

Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions

Phil J. Bouchet^{1*}, Jessica J. Meeuwig^{1,2}, Chandra P. Salgado Kent³,
Tom B. Letessier² and Curt K. Jenner⁴

¹ *The UWA Oceans Institute, School of Animal Biology, The University of Western Australia, Crawley, Western Australia 6009, Australia*

² *Centre for Marine Futures, The University of Western Australia, Crawley, Western Australia 6009, Australia*

³ *Centre for Marine Science and Technology, Curtin University, Perth, Western Australia 6845, Australia*

⁴ *Centre for Whale Research (WA) Inc., Fremantle, Western Australia 6959, Australia*

ABSTRACT

Despite being identified as a driver of mobile predator aggregations (hotspots) in both marine and terrestrial environments, topographic complexity has long remained a challenging concept for scientists to visualise and a difficult parameter to estimate. It is only with the advent of high-speed computers and the recent popularisation of geographical information systems (GIS) that terrain attributes have begun to be quantitatively measured in three-dimensional space and related to wildlife dynamics, making the well-established field of geomorphometry (or ‘digital terrain modelling’) a discipline of growing appeal to biologists. Although a diverse array of numerical metrics is now available to describe the shape, geometry and physical properties of natural habitats, few of these are known to, or adequately used by, ecologists. In this review, we examine the nature and usage of 56 geomorphometrics extracted from the ecological modelling literature over a period of 32 years (1979–2011). We show that, in studies of mobile predators, numerous topographic variables have largely been overlooked in favour of single basic metrics that do not, on their own, fully capture the complexity of continuous landscapes. Based on a simulation approach, we assess the redundancy and correlation structure of these metrics and demonstrate that a majority are highly collinear. We highlight a suite of 7–8 complementary metrics which best explain topographic patterns across a bathymetric grid of the west Australian seafloor, and contend that field and analytical protocols should prioritise variables of these types, particularly when the responses of predator populations to physical habitat features are of interest. We suggest that prominent structures such as canyons, seamounts or mountain chains can serve as useful proxies for predator hotspots, especially in remote locations where access to high-resolution biological data is often limited.

Key words: predators, hotspots, metrics, topography, complexity, geomorphometry, aggregations, landscape.

CONTENTS

I. Introduction	700
(1) Background	700
(2) Nomenclature	701
(a) Hotspots	701
(b) Mobile predators	701
(c) Topographic complexity	701
II. Methods	701

* Address for correspondence (Tel: +61 (08) 6488 8118; E-mail: philippe.bouchet@research.uwa.edu.au).

[Correction added on 13 June 2015 after first online publication: under the “Aspect” section of Table 1, in the Definition column, the variable “Easting” and “Northing” were changed to “Sine of terrain orientation” and “Cosine of terrain orientation” respectively. Also, the unit for both were changed from “m” to “rad”].

(1) Literature survey and article selection	701
(2) Multivariate simulation	701
III. Results	712
(1) Topographic drivers of predator hotspots	712
(a) Foraging	712
(b) Migration and dispersal	713
(c) Breeding	714
(d) Roosting and resting	714
(2) Landscape measures and models of predator hotspots	715
(a) Metric usage and prevalence	715
(b) Metric redundancy	715
(c) Metric relevance	718
IV. Discussion	719
V. Conclusions	723
VI. Acknowledgements	724
VII. References	724

I. INTRODUCTION

(1) Background

As a consequence of conspecific attraction, niche partitioning, resource competition or collective feeding behaviours, wildlife distributions often exhibit patchy ‘hotspot’ areas of higher animal density, greater taxonomic diversity, or more intense use (Camazine *et al.*, 2001; Worm, Lotze & Myers, 2003; Bestley *et al.*, 2009; Kouakou, Boesch & Kuehl, 2011; Nur *et al.*, 2011). Even though aggregations are regarded as an evolutionarily beneficial strategy (Vucetich, Peterson & Waite, 2004; Ritz *et al.*, 2011) and occur across a broad range of body sizes, phyla, and spatio-temporal scales (e.g. Vulinec, 1990; Weilgart & Whitehead, 1997; Scott & Cattanch, 1998; Watkins, 2008; Parsons *et al.*, 2009; de la Parra Venegas *et al.*, 2011), they also make organisms more susceptible to catastrophic events and anthropogenic threats (Williams, Lusseau & Hammond, 2009). Upper trophic level species prove particularly vulnerable to such threats because of their limited phenotypic plasticity, conservative life histories, specialist dietary requirements, and position on or near the top of the food pyramid (Lewison *et al.*, 2004; Simmonds & Isaac, 2007). Conspicuous and relatively easy to locate, aggregations of marine predators are indeed highly exploitable and prone to overharvest (Sadovy & Domeier, 2005), a trait which has contributed to the depletion of major open-ocean fisheries and the collapse of numerous pelagic populations (see Baum *et al.*, 2003; Myers & Worm, 2005; Robbins *et al.*, 2006; Jackson, 2008). Subsequent to hunting or habitat fragmentation, similar trophic downgrades (losses of apex consumers, *sensu* Estes *et al.*, 2011) have also been observed on land, and a number of terrestrial species of current conservation concern have undergone comparable extinction crises (Bailey *et al.*, 1986; Breitenmoser, 1998; Woodroffe, 2000; Ceballos & Ehrlich, 2002; Cardillo *et al.*, 2004; Ferrer & Negro, 2004; Laliberte & Ripple, 2004; Carrete *et al.*, 2007).

Predators act as key regulators of biodiversity (Sergio *et al.*, 2006a; Letnic, Ritchie & Dickman, 2012) and ecosystem

stability (Sala, 2006; Bossart, 2011), yet the consequences of their loss remain poorly grasped (Heithaus *et al.*, 2008; McCauley *et al.*, 2012). As such, mapping and predicting the location of predator hotspots to assist resource management and set priorities for conservation planning has become a rapidly expanding field of research (Reese & Brodeur, 2006). Importantly, following mounting evidence that some prominent land- and seascape structures (e.g. mountain peaks, canyons, seamounts, cliffs, sills, continental shelf edges or oceanic shoals and banks) consistently attract large wildlife (Tews *et al.*, 2004; Vetter, Smith & De Leo, 2010), assessments of species–topography relationships have gained momentum in past decades.

Notwithstanding, progress in quantifying these associations has been limited on a global scale, because: (i) ecologists have, until recently, typically defined terrain attributes in descriptive terms (for instance ‘abrupt’, ‘craggy’, ‘precipitous’, ‘steep’, ‘rugged’, or ‘broken’) (Riley, Degloria & Elliot, 1999); (ii) the search for measures of landscape patterns has long favoured the development of two-dimensional indices which describe pattern variations on a horizontal plane (e.g. mean patch area), rather than three-dimensional relief indicators (e.g. curvature) (Pike, 2002); (iii) there is little consensus on the best approach to measuring terrain complexity in a biologically meaningful way; (iv) emerging concepts in geomorphometry – the quantitative analysis of ground surface topography, also known as ‘digital terrain modelling’ (Pike, 2000) – have typically matured within the disciplines of biophysics, engineering, mathematics and earth and planetary science, with rarer applications to animal ecology; (v) even though a constantly widening array of geomorphometric variables now exists, guidelines on how to choose and apply them are virtually absent (Sappington, Longshore & Thompson, 2007).

To address these caveats, we present a quantitative examination of the literature pertaining to the topographic drivers of predator hotspots. Our aims are to provide a summary of the current state of knowledge on predator–topography associations in both terrestrial and marine

systems, and to discuss the nature and usage of geomorphometric variables in wildlife biogeography and habitat preference research over the past three decades. Additionally, we conduct simulations to assess the degree of redundancy of 56 metrics derived from the literature, and we illustrate ways in which functional groupings can be established to assist in detecting the variables that best translate the terrain patterns present amongst samples within a given region. Our resulting analysis suggests a minimum working subset of geomorphometric variables and variable types best suited for the characterisation of topographic complexity, with implications for the monitoring of large predator species.

(2) Nomenclature

(a) Hotspots

Broadly speaking, hotspots correspond to locations where an ‘out-of-the-ordinary’ phenomenon takes place (Ord & Getis, 2001; Nelson & Boots, 2008). In this study, as is routinely the case with free-ranging wildlife, we see it as a species’ critical foraging ground, breeding site, or migratory corridor, although it can by extension refer to any region of high occupancy (Block, Costa & Bograd, 2010), high species richness (Worm *et al.*, 2003), or intense biological activity (Drazen *et al.*, 2003).

(b) Mobile predators

Drawing on the animal dispersal and migration literature, mobile predators were defined as those large-bodied, upper-trophic-level species that (i) primarily derive their nourishment from other animal matter during part or the entirety of their life cycles, (ii) actively seek out, hunt and capture live prey, and (iii) are capable of sustained, repeated, undistracted and directionally consistent movements over a potentially wide range of geographic domains, habitats, landscapes, and/or across national jurisdictional boundaries, with possible ‘consequences for gene flow across space’ (Curio, 1978; Knutsen *et al.*, 2003; Dingle & Drake, 2007; Ronce, 2007; Milner-Gulland, Fryxell & Sinclair, 2011).

(c) Topographic complexity

Topographic complexity is also a broad term (Lu, 2008), but it is understood here to describe the shape, geometry and configuration of natural terrain surfaces in three-dimensional space. From a purely statistical viewpoint, this reflects variability in one or multiple quantitatively measured geomorphometric variables such as elevation, slope, aspect, curvature, fractal dimension or rugosity.

II. METHODS

(1) Literature survey and article selection

Data on species–topography linkages and the use of landforms by mobile predators were extracted from Thompson Reuters’ *BIOSIS Previews* and *Web of Science*

databases (<http://ip-science.thomsonreuters.com/>) over a 32-year search period (1979–2011) and based on appropriate key words, including multiple Boolean combinations of the words *Predator**, *Topograph**, *Terrain*, *Relief*, *Geomorph**, *Complex**, *Heterogen**, *Hotspot**, *Metric**, *Index*, *Indices*, *Model**, *Landscape**, *Seascape**, *Prey*, *Feed**, *Habitat*, *Megafauna*, *Carnivor**, among others (where asterisks represent wildcard characters). All documents were evaluated iteratively for relevance to the topic and research papers were retained if they fulfilled the following conditions: the article (i) was published in a peer-reviewed scientific journal in the English language; (ii) focused on one or more predator groups/taxa/species; (iii) was based on empirical information (e.g. review papers or personal perspective statements were omitted); and (iv) relied upon at least one geomorphometric variable within a statistical framework, regardless of the tool(s) employed (conditions adapted from Wedding *et al.*, 2011). A cross check of the reference list of each article was also undertaken and permitted the collation of further material. Manuscripts describing the development of metrics with application to predator habitat suitability models were also referenced for use in simulations (see Section II.2). All identifiable geomorphometric variables were listed (Table 1) and a purpose-built database was populated with the following metadata for each entry: article title, author name, journal title, year of publication, and type and number of metric(s) used. Results were compiled and synthesised for both marine and terrestrial taxa.

(2) Multivariate simulation

As numerous metrics often convey similar information about surface forms and are hence redundant (Gessler *et al.*, 2009), we sought to determine the degree to which each geomorphometric variable identified in the literature contributed uniquely to the representation of topographic complexity. We used the ArcGIS 10.0 software (ESRI, 2011) to simulate 150 sampling sites distributed randomly across the west Australian exclusive economic zone (EEZ), that is, the area lying between 12 and 200 nautical miles seaward of the state’s territorial sea baseline (Fig. 1), and comprised between -10 and -38.5 degrees of latitude (mean \pm S.D. site depth range = 731.3 ± 691.3 m). This maritime jurisdiction was chosen as a representative test scenario for a variety of reasons: (i) it displays a distinctively heterogeneous and highly complex seabed (Schlich, 1982); (ii) it exhibits exceptional levels of marine diversity and endemism (Costello *et al.*, 2010) with important ecological conservation values [e.g. feeding aggregations of endangered blue whales in the Perth Canyon (Rennie *et al.*, 2009), seasonal aggregations of whale sharks and sea turtles at Ningaloo Reef (Preen *et al.*, 1997; Wilson, Taylor & Pearce, 2001)]; (iii) although vertebrates are a comparatively well-understood taxon, biological sampling remains scant in most of the EEZ, especially in the deeper, offshore end of the range (Butler *et al.*, 2010); (iv) it is a region where world-renowned measures in ocean protection enter into conflict with booming industrial activities and rapid

Table 1. Geomorphometrics used to characterise and quantify topographic complexity in ecological studies of marine and terrestrial vertebrate predators

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Elevation			Height above sea level					
Mean	E.AVG	μ_z	Mean elevation.	m	$\mu_z = \sum_{i=1}^n \frac{z_i}{n}$	Milakovic <i>et al.</i> (2011) [†]	—	No
Median	E.MED	\tilde{z}	Median elevation.	m	—	Kobler & Adamic (2000) [†]	—	No
Standard deviation	E.STD	σ_z	Dispersion of elevation values about the mean.	m	$\sigma_z = \sqrt{\frac{1}{n-1} \sum_{i=1}^n (z_i - \mu_z)^2}$	Joly & Myers (2001) [†]	—	No
Coefficient of variation	E.COV	CV_z	Normalised measure of dispersion of elevation values.	d.u.	$CV_z = \frac{\sigma_z}{\mu_z}$	Osborne, Alonso & Bryant (2001) [†]	—	No
Minimum	E.MIN	z_{\min}	Smallest elevation.	m	—	Martínez, Serrano & Zuberogitia (2003) [†]	—	No
Maximum	E.MAX	z_{\max}	Largest elevation.	m	—	Murphy, Zysik & Pierce (2004) [†]	—	No
Range	E.RGE	$[z_{\min}, z_{\max}]$	Difference between highest and lowest elevations.	m	$z_{\max} - z_{\min}$	Moreno-Rueda & Pizarro (2007) [†]	—	No
Domains	E.DOM	$[z_1, z_2]; [z_3, z_4]$	Arbitrarily defined intervals.	m	—	Dean (1987) [†]	—	No
Topographic position (Hypsometric) index <i>3 × 3 rectangular neighbourhood</i>	E.TPI	TPI (HI)	Location height relative to immediate focal neighbourhood. Indicates whether a point is low or high with reference to those around it.	m	$z_i - \text{focal}[\mu_z]$ where focal $[\mu_z]$ denotes the focal mean in an annulus neighbourhood of pre-determined inner and outer radii	Dickson & Beier (2007) [†] and Moore, Harvey & Van Niel (2009)	Land Facet Corridor Tools for ArcGIS 10.0	Yes
Terrain ruggedness index (1)	E.TRI	TRI	Sum change in elevation between focal site and neighbouring sites.	m	$TRI_1 = \sqrt{\sum (z_{ij} - z_{0,0})^2}$	Riley & Malecki (2001) [†]	ArcGIS 10.0	Yes

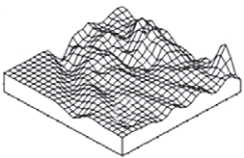


Table 1. Continued

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Terrain ruggedness index (2) <i>20 m contours</i>	E.TR2	TRI	Combined index of slope and terrain undulations ('ups and downs') which captures the number of separate aspects along a linear transect spanning the width of the study area. An area with considerable changes in relief (many bluffs and hollows) and many contour intercepts will obtain high values of ruggedness, while smooth but steep terrain will receive low values.	d.u.	$TRI_2 = \frac{TNC \times TNF}{TNC + TNF}$ where TNC equals the total number of contour intercepts along a transect line and TNF equals the total number of fluctuations ('ups and downs'), defined by the number of separate aspects along that transect. Here taken as the maximum value obtained on transects running north–south and east–west across each sampling site.	Szor, Berteaux & Gauthier (2008) [†]	ArcGIS 10.0	Yes
Slope			Maximum rate of change in elevation					
Mean	S.AVG	μ_s	Mean slope.	deg or %	$\mu_s = \sum_{i=1}^n \frac{s_i}{n}$	Milakovic <i>et al.</i> (2011) [†]	ArcGIS 10.0	Yes
Median	S.MED	\tilde{s}	Median slope.	deg or %	—	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Standard deviation	S.STD	σ_s	Dispersion of slope values about the mean.	deg or %	$\sigma_s = \sqrt{\frac{1}{n-1} \sum_{i=1}^n (s_i - \mu_s)^2}$	Macleod <i>et al.</i> (2004) [†]	ArcGIS 10.0	Yes
Coefficient of variation	S.COV	CV_s	Normalised measure of dispersion of slope values.	d.u.	—	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Minimum	S.MIN	s_{\min}	Minimum slope value.	deg or %	—	Gowans & Whitehead (1995) [†]	ArcGIS 10.0	Yes
Maximum	S.MAX	s_{\max}	Maximum slope value.	deg or %	—	Dickson, Jenness & Beier (2005) [†]	ArcGIS 10.0	Yes
Range	S.RGE	$[s_{\min}, s_{\max}]$	Difference between highest and lowest slopes.	deg or %	$s_{\max} - s_{\min}$	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Domains	S.DOM	$[s_1, s_2]; [s_3, s_4]$	Arbitrarily defined intervals.	deg or %	—	Logan & Irwin (1985) [†]	ArcGIS 10.0	Yes
Slope index 1	S.SI1	SI	Measure of terrain flatness. Ranges from 200 for flat ground to 0.02 if all slopes exceed 20%.	d.u.	$SI_1 = \frac{2AC}{BD}$ where A = % of total plot area ≤20%, B = % of total area >20%, C = % total area ≤5%, D = % total area ≤15%	Dean (1987) [†]	ArcGIS 10.0	Yes
Slope index 2	S.SI2	SI	Measure of terrain relief of a specific quadrant as a percentage of change of the topography to the whole study area.	d.u.	$SI_2 = 100 \times \frac{z_{\max} - z_{\min}}{z_M}$ where z_M is the maximum depth/elevation in the entire study area	Oviedo (2007) [†]	ArcGIS 10.0	Yes

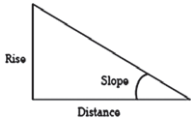


Table 1. Continued

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Slope index 3	S.SI3	SI	Average absolute deviation from maximum elevation or depth.	m	$SI_3 = \sum_{i=1}^n \frac{ z_i - z_{\max} }{n-1}$	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Aspect			Azimuthal direction of slope (α) expressed as clockwise deviation from North and measured in compass degrees from 0 to 360					
Mean	A.AVG	μ_α	Mean aspect.	deg or %	$\mu_\alpha = \text{atan2} \left(\frac{1}{n} \times \sum_{j=1}^n \sin \alpha_j, \frac{1}{n} \times \sum_{j=1}^n \cos \alpha_j \right)$	López-López <i>et al.</i> (2007) [†]	ArcGIS 10.0	Yes
Domains	A.DOM	$[\alpha_1, \alpha_2]; [\alpha_3, \alpha_4]$	Arbitrarily defined intervals.	deg or %	—	Dean (1987) [†]	—	No
Aspect index	A.ASP	AI	Measure of the distribution of aspect values across eight compass octants. Ranges from 0 for flat ground to 12.5 for a uniform aspect distribution to 300 for a plot entirely tilted in one direction.	d.u.	$AI = (A - B) + (C - D) + E$ where a half-sum is the sum of any four contiguous octant percentages, and A = largest half-sum, B = 100-A, C and D = half-sums at right angles to A, and E = mean value for non-zero octants in A.	Dean (1987) [†]	ArcGIS 10.0	Yes
Easting	A.EAS	—	Sine of terrain orientation.	rad	$\sin(\alpha)$	Moore, Harvey & Van Niel (2010)	ArcGIS 10.0	Yes
Standard deviation of easting	A.ESD	—	Dispersion of easting values about the mean.	m	$\sigma_{\sin \alpha} = \sqrt{\frac{1}{n-1} \sum_{i=1}^n (\sin \alpha_i - \mu_{\sin \alpha})^2}$	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Northing	A.NOR	—	Cosine of terrain orientation.	rad	$\cos(\alpha)$	Moore <i>et al.</i> (2010)	ArcGIS 10.0	Yes
Standard deviation of northing	A.NSD	—	Dispersion of northing values about the mean.	m	$\sigma_{\cos \alpha} = \sqrt{\frac{1}{n-1} \sum_{i=1}^n (\cos \alpha_i - \mu_{\cos \alpha})^2}$	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes

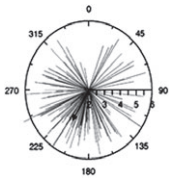


Table 1. Continued


Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Curvature								
	Profile	—	Concavity or convexity of a terrain surface Curvature along the line of maximum slope, where the surface is intersected with the plane formed by the aspect and the z-axis. Also defined as the rate of change of gradient. Determines whether particles accelerate or decelerate when flowing over a terrain. Negative values indicate convex terrain; positive values denote concave terrain.	rad m ⁻¹	$-\frac{p^2 r + 2pq s + q^2 t}{(p^2 + q^2) \times (\sqrt{1 + p^2 + q^2})^3}$ <p>where p, q, r, t and s are partial derivatives of elevation and $p = \frac{\partial z}{\partial x}$ (east–west gradient); $q = \frac{\partial z}{\partial y}$ (north–south); $r = \frac{\partial^2 z}{\partial x^2}$ (change of slope in the x direction); $t = \frac{\partial^2 z}{\partial y^2}$ (change of slope in the y direction); $s = \frac{\partial^2 z}{\partial x \partial y}$ (change of slope along the diagonal).</p>	Schmidt, Evans & Brinkmann (2003)	DEM Surface Tools	Yes
	Plan (or planform)	—	Curvature along the line of intersection between the surface and the xy plane. Indicates whether particles converge or diverge when flowing over a terrain.	rad m ⁻¹	$\frac{q^2 r - 2pq s + p^2 t}{(\sqrt{p^2 + q^2})^3}$	Schmidt <i>et al.</i> (2003)	DEM Surface Tools	No
	Tangential	—	Curvature along the line orthogonal to the line of steepest gradient. Indicates whether particles converge or diverge when flowing over a terrain.	rad m ⁻¹	$-\frac{q^2 r - 2pq s + p^2 t}{(p^2 + q^2) \times \sqrt{1 + p^2 + q^2}}$	Schmidt <i>et al.</i> (2003)	DEM Surface Tools	Yes
	Longitudinal	—	Conceptually similar to profile curvature. Indicates whether particles accelerate or decelerate when flowing over a terrain. Undefined when the slope is exactly 0 (when the east–west and north–south gradients p and $q = 0$).	rad m ⁻¹	$-2 \left(\frac{p^2 r + pq s + q^2 t}{p^2 + q^2} \right)$	Moore <i>et al.</i> (2010) and Schmidt <i>et al.</i> (2003)	DEM Surface Tools	Yes
	Cross-sectional	—	Conceptually similar to tangential curvature. Indicates whether particles converge or diverge when flowing over a terrain. Negative values indicate concave curvature where stream flows converge. Undefined when the slope is exactly 0 (when the east–west and north–south gradients p and $q = 0$).	rad m ⁻¹	$2 \left(\frac{q^2 r - pq s + p^2 t}{p^2 + q^2} \right)$	Moore <i>et al.</i> (2010) and Schmidt <i>et al.</i> (2003)	DEM Surface Tools	Yes

Table 1. Continued

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Total	C.TOT	—	General measure of the curvature of a surface itself, rather than the curvature of some line across it. Always positive although a value of 0 simply means that the surface is a plane, not necessarily that it is horizontal.	rad m ⁻¹	$r^2 + 2s^2 + t^2$	Schmidt <i>et al.</i> (2003)	DEM Surface Tools	Yes
General	C.GEN	—	General measure of the convexity of landscapes, where sinks/valleys are considered concave (<0) and peaks are considered convex (>0). Near-zero values represent either flat areas or areas where the convexity in one direction is balanced by the concavity in the perpendicular direction, such as on a saddle.	rad m ⁻¹	$-2(r+t)$	Olivier & Wotherspoon (2008) [†] and Moore <i>et al.</i> (1993)	DEM Surface Tools	Yes
Relief			Elevations and depressions of the earth's surface, including those of the ocean floor					
Micro-ruggedness index	R.MIR	—	Number of 10 m contour lines crossed by two N–S and E–W transects of 200 m.	d.u.	—	Sergio, Marchesi & Pedrini (2004) [†]	—	No
Macro-ruggedness index	R.MAR	—	Number of 10 m contour lines crossed by two N–S and E–W transects of 1.4 km.	d.u.	—	Sergio <i>et al.</i> (2005) [†]	—	No
Topographic complexity	R.TCO	—	Index of surface ruggedness derived by multiplying scaled values for slope and aspect curvature. High values denote steep and irregular terrain.	d.u.	—	Carroll, Noss & Paquet (2001) [†]	ArcGIS 10.0	Yes
Topographic irregularity index 10–20–50–100 m	R.TIN R.TIN10 R.TIN20 R.TIN50 R.TIN100	TOPIND	Number of 20 m contour lines cut by two lines equivalent to 2 km and designed on 1:50000 topographic maps in the directions N–S and E–W and crossed at the location of the sampling site.	d.u.	—	Ontiveros (1999) [†]	ArcGIS 10.0	Yes
			<i>or</i> Number of 20 m contour lines cut by two lines diametric to the sampling circle in the directions N–S and E–W.	d.u.	—	González, Bustamante & Hiraldo (1992) [†]	ArcGIS 10.0	—
			<i>or</i> Number of 20 m contour lines cut by four 1 km lines starting from the focal site in N, S, E, W directions.	d.u.	—	Donazar, Hiraldo & Bustamante (1993) [†]	ArcGIS 10.0	—
			<i>or</i> Number of 100 m contour lines cut by four lines starting from the centre of the focal area in N, S, E, W directions.	d.u.	—	Martínez <i>et al.</i> (2003) [†]	ArcGIS 10.0	—



Table 1. Continued

Geomorphic*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Topographic roughness	R.TRO	—	Number of depth categories along a 6 m-long string suspended parallel to the ground, where 'depth' is measured as the distance from the string to the lowest possible point on the substrate surface. Index measured in 1 m (coarse) or 10 cm (fine) intervals.	d.u.	—	Matheson & Larson (1998) [†]	—	No
Topographic ruggedness [P] 10–20–50–100 m	R.TRU <i>R.TRU10</i> <i>R.TRU20</i> <i>R.TRU50</i> <i>R.TRU100</i>	—	Length of contour lines contained within each quarter section of a 7.5 min map.	m	—	Warrick & Cypher (1998) [†]	ArcGIS 10.0	Yes
Land surface ruggedness index 10–20–50–100 m	R.LSR <i>R.LSR10</i> <i>R.LSR20</i> <i>R.LSR50</i> <i>R.LSR100</i>	LSRI	Number of dot-contour line intersections when overlaying a grid of 96 uniformly spaced dots in a circle representing an area of 40 ha on a 7.5 min map and oriented with rows of dots parallel to the cardinal compass axes.	d.u.	—	Beasom, Wiggers & Giardino (1983)	ArcGIS 10.0	Yes
Cirque denning	R.CDN	—	Index of occurrence of north-facing cirques suitable for predator denning.	d.u.	—	Carroll <i>et al.</i> (2001) [†]	—	No
Texture 3 × 3, 5 × 5, 7 × 7 neighbourhoods	R.TEX <i>R.TEX33</i> <i>R.TEX55</i> <i>R.TEX77</i>	—	Digital number (DN) obtained by applying a Laplacian (edge enhancement) kernel filter on a matrix of location pixels. A typical kernel is placed over a 3 × 3 array of original pixels and each is multiplied by the corresponding value in the kernel. The nine resulting values are summed and added to the DN of the central pixel.	m	—	Kobler & Adamic (2000) [†]	IDRISI Selva 17.0 FILTER module	Yes
Depth			Distance from water surface					
Mean	D.AVG	μ_z	Average depth.	m	$\mu_z = \sum_{i=1}^n \frac{z_i}{n}$	Macleod <i>et al.</i> (2004) [†]	ArcGIS 10.0	Yes
Median	D.MED	\tilde{z}	Median depth.	m	—	Yen, Sydeman & Hyrenbach (2004) [†]	ArcGIS 10.0	Yes
Standard deviation	D.STD	σ_z	Dispersion of depth values about the mean.	m	$\sigma_z = \sqrt{\frac{1}{n-1} \sum_{i=1}^n (z_i - \mu_z)^2}$	Nur <i>et al.</i> (2011) [†]	ArcGIS 10.0	Yes

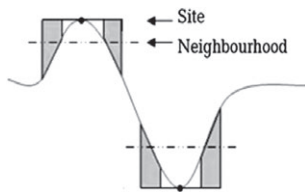
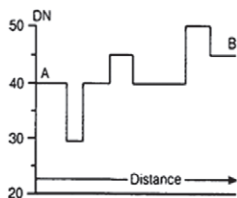


Table 1. Continued

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Coefficient of variation	D.COV	CV_z	Normalised measure of dispersion of depth values.	d.u.	$CV_z = \frac{\sigma_z}{\mu_z}$	Yen <i>et al.</i> (2005) [†]	ArcGIS 10.0	Yes
Minimum	D.MIN	z_{\min}	Smallest depth.	m	—	Laidre <i>et al.</i> (2004) [†]	ArcGIS 10.0	Yes
Maximum	D.MAX	z_{\max}	Largest depth.	m	—	Scott <i>et al.</i> (2010) [†]	ArcGIS 10.0	Yes
Range	D.RGE	$[z_{\min}, z_{\max}]$	Difference between largest and smallest depths.	m	$z_{\max} - z_{\min}$	Bouchet <i>et al.</i> (present paper)	ArcGIS 10.0	Yes
Domains	D.DOM	$[z_1, z_2]; [z_3, z_4]$	Arbitrarily defined intervals.	m	—	Haney <i>et al.</i> (1995) [†]	—	No
Contour index	D.CIN	CI	Combined measure of both change in depth and maximum depth at a site. Indicates the per cent change in depth in a sample area. Ranges from 0 to 100, with higher values reflecting steeper bathymetry.	d.u.	$CI = 100 \times \frac{z_{\max} - z_{\min}}{z_{\max}}$	Hui (1979) [†]	ArcGIS 10.0	Yes
Bathymetric position index [P]	D.BBPI D.FBPI	BPI	Scale-dependent index representing a site's position within the seascape relative to its local surrounding. It is a modification of the TPI/HI in use in terrestrial environments (see above), and is derived via a focal function which compares each cell's depth to the mean depth of the surrounding cells within a user-defined rectangle, annulus (donut shape) or circle. Positive values denote crests and high points or terrain features; zero values correspond to flat terrains or constant slopes; negative values represent depressions and low points or terrain features. Can be calculated on broad (BBPI) or fine (FBPI) scales.	d.u.	See TPI	Lander <i>et al.</i> (2011) [†]	NOAA Benthic Terrain Modeller (BTM) 3.0	Yes
Other								
Fractal dimension $9 \times 9, 25 \times 25$ neighbourhoods	O.FRD	D, Fd	Statistical index of the geometric irregularity of isotropic surfaces. Can take any value between 2 (flat plane) and 3 (infinitely crumpled surface which goes through every point within a volume).	d.u.	$D = 3 - H$ where H is a landscape-dependent parameter indicative of relief complexity and derived from a fractional Brownian motion model $z(x, y)$ defined by $E[z(x + \Delta_x, y + \Delta_y) - z(x, y)] = \sigma \sqrt{\frac{2}{\pi} \sqrt{\Delta_x^2 + \Delta_y^2}^H}$	Pittman, Costa & Battista (2009)	FocalID script in LandSerf 2.2	Yes



Table 1. Continued

Geomorphometric*	Code	Notation	Definition	Unit	Formula	Source	Software	Included in simulation
Rugosity (surface-area ratio)	O.RUG	r, SAR	Ratio of true surface area to planimetric area (scaled to minimum value of 0).	d.u.	$\frac{\sum_{i=1}^n \sqrt{s_i (s_i - a_i) (s_i - b_i) (s_i - c_i)}}{\text{Total planar area}}$ <p>where i represents three-dimensional triangles radiating out of the focal cell of a triangulated irregular network (TIN) surface draped over the raster of elevations and $s = \frac{a+b+c}{2}$ with a, b, and c the edges of each triangle.</p>	Connell & Kingsford (1998) [†] , Moore <i>et al.</i> (2010) and Jenness (2004)	DEM Surface Tools for ArcGIS 10.0	Yes
Volume [P]	O.VOL	V	Three-dimensional space under the surface to the minimum elevation or maximum depth value.	m ³	—	Walker, Jordan & Spieler (2009) [†]	ArcGIS 10.0	Yes
Vector ruggedness measure [P] <i>8 × 8 neighbourhood</i>	O.VRM	VRM	Multivariate representation of topography which incorporates variability in both the aspect and the gradient components of slope. Derived from the three-dimensional dispersion of vectors orthogonal to planar facets on a landscape. The magnitude of the resultant vector in standardized form (vector strength divided by the number of cells in the neighbourhood) is a measure of the ruggedness of the landscape for the selected scale.	d.u.	$VRM = \frac{1}{\sqrt{\left(\frac{\sum x}{n}\right)^2 + \left(\frac{\sum y}{n}\right)^2 + \left(\frac{\sum z}{n}\right)^2}}$ <p>where n is the number of cell in the neighbourhood; $z = \cos(\theta)$; $x = xy \times \sin(\alpha)$; $xy = \sin(\alpha)$; and $y = xy \times \cos(\alpha)$</p>	Sappington <i>et al.</i> (2007)	NOAA Benthic Terrain Modeller (BTM) 3.0	Yes

ArcGIS 10.0: combination of ArcGIS 10.0 + Spatial Analyst and 3D analyst extensions where appropriate + Python 2.7.

Benthic Terrain Modeler - Wright *et al.* (2012); DEM Surface Tools - Jenness (2013); IDRISI Selva 17.0 - Eastman (2012); Land Facet Corridor Tools - Jenness, Brost & Beier (2011); LandSerf 2.2 - Wood (2005).

[P], Projected - GDA94 Lambert conformal conic projection, central meridian at 115°E.

d.u., dimensionless unit.

*Metric-specific parameters shown in *italics*.

[†]Papers included in quantitative analysis of the literature (satisfied search criteria).

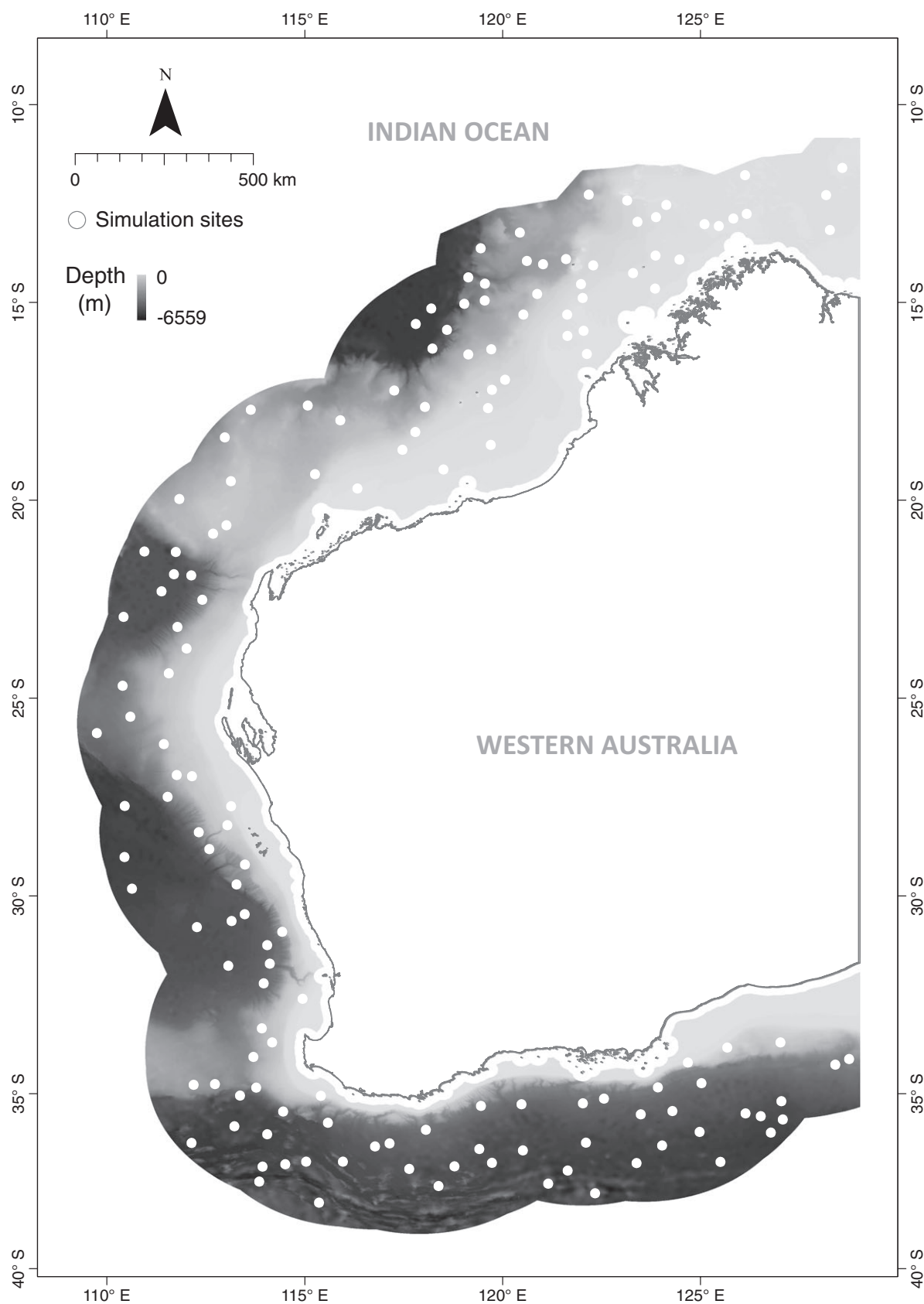


Fig. 1. Location of simulation sites within the west Australian exclusive economic zone (EEZ, $N = 150$).

human population growth; (v) developing new methods of predicting and mapping marine biodiversity using a biological interpretation of physical surrogates has been identified as a research priority by Australia's Marine Biodiversity Hub (<http://www.nerpmarine.edu.au/>) (Butler *et al.*, 2010); and (vi) lastly, because high-quality, 9 arc-second (0.0025° or approximately 250 m at the equator) depth data from a digital bathymetric grid of Australian waters (<http://www.ga.gov.au/meta/ANZCW0703013116.html>) were readily available (Whiteway, 2009). All sampling sites were square-shaped and equal in size ($25 \times 25 \text{ km}^2$, i.e. 625 km^2) so that each would encompass an identical sub-area on the surface of the Earth and contain a comparable amount of topographic information for simulation purposes. The values of each geomorphometric variable were calculated at each site based on a WGS84 geographic coordinate system or a modified GDA94 Lambert conformal conic projection (with central meridian at 115°E) where required. Data were projected using a standard nearest-neighbour resampling algorithm in ArcGIS, and projected metrics are labelled in Table 1. While some areal-based metrics (e.g. mean depth) are naturally estimated over entire landscape patches, many other 'focal' geomorphometrics (i.e. computed within a specified neighbourhood of a focal point) are calculated on a per cell basis (e.g. topographic position index, E.TPI), and it was necessary to average them to obtain comparable estimates for a given site. In order to avoid edge effects, the values of these variables were first computed on the entire EEZ and then evaluated at each site by clipping the resultant GIS layer according to the sites' boundaries. We chose not to model all elevation metrics as some essentially carried the same information (with opposite signs) as depth metrics (Table 1). Mean slopes were expressed in degree units and mean aspects were computed as circular means (*not* arithmetic means) in keeping with the requirements of directional statistics (Mardia & Jupp, 2000). All raster manipulations and computations were completed using custom-built Python 2.7 and MATLAB 2012a scripts, and raw bathymetry data were processed using ArcGIS's Spatial Analyst and 3D Analyst extensions as well as specialised geostatistical software (Wood, 2005; Jenness *et al.*, 2011; Eastman, 2012; Wright *et al.*, 2012; Jenness, 2013).

To explore redundancy among variables and prune the initial data matrix into a subset that best explained topographic complexity across the west Australian seafloor, we first calculated all pairwise Spearman rank correlation coefficients among variables according to the following equation:

$$r_s = 1 - \frac{6 \sum_{i=1}^n d_i^2}{n(n^2 - 1)}$$

where d_i denotes the differences between the ranks of each data pair (Kendall & Gibbons, 1990).

We then discarded one of the two variables in each pair where correlations were larger than $r_s = -0.9$ (avoiding effective multi-collinearity). Selection was a function of

each metric's conceptual and mathematical simplicity, commonness in the literature, or implementation in computer software, and was validated with the *caret* R package (Kuhn *et al.*, 2013), which removes variables with the largest mean absolute correlation within pairs. We tested for the presence of any further statistically significant correlations within both samples and variables by using programme PRIMER v6 (<http://www.primer-e.com>) (Clarke & Gorley, 2006) to respectively conduct Type 1 (Q-mode) and Type 2 (r-mode) similarity profile (SIMPROF) analyses on the remaining data, which were rank-transformed to satisfy linearity and symmetry assumptions. Clarke, Somerfield & Gorley (2008) and Somerfield & Clarke (2013) give exhaustive descriptions of the methods. Conditional on successfully detecting multivariate structure, we looked to answer two related but conceptually distinct questions: (i) which metrics vary coherently across samples and are therefore associated? (ii) Which metrics best explain sample patterns overall?

The first question was addressed *via* hierarchical agglomerative classification (using the CLUSTER routine inside PRIMER v6) and non-metric multidimensional scaling (MDS). The former technique investigates variable kinship by striving to find 'natural' groupings of items such that within-group similarities are maximised (Clarke, 1993), while the latter constructs a 'map' of the items in a low-dimensional space where elements close together are more alike than elements farther apart. Clarke & Warwick (2001, pp. 5–7) advocate combining ordination and clustering techniques as a means of 'checking the adequacy and mutual consistency of both representations'. The clustering was completed with a group average link [the most adequate method, according to Field, Clarke & Warwick (1982)], and Type 3 SIMPROF tests (Somerfield & Clarke, 2013) were carried out iteratively at each node of the clustering tree to validate the null hypothesis of no group divisions (mean profile derived from 1000 permutations, at a significance level of $\alpha = 0.05$).

There are two drawbacks to this approach. Firstly, any variables with strong negative correlations will be regarded as 'different' and assigned to separate groups, even though they may in fact be closely linked, as would happen if they were simply measured in opposite ways. To overcome this issue, chosen metrics were reversed (Somerfield & Clarke, 2013) by taking their ranks away from the total number of sites +1 such that correlation values in the associated Spearman rank resemblance matrix would never be less than $r_s = -0.5$. Secondly, the default permutation procedure implemented in the current release of software PRIMER does not support Type 3 SIMPROF tests, and will return spurious manipulations of the data (Somerfield & Clarke, 2013). To obtain the correct permutations, one should be cautious to temporarily 'switch' the definition of 'samples' and 'variables' prior to running the analyses.

The second question was examined *via* a Biota-Environment + Stepwise (BEST) analysis, which is designed to extract a parsimonious (minimal) subset of variables that best summarise the patterns present in the whole set

(and thus do not reject more than a negligible amount of sample information) (Clarke & Ainsworth, 1993; Clarke & Warwick, 1998). To assess performance, we used a twofold cross-validation technique where the data were split into equal-sized training (50%) and test (50%) sets, and two partitioning schemes were trialled: in the first, every second site along a latitudinal gradient running north to south was selected (systematic sampling, starting at the northernmost location), and in the second, sites were selected completely at random (random sampling). BEST metrics were identified from the training dataset and validated against the test dataset *via* a RELATE test, a non-parametric permutational form of the Mantel test. Exploring all possible combinations of metrics was unrealistic for computational reasons (as 50 variables, say, would yield 2^{50} solutions). We thus relied on the BVSTEP algorithm (Valesini *et al.*, 2003; Bremner, Rogers & Frid, 2006), which performs an incremental forward-stepping/backward-eliminating search for the best variable subset, i.e. the one whose resemblance matrix (of Euclidean distances based on normalised data, in this case) shows maximum agreement with that of the full set, as measured by the Spearman rank correlation coefficient. A natural consequence of stepwise selection is that only a small fraction of the total number of possible metric combinations is ultimately considered. We bypassed this issue by repeating the search from a different start position (i.e. a random combination of x start variables, formally called a 'restart').

The following parameters were used: (i) stop criteria of $\rho > 0.9$ and $\Delta\rho < 0.001$, meaning that the stepwise selection would terminate in one of three cases: when a similarity value greater than 0.9 (based on the chosen matching coefficient ρ – here, the Spearman rank) was achieved upon adding a new variable to the current set, *or* when dropping any variable would reduce that value to less than 0.9, *or* when no improvements in similarity greater than 0.001 could be made with the removal or addition of variables (model convergence); (ii) number of random restarts from 0 (null model empty of variables) to 6 in increments of 2; (iii) $n = 999$ permutations for the global BEST test [which evaluates the significance of the optimum ρ value while correcting for selection bias, see Clarke & Gorley (2006) for details].

Lastly, the BIOENV routine is a closely related algorithm to BVSTEP which performs an exhaustive comparison of all variable combinations based on a specified number of input items. We used it to determine the best sets of 1–4 metrics (for reasons outlined in Section III.2c).

Note that when working with biotic data, some species may only show weak links with the rest of their assemblage (and will therefore be retained by SIMPROF, or even assigned their own cluster), yet will still exert little impact on the overall sample patterns, because they may have low abundance or simply are largely absent (and will as such be dispensed by BEST). This type of disagreement cannot happen with equally weighted normalised environmental covariates (K. R. Clarke, personal communication), so we saw CLUSTER/MDS as a useful way of validating the output from BEST.

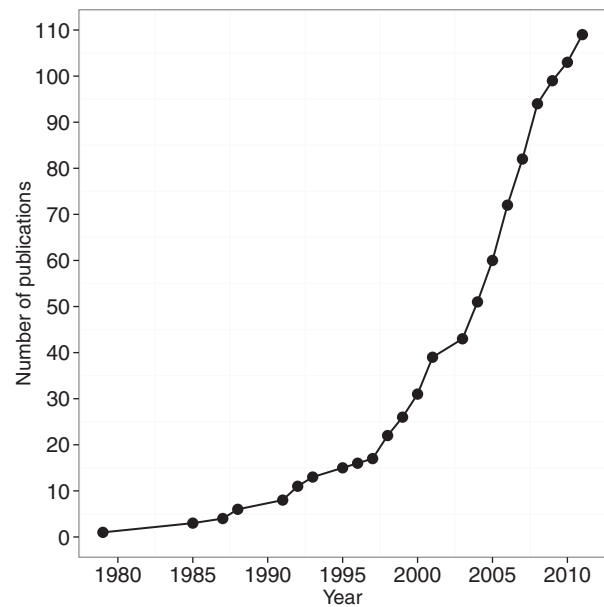


Fig. 2. Cumulative temporal distribution of the research articles surveyed ($N = 109$). See Section II for details on selection and filtering protocols.

III. RESULTS

(1) Topographic drivers of predator hotspots

Prior to the mid-1980s, technological limitations precluded the quantitative depiction of topographic complexity almost entirely, and virtually no geomorphometric variables were included as explanatory terms in predator models (Fig. 2). Following exponential improvements in computer power and algorithm sophistication (Petrovskii & Petrovskaya, 2012), wildlife–topography associations received increasing interest, with in excess of 10 research papers being published annually by the late 2000s. Based on this growing body of knowledge, and even though mechanistic drivers can be contrasting and sometimes not fully understood, our survey of the literature suggests that four major types of landscape-mediated predator aggregation pathways are at play in marine and terrestrial systems: foraging, migration/dispersal, breeding, and roosting/resting.

(a) Foraging

Topographically complex landscapes centralise resources and many have been described as key feeding grounds for mobile species, including spotted owls (*Strix occidentalis*; Irwin *et al.*, 2007), golden eagles (*Aquila chrysaetos*; Sergio *et al.*, 2006b), short-tailed albatrosses (*Phoebastria albatrus*; Piatt *et al.*, 2006), and pygmy blue whales (*Balaenoptera musculus breviceauda*; Rennie *et al.*, 2009).

The majority of topography-induced trophic subsidies to predators arise from physical–biological coupling. For example, on land, in addition to defining strong climatic gradients by interacting with wind and atmospheric

circulation patterns (Ruggiero & Hawkins, 2008), complex terrains modulate incoming solar radiation, nutrient inputs, water drainage and soil hydrology, ultimately controlling the phenology and spatial organisation of the vegetative cover (Ivanov, Bras & Vivoni, 2008; Moeslund *et al.*, 2013). In doing so, they create a mosaic of unique micro-niches which favour the fragmentation and diversification of prey populations, effectively building ladders of which mobile predators can take advantage. Similarly, in the ocean, isolated seabed features like guyots, canyons, headlands, or shelf breaks frequently alter currents and contribute to localised boosts of net productivity through vertical mixing, a process referred to as 'bathymetric steering' (Ladd, Stabeno & Cokelet, 2005b). In some cases, the resultant turbulence fuels the formation of episodic upwelling cells which promote the injection of near-bottom inorganic matter into the photic zone and thereby stimulate the growth of primary producers in surface layers (Genin, 2004). By percolating up the trophic ladder, this fertilisation effect (the magnitude of which can be substantial, i.e. as much as 10^3 times greater than in offshore waters; Carter & Gregg, 2002) attracts herbivorous zooplankton, and encourages visits by an array of mobile predators (Morato *et al.*, 2008).

Albeit well documented in some regions (e.g. Gill, 2002; Croll *et al.*, 2005), empirical evidence of persistent nutrient enrichment remains limited to a few cases (Mendonça *et al.*, 2012). This is especially apparent around many of the world's charted seamounts, which are often situated in characteristically oligotrophic areas away from continental influences and exhibit pronounced spatial and temporal variations in productivity (White *et al.*, 2007). Because these sites still display considerable levels of biomass (Morato *et al.*, 2010), the import and retention of allochthonous material by 'topographic trapping' has been postulated as an additional driver of predator feeding hotspots (Dower & Brodeur, 2004). For example, narrow seabed channels can act as physical bottlenecks for migrating fish (Wilson, Thompson & Hammond, 1997) and strong haloclines in the vicinity of seafloor structures are believed to disorient travelling Pacific salmon (*Oncorhynchus* spp.) and force them to cluster temporarily (Quinn & teHart, 1987; Hastie, Wilson & Thompson, 2003). Further evidence exists that the recurrent formation of eddies, vortices or Taylor caps around oceanic seamounts may advect negatively phototactic plankton over the features' summits during the night time, blocking the animals' pre-dawn descent to depth (Wolanski & Hamner, 1988; Lavoie, Simard & Saucier, 2000; Genin, 2004). Irrespective of the underlying mechanism, trapping regimes can result in the accumulation of zooplankton and zooplanktivores in well-lit epi- and mesopelagic depths, where they become readily accessible to both resident and transient predators. In some locations, the potential of this 'trophic focusing' pathway (*sensu* Genin, 2004) to aggregate predators has been estimated to exceed that of primary production by several orders of magnitude (Genin & Dower, 2007).

In addition, foraging theory predicts that hunting success is a direct function of terrain characteristics (Andersson,

Wallander & Isaksson, 2009), and that complex landscapes also facilitate prey capture by offering predators stalking cover (Chundawat, 1990; Sweanor, Logan & Hornocker, 2000), enabling concealed approaches (Dickson *et al.*, 2013), slowing down the escape of fleeing individuals, or providing physical barriers against which to corral prey. These properties have been verified in a variety of felids, including cougars (*Puma concolor*; Pike *et al.*, 1999) and African lions (*Panthera leo*; Funston, Mills & Biggs, 2001), as well as in some marine mammals such as killer whales (*Orcinus orca*; Heimlich-Boran, 1988).

However, relatively little research has looked at the direct influence of topography on species' energy expenditures during foraging, and to our knowledge, most examples of this come from the ornithological and fish literature. In raptors such as the golden eagle (*Aquila chrysaetos*), the selection of perched cliff platforms and sites of complex terrain allows animals to initiate chases from hidden positions at height (Sergio *et al.*, 2006b). It has also been suggested that uneven heating of complex ground by the sun favours the development of thermal draughts which may assist hunting by creating good soaring conditions and reducing the metabolic costs associated with high-altitude flight (Newton, 2007).

Analogously, Genin & Dower (2007) proposed the 'feed-rest' hypothesis to describe how some seamount-associated benthopelagic fish like the orange roughy (*Hoplostethus atlanticus*) or the pelagic armourhead (*Pseudopentaceros richardsoni*) may be able to save energy by alternating between non-foraging intervals spent motionless in quiescent shelters defined by the rough surface of the seafloor, and short, sporadic phases of active swimming in topography-induced currents, where their exposure to food-replete waters is renewed.

Michaelsen, Jensen & Høgstvedt (2011) also provide an interesting example of how soprano pipistrelles (*Pipistrellus pygmaeus*) select against open flat landscapes. As nocturnal hunters, these bats rely on celestial cues to time their foraging efforts, departing from communal roosts as soon as light levels drop. By colonising steep mountain slopes where the sun becomes shaded before astronomical sunset and remains so after sunrise, the animals are able to emerge early and extend their feeding time window by up to 2 h, thereby gaining access to a potentially wider prey field and maximising energy gains.

(b) Migration and dispersal

Our understanding of the movement behaviour of predators has long remained obscure, due in part to technical constraints. However, the relatively recent development of radio-telemetry and GPS tracking tools has revolutionised the field of bio-logging (Block, 2005), allowing wildlife trajectories to become spatially resolved and shedding new light onto the broad-scale dispersal patterns of diverse marine and terrestrial taxa (Jonker & Bester, 1998).

Numerous mobile species are now known to follow predictable pathways defined by clear topographic signatures

and to utilise terrain features as potential navigational waypoints when crossing vast expanses of open ground (McCarthy, Fuller & Munkhtsog, 2005; Holland & Grubbs, 2007). For instance, soaring birds like hawks, buzzards, ospreys or eagles appear to use ridges and summits as both guiding lines to compensate for wind drift and as a means of expediting movement by gaining lift from updrafts created where crosswinds are deflected upwards from cliffs or slopes (Mueller & Berger, 1967; Titus & Mosher, 1982; Newton, 2007; Goodrich & Smith, 2008). Recently, Brandes & Ombalski (2004) developed mathematical models of golden eagle (*Aquila chrysaetos*) spring migration based on an analogy with fluid flow dynamics. Their results showed a clear effect of mountain ridges in delineating the animals' movement pathways, with flight trajectories commonly adjoining these features for up to 100 km. Likewise, connectivity between sub-populations of pumas (*Puma concolor*) in the south-western United States appears to be maintained by a network of terrain structures (e.g. mountain ranges) that young individuals travel along as they disperse to new high-quality habitats (Dickson *et al.*, 2013).

Although long-distance visual perception may assist some species in adjusting their course, exactly how unaccomplished juvenile migrants acquire knowledge of remote physical targets outside their sensory detection range remains enigmatic (Hays, 2008). Assuming that naive individuals do not possess an inherited map of landscape topography, it has been hypothesised that infrasound sensing and magnetic field perception may aid navigation. The use of infrasonic signals radiating from steep-sided topographic features has for example been put forward in falcons and other land birds (Gschweng *et al.*, 2008). Similarly, some seamounts are known to present unique acoustic, magnetic, thermal and olfactory footprints which could act as signposts for the ocean-basin-wide movements of many elasmobranchs, cetaceans and reptiles (Montgomery & Walker, 2001).

(c) Breeding

Even though little information exists on the use of topographic structures by predators for mating purposes, available data from investigations of bird nest selection or fish spawning habits support the idea that topographically complex landscapes can optimise the breeding performance of some species. This strategy is partly based on the premise that successful reproduction is a corollary of successful resource acquisition. Insofar as an organism's foraging efficiency is a critical determinant of its condition (Pinaud & Weimerskirch, 2002), greater hunting success should lead to a faster rate of growth, a larger body mass, and an increased capacity to withstand competition for dominance and access to reproductive partners, which translates into enhanced fitness. This concept is apparent in the Pyrenean bearded vulture (*Gypaetus barbatus*), which shows strong preferences for topographically complex nesting habitats (Donazar *et al.*, 1993) where slope winds may facilitate food search and where outcrops with lower snow cover and good wind exposure will provide ossuaries where animals can store

food and easily break the bones of their prey (Margalida & Bertran, 2001). Nesting on high escarpments is also thought to minimise human disturbance during reproduction, a significant cause of breeding failure for this species (Arroyo & Razin, 2006).

In common puffins (*Fratercula arctica*), slope is also strongly correlated with measures of nest density, with flat grounds being associated with a more pronounced exposure of eggs to predation and a reduced probability of escape from gull (*Larus* spp.) aggression (Nettleship, 1972). Access to shelters and hard substrate for both the protection of young and the attachment of eggs appears equally essential to a number of oviparous deep-sea fish such as the blob sculpin (*Psychrolutes phrictus*), which have been reported to clump over the 'steepest topography and [...] roughest terrain' likely as a result of the increased availability of rocky seabed for both their offspring and their bivalve prey (Drazen *et al.*, 2003, pp. 1–2).

Responses to topographic complexity can also be sex dependent. In the grey seal (*Halichoerus grypus*) for example, pup provisioning and attendance by mothers may be diminished where within-site movements and access to water pools are restricted by broken ground, and females of this species have been shown to engage in more energetically costly behaviours at the expense of interactions with their newborns in some complex areas (Twiss *et al.*, 2000). By contrast, bulls may favour haul-outs where receptive females are spatially aggregated by terrain complexity, as this likely promotes mate monopolisation and guarding, territorial defence and the maintenance of harem hierarchy (Anderson & Harwood, 1985; Twiss & Thomas, 1999). That said, the true extent of behavioural polygyny in pinnipeds and the effects of topography on the likelihood of male copulation are subject to controversy (Baldi *et al.*, 1996; Ambs *et al.*, 1999).

(d) Roosting and resting

The availability of suitable roosting and resting sites can be a critically limiting factor for predator populations (Zielinski *et al.*, 2004; Lesmeister, Gompfer & Millspaugh, 2008). Even though studies examining the effects of terrain attributes on roost selection are still admittedly rare (Perry, Thill & Leslie, 2008), evidence exists that topographic complexity may influence roost and nest locations in some mammals and birds, mostly by providing direct concealment or camouflaging from other predators, and/or creating microrefugia which buffer against weather extremes and help minimise thermal stress. Terrain steepness (slope) and orientation (aspect) seem to be especially influential factors in this regard, and May, Petersburg & Gutiérrez (2004) for instance reported that the likelihood of Mexican spotted owls (*Strix occidentalis lucida*) nesting in an area was a function of per cent slope, with similar observations being made in fishers (*Martes pennanti*) (Zielinski *et al.*, 2004) and northern bats (*Myotis septentrionalis*) (Lacki & Schwierjohann, 2001). Likewise, resting snow leopards (*Uncia uncia*) have been shown to prefer steep slopes associated with ridge tops and cliffs as these often constitute ideal positions with good views of the animals' territories

(Chundawat, 1990). Topographic complexity and greater crevice volume were also found to be the most consistent biophysical features distinguishing the resting positions of ornate wobbegong sharks (*Orectolobus ornatus*) (Carraro & Gladstone, 2006), although the authors point out that this may come at a cost since prey capture could prove more difficult in topographically heterogeneous environments.

(2) Landscape measures and models of predator hotspots

In spite of the role of topography in shaping the dynamics of many wildlife species, an impediment to testing theories about predator habitat selection has been the lack of robust ways of expressing, visualising and summarising continuous surface forms. Typically, ecologists have received limited exposure to appropriate geoprocessing methods, and inconsistencies in the accuracy, coverage, and accessibility of digital terrain models have further prevented them from embracing the variety of numerical metrics that are now available.

(a) Metric usage and prevalence

We identified 41 distinct geomorphometric variables within the $N = 109$ peer-reviewed journal articles published between 1979 and 2011 that satisfied our filtering criteria (Table 1). The reporting of metrics in ecological publications varied greatly both within studies (i.e. metric diversity within a single model, see Fig. 3) and across them (i.e. frequency of use of each metric within the literature pool, see Fig. 4). A strong preference for simple models was apparent, with 34% of examined articles considering one single measure of topographic complexity only, and the vast majority (94%) never relying on more than 4. All else being equal, metric diversity was consistently higher in the marine arena (Fig. 3). For example, Macleod *et al.* (2004) recorded as many as eight different geomorphometric variables in a study of minke whale (*Balaenoptera acutorostrata*) distribution off the west coast of Scotland.

The frequency distribution of metric usage was also strongly skewed towards a select few such as mean elevation (E.AVG) and mean slope (S.AVG), which ranked by far as the most applied metrics in terrestrial predator ecology ($N = 35$ and $N = 26$ respectively, out of a total of $N = 52$). These were followed by mean aspect (A.AVG, $N = 18$), elevation domains (E.DOM, $N = 5$), and topographic irregularity index (R.TIN, $N = 4$) (Fig. 4). Likewise, mean depth (D.AVG) clearly dominated marine research ($N = 45$, out of a total of $N = 57$), followed by mean slope (S.AVG, $N = 21$), depth domains (D.DOM, $N = 11$), contour index (D.CIN, $N = 9$), and maximum depth (D.MAX, $N = 7$), with mean aspect (A.AVG), standard deviation of depth (D.STD) and minimum depth (D.MIN) showing only marginal contributions. Irrespective of the conceptual similarities between some variables, very little overlap occurred across research areas, as only 5 of the 41 metrics [mean elevation (E.AVG), mean slope (S.AVG), slope domains (S.DOM),

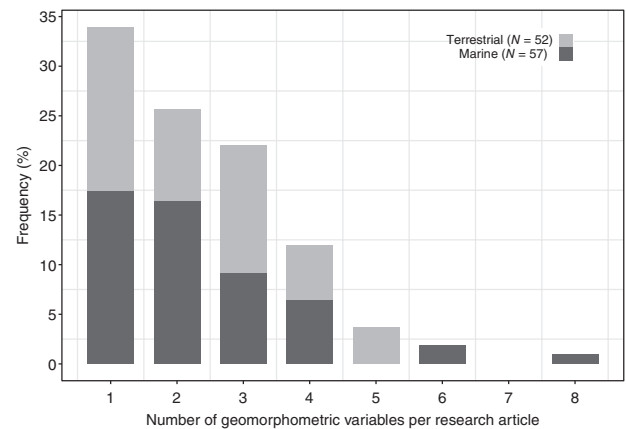


Fig. 3. Usage of geomorphometric variables in the ecological literature surveyed ($N = 109$). Values expressed as percentage of total number of articles analysed.

maximum slope (S.MAX), and mean aspect (A.AVG)] were common to both marine and terrestrial articles. This is arguably a conservative estimate as we made the distinction between measures of depth and elevation although some of them are in fact numerically equivalent (e.g. mean elevation is the mathematical opposite of mean depth).

(b) Metric redundancy

This exercise was concerned with overall metric dependence and correlation patterns, and we analysed an extra 15 complementary variables, which were either (i) derivatives of existing variables appraised on different scales, (ii) new variables drawn from monographs, reports and technical articles (or their associated supplementary materials) which were returned by the online search engines but did not pass our acceptance filters, or (iii) additional constructs which the authors deemed of relevance (Table 1). The pairwise Spearman coefficients between these 56 metrics are shown in Fig. 5. As anticipated, many variables were strongly or even perfectly correlated [e.g. depth range (D.RGE) vs. slope index(2)(S.SI2), which are purely multiples of one another], and the preliminary screening of the matrix eliminated 34 of them. Discrepancies in the scale sensitivity of multi-scale variables (Table 1) were apparent; for instance, the values of topographic ruggedness were severely correlated at multiple resolutions, whereas the bathymetric position index seemed unaffected. Interestingly, minimum (D.MIN), maximum (D.MAX), median (D.MED), and mean depth (D.AVG) were also found to be highly collinear. Due to its widespread adoption in habitat models (Fig. 4), we were inherently interested in evaluating the relevance of mean depth (D.AVG) as a predictor of topographic complexity, and we intentionally retained this metric over others in its group.

Type 2 and Type 1 SIMPROF tests revealed the presence of further internal structure within the remaining 22 variables (test statistic π : 0.152, $P < 0.001$, number of permutations: $T = 999$), as well as within samples (test statistic π : 0.093,

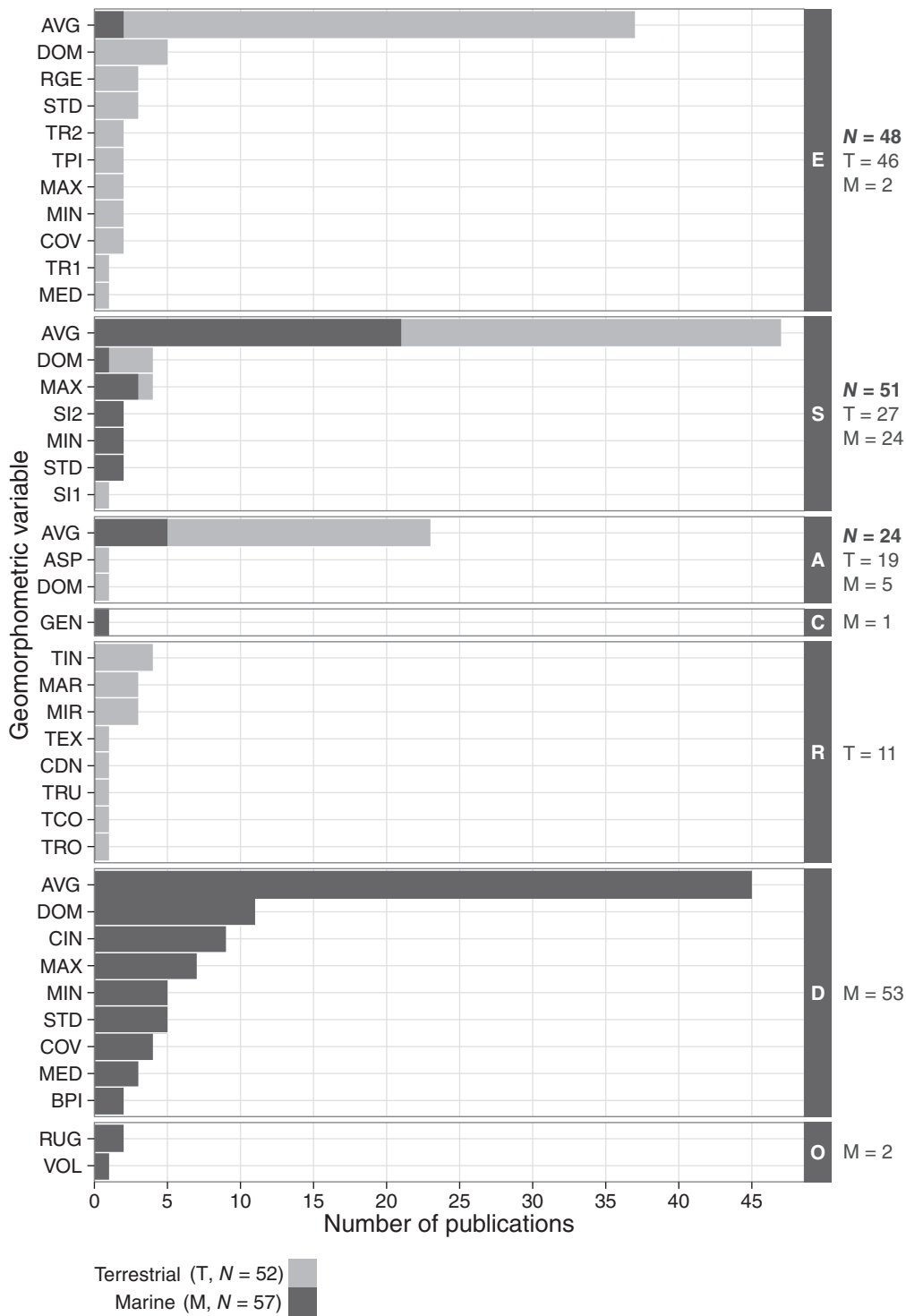


Fig. 4. Prevalence of geomorphometric variables in the ecological literature surveyed ($N = 109$; metrics not shown had a value of 0). A, aspect; C, curvature; D, depth; E, elevation; O, other; R, relief; S, slope. ASP, aspect index; AVG, mean; BPI, bathymetric position index; CDN, Cirque denning; CIN, contour index; COV, coefficient of variation; DOM, domains; GEN, general curvature; MAR, macro-ruggedness index; MAX, maximum; MED, median; MIN, minimum; MIR, micro-ruggedness index; RGE, range; RUG, rugosity; SI(1,2), slope index 1 & 2; STD, standard deviation; TCO, topographic complexity; TEX, texture; TIN, topographic irregularity index; TPI, topographic position index; TR(1,2), terrain ruggedness index 1 & 2; TRO, topographic roughness; TRU, topographic ruggedness; VOL, volume. For details see Table 1.

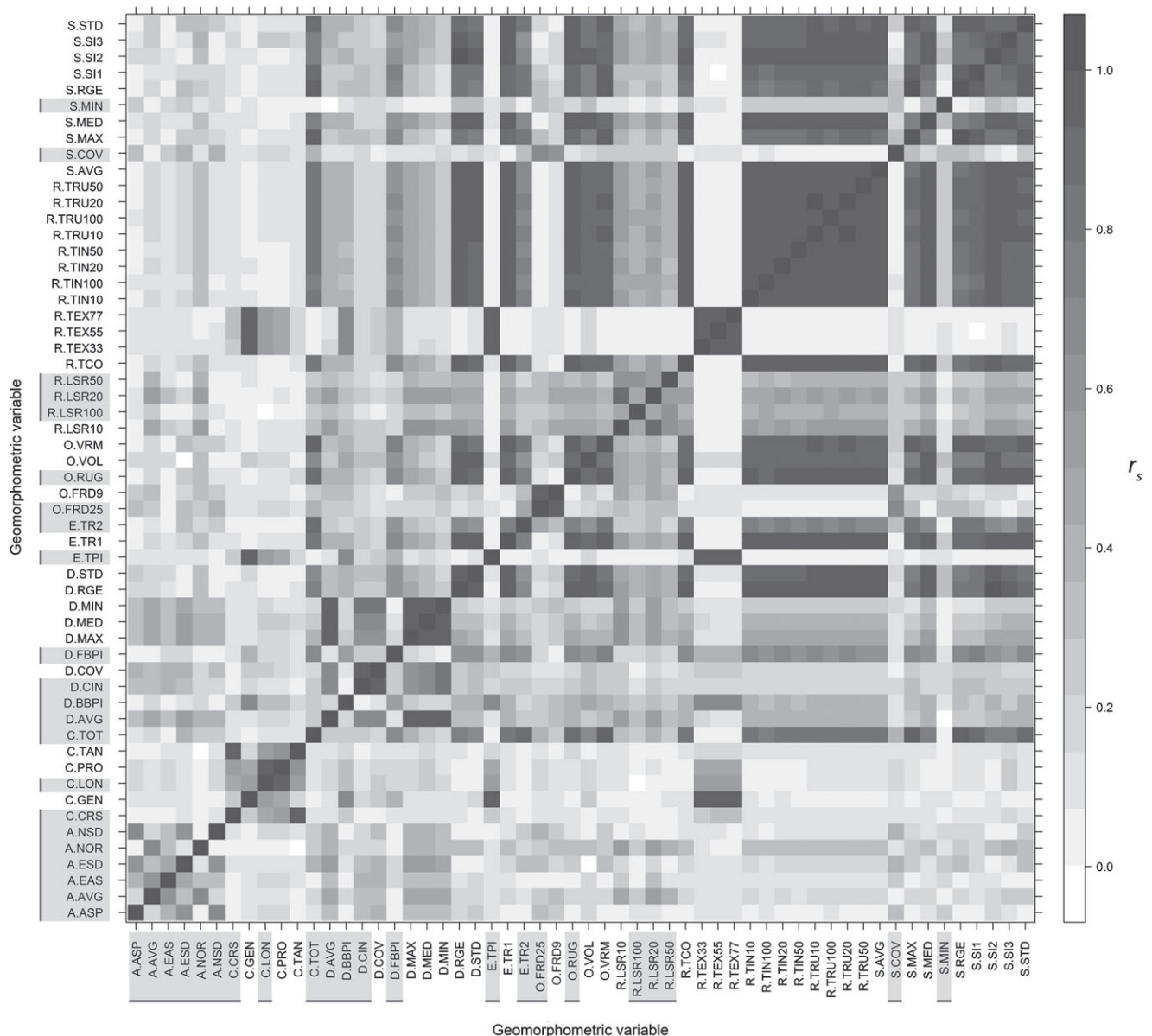


Fig. 5. Spearman rank correlation (r_s) matrix between all simulated geomorphometric variables ($N = 56$). For graphical purposes, coefficients have been converted to absolute values. Retained variables are highlighted in grey. For a full description of code names, see Table 1. A.ASP, aspect index; A.AVG, average aspect; A.EAS, average easting; A.ESD, standard deviation of easting; A.NOR, average northing; A.NSD, standard deviation of northing; C.CRS, cross-sectional curvature; C.GEN, general curvature; C.LON, longitudinal curvature; C.PRO, profile curvature; C.TAN, tangential curvature; C.TOT, total curvature; D.AVG, average depth; D.BBPI, bathymetric position index (broad scale); D.CIN, contour index; D.COV, coefficient of variation of depth; D.FBPI, bathymetric position index (fine scale); D.MAX, maximum depth; D.MED, median depth; D.MIN, minimum depth; D.RGE, depth range; D.STD, standard deviation of depth; E.TPI, topographic position index; E.TR1-2, terrain ruggedness index 1 & 2; O.FRD(9,25), fractal dimension (9 × 9, 25 × 25 neighbourhoods); O.RUG, rugosity; O.VOL, volume; O.VRM, vector ruggedness measure; R.LSR(10,20,50,100), land surface ruggedness (10, 20, 50 or 100 m contours); R.TCO, topographic complexity; R.TEX(33,55,77), texture (3 × 3, 5 × 5, 7 × 7 neighbourhoods); R.TIN(10,20,50,100), topographic irregularity index (10, 20, 50, or 100 m contours); R.TRU(10,20,50,100), topographic ruggedness (10, 20, 50, 100 m contours); S.AVG, average slope; S.COV, coefficient of variation of slope; S.MAX, maximum slope; S.MED, median slope; S.MIN, minimum slope; S.RGE, slope range; S.SI(1,2,3), slope indices 1, 2 & 3; S.STD, standard deviation of slope.

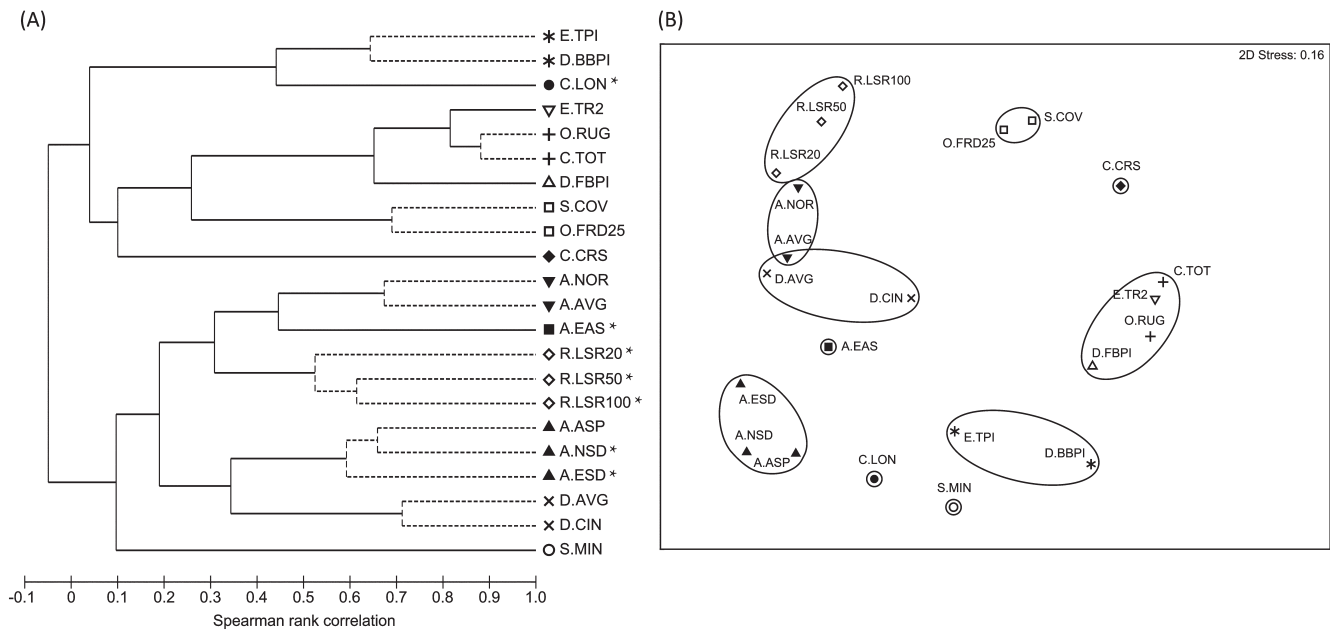


Fig. 6. (A) Dendrogram from a hierarchical, group-average linked cluster analysis of geomorphometric variables, using Spearman rank correlation similarities on rank-transformed variables ($N = 22$). Stars indicate reversed variables. Dashed lines represent groups not separated at $P < 0.05$ by Type 3 SIMPROF. Continuous lines are used where SIMPROF rejected the null hypothesis of internal group homogeneity. Individual clusters are shown using different symbols, for clarity. (B) Corresponding MDS plot. Clusters identified at an arbitrary similarity level of $r_s = 0.52$ are superimposed and shown in black. The ‘stress’ value is a measure of goodness-of-fit, and evaluates how well the two-dimensional plot reflects the structural patterns present in the multivariate data cloud. Values comprised between 0.1 and 0.2 indicate a fairly informative ordination (Clarke & Gorley, 2006). A.ASP, aspect index; A.AVG, mean aspect; A.EAS, aspect easting; A.ESD, standard deviation of easting; A.NOR, aspect northing; A.NSD, standard deviation of northing; C.CRS, cross-sectional curvature; C.LON, longitudinal curvature; C.TOT, total curvature; D.AVG, mean depth; D.BBPI, bathymetry position index (broad scale); D.CIN, contour index; D.FBPI, bathymetric position index (fine scale); E.TPI, topographic position index; E.TR2, terrain ruggedness index (2); O.FRD25, fractal dimension (25 \times 25 neighbourhood); O.RUG, rugosity; R.LSR100, land surface ruggedness index (100 m contours); R.LSR20, land surface ruggedness index (20 m contours); R.LSR50, land surface ruggedness index (50 m contours); S.COV, coefficient of variation of slope; S.MIN, minimum slope.

$P < 0.001$, number of permutations: $T = 999$), confirming that CLUSTER and BEST analyses were justified.

CLUSTER discriminated 13 groups of metrics ranging in size from 1 to 3 variables (see Fig. 6A, the dashed lines on the dendrogram representing variables that are genuinely associated, above and beyond what could have occurred by chance). Five metrics [mean aspect easting (A.EAS), minimum slope (S.MIN), longitudinal curvature (C.LON), cross-sectional curvature (C.CRS) and the fine-scale bathymetric position index (D.FBPI)] were classed as singletons, implying that they display a topographic signature not fully mirrored by the remaining variables. For minimum slope, we believe this is plausibly more an artefact of the size of our sampling sites rather than a true signal. The grouping together of several other metrics from the same category (as defined in Table 1) suggests that these variables effectively carry redundant information to some degree [e.g. land surface ruggedness based on 20 (R.LSR20), 50 (R.LSR50) and 100 m (R.LSR100) isobaths]. The agreement between the MDS ordination (Fig. 6B) and the dendrogram is also quite clear. The 11 clusters defined at a level of similarity of $r_s = 0.52$ (which is arbitrary, yet objectively corresponds

to the highest threshold beyond which *some* metrics can no longer be statistically distinguished), are indeed fairly sharp, and most would be determined in much the same way should one be tasked with drawing their boundaries by eye from the 2D plot alone. Although not optimal, the stress value (0.16) is satisfactory, confirming that metric relationships are reasonably portrayed (Clarke & Gorley, 2006).

(c) Metric relevance

Table 2 lists the best-metric combinations (of smallest size but highest rank correlation) identified by the BVSTEP algorithm for each restart configuration. Only 7–8 metrics (in all but one trial) were required to maximise the correlation between resemblance matrices, irrespective of the data-partitioning scenario. Although some discrepancies in subset composition were observed between systematic and random samples [e.g. aspect easting (A.EAS) was only extracted in the former], substantial overlap in metric identity occurred. The number of restarts had relatively little bearing on variable selection, and each RELATE test returned a highly significant P -value, meaning there

Table 2. Geomorphometric variables selected under the BEST (BVSTEP/BIOENV) matching procedure

Algorithm	Data partitioning	r	k	ρ	BEST metrics (in alphabetical order)										Relate test	
					A.AVG	C.CRS	D.AVG	D.BBPI	O.FR25	O.RUG	R.LSR50	S.MIN	R.LSR50	S.MIN	$R\rho$	P
BVSTEP	SYSTEMATIC	0	9	0.912	A.ASP	C.LON	D.CIN	O.FR25	O.RUG	R.LSR50	S.MIN	—	O.RUG	S.MIN	0.899	<0.001
BVSTEP	SYSTEMATIC	2	8	0.907	A.AVG	C.LON	D.CIN	O.FR25	O.RUG	R.LSR50	S.MIN	—	R.LSR50	S.MIN	0.887	<0.001
BVSTEP	SYSTEMATIC	4	8	0.907	A.AVG	C.LON	D.CIN	O.FR25	O.RUG	R.LSR50	S.MIN	—	R.LSR50	S.MIN	0.887	<0.001
BVSTEP	SYSTEMATIC	6	8	0.906	A.AVG	C.LON	D.AVG	O.RUG	R.LSR50	S.COV	S.MIN	—	R.LSR50	S.MIN	0.880	<0.001
BVSTEP	SYSTEMATIC	8	8	0.904	A.AVG	C.TOT	D.CIN	E.TPI	O.FR25	R.LSR50	S.MIN	—	R.LSR50	S.MIN	0.901	<0.001
BVSTEP	SYSTEMATIC	10	8	0.902	A.EAS	C.LON	D.CIN	O.RUG	R.LSR20	R.LSR50	S.MIN	—	R.LSR50	S.MIN	0.881	<0.001
BVSTEP	RANDOM	0	8	0.910	A.ESD	C.CRS	D.AVG	E.TPI	O.FR25	R.LSR50	S.MIN	—	R.LSR50	S.MIN	0.851	<0.001
BVSTEP	RANDOM	2	7	0.904	A.ASP	A.ESD	D.CIN	O.RUG	R.LSR20	R.LSR50	—	—	R.LSR50	—	0.794	<0.001
BVSTEP	RANDOM	4	7	0.904	A.ASP	A.ESD	D.CIN	O.RUG	R.LSR20	R.LSR50	—	—	R.LSR50	—	0.794	<0.001
BVSTEP	RANDOM	6	7	0.904	A.ASP	A.ESD	D.CIN	O.RUG	R.LSR20	R.LSR50	—	—	R.LSR50	—	0.794	<0.001
BVSTEP	RANDOM	8	7	0.902	A.ESD	C.LON	D.AVG	O.RUG	R.LSR50	S.COV	—	—	R.LSR50	—	0.827	<0.001
BVSTEP	RANDOM	10	7	0.904	A.ASP	A.ESD	D.CIN	O.RUG	R.LSR20	R.LSR50	—	—	R.LSR50	—	0.794	<0.001
BIOENV	—	1	—	0.432	O.FR25	—	—	—	—	—	—	—	—	—	—	—
BIOENV	—	2	—	0.586	O.RUG	R.LSR50	—	—	—	—	—	—	—	—	—	—
BIOENV	—	3	—	0.720	A.ESD	C.TOT	—	—	—	—	—	—	—	—	—	—
BIOENV	—	4	—	0.788	A.ESD	C.TOT	R.LSR50	—	—	—	—	—	—	—	—	—

r, number of start variables (BVSTEP) or number of variables (BIOENV); k, number of selected metrics; ρ , Spearman rank correlation; $R\rho$, RELATE Rho statistic (rank correlation); P , P -value obtained by permutation (level of significance).

was a good match between the sample patterns present in the subsets and those in the full set, and that our results can be deemed reliable. Overall, land surface ruggedness (based on 50 m contours) (R.LSR50), rugosity (O.RUG), longitudinal curvature (C.LON), and the contour index (D.CIN) were the most commonly selected metrics and should be considered amongst the best variables explaining topographic heterogeneity across the EEZ. Lastly, BVSTEP variable sets encompassed between 71 and 100% of the metric categories defined as per Table 1, and consistently represented in excess of 50% of the dendrogram groupings.

Since very few models have traditionally incorporated more than four variables (Fig. 3), we used BIOENV to establish which 1–4-metric combinations best explained patterns in topographic complexity (i.e. had maximum correlation with the entire data and best grouped sites in a manner consistent with the patterns observed within the whole multivariate cloud). The fractal dimension (evaluated on a 25×25 neighbourhood – O.FR25) was returned as the single variable with greatest similarity to the full dataset; rugosity (O.RUG) and land surface ruggedness (based on 50 m contours) (R.LSR50) taken together were the best pair; the standard deviation of aspect easting (A.ESD), total curvature (C.TOT) and R.LSR50 came out as the best triplet, and the best four-variable combination was identical, with the addition of the topographic position index (E.TPI).

IV. DISCUSSION

Species–topography associations have been proposed as a classic model for understanding both plant and animal biogeography (e.g. Guisan, Weiss & Weiss, 1999; Muñoz *et al.*, 2005), and there is now a growing consensus that complex landscapes can exert a variety of functional controls on wildlife abundance, diversity and behaviour. In this review, we have highlighted some of the mechanisms through which predator populations respond to terrain fluctuations at multiple resolutions. Regarded as an indicator of habitat heterogeneity as a whole, topographic complexity has for instance been put forward as the most reliable predictor of continent-wide and global vertebrate species richness both on land (Kerr & Packer, 1997; Jetz & Rahbek, 2002; Davies *et al.*, 2007), and in the sea (Worm *et al.*, 2003; Morato *et al.*, 2010). It has also repeatedly proven more significant in shaping predator hotspots than other proximate factors such as food availability, temperature or human disturbance. In Nepal, topographic complexity was shown to have a comparatively stronger effect on snow leopard (*Uncia uncia*) activity budgets than did prey occurrence (Wolf & Ale, 2009). In Namibia, foraging Cape gannets (*Morus capensis*) were consistently observed in areas of strong topography-dependent upwelling, even though their main pelagic prey were not (Grémillet *et al.*, 2008). In Spain, Aragón *et al.* (2010) found that topographic attributes were more robust predictors of bird population trends than climatic factors.

Although not fully resolved for all species, wildlife–topography relationships are nevertheless typically complex, and may be either direct or indirect. This underlines the importance of viewing topographic heterogeneity as not merely the static physical template of an organism's habitat, but also as an influential determinant of animal community dynamics, interspecific relationships, activity patterns and evolutionary histories. As an illustration, Thornthwaite (1953) coined the term 'topoclimate' to refer to the concept of 'terrain climatology', the environmental variability induced and captured by local differences in ground surface characteristics such as slope, aspect, or landscape position. Since then, it has been widely acknowledged that climate is often tightly correlated with terrestrial topography, and that the latter perturbs practically every conceivable atmospheric process, from wind turbulence (Ruel, Pin & Cooper, 1998) to cloudiness, precipitation patterns (Basist, Bell & Meentemeyer, 1994), or incident radiation and light availability (Bennie *et al.*, 2008). For instance, in the northern hemisphere, insolation is generally higher on southwest- than northeast-facing slopes, the former experiencing warmer temperatures and a higher frequency of droughts as a result. Such interactions between land and air masses fuel pronounced spatial and temporal heterogeneity in snow accumulation, water and heat balance, soil depth, moisture content, pH levels, evapotranspiration rates, and post-rainfall drainage (Tovar-Pescador *et al.*, 2006), and are responsible for the establishment of floristic gradients potentially as extreme as those induced by latitudinal changes over continental distances (Raupach & Finnigan, 1997). The deposition and capture of seeds, propagules, litter and other organic particles in regions of complex terrain can also add to this effect and contribute further to local patterns in vegetation biomass and composition (Chen *et al.*, 2007; Da Conceição Bispo, De Morisson Valeriano & Dos Santos, 2012; Moeslund *et al.*, 2013). Since access to nutritious forage is a key determinant of the aggregation behaviour and body condition of wild ruminants (e.g. Myrsetrud *et al.*, 2001; Pettorelli *et al.*, 2005), it is unsurprising that topographic parameters such as terrain orientation (aspect) have been identified as proxies of the distributions of large carnivores. A case in point is that of Canadian lynx (*Lynx canadensis*), martens (*Martes americana*) and wolves (*Canis lupus*), which are observed more frequently on south- and east-facing slopes that tend to be free of snow earlier in the year and promote the growth of grass types suitable for their ungulate prey (Alexander, 2008). Lastly and importantly, topographic complexity also determines the prevalent weather conditions at the scale of individual organisms, and may as such support the formation of locally favourable microrefugia amidst globally inclement climes, allowing pockets of wildlife to persist outside the boundaries of their documented ranges (Dobrowski, 2011).

With the recognition of the significance of topoclimate–biotic coupling and the rising perception that vertebrate predators are charismatic ecosystem 'building blocks' that generate tremendous public appeal and high rates of profit through ecotourism industries (e.g. Vianna

et al., 2012), there has been considerable interest in relating environmental variability to predator occurrence in recent years (Kerr & Packer, 1997).

Despite rapid advances in our ability to model these linkages, topographic complexity has long remained inadequately quantified (Coblentz & Riitters, 2004). This is especially apparent in the marine realm, where a dedicated seascape-driven approach to predator ecology has only just begun to emerge (Pittman, McAlpine & Pittman, 2004). As the field of geomorphometry has steadily developed into an applied sub-discipline of ecology and geology, the elaboration of numerous spatial analysis frameworks has however also been catalysed (Pike, Evans & Hengl, 2008), and a comprehensive and complex spectrum of metrics now exists for describing the properties of natural terrains.

We have shown that although all these variables are readily available for inclusion in predator models, there has been a marked bias towards the application of single basic metrics which do not suffice in many theoretical and practical contexts (Pike, 2000). For instance, mean elevation/depth (E/D.AVG) – a staple of habitat preference studies (Fig. 4) – is fundamentally no more than a referenced position in cardinal space (much like latitude or longitude), and can be a severely misleading index of topographic complexity, especially when considered as a single explanatory term. BIOENV offers a compelling illustration of this by showing that mean depth does not belong to any of the best 1–4-metric combinations. We also demonstrate this in Fig. 7, where three-dimensional models of the seafloor at four locations within the West Australian EEZ are visually compared. Although pairs of sites within a given row have identical mean depth values (to within 5 m), the shape and convolution of their underlying terrain are drastically different. Likewise, neither mean slope nor mean aspect can *independently* convey meaningful information about the intricate ridgeline or canyon features which are prone to influence animal aggregations (Dickson & Beier, 2007), at least not over dimensions relevant to most mobile predators.

The fact that no general index of topographic complexity has gained prominence (Pittman *et al.*, 2009) therefore begs the question of whether one does or should in fact exist. Sappington *et al.* (2007) and Larkin, Vivian-Smith & Zedler (2006) argued against it, declaring that an ideal measure of topographic complexity ought to be multivariate in essence, particularly because different analytical approaches or metric calculation procedures may yield dissimilar and/or contradictory results (Warren *et al.*, 2004; Dickson & Beier, 2007). Qi & Zhu (2003) concurred and cautioned that terrain characterisation exercises ought to include measures of ground curvature in addition to slope or aspect.

Our analysis provides clear empirical support for this idea, and corroborates Moeslund *et al.* (2013)'s view that different (analytical) avenues are necessary to paint a comprehensive picture of the functional role of topography on biotic assemblages. By combining CLUSTER/MDS and BEST, we were firstly able to show that most existing geomorphometrics exhibit considerable levels of

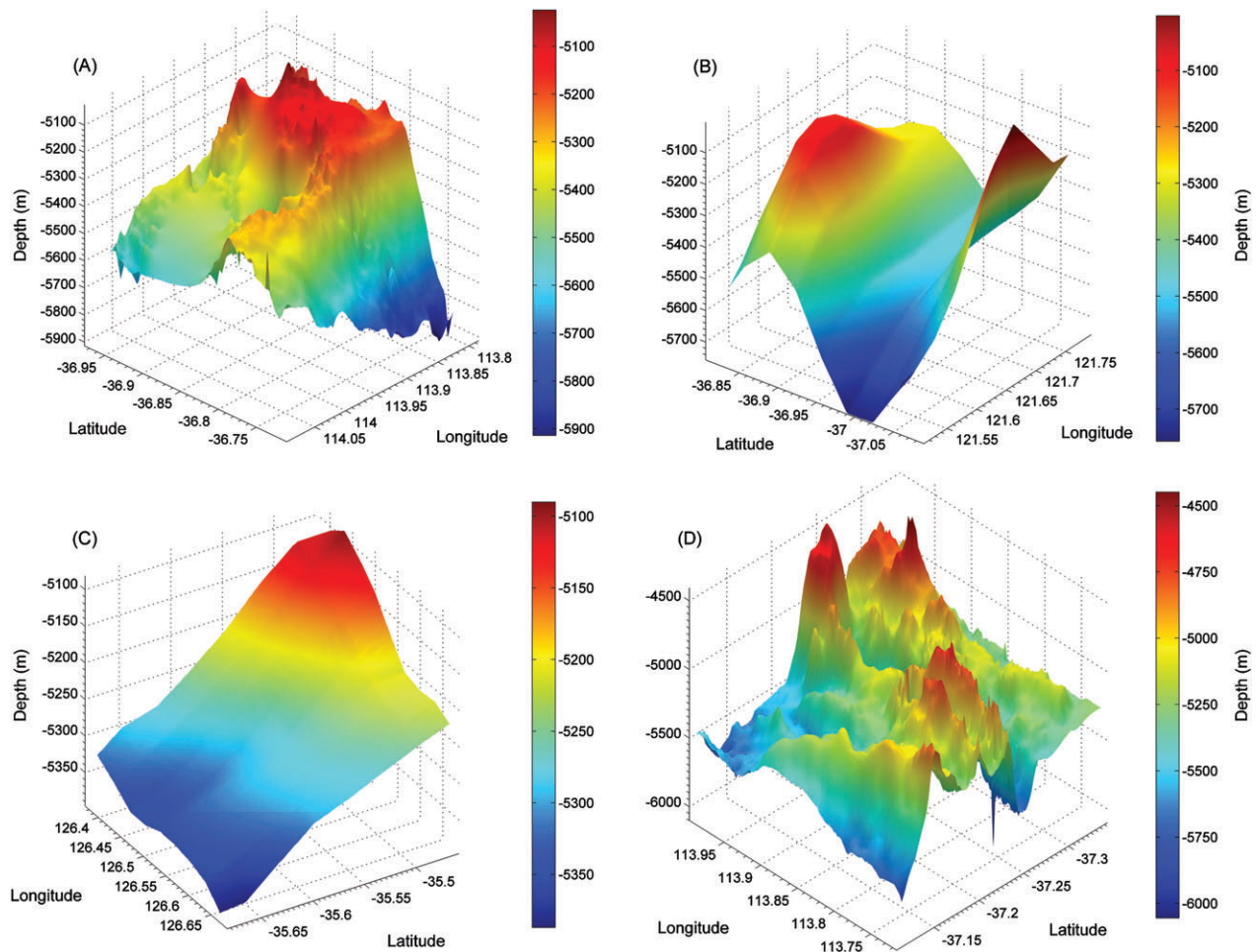


Fig. 7. Three-dimensional models of submarine topography at paired simulation sites with identical mean depths (± 5 m). Mean depth values are (A) -5367.7 m (36.84° S, 113.94° E); (B) -5365.3 m (36.95° S, 121.65° E); (C) -5259.5 m (37.23° S, 113.86° E); and (D) -5255.9 m (35.57° S, 126.53° E), respectively.

redundancy, and should hence be chosen carefully to avoid the well-documented biases that ensue from collinearity (Zuur, Ieno & Elphick, 2010). Secondly, BVSTEP was useful in providing a parsimonious view of topographic complexity. Although disputed by some (e.g. Guthery *et al.*, 2005), the concept that predictive models should place a premium on economising degrees of freedom and being no more complicated than necessary (the ‘Occam’s razor’ or ‘parsimony’ principle; Burnham & Anderson, 2002) has indeed been espoused as an overriding modelling philosophy in the past few decades (Forster, 2000). Ideally, ecologists should strive to construct models which adequately approximate patterns in the data without compromising generality, simplicity, and elegance. In this sense, BVSTEP was useful in discarding ‘noise’ variables and demonstrating that a suite of only seven or eight complementary metrics was needed to fully capture spatial variations in the West Australian seafloor. This comes in stark contrast to the trends we identified from the literature where very few authors tested more than four different metrics (Fig. 3). Importantly, we conclude that the vast majority of ecological models have

so far fallen short of appropriately assessing the effects of topographic complexity on predator species.

Cross-validation on systematic and random samples revealed a high degree of consistency in metric choice, an indication that representative variables were successfully extracted from the multivariate data cloud. Most selected metrics belonged to distinct clusters (seen best on the MDS plot in Fig. 6B). Given the metric associations captured by CLUSTER and the fact that BVSTEP could only examine a fraction of all possible combinations of variables, we see value in, and recommend, consolidating and synthesising outputs from both techniques to inform metric selection when testing hypotheses about topographic complexity from an ecological viewpoint. In particular, the dendrogram of Fig. 6A cannot help determine which metrics should be taken as representative of each cluster (as metrics within a single cluster were not statistically different). It is our experience that some parameters may be more easily measured, make greater pragmatic sense or simply be more meaningful for a given study and/or species. Metric selection will thus inevitably entail an element of subjectivity, and cluster/ordination

analyses can, in this regard, assist in finding the variables most suited to one's own purposes without undermining statistical validity. Our final proposed suite of best metrics was ultimately conditioned by our initial (although informed) approach to reducing multicollinearity. For instance, the coefficient of variation of depth (D.COV) was found to correlate highly with the contour index (D.CIN), and the former was therefore removed. It would not be unreasonable, nonetheless, to do the opposite should practical, theoretical or data-driven considerations justify it.

It should also be emphasised that speculating on causal links between predator assemblages and simulated geomorphometric variables was beyond the scope of this review, and would have necessitated access to biological field data we did not possess. The extent to which our best variables correlate with predator hotspots is therefore not immediately clear and will undoubtedly be context-specific since relationships can prove variable across taxa, geographical locations, niche conditions and time. For example, slope appears to outperform other measures of topographic complexity in accounting for the denning behaviour of arctic foxes (*Alopex lagopus*) in Canada (Szor *et al.*, 2008), but fails to explain sperm whale (*Physeter macrocephalus*) occurrence in the Mediterranean (Pirota *et al.*, 2011).

For these reasons, our conclusions should not be taken to reflect geomorphometric choices in an absolute sense. Rather, we have shown that different metric *types* (at least six, i.e. aspect, curvature, elevation/depth, relief, slope and other) are needed and of most use for the quantification of topographic complexity, and should therefore drive approaches to data collection and data handling.

That said, predator populations do not solely respond to the static properties of landscapes, and many animals also track and exploit dynamic habitat conditions, from relatively ephemeral features of the environment such as sea surface height anomaly, thermal front locations or tidal current strength (Kappes *et al.*, 2010; Weimerskirch *et al.*, 2010; Block *et al.*, 2011; Louzao *et al.*, 2011; Wedding *et al.*, 2011), to seasonal/inter-annual patterns in human presence (Muñoz, Márquez & Real, 2013). For instance, the den sites occupied by Scandinavian brown bears (*Ursus arctos*) in the vicinity of populated areas tend to be situated in more rugged terrain, likely because these offer better cover from, and reduce interactions with, humans (Sahlén, Støen & Swenson, 2011). Likewise, Rauset *et al.* (2013, p. 706) reported that wolverines (*Gulo gulo*) 'select for steep and rugged terrain [...] independent of scale and habitat availability' and postulated that this strategy maximised survival in an anthropogenic landscape where poaching activities predominate. To improve the explanatory accuracy (i.e. ability to model the observed data) and predictive power (i.e. ability to extrapolate results to independent datasets) of habitat models, a good philosophical and statistical compromise may then lie in combining an array of conventional metrics with dynamic parameters that may capture the interplay between topography, ocean/atmospheric flow, climate forcing (Nel *et al.*, 2001; Mauritzen *et al.*, 2003; Ladd *et al.*, 2005a; Pirota *et al.*, 2011), and disturbance.

Finally, as Gessler *et al.* (2009, p. 639) once stated, 'every representation of the Earth's surface height is, in some respect, flawed', and our GIS-based approach has a number of limitations. Firstly, because land- and seascapes do not have the same geological origin, nor are they subject to the same mechanical and tectonic forces, our benthic digital elevation model (DEM) may not necessarily be a reliable analogue of terrestrial surfaces. It is thus possible that metric associations may be somewhat different on land, although further research is required to fully address this knowledge gap.

Secondly, a small minority of metrics (i.e. 4 out of 56 variables, see Table 1) required projecting. While nearest-neighbour methods have the advantage of partially maintaining the integrity of the original DEM by preserving cell values (i.e. no 'new' values are introduced *via* averaging or interpolation, as may be the case with bilinear interpolation or cubic convolution), and may perform similarly to, or even better than, other techniques (e.g. Wu, Li & Huang, 2008; Hubert, Schwarzer & Jaquet, 2012), no resampling algorithm can leave a digital raster surface unaltered. Projected metrics may, therefore, have been subject to some bias, which future research should aim to quantify.

Thirdly, we recognise that different assumptions regarding sampling site dimensions, landscape conditions, or computational algorithms (e.g. terrain slope can be computed in at least eight ways; Jones, 1998) might also affect the performance of multivariate methods. Albeit not computationally straightforward, a valuable endeavour would be to reiterate the analyses on a large number of random samples in a bootstrap manner, to gain insights into the uncertainty intrinsic to the variable selection process.

Li & Wu (2004) argued that meaningful interpretations of physical habitat variables can only be achieved when they are framed into a suitable ecological context. While the authors mainly discussed two-dimensional landscape indices, we believe that their conclusions are equally as relevant for three-dimensional geomorphometrics whose shortcomings, attainable ranges, and behaviour in response to changing landscapes ought to be understood fully prior to analysis (Hargis, Bissonette & David, 1998). The lack of widespread adoption of geomorphometrics thus appears to be a by-product of the fact that the merits and weaknesses of many still remain somewhat obscure, even if their analytical properties have long been grasped (Li & Reynolds, 1994). Intuitively, metrics that prove overly complex, composite, or non-linear seem ill recommended, and ones ordered on relative scales comprised between finite boundaries (e.g. fractal dimension, which spans between 2 and 3, and was selected as the best single variable *via* BIOENV) prove more transparent and user-friendly, specifically when minimum and maximum values have inherent relevance from a biological standpoint.

Grain (the size of the units where species–environment relationships are investigated) and extent (the overall area under study; Wiens, 1989) are also crucial factors affecting perceptions of complexity. Since predators

associate with landscapes at a variety of scales, pattern detection may stall if the scales at which analyses are conducted do not match that at which the target phenomena take place. As acknowledged by other authors (e.g. Wilson *et al.*, 2007), the use of multiscale analyses is fundamental. Because reports on scale-dependence laws in two-dimensional landscape variables are abundant (e.g. Wu *et al.*, 2002; Wu, 2004) but three-dimensional metrics have yet to receive the same attention, we advocate that measurements of topographic complexity also be explicitly tested *via* scalograms (response curves to varying grain; Zhang & Li, 2013) or equivalent techniques whenever possible.

Lastly, relationships between behavioural and environmental cues can sometimes be challenging to discern (Campomizzi *et al.*, 2008), especially as different guilds, cohorts, social units or even individuals with divergent requirements may perceive habitat quality differently within the same land or seascape (Cañadas & Hammond, 2008). For example, grey seals (*Halichoerus grypus*) have been found to selectively vacate seemingly suitable breeding areas on flat terrain, possibly because the costs incurred by more frequent aggressive encounters on densely crowded open-ground haul-outs may outweigh those associated with more difficult locomotion in topographically complex sites (Pomeroy, Twiss & Duck, 2000). By contrast, large gatherings of humpback whales (*Megaptera novaeangliae*) routinely occur in flat coastal areas as sheltered embayments provide cows and calves some degree of protection against predators and inclement conditions during the mating season (Braithwaite, Meeuwig & Jenner, 2012). The factors that determine which area is occupied by these animals may accordingly be social rather than oceanographic (Oviedo & Solís, 2008), and hotspots of gregarious species may thus coincide with patches of suboptimal habitat. For this reason, Campomizzi *et al.* (2008) recommend the inclusion of a clustering parameter in predictive distribution models to account for biases ensuing from conspecific attraction and optimise the likelihood of detecting hotspots in both currently occupied, and suitable yet unoccupied, areas. Maintaining the latter is pivotal in endangered species management, where declining populations cannot physically fill their entire habitat space but may need it for successful recovery (Heppell, Walters & Crowder, 1994).

V. CONCLUSIONS

(1) Many mobile predator species are little constrained by geographical barriers and the mechanisms that produce and maintain their aggregations have hence long challenged scientists in search of conservation indicators and robust methods of mapping faunal hotspots (Wintle, Elith & Potts, 2005; Botequilha-Leitao *et al.*, 2006). While measuring topographic complexity has not necessarily been an over-arching objective for ecologists, the recent recognition that numerous hotspots consistently occur in sites defined by terrain features has fuelled a flurry of research into the application of geomorphology to biological questions.

(2) In contrast with their rapid development and diversification, topographic variables have not been adopted with matching speed in predator studies, and modellers do not seem to have embraced the full array of geomorphometrics that are now available to them. Importantly, basic terrain descriptors such as mean elevation/depth have been uncritically viewed as reliable proxies of topographic complexity when in fact they provide an inadequate and incomplete representation of surface forms.

(3) Most geomorphometrics are severely redundant, and we have described strategies that allow informed choices of explanatory variables to be made to circumvent the problematic treatment of collinearity in predictive models. Multivariate combinations of metric types are essential to encapsulate topographic variability fully, and the fact that only a minority of investigators have followed this reasoning suggests that topographically complex environments may be more important than previously understood (Le Roux, Virtanen & Luoto, 2013).

(4) Conditional on formulating unambiguous measures that integrate unique representations of both vertical and horizontal terrain characteristics, we therefore argue that topographic complexity may be a useful surrogate of predator hotspots. This has strong implications for the establishment of appropriate management policies for endangered species, especially in the face of globally intensifying anthropogenic pressures. In addition to shaping weather patterns, complex landscapes support many viable populations of keystone mobile predators. By preserving these habitats, not only may other lower trophic level species with smaller spatial ranges benefit from protection (Dickson *et al.*, 2013), but the success of biodiversity conservation measures may also be maximised under future climate scenarios. In this regard, the delineation of landscape management units (LMUs; Underwood *et al.*, 2010) or 'facets' that parse natural terrains into recurring blocks of uniform topographic signature seems a potentially attractive solution to protect the 'arenas' to the benefit of the 'actors' (Beier & Brost, 2010). As the demand for topographic data continues to grow, we anticipate that management decisions will increasingly rely on such simple but effective strategies. Compared to vegetation matrices or prey fields, spatio-temporally stable physical structures are indeed more readily observable, easier to inventory or map, and less costly to characterise.

(5) In particular, current contentions over the effectiveness of protected areas for mobile taxa have made ocean zoning a topical issue in the marine arena (Agardy *et al.*, 2003; Williams, ReVelle & Levin, 2005). Despite the fact that oceanic reserves may need to be framed around adaptive dynamic boundaries (Hooker *et al.*, 2011), we claim that large bathymetric features should still provide a robust initial foundation for delineating potentially important marine predator habitats, a view shared by an increasing number of authors (Hyrenbach, Forney & Dayton, 2000; Michael, Jahncke & Hyrenbach, 2014). This may be especially relevant in the remote and relatively inaccessible high seas, where biological data remain sparse and ephemeral

drivers of wildlife dynamics, like prey availability, are hard or impossible to assess (Grémillet *et al.*, 2004).

VI. ACKNOWLEDGEMENTS

We are grateful to Bob Clarke and Marti Anderson for their insightful advice on the multivariate analyses, and we wish to thank Jeff Jenness and Takuia Iwamura for providing stimulating and helpful comments that considerably improved the quality of the manuscript. This research received support from the Australian Government's National Environmental Research Program (NERP) Marine Biodiversity Hub. P.J.B. was the recipient of a scholarship for international research fees (SIRF) during the course of this work.

VII. REFERENCES

- AGARDY, T., BRIDGEWATER, P., CROSBY, M. P., DAY, J., DAYTON, P. K., KENCHINGTON, R., LAFFOLEY, D., MCCONNEY, P., MURRAY, P. A., PARKS, J. E. & PEAU, L. (2003). Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**, 353–367.
- ALEXANDER, S. M. (2008). Snow-tracking and GIS: using multiple species-environment models to determine optimal wildlife crossing sites and evaluate highway mitigation plans on the Trans-Canada Highway. *The Canadian Geographer* **52**, 169–187.
- AMBS, S. M., BONESS, D. J., DON BOWEN, W., PERRY, E. A. & FLEISCHER, R. C. (1999). Proximate factors associated with high levels of extraconsort fertilization in polygynous grey seals. *Animal Behaviour* **58**, 527–535.
- ANDERSON, S. S. & HARWOOD, J. (1985). Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. *Animal Behaviour* **33**, 1343–1348.
- ANDERSSON, M., WALLANDER, J. & ISAKSSON, D. (2009). Predator perches: a visual search perspective. *Functional Ecology* **23**, 373–379.
- ARAGÓN, P., LOBO, J. M., OLALLA-TÁRRAGA, M. Á. & RODRÍGUEZ, M. Á. (2010). The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography* **19**, 40–49.
- ARROYO, B. & RAZIN, M. (2006). Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation* **128**, 276–284.
- BAILEY, T. N., BANGS, E. E., PORTNER, M. F., MALLOY, J. C. & McAVINCHEY, R. J. (1986). An apparent overexploited lynx population on the Kenai Peninsula, Alaska. *Journal of Wildlife Management* **50**, 279–290.
- BALDI, R., CAMPAGNA, C., PEDRAZA, S. & LE BOEUF, B. J. (1996). Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Animal Behaviour* **51**, 717–724.
- BASIST, A., BELL, G. D. & MEENTEMEYER, V. (1994). Statistical relationships between topography and precipitation patterns. *Journal of Climate* **7**, 1305–1315.
- BAUM, J. K., MYERS, R. A., KEHLER, D. G., WORM, B., HARLEY, S. J. & DOHERTY, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**, 389–392.
- BEASOM, S. L., WIGGERS, E. P. & GIARDINO, J. R. (1983). A technique for assessing land surface ruggedness. *Journal of Wildlife Management* **47**, 1163–1166.
- BEIER, P. & BROST, B. (2010). Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology* **24**, 701–710.
- BENNIE, J., HUNTLEY, B., WILTSHIRE, A., HILL, M. O. & BAXTER, R. (2008). Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* **216**, 47–59.
- BESTLEY, S., PATTERSON, T. A., HINDELL, M. A. & GUNN, J. S. (2009). Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. *Ecology* **91**, 2373–2384.
- BLOCK, B. A. (2005). Physiological ecology in the 21st century: advancements in bioglogging science. *Integrative and Comparative Biology* **45**, 305–320.
- BLOCK, B. A., COSTA, D. P. & BOGRAD, S. J. (2010). A view of the ocean from Pacific predators. In *Life in the World's Oceans: Diversity, Distribution and Abundance* (ed. A. D. MCINTYRE), pp. 291–311. Wiley-Blackwell, Oxford.
- BLOCK, B. A., JONSEN, I. D., JORGENSEN, S. J., WINSHIP, A. J., SHAFFER, S. A., BOGRAD, S. J., HAZEN, E. L., FOLEY, D. G., BREED, G. A., HARRISON, A. L., GANONG, J. E., SWITHENBANK, A., CASTLETON, M., DEWAR, H., MATE, B. R., SHILLINGER, G. L., SCHAEFER, K. M., BENSON, S. R., WEISE, M. J., HENRY, R. W. & COSTA, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90.
- BOSSART, G. D. (2011). Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology* **48**, 676–690.
- BOTEQUILHA-LEITAO, A., MILLER, J., AHERN, J. & MCGARIGAL, K. (2006). *Measuring Landscapes: A Planner's Handbook*. Island Press, Washington.
- BRAITHWAITE, J. E., MEEUWIG, J. J. & JENNER, K. C. S. (2012). Estimating cetacean carrying capacity based on spacing behaviour. *PLoS ONE* **7**, e51347.
- BRANDES, D. & OMBALSKI, D. W. (2004). Modeling raptor migration pathways using a fluid-flow analogy. *Journal of Raptor Research* **38**, 195–207.
- BREITENMOSE, U. (1998). Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation* **83**, 279–289.
- BREMNER, J., ROGERS, S. I. & FRID, C. L. J. (2006). Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems* **60**, 302–316.
- BURNHAM, K. P. & ANDERSON, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- BUTLER, A. J., REES, T., BEESLEY, P. & BAX, N. J. (2010). Marine biodiversity in the Australian region. *PLoS ONE* **5**, e11831.
- CAMAZINE, S., DENEUBOURG, J.-L., FRANKS, N. R., SNEYD, J., THERAULAZ, G. & BONABEAU, E. (2001). *Self-Organization in Biological Systems*. Princeton University Press, Princeton.
- CAMPOMIZZI, A. J., BUTCHER, J. A., FARRELL, S. L., SNEELGROVE, A. G., COLLIER, B. A., GUTZWILLER, K. J., MORRISON, M. L. & WILKINS, R. N. (2008). Conspecific attraction is a missing component in wildlife habitat modeling. *Journal of Wildlife Management* **72**, 331–336.
- CANADAS, A. & HAMMOND, P. (2008). Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean: implications for conservation. *Endangered Species Research* **4**, 309–331.
- CARDILLO, M., PURVIS, A., SECHREST, W., GITTLEMAN, J. L., BIELBY, J. & MACE, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology* **2**, e197.
- CARRARO, R. & GLADSTONE, W. (2006). Habitat preferences and site fidelity of the ornate wobbegong shark (*Orectolobus ornatus*) on rocky reefs of New South Wales. *Pacific Science* **60**, 207–223.
- CARRETE, M., GRANDE, J. M., TELLA, J. L., SÁNCHEZ-ZAPATA, J. A., DONÁZAR, J. A., DÍAZ-DELGADO, R. & ROMO, A. (2007). Habitat, human pressure, and social behavior: partialling out factors affecting large-scale territory extinction in an endangered vulture. *Biological Conservation* **136**, 143–154.
- CARROLL, C., NOSS, R. F. & PAQUET, P. C. (2001). Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* **11**, 961–980.
- CARTER, G. S. & GREGG, M. C. (2002). Intense, variable mixing near the head of Monterey submarine canyon. *Journal of Physical Oceanography* **32**, 3145–3165.
- CEBALLOS, G. & EHRLICH, P. R. (2002). Mammal population losses and the extinction crisis. *Science* **296**, 904–907.
- CHEN, X. F., CHEN, J. M., AN, S. Q. & JU, W. M. (2007). Effects of topography on simulated net primary productivity at landscape scale. *Journal of Environmental Management* **85**, 585–596.
- CHUNDAWAT, R. S. (1990). Habitat selection by a snow leopard in Hemis National Park, India. *International Pedigree Book of Snow Leopards* **6**, 85–92.
- CLARKE, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.
- CLARKE, K. R. & AINSWORTH, M. (1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205–219.
- CLARKE, K. R. & GORLEY, R. N. (2006). *PRIMER v6: User Manual*. PRIMER-E, Plymouth.
- CLARKE, K. R., SOMERFIELD, P. J. & GORLEY, R. N. (2008). Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* **366**, 56–69.
- CLARKE, K. R. & WARWICK, R. M. (1998). Quantifying structural redundancy in ecological communities. *Oecologia* **113**, 278–289.
- CLARKE, K. R. & WARWICK, R. M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation*. Second Edition. PRIMER-E, Plymouth.
- COBLENTZ, D. D. & RIITERS, K. H. (2004). Topographic controls on the regional-scale biodiversity of the south-western USA. *Journal of Biogeography* **31**, 1125–1138.
- CONNELL, S. D. & KINGSFORD, M. J. (1998). Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs* **17**, 49–57.
- COSTELLO, M. J., COLL, M., DANOVARO, R., HALPIN, P., OJAVEER, H. & MILOSLAVICH, P. (2010). A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* **5**, e12110.
- CROLL, D., MARINOVIC, B., BENSON, S., CHAVEZ, F., BLACK, N., TERNULLO, R. & TERSHY, B. (2005). From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series* **289**, 117–130.

- CURIO, E. (1978). *The Ethology of Predation*. Springer-Verlag, New York.
- DA CONCEIÇÃO BISPO, P., DE MORISSON VALERIANO, M. & DOS SANTOS, J. R. (2012). Effects of the geomorphometric characteristics of the local terrain on floristic composition in the central Brazilian Amazon. *Austral Ecology* **37**, 491–499.
- DAVIES, R. G., ORME, C. D. L., STORCH, D., OLSON, V. A., THOMAS, G. H., ROSS, S. G., DING, T.-S., RASMUSSEN, P. C., BENNETT, P. M., OWENS, I. P. F., BLACKBURN, T. M. & GASTON, K. J. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1189–1197.
- DEAN, F. C. (1987). Brown bear density, Denali National Park, Alaska, and sighting efficiency adjustment. *International Conference on Bear Research and Management* **7**, 37–43.
- DICKSON, B. G. & BEIER, P. (2007). Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. *Journal of Zoology* **271**, 270–277.
- DICKSON, B. G., JENNESS, J. S. & BEIER, P. (2005). Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management* **69**, 264–276.
- DICKSON, B. G., ROEMER, G. W., MCRAE, B. H. & RUNDALL, J. M. (2013). Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the Southwestern United States. *PLoS ONE* **8**, e81898.
- DINGLE, H. & DRAKE, V. A. (2007). What is migration? *Bioscience* **57**, 113–121.
- DOBROWSKI, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**, 1022–1035.
- DONAZAR, J. A., HIRALDO, F. & BUSTAMANTE, J. (1993). Factors influencing nest site selection, breeding density and breeding success in the bearded vulture (*Gypaetus barbatus*). *Journal of Applied Ecology* **30**, 504–514.
- DOWER, J. F. & BRODEUR, R. D. (2004). The role of biophysical coupling in concentrating marine organisms around shallow topographies. *Journal of Marine Systems* **50**, 1–2.
- DRAZEN, J. C., GOFFREDI, S. K., SCHLINING, B. & STAKES, D. S. (2003). Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda escarpment: a reproductive hot spot. *The Biological Bulletin* **205**, 1–7.
- EASTMAN, J. R. (2012). *IDRISI Selva*. Clark University, Worcester Available at <http://www.clarklabs.org/products/idrisi.cfm>. Accessed March 2013.
- ESRI (2011). *ArcGIS Desktop Release 10*. Environmental Systems Resource Institute, Redlands.
- ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, L., OKSANEN, T., PAINE, R. T., PIKITCH, E. K., RIPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHOENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. & WARDLE, D. A. (2011). Trophic downgrading of planet Earth. *Science* **333**, 301–306.
- FERRER, M. & NEGRO, J. J. (2004). The near extinction of two large European predators: super specialists pay a price. *Conservation Biology* **18**, 344–349.
- FIELD, J. G., CLARKE, K. R. & WARWICK, R. M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* **8**, 37–52.
- FORSTER, M. R. (2000). Key concepts in model selection: performance and generalizability. *Journal of Mathematical Psychology* **44**, 205–231.
- FUNSTON, P. J., MILLS, M. G. L. & BIGGS, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology* **253**, 419–431.
- GENIN, A. (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* **50**, 3–20.
- GENIN, A. & DOWER, J. F. (2007). Seamount plankton dynamics. In *Seamounts: Ecology, Fisheries and Conservation* (eds T. J. PITCHER, T. MORATO, P. J. B. HART, M. R. CLARK, N. HAGGAN and R. S. SANTOS), pp. 85–100. Blackwell Publishing, Oxford.
- GESSLER, P., PIKE, R., MACMILLAN, R. A., HENGL, T., REUTER, H. I., TOMISLAV, H. & HANNES, I. R. (2009). The future of geomorphometry. In *Geomorphometry: Concepts, Software, Applications* (eds T. HENGL and H. I. REUTER), pp. 637–652. Elsevier, Oxford.
- GILL, P. (2002). A blue whale (*Balaenoptera musculus*) feeding ground in a southern Australian coastal upwelling zone. *Journal of Cetacean Research and Management* **4**, 179–184.
- GONZÁLEZ, L. M., BUSTAMANTE, J. & HIRALDO, F. (1992). Nesting habitat selection by the Spanish imperial eagle *Aquila adalberti*. *Biological Conservation* **59**, 45–50.
- GOODRICH, L. J. & SMITH, J. P. (2008). Raptor migration in North America. In *State of North America's Birds of Prey* (eds K. L. BILDSTEIN, J. P. SMITH, E. RUELAS INZUNZA and R. R. VEIT), pp. 37–149. Nuttall Ornithological Club, Cambridge, and American Ornithologists' Union, Washington.
- GOWANS, S. & WHITEHEAD, H. (1995). Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Canadian Journal of Zoology* **73**, 1599–1608.
- GRÉMILLET, D., KUNTZ, G., DELBART, F., MELLET, M., KATO, A., ROBIN, J. P., CHAILLON, P. E., GENDNER, J. P., LORENTSEN, S. H. & MAHO, Y. L. (2004). Linking the foraging performance of a marine predator to local prey abundance. *Functional Ecology* **18**, 793–801.
- GRÉMILLET, D., LEWIS, S., DRAPEAU, L., VAN DER LINGEN, C. D., HUGGETT, J. A., COETZEE, J. C., VERHEYE, H. M., DAUNT, F., WANLESS, S. & RYAN, P. G. (2008). Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* **45**, 610–621.
- GSCHWENG, M., KALKO, E. K. V., QUERNER, U., FIEDLER, W. & BERTHOLD, P. (2008). All across Africa: highly individual migration routes of Eleonora's falcon. *Proceedings of the Royal Society of London Series B: Biological Sciences* **275**, 2887–2896.
- GUINAN, A., WEISS, S. & WEISS, A. (1999). GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology* **143**, 107–122.
- GUTHERY, F. S., BRENNAN, L. A., PETERSON, M. J. & LUSK, J. J. (2005). Information theory in wildlife science: critique and viewpoint. *The Journal of Wildlife Management* **69**, 457–465.
- HANEY, J. C., HAURY, L. R., MULLINEAUX, L. S. & FEY, C. L. (1995). Sea-bird aggregation at a deep North Pacific seamount. *Marine Biology* **123**, 1–9.
- HARGIS, C. D., BISSONETTE, J. A. & DAVID, J. L. (1998). The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* **13**, 167–186.
- HASTIE, G. D., WILSON, B. & THOMPSON, P. M. (2003). Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique. *Canadian Journal of Zoology* **81**, 469–478.
- HAYS, G. C. (2008). Sea turtles: a review of some key recent discoveries and remaining questions. *Journal of Experimental Marine Biology and Ecology* **356**, 1–7.
- HEIMLICH-BORAN, J. R. (1988). Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *Canadian Journal of Zoology* **66**, 565–578.
- HEITHAUS, M. R., FRID, A., WIRSING, A. J. & WORTON, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* **23**, 202–210.
- HEPPELL, S. S., WALTERS, J. R. & CROWDER, L. B. (1994). Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *The Journal of Wildlife Management* **58**, 479–487.
- HOLLAND, K. N. & GRUBBS, D. R. (2007). Fish visitors to seamounts – Section A: tunas and billfish at seamounts. In *Seamounts: Ecology, Fisheries & Conservation* (eds T. J. PITCHER, T. MORATO, P. J. B. HART, M. R. CLARK, N. HAGGAN and R. S. SANTOS), pp. 189–201. Blackwell Publishing, Oxford.
- HOOKE, S. K., HYRENBACH, K. D., CORRIGAN, C., POLOVINA, J. J. & REEVES, R. R. (2011). Making protected area networks effective for marine top predators. *Endangered Species Research* **13**, 203–218.
- HUBERT, S., SCHWARZER, S. & JAQUET, J.-M. (2012). Spatial degradation of classified satellite images. *The Open Remote Sensing Journal* **5**, 64–72.
- HUI, C. (1979). Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. *Journal of Mammalogy* **60**, 521–527.
- HYRENBACH, K. D., FORNEY, K. A. & DAYTON, P. K. (2000). Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**, 437–458.
- IRWIN, L. L., CLARK, L. A., ROCK, D. C. & ROCK, S. L. (2007). Modeling foraging habitat of California spotted owls. *Journal of Wildlife Management* **71**, 1183–1191.
- IVANOV, V. Y., BRAS, R. L. & VIVONI, E. R. (2008). Vegetation-hydrology dynamics in complex terrain of semiarid areas: 2. Energy-water controls of vegetation spatiotemporal dynamics and topographic niches of favorability. *Water Resources Research* **44**, W03430.
- JACKSON, J. B. C. (2008). Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences* **105**, 11458–11465.
- JENNESS, J. S. (2004). Calculating landscape surface area from digital elevation models. *Wildlife Society Bulletin* **32**, 829–839.
- JENNESS, J. S. (2013). *DEM Surface Tools for ArcGIS*. Jenness Enterprises. Available at http://www.jennessent.com/arcgis/surface_area.htm. Accessed March 2013.
- JENNESS, J. S., BROST, B. & BEIER, P. (2011). *Land Facet Corridor Designer: Extension for ArcGIS*. Jenness Enterprises. Available at: http://www.jennessent.com/arcgis/land_facets.htm. Accessed March 2013.
- JETZ, W. & RAHBEK, C. (2002). Geographic range size and determinants of avian species richness. *Science* **297**, 1548–1551.
- JOLY, K. & MYERS, W. L. (2001). Patterns of mammalian species richness and habitat associations in Pennsylvania. *Biological Conservation* **99**, 253–260.
- JONES, K. H. (1998). A comparison of algorithms used to compute hill slope as a property of the DEM. *Computers & Geosciences* **24**, 315–323.
- JONKER, F. C. & BESTER, M. N. (1998). Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10**, 21–30.
- KAPPES, M. A., SHAFFER, S. A., TREMBLAY, Y., FOLEY, D. G., PALACIOS, D. M., ROBINSON, P. W., BOGRAD, S. J. & COSTA, D. P. (2010). Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography* **86**, 246–260.
- KENDALL, M. G. & GIBBONS, J. D. (1990). *Rank Correlation Methods*. Fifth Edition. Griffin, London.
- KERR, J. T. & PACKER, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* **385**, 252–254.
- KNUTSEN, H., JORDE, P. E., ANDRÉ, C. & STENSETH, N. C. (2003). Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology* **12**, 385–394.

- KOBLE, A. & ADAMIC, M. (2000). Identifying brown bear habitat by a combined GIS and machine learning method. *Ecological Modelling* **135**, 291–300.
- KOUAKOU, C. Y., BOESCH, C. & KUEHL, H. S. (2011). Identifying hotspots of chimpanzee group activity from transect surveys in Taï National Park, Côte d'Ivoire. *Journal of Tropical Ecology* **27**, 621–630.
- KUHN, M., WING, J., WESTON, S., WILLIAMS, A., KEEFER, C., ENGELHARDT, A. & COOPER, T. (2013). caret: classification and regression training, R package version 5.15-61. Available at <http://CRAN.R-project.org/package=caret>. Accessed March 2013.
- LACKI, M. J. & SCHWIERJOHANN, J. H. (2001). Day-roost characteristics of northern bats in mixed mesophytic forest. *The Journal of Wildlife Management* **65**, 482–488.
- LADD, C., JAHNCKE, J., HUNT, G. L., COYLE, K. O. & STABENO, P. J. (2005a). Hydrographic features and seabird foraging in Aleutian Passes. *Fisheries Oceanography* **14**, 178–195.
- LADD, C., STABENO, P. & COKELET, E. D. (2005b). A note on cross-shelf exchange in the northern Gulf of Alaska. *Deep-Sea Research Part II: Topical Studies in Oceanography* **52**, 667–679.
- LAIDRE, K. L., HEIDE-JORGENSEN, M. P., LOGSDON, M. L., HOBBS, R. C., HEAGERTY, P., DIETZ, R., JØRGENSEN, O. & TREBLE, M. (2004). Seasonal narwhal habitat associations in the high Arctic. *Marine Biology* **145**, 821–831.
- LALIBERTE, A. S. & RIPPKE, W. J. (2004). Range contractions of North American carnivores and ungulates. *Bioscience* **54**, 123–138.
- LANDER, M. E., LOGSDON, M. L., LOUGHLIN, T. R. & VAN BLARICOM, G. R. (2011). Spatial patterns and scaling behaviors of Steller sea lion (*Eumetopias jubatus*) distributions and their environment. *Journal of Theoretical Biology* **274**, 74–83.
- LARKIN, D., VIVIAN-SMITH, G. & ZEDLER, J. B. (2006). Topographic heterogeneity theory and ecological restoration. In *Foundations of Restoration Ecology* (eds D. A. FALK, M. A. PALMER and J. B. ZEDLER), pp. 142–165. Island Press, Washington.
- LAVOIE, D., SIMARD, Y. & SAUCIER, F. J. (2000). Aggregation and dispersion of krill at channel heads and shelf edges: the dynamics in the Saguenay-St. Lawrence Marine Park. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1853–1869.
- LE ROUX, P. C., VIRTANEN, R. & LUOTO, M. (2013). Geomorphological disturbance is necessary for predicting fine-scale species distributions. *Ecography* **36**, 800–808.
- LESMEISTER, D. B., GOMPPER, M. E. & MILLSAUGH, J. J. (2008). Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. *Journal of Mammalogy* **89**, 1512–1520.
- LETNIC, M., RITCHIE, E. G. & DICKMAN, C. R. (2012). Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* **87**, 390–413.
- LEWISON, R., CROWDER, L., READ, A. J. & FREEMAN, S. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution* **19**, 598–604.
- LI, H. & REYNOLDS, J. F. (1994). A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* **75**, 2446–2455.
- LI, H. & WU, J. (2004). Use and misuse of landscape indices. *Landscape Ecology* **19**, 389–399.
- LOGAN, K. A. & IRWIN, L. L. (1985). Mountain lion habitats in the Big Horn mountains, Wyoming. *Wildlife Society Bulletin* **13**, 257–262.
- LÓPEZ-LÓPEZ, P., GARCÍA-RIPOLLÉS, C., SOUTULLO, Á., CADAHÍA, L. & URIOS, V. (2007). Identifying potentially suitable nesting habitat for golden eagles applied to 'important bird areas' design. *Animal Conservation* **10**, 208–218.
- LOUZAQ, M., PINAUD, D., PÉRON, C., DELORD, T., WIEGAND, T. & WEIMERSKIRCH, H. (2011). Conserving pelagic habitats: seascape modelling of an oceanic top predator. *Journal of Applied Ecology* **48**, 121–132.
- LU, H. (2008). Modelling terrain complexity. In *Advances in Digital Terrain Analysis* (eds Q. ZHOU, B. LEES and T. GUO-AN), pp. 159–176. Springer, Berlin.
- MACLEOD, K., FAIRBAIRNS, R., GILL, A., FAIRBAIRNS, B., GORDON, J., BLAIR-MYERS, C. & PARSONS, E. (2004). Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. *Marine Ecology Progress Series* **277**, 263–274.
- MARDIA, K. V. & JUPP, P. E. (2000). *Directional Statistics*. Academic Press, London.
- MARGALIDA, A. & BERTRAN, J. (2001). Function and temporal variation in use of ossuaries by bearded vultures (*Gypaetus barbatus*) during the nestling period. *The Auk* **118**, 785–789.
- MARTÍNEZ, J. A., SERRANO, D. & ZUBEROGOTIA, I. (2003). Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. *Ecography* **26**, 21–28.
- MATHESON, J. D. & LARSON, D. W. (1998). Influence of cliffs on bird community diversity. *Canadian Journal of Zoology* **76**, 278–287.
- MAURITZEN, M., DEROCHE, A. E., PAVLOVA, O. & WIIG, Ø. (2003). Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. *Animal Behaviour* **66**, 107–113.
- MAY, C. A., PETERSBURG, M. L. & GUTIÉRREZ, R. J. (2004). Mexican spotted owl nest- and roost- site habitat in northern Arizona. *The Journal of Wildlife Management* **68**, 1054–1064.
- MCCARTHY, T. M., FULLER, T. K. & MUNKHTSOG, B. (2005). Movements and activities of snow leopards in Southwestern Mongolia. *Biological Conservation* **124**, 527–537.
- MCCAULEY, D. J., YOUNG, H. S., DUNBAR, R. B., ESTES, J. A., SEMMENS, B. X. & MICHELI, F. (2012). Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* **22**, 1711–1717.
- MENDONÇA, A., ARISTEGUI, J., VILAS, J. C., MONTERO, M. F., OJEDA, A., ESPINO, M. & MARTINS, A. (2012). Is there a seamount effect on microbial community structure and biomass? The case study of Seine and Sedlo Seamounts (Northeast Atlantic). *PLoS ONE* **7**, e29526.
- MICHAEL, P. E., JAHNCKE, J. & HYRENBACH, K. D. (2014). Relative influence of static and dynamic features on black-footed albatross (*Phoebastria nigripes*) habitat use in central California Sanctuaries. *Fisheries Oceanography* **23**, 18–31.
- MICHAELSEN, T. C., JENSEN, K. H. & HÖGSTEDT, G. (2011). Topography is a limiting distributional factor in the soprano pipistrelle at its latitudinal extreme. *Mammalian Biology - Zeitschrift für Säugetierkunde* **76**, 295–301.
- MILAKOVIC, B., PARKER, K. L., GUSTINE, D. D., LAY, R. J., WALKER, A. B. D. & GILLINGHAM, M. P. (2011). Habitat selection by a focal predator (*Canis lupus*) in a multiprey ecosystem of the northern Rockies. *Journal of Mammalogy* **92**, 568–582.
- MILNER-GULLAND, E. J., FRYXELL, J. M. & SINCLAIR, A. R. E. (2011). *Animal Migration: A Synthesis*. Oxford University Press, Oxford.
- MOESLUND, J. E., ARGE, L., BØCHER, P. K., DALGAARD, T. & SVENNING, J.-C. (2013). Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany* **31**, 129–144.
- MONTGOMERY, J. C. & WALKER, M. M. (2001). Orientation and navigation in elasmobranchs: which way forward? *Environmental Biology of Fishes* **60**, 109–116.
- MOORE, I. D., GESSLER, P. E., NIELSEN, G. A. & PETERSON, G. A. (1993). Soil attribute prediction using terrain analysis. *Soil Science Society of America Journal* **57**, 443–452.
- MOORE, C. H., HARVEY, E. S. & VAN NIEL, K. P. (2009). Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships. *ICES Journal of Marine Science* **66**, 2068–2075.
- MOORE, C., HARVEY, E. & VAN NIEL, K. (2010). The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Marine Biology* **157**, 2717–2729.
- MORATO, T., HOYLE, S. D., ALLAIN, V. & NICOL, S. J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences* **107**, 9707–9711.
- MORATO, T., VARKEY, D. A., DAMASO, C., MACHETE, M., SANTOS, M., PRIETO, R., SANTOS, R. S. & PITCHER, T. J. (2008). Evidence of a seamount effect on aggregating visitors. *Marine Ecology Progress Series* **357**, 23–32.
- MORENO-RUEDA, G. & PIZARRO, M. (2007). The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. *Acta Oecologica* **32**, 50–58.
- MUELLER, H. C. & BERGER, D. D. (1967). Wind drift, leading lines, and diurnal migration. *The Wilson Bulletin* **79**, 50–63.
- MUÑOZ, A.-R., MÁRQUEZ, A. L. & REAL, R. (2013). Updating known distribution models for forecasting climate change impact on endangered species. *PLoS ONE* **8**, e65462.
- MUÑOZ, A. R., REAL, R., BARBOSA, A. M. & VARGAS, J. M. (2005). Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. *Diversity and Distributions* **11**, 477–486.
- MURPHY, M. T., ZYSIK, J. & PIERCE, A. (2004). Biogeography of the birds of the Bahamas with special reference to the island of San Salvador. *Journal of Field Ornithology* **75**, 18–30.
- MYERS, R. A. & WORM, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **360**, 13–20.
- MYSTERUD, A., LANGVATN, R., YOCOZ, N. G. & STENSETH, N. C. (2001). Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* **70**, 915–923.
- NEL, D. C., LUTJEHARMS, J. R. E., PAKHOMOV, E. A., ANSORGE, I. J., RYAN, P. G. & KLAGES, N. T. W. (2001). Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series* **217**, 15–26.
- NELSON, T. A. & BOOTS, B. (2008). Detecting spatial hot spots in landscape ecology. *Ecography* **31**, 556–566.
- NETTLESHIP, D. N. (1972). Breeding success of the common puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs* **42**, 239–268.
- NEWTON, I. (2007). *The Migration Ecology of Birds*. Academic Press, London.
- NUR, N., JAHNCKE, J., HERZOG, M. P., HOWAR, J., HYRENBACH, K. D., ZAMON, J. E., AINLEY, D. G., WIENS, J. A., MORGAN, K., BALLANCE, L. T. & STRALBERG, D. (2011). Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. *Ecological Applications* **21**, 2241–2257.
- OLIVIER, F. & WOTHERSPOON, S. J. (2008). Nest selection by snow petrels *Pagodroma nivea* in East Antarctica: validating predictive habitat selection models at the continental scale. *Ecological Modelling* **210**, 414–430.
- ONTIVEROS, D. (1999). Selection of nest cliffs by Bonelli's eagle (*Hieraetus fasciatus*) in southeastern Spain. *Journal of Raptor Research* **33**, 110–116.

- ORD, J. K. & GETIS, A. (2001). Testing for local spatial autocorrelation in the presence of global autocorrelation. *Journal of Regional Science* **41**, 411–432.
- OSBORNE, P. E., ALONSO, J. C. & BRYANT, R. G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology* **38**, 458–471.
- OVIDO, L. (2007). Dolphin sympatric ecology in a tropical fjord: habitat partitioning by bathymetry and topography as a strategy to coexist. *Journal of the Marine Biological Association of the United Kingdom* **87**, 1327–1335.
- OVIDO, L. & SOLÍS, M. (2008). Underwater topography determines critical breeding habitat for humpback whales near Osa Peninsula, Costa Rica: implications for Marine Protected Areas. *Revista de Biología Tropical* **56**, 591–602.
- DE LA PARRA VENEGAS, R., HUETER, R., GONZÁLEZ CANO, J., TYMINSKI, J., GREGORIO REMOLINA, J., MASLANKA, M., ORMOS, A., WEIGT, L., CARLSON, B. & DOVE, A. (2011). An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean Sea. *PLoS ONE* **6**, e18994.
- PARSONS, K. M., BALCOMB III, K. C., FORD, J. K. B. & DURBAN, J. W. (2009). The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Animal Behaviour* **77**, 963–971.
- PERRY, R. W., THILL, R. E. & LESLIE, D. M. (2008). Scale-dependent effects of landscape structure and composition on diurnal roost selection by forest bats. *The Journal of Wildlife Management* **72**, 913–925.
- PETROVSKII, S. & PETROVSKAYA, N. (2012). Computational ecology as an emerging science. *Interface Focus* **2**, 241–254.
- PETTORELLI, N., MYSTERUD, A., YOCOZO, N. G., LANGVATN, R. & STENSETH, N. C. (2005). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **272**, 2357–2364.
- PIATT, J. F., WETZEL, J., BELL, K., DEANGE, A. R., BALOGH, G. R., DREW, G. S., GEERNAERT, T., LADD, C. & BYRD, G. V. (2006). Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: implications for conservation. *Deep-Sea Research Part II: Topical Studies in Oceanography* **53**, 387–398.
- PIKE, R. J. (2000). Geomorphometry – Diversity in quantitative surface analysis. *Progress in Physical Geography* **24**, 1–20.
- PIKE, R. J. (2002). *A Bibliography of Terrain Modeling (Geomorphometry), the Quantitative Representation of Topography* (Volume 4) Open-File Report 02–465. US Geological Survey, Bibliogov, Washington D.C.
- PIKE, R. J., EVANS, I. S. & HENGL, T. (2008). Geomorphometry: a brief guide. In *Geomorphometry: Concepts, Software, Applications* (eds T. HENGL and H. I. REUTER), pp. 1–28. Elsevier, Oxford.
- PIKE, J. R., SHAW, J. H., LESLIE, D. M. JR. & SHAW, M. G. (1999). A geographic analysis of the status of mountain lions in Oklahoma. *Wildlife Society Bulletin* **27**, 4–11.
- PINAUD, D. & WEIMERSKIRCH, H. (2002). Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* **99**, 141–150.
- PIROTTA, E., MATTHIOPOULOS, J., MACKENZIE, M., SCOTT-HAYWARD, L. & RENDELL, L. (2011). Modelling sperm whale habitat preference: a novel approach combining transect and follow data. *Marine Ecology Progress Series* **436**, 257–272.
- PITTMAN, S. J., COSTA, B. M. & BATTISTA, T. A. (2009). Using Lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *Journal of Coastal Research* **53**, 27–38.
- PITTMAN, S. J., MCALPINE, C. A. & PITTMAN, K. M. (2004). Linking fish and prawns to their environment: a hierarchical landscape approach. *Marine Ecology Progress Series* **283**, 233–254.
- POMEROY, P. P., TWISS, S. D. & DUCK, C. D. (2000). Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *Journal of Zoology* **250**, 1–12.
- PREN, A. R., MARSH, H., LAWLER, I. R., PRINCE, R. I. T. & SHEPHERD, R. (1997). Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research* **24**, 185–208.
- QI, F. & ZHU, A.-X. (2003). Knowledge discovery from soil maps using inductive learning. *International Journal of Geographical Information Science* **17**, 771–795.
- QUINN, T. & TEHART, B. (1987). Movements of adult sockeye salmon (*Oncorhynchus nerka*) in British Columbia coastal waters in relation to temperature and salinity stratification: ultra-sonic telemetry results. *Canadian Special Publication of Fisheries and Aquatic Sciences* **96**, 61–77.
- RAUPACH, M. R. & FINNIGAN, J. J. (1997). The influence of topography on meteorological variables and surface-atmosphere interactions. *Journal of Hydrology* **190**, 182–213.
- RAUSET, G., MATTISSON, J., ANDRÉN, H., CHAPRON, G. & PERSSON, J. (2013). When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* **172**, 701–711.
- REESE, D. C. & BRODEUR, R. D. (2006). Identifying and characterizing biological hotspots in the northern California Current. *Deep-Sea Research Part II: Topical Studies in Oceanography* **53**, 291–314.
- RENNIE, S., HANSON, C. E., MCCAULEY, R. D., PATTIARATCHI, C., BURTON, C., BANNISTER, J., JENNER, C. & JENNER, M. N. (2009). Physical properties and processes in the Perth Canyon, Western Australia: links to water column production and seasonal pygmy blue whale abundance. *Journal of Marine Systems* **77**, 21–44.
- RILEY, S. J., DEGLORIA, S. D. & ELLIOT, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* **5**, 23–27.
- RILEY, S. J. & MALECKI, R. A. (2001). A landscape analysis of cougar distribution and abundance in Montana, USA. *Environmental Management* **28**, 317–323.
- RITZ, D. A., HOBDAV, A. J., MONTGOMERY, J. C., WARD, A. J. W. & MICHAEL, L. (2011). Social aggregation in the pelagic zone with special reference to fish and invertebrates. In *Advances in Marine Biology* (Volume 60, ed. M. LESSER), pp. 161–227. Academic Press, London.
- ROBBINS, W. D., HISANO, M., CONNOLLY, S. R. & CHOAT, J. H. (2006). Ongoing collapse of coral-reef shark populations. *Current Biology* **16**, 2314–2319.
- RONCE, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics* **38**, 231–253.
- RUEL, J.-C., PIN, D. & COOPER, K. (1998). Effect of topography on wind behaviour in a complex terrain. *Forestry* **71**, 261–265.
- RUGGIERO, A. & HAWKINS, B. A. (2008). Why do mountains support so many species of birds? *Ecography* **31**, 306–315.
- SADOVY, Y. & DOMEIER, M. (2005). Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* **24**, 254–262.
- SAHLÉN, E., STØEN, O.-G. & SWENSON, J. E. (2011). Brown bear den site concealment in relation to human activity in Sweden. *Ursus* **22**, 152–158.
- SALA, E. (2006). Top predators provide insurance against climate change. *Trends in Ecology & Evolution* **21**, 479–480.
- SAPPINGTON, J. M., LONGSHORE, K. M. & THOMPSON, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave desert. *Journal of Wildlife Management* **71**, 1419–1426.
- SCHLICH, R. (1982). The Indian Ocean: aseismic ridges, spreading centers, and oceanic basins. In *The Ocean Basins and Margins, The Indian Ocean* (Volume 6, eds A. E. M. NAIRN and F. G. STEHLI), pp. 51–147. Plenum Press, New York.
- SCHMIDT, J., EVANS, I. S. & BRINKMANN, J. (2003). Comparison of polynomial models for land surface curvature calculation. *International Journal of Geographical Information Science* **17**, 797–814.
- SCOTT, M. D. & CATTANACH, K. L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the Eastern Pacific. *Marine Mammal Science* **14**, 401–422.
- SCOTT, B. E., SHARPLES, J., ROSS, O. N., WANG, J., PIERCE, G. J. & CAMPHUYSEN, C. J. (2010). Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series* **408**, 207–226.
- SERGIO, F., MARCHESI, L. & PEDRINI, P. (2004). Integrating individual habitat choices and regional distribution of a biodiversity indicator and top predator. *Journal of Biogeography* **31**, 619–628.
- SERGIO, F., NEWTON, I. A. N., MARCHESI, L. & PEDRINI, P. (2006a). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* **43**, 1049–1055.
- SERGIO, F., PEDRINI, P., RIZZOLLI, F. & MARCHESI, L. (2006b). Adaptive range selection by golden eagles in a changing landscape: a multiple modelling approach. *Biological Conservation* **133**, 32–41.
- SERGIO, F., SCANDOLARA, C., MARCHESI, L., PEDRINI, P. & PENTERIANI, V. (2005). Effect of agro-forestry and landscape changes on common buzzards (*Buteo buteo*) in the Alps: implications for conservation. *Animal Conservation* **8**, 17–25.
- SIMMONDS, M. P. & ISAAC, S. J. (2007). The impacts of climate change on marine mammals: early signs of significant problems. *Oryx* **41**, 19–26.
- SOMERFIELD, P. J. & CLARKE, K. R. (2013). Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. *Journal of Experimental Marine Biology and Ecology* **449**, 261–273.
- SWEANOR, L. L., LOGAN, K. A. & HORNOCKER, M. G. (2000). Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* **14**, 798–808.
- SZOR, G., BERTEAUX, D. & GAUTHIER, G. (2008). Finding the right home: distribution of food resources and terrain characteristics influence selection of denning sites and reproductive dens in arctic foxes. *Polar Biology* **31**, 351–362.
- TEWS, J., BROSE, U., GRIMM, V., TIELBÖRGER, K., WICHMANN, M. C., SCHWAGER, M. & JELTSCH, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.
- THORNTWHAITE, C. W. (1953). A charter for climatology. *World Meteorological Organization Bulletin* **2**, 40–46.
- TITUS, K. & MOSHER, J. A. (1982). The influence of seasonality and selected weather variables on autumn migration of three species of hawks through the Central Appalachians. *The Wilson Bulletin* **94**, 176–184.
- TOVAR-PESCADOR, J., POZO-VÁZQUEZ, D., RUIZ-ARIAS, J. A., BATLLES, J., LÓPEZ, G. & BOSCH, J. L. (2006). On the use of the digital elevation model to estimate the solar radiation in areas of complex topography. *Meteorological Applications* **13**, 279–287.

- TWISS, D. S., CAUDRON, A., POMEROY, P. P., THOMAS, C. J. & MILLS, J. P. (2000). Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. *Animal Behaviour* **59**, 327–338.
- TWISS, D. S. & THOMAS, C. J. (1999). Fine scale topographical influences on Environmental Potential for Polygamy (EPP) and male reproductive success in grey seals. In *Proceedings of the 13th Annual Conference of the European Cetacean Society*, Valencia, Spain, pp. 191–195.
- UNDERWOOD, E., VIERS, J., QUINN, J. & NORTH, M. (2010). Using topography to meet wildlife and fuels treatment objectives in fire-suppressed landscapes. *Environmental Management* **46**, 809–819.
- VALESINI, F. J., CLARKE, K. R., ELIOT, I. & POTTER, I. C. (2003). A user-friendly quantitative approach to classifying nearshore marine habitats along a heterogeneous coast. *Estuarine, Coastal and Shelf Science* **57**, 163–177.
- VETTER, E. W., SMITH, C. R. & DE LEO, F. C. (2010). Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. *Marine Ecology* **31**, 183–199.
- VIANNA, G. M. S., MEEKAN, M. G., PANNELL, D. J., MARSH, S. P. & MEEUWIG, J. J. (2012). Socio-economic value and community benefits from shark-diving tourism in Palau: a sustainable use of reef shark populations. *Biological Conservation* **145**, 267–277.
- VUCETICH, J. A., PETERSON, R. O. & WAITE, T. A. (2004). Raven scavenging favours group foraging in wolves. *Animal Behaviour* **67**, 1117–1126.
- VULINEC, K. (1990). Collective security: aggregation by insects as a defense. In *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators* (eds D. L. EVANS and J. O. SCHMIDT), pp. 251–288. State University of New York Press, New York.
- WALKER, B. K., JORDAN, L. K. B. & SPIELER, R. E. (2009). Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. *Journal of Coastal Research* **53**, 39–48.
- WARREN, S. D., HOHMANN, M. G., AUERSWALD, K. & MITASOVA, H. (2004). An evaluation of methods to determine slope using digital elevation data. *Catena* **58**, 215–233.
- WARRICK, G. D. & CYPHER, B. L. (1998). Factors affecting the spatial distribution of San Joaquin kit foxes. *Journal of Wildlife Management* **62**, 707–717.
- WATKINS, J. (2008). Aggregation and vertical migration. In *Krill: Biology, Ecology and Fisheries* (ed. I. EVERSON), pp. 80–102. Blackwell Science, Oxford.
- WEDDING, L., LEPCZYK, C., PITTMAN, S., FRIEDLANDER, A. & JORGENSEN, S. (2011). Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. *Marine Ecology Progress Series* **427**, 219–232.
- WEILGART, L. & WHITEHEAD, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology* **40**, 277–285.
- WEIMERSKIRCH, H., CORRE, M. L., KAI, E. T. & MARSAC, F. (2010). Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. *Progress in Oceanography* **86**, 204–213.
- WHITE, M., BASHMACHNIKOV, I., ARISTEGUI, J. & MARTINS, A. (2007). Physical processes and seamount productivity. In *Seamounts: Ecology, Fisheries & Conservation* (eds T. J. PITCHER, T. MORATO, P. J. B. HART, M. R. CLARK, N. HAGGAN and R. S. SANTOS), pp. 65–84. Blackwell Publishing, Oxford.
- WHITEWAY, T. G. (2009). *Australian Bathymetry and Topography Grid, June 2009*. Geoscience Australia. Available at https://www.ga.gov.au/products/servlet/controller?event=GEOCAT_DETAILS&catno=67703. Accessed March 2013.
- WIENS, J. (1989). Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- WILLIAMS, R., LUSSEAU, D. & HAMMOND, P. S. (2009). The role of social aggregations and protected areas in killer whale conservation: the mixed blessing of critical habitat. *Biological Conservation* **142**, 709–719.
- WILLIAMS, J., REVELLE, C. & LEVIN, S. (2005). Spatial attributes and reserve design models: a review. *Environmental Modeling and Assessment* **10**, 163–181.
- WILSON, M. F. J., O'CONNELL, B., BROWN, C., GUINAN, J. C. & GREHAN, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geology* **30**, 3–35.
- WILSON, S., TAYLOR, J. & PEARCE, A. (2001). The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/Southern Oscillation. *Environmental Biology of Fishes* **61**, 1–11.
- WILSON, B., THOMPSON, P. M. & HAMMOND, P. S. (1997). Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* **34**, 1365–1374.
- WINTLE, B. A., ELITH, J. & POTTS, J. M. (2005). Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of New South Wales. *Austral Ecology* **30**, 719–738.
- WOLANSKI, E. & HAMNER, W. M. (1988). Topographically controlled fronts in the ocean and their biological influence. *Science* **241**, 177–181.
- WOLF, M. & ALE, S. (2009). Signs at the top: habitat features influencing snow leopard *Uncia uncia* activity in Sagarmatha National Park, Nepal. *Journal of Mammalogy* **90**, 604–611.
- WOOD, J. (2005). *LandSerf*. London University, Department of Information Science. Available at <http://www.soi.city.ac.uk/~jwo/landserf/>. Accessed March 2013.
- WOODROFFE, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* **3**, 165–173.
- WORM, B., LOTZE, H. & MYERS, R. (2003). Predator diversity hotspots in the blue ocean. *Proceedings of the National Academy of Sciences* **100**, 9884–9888.
- WRIGHT, D. J., PENDLETON, M., BOULWARE, J., WALBRIDGE, S., GERLT, B., ESLINGER, D., SAMPSON, D. & HUNTLEY, E. (2012). *ArcGIS Benthic Terrain Modeler (BTM)*. NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management, Environmental Systems Research Institutes. Available at <http://www.csc.noaa.gov/digitalcoast/tools/btm>. Accessed March 2013.
- WU, J. (2004). Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology* **19**, 125–138.
- WU, S., LI, J. & HUANG, G. H. (2008). A study on DEM-derived primary topographic attributes for hydrologic applications: sensitivity to elevation data resolution. *Applied Geography* **28**, 210–223.
- WU, J., SHEN, W., SUN, W. & TUELLER, P. (2002). Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology* **17**, 761–782.
- YEN, P. P. W., SYDEMAN, W. J. & HYRENBACH, K. D. (2004). Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems* **50**, 79–99.
- YEN, P. P. W., SYDEMAN, W. J., MORGAN, K. H. & WHITNEY, F. A. (2005). Top predator distribution and abundance across the eastern Gulf of Alaska: temporal variability and ocean habitat associations. *Deep-Sea Research Part II: Topical Studies in Oceanography* **52**, 799–822.
- ZHANG, N. & LI, H. (2013). Sensitivity and effectiveness of landscape metric scalograms in determining the characteristic scale of a hierarchically structured landscape. *Landscape Ecology* **28**, 343–363.
- ZIELINSKI, W. J., TRUEX, R. L., SCHMIDT, G. A., SCHLEXER, F. V., SCHMIDT, K. N. & BARRETT, R. H. (2004). Resting habitat selection by fishers in California. *Journal of Wildlife Management* **68**, 475–492.
- ZUUR, A. F., IENO, E. N. & ELPHICK, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3–14.

(Received 27 June 2013; revised 22 June 2014; accepted 23 June 2014; published online 15 August 2014)