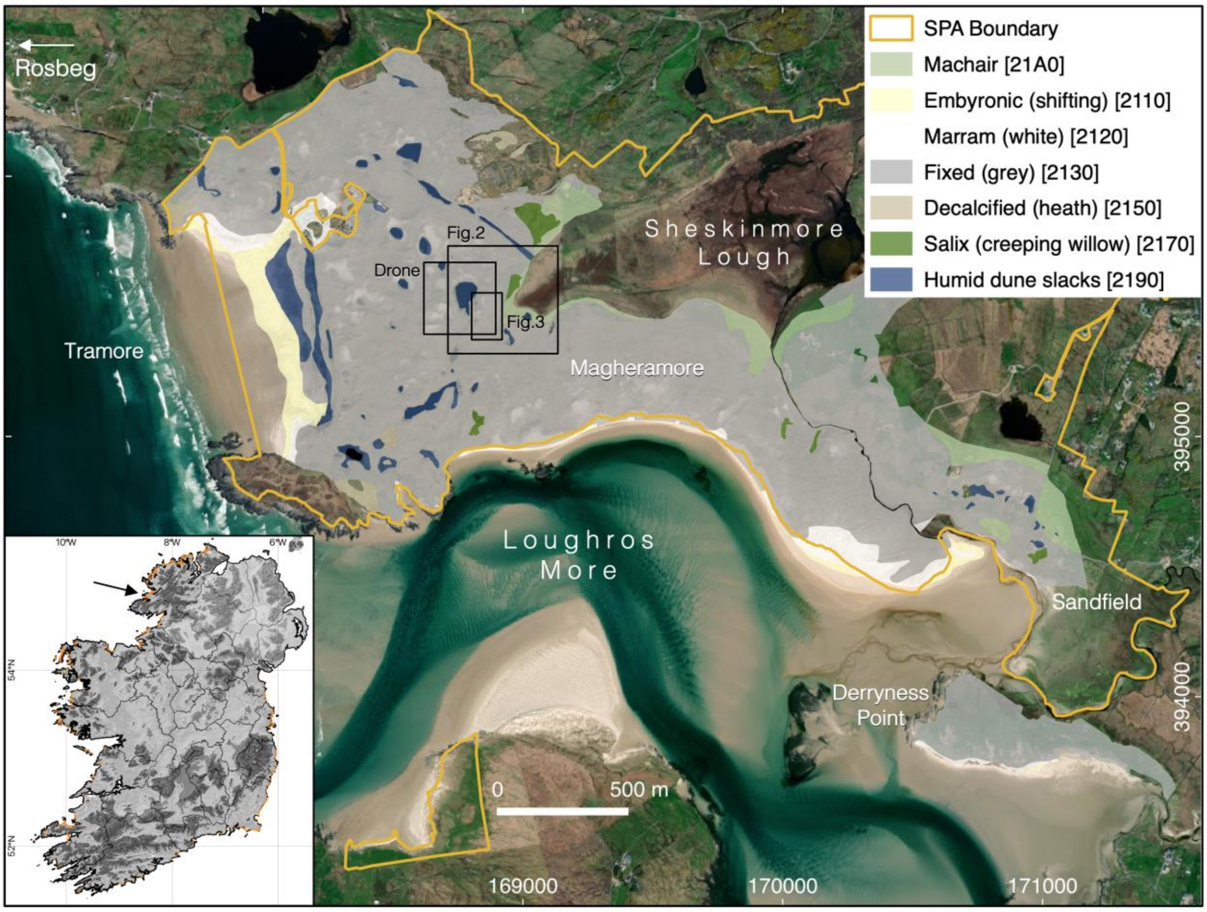


Fig. 1: The Sheskinmore dune system in northwest Ireland, showing the location of key dune habitats and protected area boundaries, and specific regions covered in subsequent figures.

METHODS

Research design

Monitoring and mapping rabbit populations and activity across a dune system is challenging as a field-based approach, requiring considerable time on the ground. Although field observations of rabbit activity at Sheskinmore have loosely guided decision-making around culling, no formal records or monitoring exists. Access restrictions brought about by the Covid-19 pandemic prompted an evaluation based on existing geospatial resources that could underpin a sustainable methodology going forward. Rabbit burrow entrances are distinctly visible in aerial and satellite imagery and prominent features in drone imagery, with a strong spectral signature reflecting a local bare-sand patch within a well-vegetated habitat mosaic (**Fig. 2**). In this study, we explored rabbit activity across the dune system using available remotely sensed data, based on the underlying principle that active entrances are evidence of rabbit burrowing and warren usage at the time of image acquisition (Ruiz-Aizpurua and Tortosa 2018). Distribution patterns and targeted areas were outlined and analysed, using spatial statistical tools.

Data Collection

Burrow entrances were digitised into point layers for four sets of aerial and satellite images obtained from Ordnance Survey of Ireland (1995), ESRI World Imagery (November 2011 and April 2014) and Google Earth Pro (CNES image from September 2019) in QGIS (QGIS Development Team 2020); see **Table 1**). This process was repeated for a set of drone orthomosaics (previous surveys undertaken to support a separate study on dune pond habitats) that covered a smaller area of the dune system (boundary delineation marked as Drone in **Fig. 1**) (**Table 1**). We purposefully chose satellite imagery which was high enough resolution to see burrow entrances and also freely available, in the perspective of easily repeatable and accessible methods.

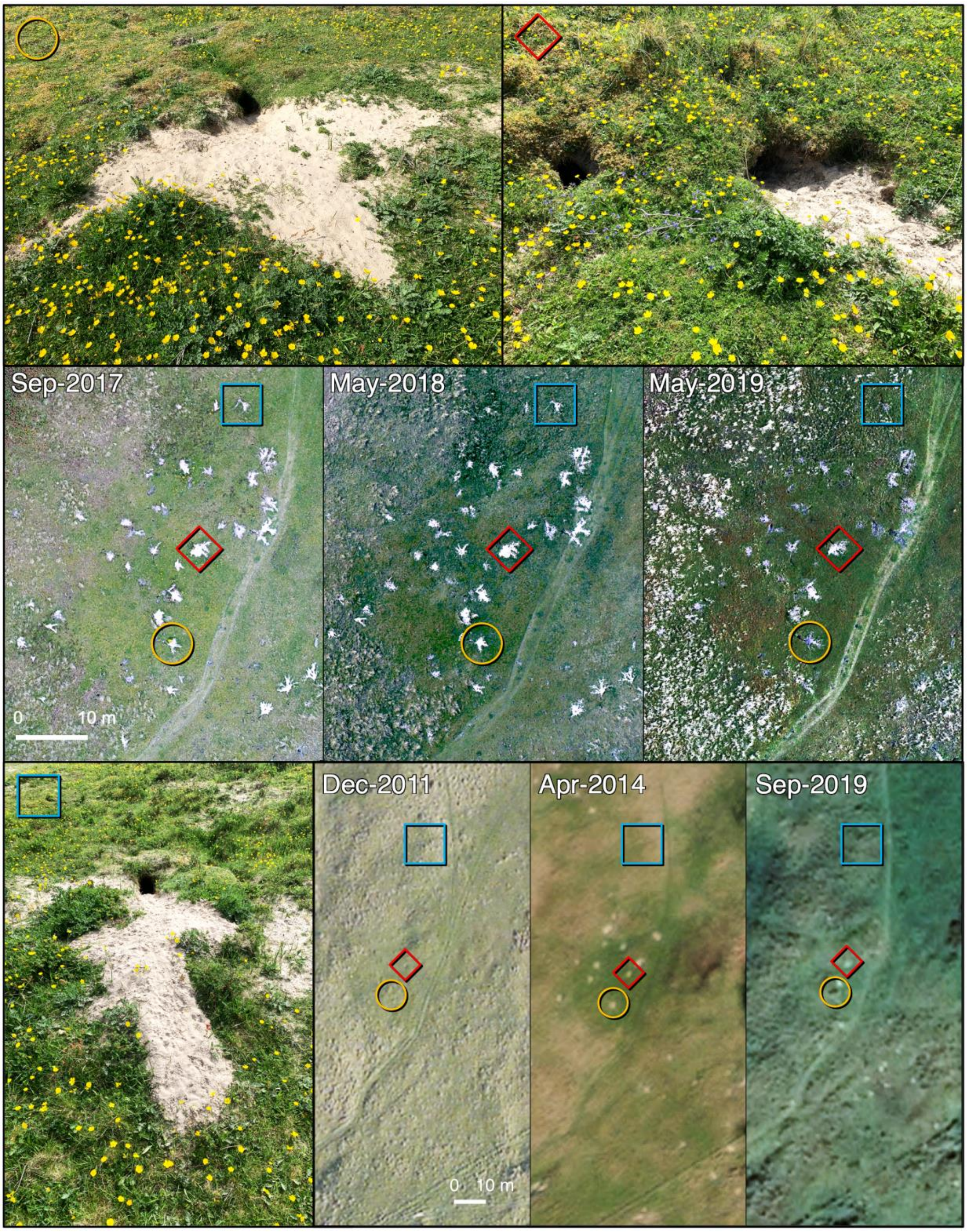


Fig. 2: Rabbit warren entrances in the Sheskinmore dune system in northwest Ireland, and their signature in drone (2017-2019) and satellite (2011-2019) imagery, (follow symbol references). Note that the ground photos relate to 2021 and not at the time of aerial/satellite image acquisition. Also note the presence of both active and inactive entrances in the top-right (◇) photograph.

Table 1: Summary of the geospatial resources used.

Source	Date	Pixel resolution	Positioning accuracy	Imagery type
Ordnance Survey of Ireland	14 Jun 1995	0.5 m	12.7 m	Aerial
Esri World Imagery (Clarity) Beta, formerly available through Bing	7 Nov 2011	0.3 m	5.4 m	Satellite
Microsoft (UC-G)				
ESRI Satellite (ArcGIS/World_Imagery)	20 Apr 2014	0.5 m	8.5 m	Satellite
DigitalGlobe (WV02)				
Google Earth Pro	20 Sep 2019	0.5 m	4.9 m	Satellite
CNES Airbus				
DJI Phantom 4	15 Sep 2017	0.05 m	0.8 m	Drone
DJI Phantom 4	25 May 2018	0.05 m	0.2 m	Drone
DJI Phantom 4	27 May 2019	0.05 m	2.4 m	Drone

Geospatial analyses were later supported by on-site observation of warren entrances in September 2021. Formal ground-truthing was not possible due to the asynchronous timing of geospatial resources (from the past) and site access. Evidence of entrances within the drone imagery were indisputable, and this supported analysis of the satellite imagery. Site-based assessment in 2021 therefore simply checked, as far as possible, interpretation of the 2019 imagery.

Spatiotemporal analyses

The spatial distribution of burrows were initially visualised using density maps in QGIS for both satellite and drone imagery. Changes in burrow density across the site between 1995 and 2019, were examined through point pattern analysis and grid count densities. Average nearest neighbour (ANN) distances and the nearest neighbour index (NNI) were calculated from the entrance point data distances for each year using the *spatstat* package in R (Baddeley et al. 2015). To explore the patterns in entrance density, a hexagonal grid system was generated (using the *sp* package (Bivand et al. 2013)) to cover the dune environment of Sheskinmore, within which the spatial distribution in entrance density could be assessed. Previous studies have estimated rabbits stray from 80 to 400 m maximum from their burrows (Kolb 1991; Gibb 1993; Martins et al. 2002), with no clear indicator of the spatial range associated with rabbit use and entry to warrens. For consistency, 100 m was used as the neighbourhood radius underpinning all density-based analyses here. Entrance counts per grid cell were calculated and visualised as a gridded representation, and counts were also analysed for evidence of trends over time at each cell.

The spatial autocorrelation of the warren entrance density was calculated using the global Moran's I and Geary's contiguity ratio (C). These metrics use defined attributes of neighbouring features to test whether a set of points is randomly distributed. The neighbourhood represents the area around feature *i*, where any other feature found is a neighbour (*j*), exerting an influence on the location of *i*. The neighbour's list object was constructed using the queen contiguity condition and used to perform the Moran's I and Geary's C analysis of entrance density. All steps were performed using the *spdep* (Pebesma and Bivand 2023) package in R. Moran's I indices closer to 1 indicate spatial clustering of the features according to the variable tested (i.e. entrance density). Pseudo p-values from these tests are prone to inflate Type I errors, particularly as the number of tests increases (Ord and Getis 1995; Anselin 2019), so Monte-Carlo permutation tests of 10,000 simulations were used to re-evaluate indices and p-values. The local Moran's I was also calculated, using the GeoDa (Anselin et al. 2006) package (*rgeoda*) to examine the spatial distribution and clustering of high and low entrance densities.

Multivariate analyses

To evaluate the importance of different variables in explaining the patterns observed across the site, Principal Component Analysis (PCA) was performed on a suite of variables representing the local environment around the digitised entrances , using the *stats* package in R. Spatial position was represented as the X and Y coordinates, and a series of topographic measures were derived to capture the physical environment.

A digital elevation model (DEM) at 1m spatial resolution (derived from multiple dGPS surveys over several years) was available for Sheskinmore following the work of Gardner (2016) and Maher-Mcwilliams (2013). Data beyond the main Tramore-Magheramore dunes were obtained from the 25m resolution EU-DEM v1.1, downloaded from https://land.copernicus.eu. All data were reprojected to the Irish Transverse Mercator IRENET95 coordinate reference system (EPSG; 2157). Topographic slope, aspect, and roughness were derived in QGIS from the DEM data, and extracted for each warren location. Aspect and roughness respectively describe the direction a slope faces, ranging from 0 to 360° (Cone 1998), and the maximum irregularity of a surface in a cell compared to its neighbours (Wilson et al. 2007). In the PCA, aspect was reclassified as northeast-facing (NtoE, i.e. facing between 315º and 135º N) or not, based on the predominance of southwesterly winds .

The potential for human disturbance in influencing spatial patterning of the burrows was considered: a Euclidean Distance analysis was performed in QGIS to derive distance to the nearest human habitation (campsite within the reserve, and housing scattered around the reserve), and extracted for each warren location (hereafter referred to as proximity). To include a local measure of density, the local kernel density estimate (KDE) was calculated with a quartic kernel and radius of 100 m for each coverage, using the *spatstat* package in R. The KDE was extracted for each entrance site, completing a multivariate spatial description of warren entrances.

Habitat data were obtained from the National Parks and Wildlife Service Maps and Data portal (https://www.npws.ie/maps-and-data) as spatial datasets (shapefiles) and used as supplementary variables in the PCA analysis.

RESULTS

Throughout the digitisation process, differences in the level of detection and type of spectral signature were evident (**Fig. 2**). Assessment of the satellite and drone imagery alongside ground-truthing observations confirmed that both methods could successfully identify active burrow entrances (**Fig. 2,3**). In satellite imagery, burrow entrances were distinguishable as a bright sandy lobe contrasted by darker surrounding vegetated ground, and their discrete extent and distribution across different imagery gave confidence to their correct identification (**Fig. 3**). Recent excavation can promote localised erosion and degradation of vegetation, but can also lead to large amounts of sand being deposited at the mouth of the burrow, thus burying the vegetation. Indeed, such sand piles at the mouth of rabbit burrows have previously been studied in the De Blink dunes, Netherlands (Rutin 1992).

The higher resolution drone imagery captured a more detailed representation of active entrance morphology (in terms of the bare sand deposit). At high resolution, active entrances usually comprise a star-shaped pattern indicative of repeated use of multiple directions into and out of the warren (**Fig. 2**). In places, these features were more extended as a consequence of erosion and collapse of the initial part of the tunnel, meaning entrances that were well used or long-lived comprised a larger area of bare sand than less well-used or more recent entrances (**Fig. 4**). In a few cases, a single sandy lobe is associated with more than one entrance (**Fig. 2**), but this was only encountered in a small number of ground and drone image observations. Excavation deposition (as seen in Rutin (1992)) and erosion both seemed plausible processes when examining the detail of “active” burrows visible in drone imagery.

Lastly, inactive entrances were also distinctly visible in drone imagery as discrete, isolated black features. Field surveys of burrow density performed by Kolb (1991) classified burrows as disused (i.e. inactive) when the entrance had a “rough edge” or was grassy, which is distinctly different to active entrances that comprise a localised but significant area of bare sand (**Fig. 4**). These inactive entrances were not at all detectable in the satellite imagery.

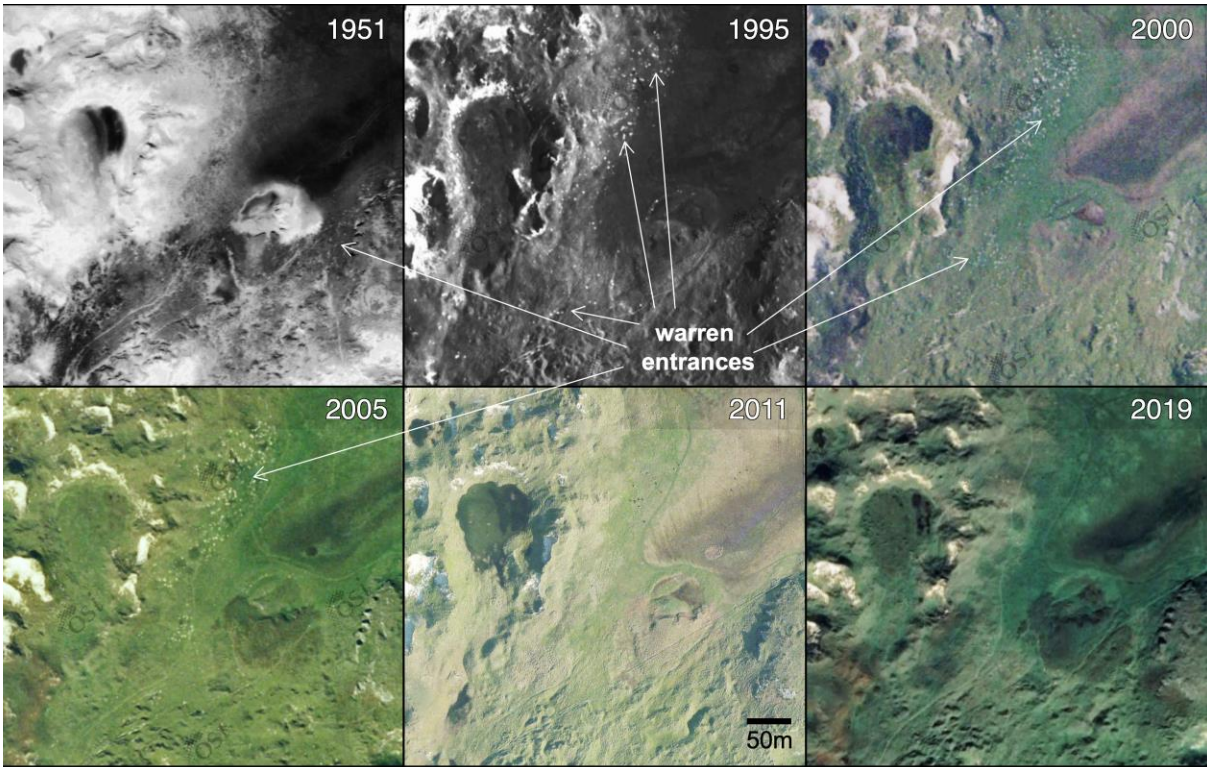
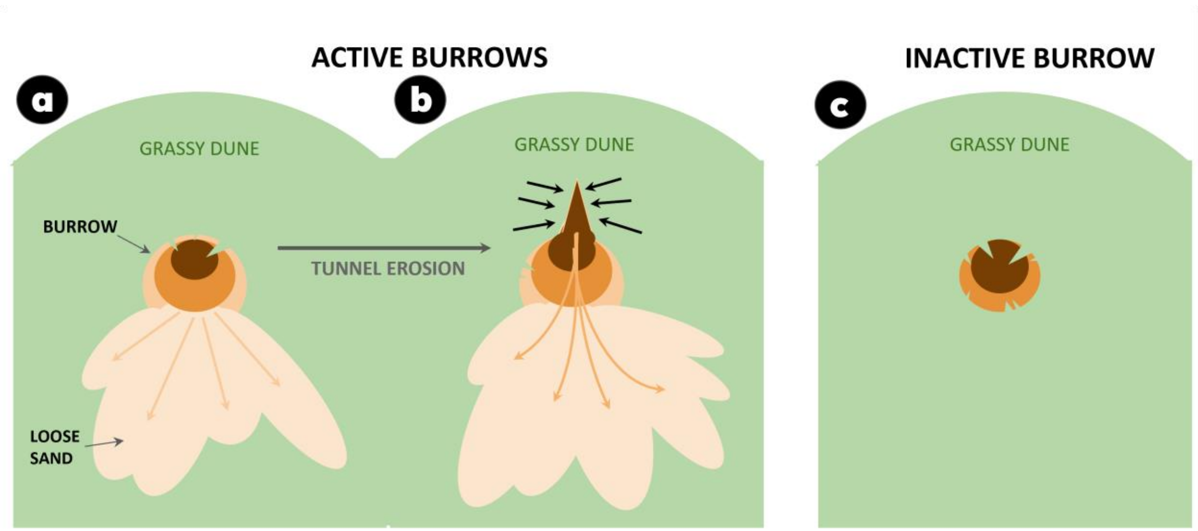


Fig. 3: Variation in the evidence of rabbit warren entrances within a range of aerial and satellite imagery: physical aerial photographs from 1951 (Irish Air Corps) and 1995 (Ordnance Survey of Ireland) and shown alongside satellite imagery (2000, 2005) available online (but not as WMS) through the GeoHive Irish geospatial data hub (www.geohive.ie), and 2011 Microsoft and 2019 Google Earth imagery.



(a) Excavation of burrow with displacement of sand to the entrance. Use and maintenance of the entrance causing piles of loose sand to remain at the entrance in irregular patterns, visible in satellite and drone imagery. **(b)** Use over time causing the roof of the tunnel to collapse; the collapsed sand is continuously excavated to the outside of the entrance, maintaining and feeding the piles of sand. The prolongation of the burrow entrance is visible in drone imagery. **(c)** Lack of occupation leading to vegetation growth over the entrance. The sand piles are also overgrown and the burrow entrance becomes indiscernible in satellite images.

Fig. 4: Interpreted structure and form of rabbit warren entrances evident in remote- and near-sensing imagery, corroborated through ground observations.

As expected, large numbers of burrow entrances throughout the dune system were detected in the imagery. The digitisation process yielded a site-wide minimum of 634 burrows (in 2019) and maximum of 2,483 (in 2014), which equated to a range in density from 2.01 to 7.88 per hectare (ha). In 1995, 2,097 entrances were visible in the aerial imagery (site-wide average density 6.66/ha), but this had reduced to 772 (2.45/ha) in 2011 (**Fig. 5**). Position accuracy prevented systematic estimation of the proportion of burrows re-used across years, but visually, it was clear that some burrows were sustained throughout the period covered, suggesting on-going or re-use.

Entrance densities mapped from the drone imagery were substantially higher, but also variable and specifically show a distinct decline in activity over the period 2017 to 2019. The drone-mapped zone was a small area toward the rear of the Tramore dunes where rabbit activity is generally more prevalent, and here, 381, 251 and 172 entrances were mapped from the 2017 (42/ha), 2018 (28/ha), and 2019 (19/ha) imagery respectively (**Fig. 5**). The higher resolution afforded by the drone mapping permitted greater detection capability. Considering just this subset area (delineated in **Fig. 1**), 83 entrances were evident in the 2019 satellite imagery (9.2/ha) which equates to 48% of those evident in the drone imagery. The time of year of images differs, but undoubtedly the difference is due to resolution. The nature of change in number and density shown across the whole site is also reflected in the densities specific to the drone survey area (**Fig. 5**) meaning that this region of interest is a good representation of total activity across the dune system.

The imagery, and entrances mapped, show that there have been notable shifts through time in rabbit activity across the dune system. Although rabbit populations are not monitored on site, the observation of increased rabbit degradation and the utilisation of culling during the mid-2010s aligns with a distinct peak in the rabbit activity derived from the mapping of entrances from both satellite and drone imagery, implying a peak in rabbit population at that time (**Fig. 5**). It is likely that the elevated activity in the mid-1990s is also associated with another peak in rabbit population.

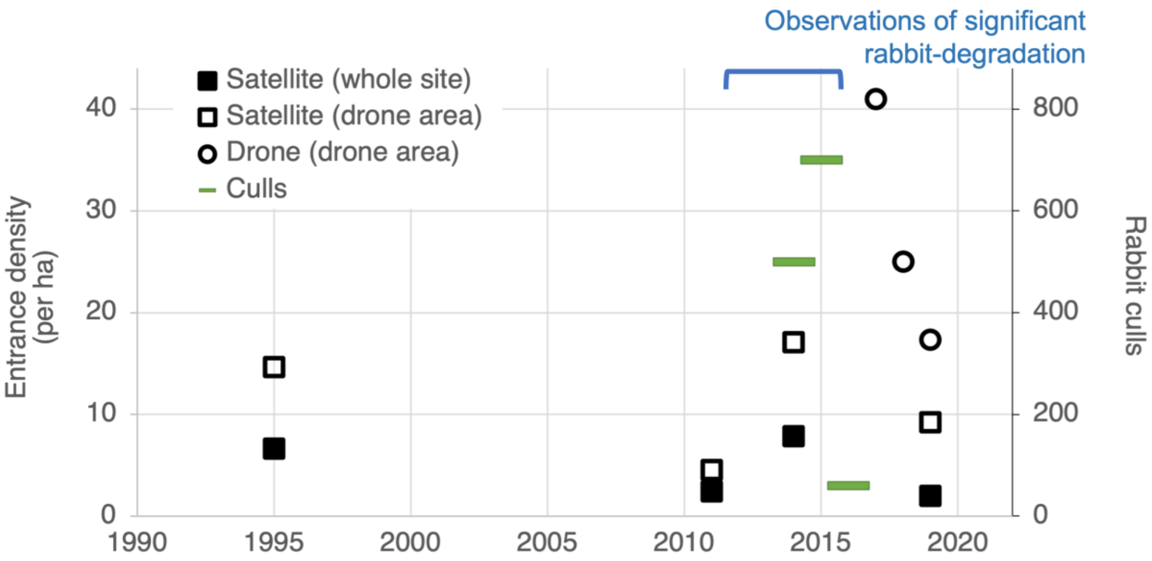


Fig. 5: Number of warren entrances identified in aerial (1995), satellite (2011, 2014, 2019) and drone (2017-2019) imagery per hectare, based on whole site (aerial/satellite) or reduced area (drone) measurements. Entrances were also counted within the reduced (drone) area for aerial/satellite imagery as this region contained a higher density of warrens than average across the dune. Also shown are the limited records of rabbit culls (2014-2016) that were undertaken due to site observations of significant rabbit degradation.

Burrow entrances were generally found clustered around the rear of Tramore dunes, the rear of the Magheramore dunes, throughout the Sandfield dune area, and variably present on Derryness Point (**Fig. 6**: 1995 to 2019). Entrances were generally not present on the seaward or estuary-facing dunes except for further into the estuary around Sandfield and Derryness. The distribution of entrances has changed through time largely as a result of changing levels of activity, but the mean density (**Fig. 6**: Mean) over this period highlights locations within the dunes where entrances have persisted, particularly around the central and eastern part of Magheramore into the Sandfield area. The calculation of linear trends in density over time (**Fig. 6**: Trend) illustrates areas within the dunes that have experienced a more systematic increase or decrease over the 24-year period. In the most part, this emphasises the loss of active entrances across the east-central (higher density) area of Magheramore, but also suggests that there has been a small southeast shift in the zone of activity. The north end of Tramore dunes, within the vicinity of the caravan site, is now almost devoid of warren entrances relative to the 1990s.

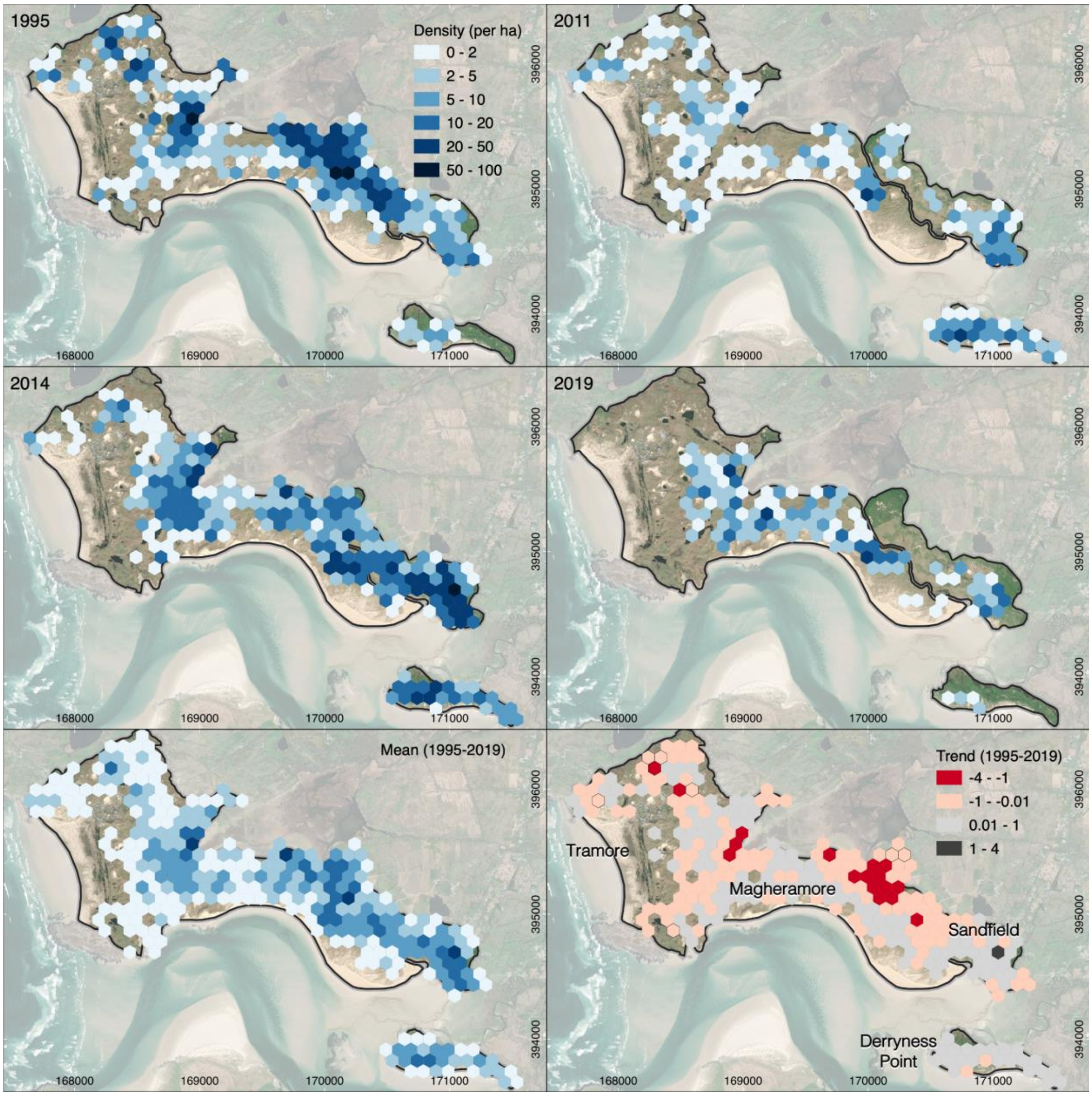


Fig. 6: Warren entrance density (entrances per ha) mapped from aerial (1995) and satellite (2011, 2014, 2019) imagery visualised on a hexagonal grid (100 m spacing). The average density across the site and trend in the density between 1995 and 2019 is also shown; those trends significant at the 90% level are delineated in black.

Spatial statistics confirmed clustering of burrow entrances across all years (**Table 2**). The lower site-wide density of entrances in 2011 and 2019 is evidenced in larger measures of average nearest neighbour (ANN) distance, but the greater ANN and nearest neighbour index (NNI) for 2011 captures the fact that warren entrances had a greater geographic range in 2011 than in 2019 (**Fig. 6**). Application of global spatial autocorrelation metrics Moran's I and Geary's C suggests that the localised entrance densities were most clustered in 1995 and most dispersed in 2019.

Table 2: Results of global spatial distance and distribution metrics.

	Warren entrances		**Warren entrance density**	
Year	**Average Nearest Neighbour** (in metres)	**Nearest Neighbour Index** <1 Clustered >1 Dispersed	**Moran's I** 1 Clustered 0 no pattern -1 Dispersed	**Geary's C** >1 Dissimilar values clustered 1 No spatial autocorrelation <1 Similar values clustered
1995	9.3	0.480**	0.522**	0.496**
2011	16.51	0.517**	0.373**	0.686**
2014	7.91	0.444**	0.463**	0.557**
2019	10.26	0.291**	0.319**	0.704**

** p<0.01

Calculation of the local Moran's I for each grid cell and for each coverage year identified distinct clusters of high entrance density within the dunes, and that these hotspots were not persistent through the changing cycle of rabbit activity (**Fig. 7**). The greater activity evident in 1995 was characterised by clusters of high entrance density in the centre-east and centre-west of the Magheramore system. When activity (site-wide density) was lower in 2011, the hotspot of entrance density moved to Derryness Point in the southeast, with localised high density around Sandfield. A small hotspot remained at Derryness when activity increased in 2014, but a more robust hotspot was built at Sandfield. As rabbit activity dropped again in 2019, the main hotspot in high entrance density moved back into the centre-south of Magheramore.

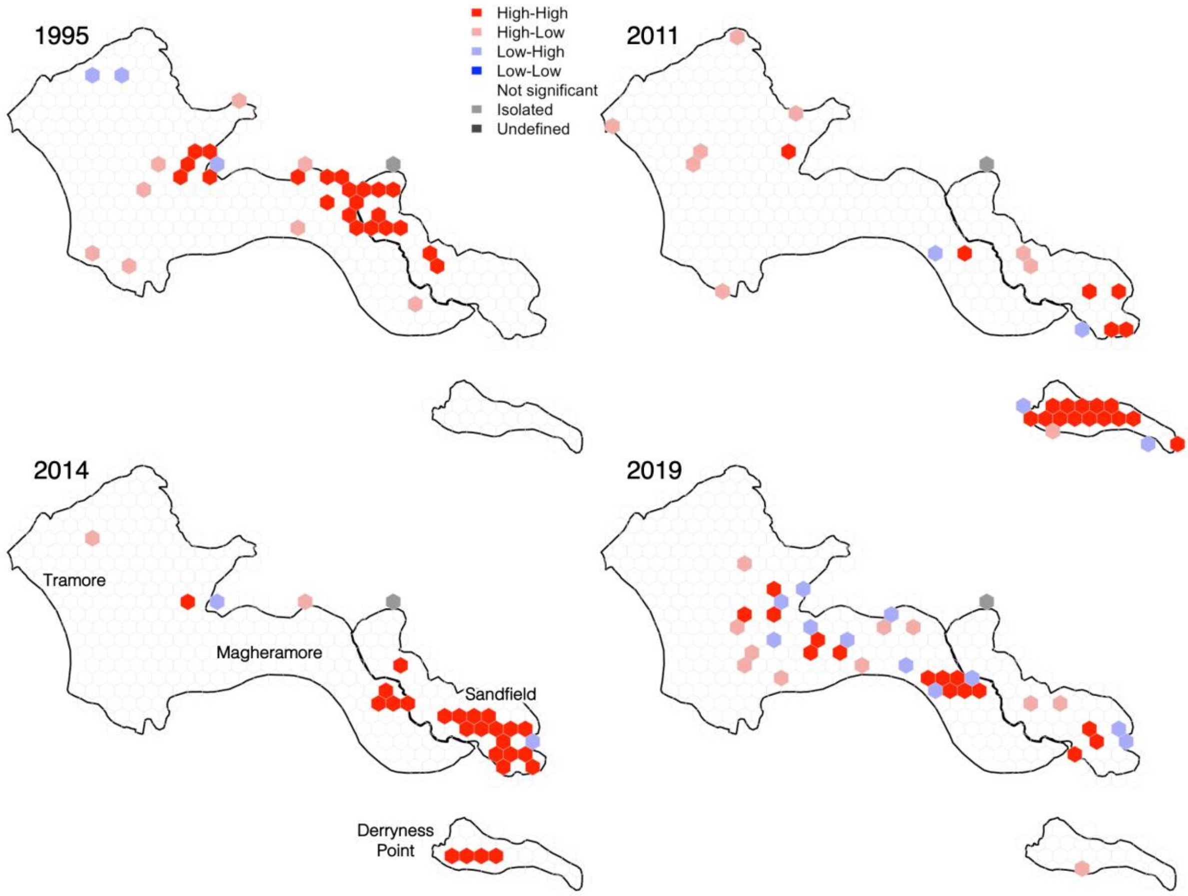


Fig. 7: Results of the Local Moran's I analysis (GeoDa) of warren entrance density.

Following these observations, we sought to explore some of the underlying drivers of the spatial patterns. A PCA of key environmental variables showed that the first 3 components explained over 73% of the within-data variance (**Fig. 8**). Overall, the PCA did not single out a particular variable explaining the observed patterns, but the first component (41.5%) showed that east-west position (X coordinate) and elevation were dominant gradients within the distribution of warren entrances; those to the east were at lower elevations than those to the west, and higher entrance densities were also found to the east (**Fig. 8a**). The second (16.8%) and third (15.6%) components reflected gradients in topographic structure (slope, roughness) and proximity and aspect (NtoE), respectively. Higher densities of entrances were associated with southwest facing slopes closer to the margins of the site (and closer to human activity, **Fig. 8c**), but on lower elevations (**Fig. 8a**).

The consistent spread of data points across multivariate space between the different years suggests that there was little difference in the importance of these variables to each time step (**Fig. 8**), even though there were clear geographic shifts in rabbit warren activity. The increased rabbit activity evident in the 1995 and 2014 imagery aligned with increased entrance densities as more entrances were formed (**Fig. 8a** and **c**, **kde variable**). Additionally, supplementary variables describing habitat showed that the warren entrances to the east of the system were more associated with machair habitat, and those to the west with fixed dune habitat (**Fig. 8a-b**).

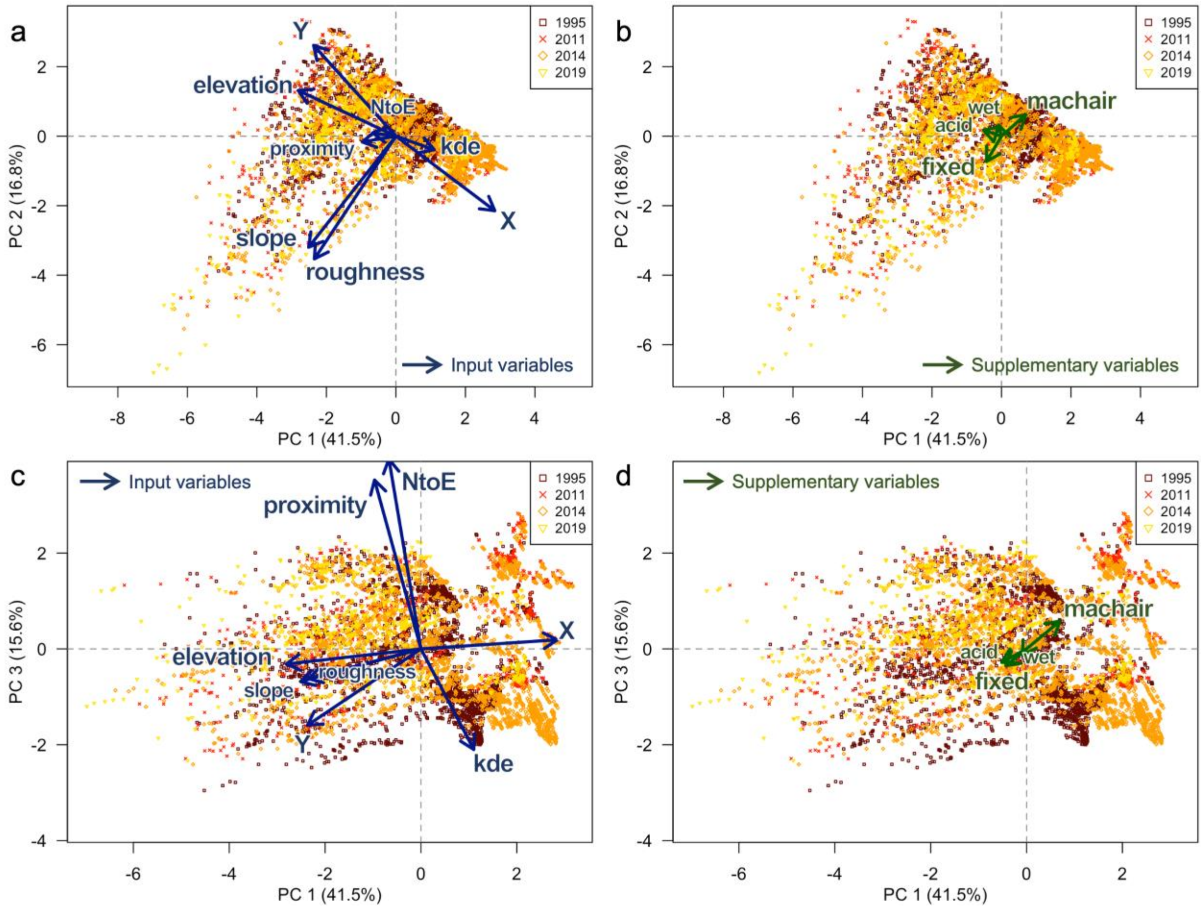


Fig. 8: Biplots of principal components 1 and 2 (**a,b**) and 1 and 3 (**c,d**) following a PCA of geography (X, Y coordinates), elevation, slope, aspect (simplified to northeasterly), topographic roughness, proximity to anthropogenic centres, and entrance density (kde) (**a,c**); supplementary variables capturing habitat type are shown in (**b,d**).

DISCUSSION

In the context of the Sheskinmore dunes, aerial and satellite imagery provide interesting insights into the spatiotemporal dynamics of rabbit activity and burrowing behaviour, with implications for rabbit population change monitoring and management. Ground-truthing confirmed appropriate interpretation of spectral features within both ultra-high resolution drone image and high-resolution satellite imagery. Whilst drone mapping is an increasingly popular approach for the mapping and monitoring of dune environments, it can only support recent and current monitoring practices. Meanwhile here, previously acquired satellite imagery and aerial photography can also support burrow entrance mapping, and opens an interesting door for the analysis of past to present changes in rabbit activity as a proxy for rabbit populations in coastal dune systems.

Higher resolution satellite imagery could be an accessible alternative to capturing this information. In the case of the Sheskinmore dunes, remote sensing confirmed the presence of a fluctuating wild European rabbit population. Rapid changes in rabbit populations are not unusual; myxomatosis can drive population changes of up to 300% in 2 years (Trout et al. 1992). The changes in burrow density and shifts in burrow clustering patterns were also consistent with rabbit culls driving a decline in population density in recent years.

This method of detection further creates an opportunity to model rabbit (and/or mammal) fossorial behaviour based on historical patterns, which would improve understanding of coastal dune dynamics and management where applicable. However, predicting rabbit burrowing patterns will require better understanding of (and likely more data for) the variables describing the burrowing behaviour and preferences of rabbits. A study predicting breeding habitat selection of western burrowing owls according to black-tailed prairie dog colonies in the USA used a similar approach (Lantz et al. 2007). They identified variables with potential to influence owl nesting (such as distance to prairie dog activity) and used logistic regression to determine the likelihood of burrow use.

Unlike that study, which required collection of data in the field, rabbit burrowing behaviour may be easier to model based on remotely sensed variables. Social behaviour (ie. aggregation of burrows into warrens) and substrate type (usually known through habitat assessments in protected areas) may be good candidates to start with: as shown in this study, rabbit burrows tend to cluster within warrens in fixed dune habitat. Several terrain variables were important in explaining spatial patterns, including elevation, slope and aspect, position, which are all easily derived from DEMs. Further research, including ground observations and at other dune sites is recommended to determine if these patterns are generalisable. Disease outbreak dynamics are also likely to influence spatial patterns of burrow use over time and should be further investigated.

In addition, using satellite imagery from different sources, resolutions, and times of the year highlights several important factors influencing the detection of entrances which should be taken into account. Resolution is key to maximising the potential for entrance mapping: warren entrance holes are 20-30 cm in diameter, so detecting these requires imagery with a pixel resolution of <30 cm. At 5 cm pixel resolution, the drone imagery is ideal for this, and even inactive entrances were visible (but not digitised). At >50 cm resolution, satellite imagery can only be used to map the bare ground patches found at active entrances.

Light conditions are also important: in bright light and low sun elevation (i.e. during the winter and nearer dawn and dusk), bare ground patches have a stronger spectral contrast to the surrounding vegetation and entrance holes can appear as a distinct, localised shadow. Even with consistent sensors, it is likely that the level of detection can vary according to the weather and season. Rutin (1992) noted burrowing patterns were significantly influenced by rainfall, where burrow erosion could occur. Myers and Parker (1975) also observed that large warrens tended to be inactive after summer, and little burrowing activity occurred outside the breeding season, meaning patterns in burrow visibility could vary significantly according to the timing of imagery. Satellite and drone imagery are useful to survey rabbit population trends and burrow use over time, but digitisation and data analysis should be undertaken keeping this in mind.

With the recent advances in image processing, digitisation of burrow entrances from remote sensing imagery could also be semi-automated and potentially enhanced using AI-assisted segmentation, which would facilitate data extraction from larger (or more) datasets. Such methods have been successfully employed in other fields (e.g.: González-Rivero et al. 2016; Leckie et al. 2003; Whiteside et al. 2020; Kopecky et al.

2023), where the combined advances in near sensing surveys and computer science have revolutionised ecological mapping. Some experimentation with optical image classification and segmentation of the drone images used here showed some potential, but required considerable training effort due to the small scale of the entrance hollows and sand patches relative to the scale of the dune, and the degree of spectral variability within the dune vegetation. Following a machine learning approach might lead to a more efficient segmentation, but ultimately, considerably more data is needed to provide the necessary training resource. Manual digitising might be the more accessible option for those working at a specific dune site, and to mitigate inconsistencies, imagery could be selected from a common season and under similar light and visibility conditions, if available.

Although it can become a powerful monitoring tool, remote sensing alone is, for the time being, too limited for an assessment of the impact of fossorial activity on coastal dune erosion. To the best of our knowledge, the only useful data gathered so far comes from Rutin (1992), who estimated the area of sand excavated for a single burrow ranged from 121 to 1,129 g (av. 436 g), and in the case of a shallow burrow dug for feeding, about 1 kg of sand was displaced. At 500 g per burrow entrance, this would amount to up to 1,200 kg of sand excavation across the Sheskinmore dunes based on the maxima in 2014. If satellite estimations are around 50% of the total entrances present, this value could be closer to 2,400 kg. At a density of 1,500 kg m^{-3}, this would contribute to mobilisation of at least 1.6 m^3 of sand. In the context of the potential volume of sand present within the Sheskinmore dunes (at 315 ha, even if the sand depth were only 1 m, the dune sediment volume would be $3x10^6$ m^3), this is a very small amount, but the warren network structure and rabbit activity lead to a range of other degradational processes, e.g. overgrazing and destabilisation (Provoost et al. 2011), that play an important role in coastal dune dynamics. Excavation can also contribute to overall sediment transport by reducing the consolidating role of vegetation and exposing loose particles to wind and rain. Rutin (1992) further noted that tunnelling promoted soil permeability and reduced runoff, which could simultaneously be argued to promote stabilisation. However, data are very local and approximate, and knowledge of the underground connectivity of burrows (and by association, warren size) is lacking, particularly in Sheskinmore's case.

Other studies have found that the mean number of burrow entrances per warren is generally lower in sandy environments. Approximately 3.4 to 6.8 entrances per warren have been recorded across sites (Myers and Parker 1975; Palomares 2003), possibly because looser soils provide lesser stability and increases the chances of burrow collapse (Myers and Parker 1965). However, this remains debatable without field confirmation, as in sandy-soil warrens up to 126 burrow entrances have been counted for a single warren (Palomares 2003). While warrens in sandy environments may be smaller, the densification of entrances suggests warrens may become larger and more complex at greater population levels, rather than more spread out across the entire dune system. In some sites, this is likely to reflect range-limitations of the specific substrate, landuse/landcover and environment but at Sheskinmore, there is a clear indication of shifts in geography in addition to densification.

Further surveys, for example to determine the depth of sand to bedrock, would help in determining the erosive impact of rabbit burrowing behaviour. Clustering patterns indicate excavations are concentrated in strategic areas. However, the realistic impact of the burrows cannot be determined unless the dune stratigraphy is better known. Further investigation of burrow density, burrow use and the local geology would therefore offer valuable insight on whether population controls may be necessary to mitigate risks of erosion in the future.

A major issue in coastal dune conservation has been determining whether dunes should be actively de-stabilised (e.g: Pye and Blott, 2017), or if the process of fixation should run its course (van Boxel et al. 1997; Pye et al. 2014; Pye and Blott 2017; Cooper and Jackson 2021). Historical aerial imagery from Sheskinmore (**Fig. 3**) effectively illustrates the *greening up* of coastal dunes; the dune surface of the 1950s was dominated by bare sand that has gradually been revegetated, and blowouts that were still unvegetated at the turn of the 21st century are now substantially fixed by comparison. There is wide recognition that the introduction of myxomatosis in the 1950s to Ireland and the UK to specifically control rabbit populations is linked directly to a marked shift in succession in coastal dunes, vegetation growth and dune stabilisation (see review in Provoost et al. 2011). Over the decades, ongoing cycles in myxomatosis have driven local changes in rabbit populations, and it is clear from the imagery that population cycles drive burrowing and erosional activity of rabbits across the dune environment, meaning that they play a distinct role in the geomorphological evolution of coastal dunes (see also Moulton et al. 2020).

Patterns of resistance and resilience differ among dune systems according to their ecological and geomorphological characteristics (Stallins and Parker 2003; Stallins and Corenblit 2018). Recent studies have supported a paradigm shift proposing less interventionist approaches to coastal dune system conservation, as they will naturally evolve differently according to their unique coastal-geological context, abiotic and biotic dynamics (Barrett-Mold and Burningham 2010; Delgado-Fernández et al. 2019; Cooper and Jackson 2021). Thus, the importance of pursuing studies on the role of invasive rabbit populations on coastal dune systems falls within the pressing need to better inform conservation management. This is especially true in contexts where coastal environments may be more prone to erosion by sea level rise and changing weather patterns (Pye and Blott 2020; Gao et al. 2020). In this context, coastal dune fixation is perhaps even desirable, as increased vegetation cover may buffer erosion (Cooper and Jackson 2021).

A more distinct evaluation of the change in rabbit activity across dune systems in the past is needed, but also a clearer outline of the near- and remote- sensing opportunities for contemporary monitoring. Clearer conservation aims are arguably a prerequisite to determining whether, and how, rabbit populations should be managed on coastal dune systems. Maintaining a case-by-case management approach appears more appropriate, as coastal dune systems evolve naturally differently. In this perspective, invasive rabbits are likely to play a role in both erosion (through burrowing) and stabilisation (through grazing) patterns which vary with population dynamics. Ideally, conservation approaches could aim for populations that coexist in harmony with the natural evolution of the dunes, without compromising the diversity they host or their existence in the future. Ultimately, populations need to be monitored, and their potential biogeomorphological role better evaluated. This study has demonstrated the potential for both freely available satellite imagery and high resolution drone imagery in this application.

CONCLUSION

The use of remote sensing proved efficient in detecting a large wild European rabbit population established on the remote coastal dune system of Sheskinmore, Co. Donegal, Ireland. By comparing satellite and drone imagery data, we came to the conclusion that satellite imagery is particularly useful to monitor active rabbit populations since its relatively lower resolution can exclusively sample burrows which are being actively used. On the other hand, higher resolution imagery can provide an additional insight on the dynamics of the population, since they allow the detection of inactive burrows as well. This type of data is even more appropriate in the current research context, where remote data collection from accessible, reliable and free sources is practical and preferred. It also opens up possibilities in terms of modelling rabbit burrowing behaviour, and enhanced efficiencies in detection and mapping that might come from advances in automated classification and segmentation.

This case study also highlighted a gap in coastal dune research and conservation - which have overlooked the implications of this invasive species' fossorial behaviour, prone to colonising these environments. This falls within a wider conservation imperative to clarify conservation aims and better management. Hence, further field studies on burrow connectivity, burrowing behaviours, their interaction with grazing patterns, and their impact on dune dynamics in different geomorphological contexts is key to more informed coastal dune conservation practises.

FUNDING

No funding was received for completion of this study.

DECLARATIONS

Conflict of Interest. The researchers declare having no financial or non-financial interests related to or influencing the work in this paper.

REFERENCES

Anselin L (2019) A Local Indicator of Multivariate Spatial Association: Extending Geary's c. Geographical Analysis 51:133–150. https://doi.org/10.1111/gean.12164

Anselin L, Syabri I, Kho Y (2006) GeoDa : An Introduction to Spatial Data Analysis. Geographical Analysis 38:5–22. https://doi.org/10.1111/J.0016-7363.2005.00671.X

Arens SM, Slings QL, Geelen LHWT, van der Hagen HGJM (2007) Implications of environmental change for dune mobility in the Nether lands. International Conference on Management and Restoration of Coastal Dunes. Minist. de Medio Ambiente, Santander, Spain, pp 3–5

Baddeley A, Rubak E, Turner R (2015). Spatial Point Patterns: Methodology and Applications with R.

Barrett-Mold C, Burningham H (2010) Contrasting ecology of prograding coastal dunes on the northwest coast of Ireland. Journal of Coastal Conservation 14:81–90. https://doi.org/10.1007/s11852-009-0069-4

Carter B, Wilson P (1988) Geomorphological, sedimentological and pedological influences on coastal dune development in Ireland. J Coastal Res

Carter R, Wilson P (1991) Chronology and geomorphology of the Irish dunes. A Guide to the Sand Dunes of Ireland. European Union for Dune Conservation and Coastal Management, ISBN 0951777904, pp18–41

Carter RWG (1991) Near-future sea level impacts on coastal dune landscapes. Landscape Ecology 6:29–39. https://doi.org/10.1007/BF00157742

Chapman and Hall/CRC Press, Lo ndon. ISBN 9781482210200 Bivand R, Pebesma E, Gomez-Rubio V (2013). Applied spatial data analysis with R, Second edition. Springer, NY. https://asdar-book.or g/

Cone J (1998) Principles of Geographical Information Systems by Peter A. New Zealand Geographer 54:56–57. https://doi.org/10.1111/j.1745-7939.1998.tb02089.x

Cooper A, Jackson D (2021) Dune gardening? A critical view of the contemporary coastal dune management paradigm. Area 53: 345–352. https://doi.org/10.1111/area.12692

Cox TE, Matthews R, Halverson G, Morris S (2021) Hot stuff in the bushes: Thermal imagers and the detection of burrows in vegetated sites. Ecology and Evolution 11:6406–6414. https://doi.org/10.1002/ECE3.7491

de Winter RC, Ruessink BG (2017) Sensitivity analysis of climate change impacts on dune erosion: case study for the Dutch Holland coast. Climate Change 141:685–701. https://doi.org/10.1007/s10584-017-1922-3

Delgado-Fernández I, Davidson-Arnott RGD, Hesp PA (2019) Is 're-mobilisation' nature restoration or nature destruction? A commentary. Journal of Coastal Conservation 23:1093–1103. https://doi.org/10.1007/s11852-019-00716-9

Dellafiore CM, Gallego Fernández JB, Vallés SM (2008) Habitat use for warren building by European rabbits (Oryctolagus cuniculus) in relation to landscape structure in a sand dune system. Acta Oecologica 33:372–379. https://doi.org/10.1016/j.actao.2008.02.002

Eldridge DJ, Myers CA (2001) The impact of warrens of the European rabbit (Oryctolagus cuniculus L.) on soil and ecological processes in a semi-arid Australian woodland. Journal of Arid Environments 47:325–337. https://doi.org/10.1006/jare.2000.0685

Everard M, Jones L, Watts B (2010) Have we neglected the societal importance of sand dunes? An ecosystem services perspective. Aquatic Conservation 20:476–487. https://doi.org/10.1002/aqc.1114

Gao J, Kennedy DM, Konlechner TM (2020) Coastal dune mobility over the past century: A global review. Progress in Physical Geography: Earth and Environment 44:814–836. https://doi.org/10.1177/0309133320919612

Gardner E (2016) The ecohydrology and conservation of a coastal sedimentary lake and wetland system: Sheskinmore Lough, Donegal, Ireland. University College London

Gibb JA (1993) Sociality, time and space in a sparse population of rabbits (Oryctolagus cuniculus). Journal of Zoology 229:581–607. https://doi.org/10.1111/J.1469-7998.1993.TB02658.X

González-Rivero M, Beijbom O, Rodriguez-Ramirez A, Holtrop T, González-Marrero Y, Ganase A, Roelfsema C, Phinn S, Hoegh-Guldberg O (2016) Scaling up Ecological Measurements of Coral Reefs Using Semi-Automated Field Image Collection and Analysis. Remote Sensing. 8(1):30. https://doi.org/10.3390/rs8010030

Hayden TJ, Harrington Rory, Clarke Billy (2001) Exploring Irish mammals. Town House & Country House Ltd, Dublin, Ireland. ISBN 97 81860590931

Herron LE (2014) Quantifying the impact of grazing by wild rabbits and conservation grazing by cattle on sand dunes in Northern Irelan d. PhD thesis, Queen's University Belfast, https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.676515

Hesp P, Schmutz P, Martinez ML (Marisa), et al (2010) The effect on coastal vegetation of trampling on a parabolic dune. Aeolian Research 2:105–111. https://doi.org/10.1016/j.aeolia.2010.03.001

Jackson DWT, Cooper JAG (2011) Coastal dune fields in Ireland: rapid regional response to climatic change. In: 11th International Coast al Symposium. J Coastal Res Szczecin, Poland, 293–297

Jackson DWT, Costas S, González-Villanueva R, Cooper A (2019) A global 'greening' of coastal dunes: An integrated consequence of climate change? Global and Planetary Change 182:103026. https://doi.org/10.1016/j.gloplacha.2019.103026

Jiang J, Gao D, DeAngelis DL (2012) Towards a theory of ecotone resilience: Coastal vegetation on a salinity gradient. Theor Popul Biol 82:29–37. https://doi.org/10.1016/j.tpb.2012.02.007

Jones ML, Wallace H, Norris D, Brittain SA, Haria S, Jones RE, Rhind PM, Reynolds B, & Emmett BA (2004) Changes in vegetation and soil characteristics in coastal sand dunes along a gradient of atmospheric nitrogen deposition. Plant biology, 6(5):598-605.

Kolb BYHH (1991) Use of Burrows and Movements by Wild Rabbits (Oryctolagus cuniculus) on an Area of Sand Dunes. Journal of Applied Ecology 28:879–891

Kopecky KL, Pavoni G, Nocerino E, Brooks AJ, Corsini M, Menna F, Gallagher JP, Capra A, Castagnetti C, Rossi P, et al. (2023) Quantifying the Loss of Coral from a Bleaching Event Using Underwater Photogrammetry and AI-Assisted Image Segmentation. Remote Sensing 15(16):4077. https://doi.org/10.3390/rs15164077

Lantz SJ, Conway CJ, Anderson SH (2007) Multiscale Habitat Selection by Burrowing Owls in Black-Tailed Prairie Dog Colonies. Journal of Wildlife Management 71(8):2664-2672. https://doi.org/10.2193/2006-221

Leckie DG, Gougeon FA, Walsworth N, Paradine D (2003) Stand delineation and composition estimation using semi-automated individual tree crown analysis. Remote Sensing of Environment 85(3):355-369. https://doi.org/10.1016/S0034-4257(03)00013-0

Levin N, Kidron GJ, Ben-Dor E (2006) The spatial and temporal variability of sand erosion across a stabilizing coastal dune field. Sedimentology 53:697–715. https://doi.org/10.1111/j.1365-3091.2006.00787.x

Lombardi L, Fernández N, Moreno S, Villafuerte R (2003) Habitat-related differences in Rabbit (Oryctolagus cuniculus) abundance, distribution and activity. Journal of Mammalogy 84:26–36. https://doi.org/10.1644/1545-1542(2003)084<0026:HRDIRO>2.0.CO;2

Maher-McWilliams D (2013) Geomorphic and Hydrological Mapping of Sheskinmore Lough and Wetland, Co. Donegal, Ireland. Master's thesis, University College London, https://sheskinmore.files.wordpress.com/2013/10/mahermcwilliams13sheskinmore-topography.pdf

Martínez ML, Maun MA, Psuty NP (2008) The Fragility and Conservation of the World’s Coastal Dunes: Geomorphological, Ecological and Socioeconomic Perspectives. Springer, Berlin, Heidelberg, pp 355–369

Martins H, Miller DR, Elston DA, et al (2002) Factors influencing the location and number of entrances of European wild rabbit (Oryctolagus cuniculus L.) warrens in a Southern Portuguese montado. Journal of Mediterranean Ecology 3:31–40

Mentaschi L, Vousdoukas MI, Pekel J-F, et al (2018) Global long-term observations of coastal erosion and accretion. Scientific Reports 8:12876. https://doi.org/10.1038/s41598-018-30904-w

Moulton MAB, Hesp PA, da Silva GM, et al (2020) Effects of the Increase in Vegetation Cover and Impact of Rabbits on the Geomorphology of Parabolic Dunes (Younghusband Peninsula - SA, Australia). Journal of Coastal Research 95:108. https://doi.org/10.2112/SI95-021.1

Myers K, Parker BS (1965) A study of the biology of the wild rabbit in climatically different regions in Eastern Australia. CSIRO Wildl R es 10: 1-32

Myers K, Parker BS (1975) Effect of severe drought on rabbit numbers and distribution in a refuge area in semiarid North-Western New South Wales. Wildlife Research 2:93–101. https://doi.org/10.1071/WR9750103

NPWS (2019) The Status of EU Protected Habitats and Species in Ireland. Volume 3: Species Assessment. Unpublished NPWS report. Ed ited by: Deirdre Lynn and Fionnuala O'Neill. https://www.npws.ie/sites/default/files/publications/pdf/NPWS_2019_Vol3_Species_Article 17.pdf

O'Briain M (2005) 'EU biodiversity policy context for the conservation of estuaries and dunes.' International Conference on Nature Resto ration Practices in European Coastal Habitats, Koksijde, Belgium, 19-23 September 2005, VLIZ Special Publication 19: 7–12.

Ord JK, Getis A (1995) Local Spatial Autocorrelation Statistics: Distributional Issues and an Application. Geogr Anal 27:286–306. https://doi.org/10.1111/j.1538-4632.1995.tb00912.x

Palomares F (2003) Warren building by European rabbits (Oryctolagus cuniculus) in relation to cover availability in a sandy area. Journal of Zoology 259:63-67. https://doi.org/10.1017/S0952836902002960

Pebesma E, Bivand R (2023). Spatial Data Science With Applications in R. Chapman & Hall. https://r-spatial.org/book/ .

Provoost S, Jones MLM, Edmondson SE (2011) Changes in landscape and vegetation of coastal dunes in northwest Europe: A review. Journal of Coastal Conservation 15:207–226. https://doi.org/10.1007/s11852-009-0068-5

Pye K, Blott SJ (2017) Evolution of a sediment-starved, over-stabilised dunefield: Kenfig Burrows, South Wales, UK. Journal of Coastal Conservation 21:685–717. https://doi.org/10.1007/s11852-017-0506-8

Pye K, Blott SJ (2020) Is 're-mobilisation' nature restoration or nature destruction? A commentary. Discussion. Journal of Coastal Conservation 24:10. https://doi.org/10.1007/s11852-020-00730-2

Pye K, Blott SJ, Howe MA (2014) Coastal dune stabilization in Wales and requirements for rejuvenation. Journal of Coastal Conservation 18:27–54. https://doi.org/10.1007/s11852-013-0294-8

QGIS Development Team (2020) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Quigley MB (1991) A guide to the sand dunes of Ireland. European Union for Coastal Conservation, Dublin.

Ranwell DS (1960) Newborough Warren, Anglesey : III . Changes in the Vegetation on Parts of the Dune System After the Loss of Rabbit s by Myxomatosis. J of Ecology 48(2):385–395. https://doi.org/10.2307/2257524

Ranwell DS (1972) Ecology of salt marshes and sand dunes. Chapman and Hall

Rogers PM, Myers K (1979) Ecology of the European Wild Rabbit, Oryctolagus cuniculus (L.), in Mediterranean Habitats. I. Distribution in the Landscape of the Coto

Donana, S. Spain. Journal of Applied Ecology 16:691. https://doi.org/10.2307/2402846

Ruiz-Aizpurua L, Tortosa FS (2018) When more is less: the negative effect of European rabbit release upon local warren occupancy. Acta Ethologica 21:101–107. https://doi.org/10.1007/s10211-018-0286-7

Rutin J (1992) Geomorphic activity of rabbits on a coastal sand dune, De Blink dunes, the Netherlands. Earth Surfaces Processes and Landforms 17:85–94. https://doi.org/10.1002/esp.3290170107

Sanchez DM, Rachlow JL, Robinson AP, Johnson TR (2009) Survey Indicators for Pygmy Rabbits: Temporal Trends of Burrow Systems and Pellets. West North American Naturalist 69:426–436. https://doi.org/10.3398/064.069.0402

Slingsby D, Cook C (1986) *Practical Ecology*. Macmillan Education UK, London

Stallins JA, Corenblit D (2018) Interdependence of geomorphic and ecologic resilience properties in a geographic context. Geomorphology 305:76–93

Stallins JA, Parker AJ (2003) The influence of complex systems interactions on barrier Island dune vegetation pattern and process. Annals of the Association of American Geographers 93:13–29. https://doi.org/10.1111/1467-8306.93102

Sumption KJ, Flowerdew JR (1985) The ecological effects of the decline in Rabbits (Oryctolagus cuniculus L.) due to myxomatosis. Mamm Review 15:151–186. https://doi.org/10.1111/j.1365-2907.1985.tb00396.x

Trout RC, Ross J, Tittensor AM, Fox AP (1992) The effect on a british wild rabbit population (Oryctolagus cuniculus) of manipulating myxomatosis. Journal of Applied Ecology 29:679–686. https://doi.org/10.2307/2404476

van Boxel JH, Jungerius PD, Kieffer N, Hampele N (1997) Ecological effects of reactivation of artificially stabilized blowouts in coastal dunes. Journal of Coastal Conservation 3:57–62. https://doi.org/10.1007/BF02908179 van Dijk HW (1992) 'Grazing domestic livestock in Dutch coastal dunes: Experiments, experiences and perspectives.' 3rd European Dune Congress. Rotterdam, Galway, Ireland,17-21 June 1992.

Whiteside TG, Esparon AJ, Bartolo RE (2020) A semi-automated approach for quantitative mapping of woody cover from historical time series aerial photography and satellite imagery. Ecol Informatics 55. https://doi.org/10.1016/j.ecoinf.2019.101012

Whitford WG, Kay FR (1999) Bioperturbation by mammals in deserts: A review. Journal of Arid Environments 41:203–230. https://doi.org/10.1006/jare.1998.0482

Wilson MFJ, O'Connell B, Brown C, et al (2007) Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the Continental Slope. Marine Geodesy 30:3–35. https://doi.org/10.1080/01490410701295962

Wood DH (1984) The rabbit (Oryctolagus cuniculus L.) as an element in the arid biome of Australia. In: Cogger HG, Cameron EE (eds) Arid Australia. Australian Museum, Sydney, pp 273–287