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Causal explanations for the evolution of 'low gear' locomotion in insular ruminants

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Abstract

Aim: Mammals on islands often undergo remarkable evolutionary changes. The acquisition of 'low gear' locomotion, namely short and robust limb elements, has been typically associated with the island syndrome in large mammals and, especially, ruminants. Here we provide an investigative framework to examine biotic and abiotic selective factors hypothesized to influence evolution of this peculiar type of gait.

Location: Islands worldwide.

Taxon: Bovidae.

Methods: We calculated response variables associated with 'low gear' locomotion in 21 extinct and extant insular bovids. We assembled data on the physiography of 11 islands and on life history and ecological traits of the focal taxa. We estimated 10 predictors (island area and four topographic indices, body mass, body size divergence, number of predators and competitors, large mammal richness) and used multiple regressions, regression trees, and random forests to assess their contextual importance.

Results: The acquisition of 'low gear' locomotion generally happens on islands with a small number of competitors. However, the roughness of the island terrain appears to be also important, without being a main driver. Finally, although the most extreme cases of 'low gear' locomotion occurred on islands with no mammalian predators, our models show a non-significant relationship with this factor.

Main conclusions: The evolution of 'low gear' locomotion in insular ruminants does not simply result from phyletic dwarfing and predatory release. Variation in morphological responses within Bovidae to ecological and topographic traits suggests, instead, a complex interplay of biotic and abiotic factors. Current understanding on the main drivers of species evolutionary pathways and biogeographic patterns are disproportionally based on few taxa, mainly vertebrates, and in some extreme cases (like this one) even on few species. Here we show how adding more data, even within the same taxonomic group, can challenge historically accepted macroevolutionary and macroecological concepts.

KEYWORDS

Bovidae, fossils, island evolution, island syndrome, islands, mammals, palaeoecology

1 | INTRODUCTION

Mammals are a prime target to investigate the suite of responses to the geographic isolation and ecological simplicity of island environments known as the island syndrome (Adler & Levins, 1994; Heaney, 1978; Lomolino, 1985; Lomolino et al., 2013; Wallace, 1880). The best-known trait shift that characterizes insular mammals is body size change, a graded trend from gigantism in small species to dwarfism in large species (e.g. Faurby & Svenning, 2016; Foster, 1964; Lomolino, 1985, 2005; Lomolino, Riddle, & Whittaker, 2017; McClain, Durst, Boyer, & Francis, 2012; Van Valen, 1973). Its magnitude and direction result from a combination of selective biotic and abiotic factors (Durst & Roth, 2015; Heaney, 1978; Lomolino, Sax, Palombo, & Van der Geer, 2012; Meiri, Cooper, & Purvis, 2008; Palombo, 2007; Rozzi & Lomolino, 2017; Van der Geer, Lyras, Lomolino, Palombo, & Sax, 2013; Van der Geer et al., 2016). However, in addition to shifts in body size towards that of intermediate-sized taxa, mammals on islands often undergo morphological changes in their skull, brain, teeth and appendicular skeleton (Angelone et al., 2018; Bover & Alcover, 1999a; Bover & Fornós, 2005; De Vos, 2000; Diniz-Filho & Raia, 2017; Jordana, Marín-Moratalla, DeMiguel, Kaiser, & Köhler, 2012; Köhler & Moyà-Solà, 2004; Larramendi & Palombo, 2015; Lyras, 2018; Palombo, Rozzi, & Bover, 2013; Quintana, Köhler, & Moyà-Solà, 2011; Rozzi, 2017; Rozzi, Winkler, De Vos, Schulz, & Palombo, 2013; Sondaar, 1977; Van der Geer, Lyras, Mitteroecker, & MacPhee, 2018; Weston & Lister, 2009; Winkler et al., 2013). Extinct and extant insular ruminants, and to a lesser degree insular elephants and hippopotamuses, often evolved a peculiar structure of the limbs by shortening limb elements—most markedly the metapodials, increasing their robustness, and occasionally developing bone fusions (Bover & Fornós, 2005; Bover, Quintana, & Alcover, 2010; Leinders & Sondaar, 1974; Rozzi & Palombo, 2014; Sondaar, 1977; Van der Geer, 2014a; Van der Geer, Lyras, De Vos, & Dermitzakis, 2011). This has been explained as an adaptation for what P.Y. Sondaar (Sondaar, 1977) described as 'low gear' locomotion—a frequent phenomenon believed to be advantageous, in the absence of predators, for low-speed walking in mountainous environments. The acquisition of this type of locomotion would result in increased mediolateral bending strength of distal limb bones (Higgins, 2014) and overall better stability on uneven terrain (Rozzi & Palombo, 2014; Van der Geer et al., 2011). Furthermore, there would not be any downside in the consequent loss of cursorial aptitude in the focal taxa, due to the lack of mammalian predators that generally characterizes insular faunas (Sondaar, 1977). Lack of predators may select for increasing body stability, while decreasing running speed and manoeuvrability (Lyras, Giannakopoulou, Lillis, Veis, & Papadopoulos, 2016; Palombo & Zedda, 2016; Van der Geer et al., 2011).

Relative shortening and/or thickening of metapodials is recorded in several fossil and extant insular ruminants, such as dwarf buffaloes (*Bubalus cebuensis*, *B. mindorensis*, *B. depressicornis*, *B. quarlesi*; Croft, Heaney, Flynn, & Bautista, 2006; Rozzi, 2017; Rozzi & Palombo, 2014), the Formosan serow (*Capricornis swinhoei*; Rozzi

& Palombo, 2014), all species of *Myotragus* (Bover, 2004; Bover et al., 2010), the smallest *Hoplitomeryx* (*H. matthei* and *H. devosi* sensu Van der Geer, 2014b; see Mazza et al., 2016; Van der Geer, 2014b), the Ryukyu deer (*Cervus astylodon*; Van der Geer, 2014a; Van der Geer et al., 2011), the Kassos deer (*Candiacervus cerigensis*; Van der Geer, 2014a; Van der Geer et al., 2011), the Karpathos deer (*C. pygadiensis*; Van der Geer, 2014a; Van der Geer et al., 2011) and some species of Cretan deer (*C. ropalophorus*, *C.* sp. (size II), *C. cretensis*; Van der Geer, 2014a, 2018; Van der Geer et al., 2011). In a few cases (*Myotragus balearicus*, *C. ropalophorus*, and the smallest *Hoplitomeryx*) short and robust distal limb bones are already present at birth, but they become even more stout during postnatal ontogeny (Bover & Alcover, 1999b; Van der Geer, 2014a; Van der Geer et al., 2011). Bone fusions likely dampen instability of the joints and reduce lateral movement of the stride by restricting functionally undesirable lateral and planar movement (e.g. Bover & Fornós, 2005; Rozzi & Palombo, 2014; Van der Geer et al., 2011). However, they are rare in insular ruminants, except for the fusion of the metatarsal with the naviculo-cuboid and cuneiforms in *Myotragus* and *Hoplitomeryx* (see e.g. Bover & Fornós, 2005; Van der Geer, 2014a). *Myotragus balearicus* is also characterized by shortened phalanges, that is, shorter feet, rare fusion of the distal fibula (*os malleolare*) and tibia (observed also in *Hoplitomeryx*), and occasional carpal fusions (scapholunar and pisiform-cuneiform fusions), making this species the most extreme case of 'low gear' locomotion (see e.g. Bover & Fornós, 2005; Sondaar, 1977; Van der Geer, 2014a).

A few studies presented an overview of taxa exhibiting morphological features associated with 'low gear' locomotion, discussed problems in assessing its generality and suggested that the main driver behind this evolutionary pathway would be the lack of mammalian predators on the focal islands (Palombo & Rozzi, 2013; Rozzi & Palombo, 2014; Sondaar, 1977; Van der Geer, 2005, Van der Geer, 2014; Van der Geer et al., 2011). Nevertheless, a quantitative investigation of the causal forces influencing the acquisition of this peculiar type of locomotion in insular ruminants has yet to be conducted. Bovidae is a highly diverse clade of large mammals (e.g. Bibi, 2013; Bibi et al., 2009), which provides an excellent opportunity to study how locomotion on different terrains affects loading regimes experienced by distal limb elements and, consequently, their morphology (Higgins, 2014). Here we focus on insular bovids, which encompass a variety of species exhibiting different degrees of metapodial shortening and thickening (see also Rozzi & Palombo, 2014) and which inhabited or are still living on islands located in different regions and characterized by varied palaeogeographic histories and evolutionary pressures. We expand the dataset for insular bovids as given in Rozzi and Palombo (2014) and investigate the selective factors hypothesized to influence the evolution of 'low gear' locomotion extensively for the first time. We concentrate on the two main morphological traits associated with this peculiar type of locomotion (i.e. short and robust metapodials) and we predict that they should be most pronounced for:

1. Smaller species and/or species that are strongly reduced in size relative to their mainland ancestors or closest mainland relatives.

2. Species that inhabited or are still living on islands with the fewest predators (Figure 1).
3. Species that inhabited or are still living on islands characterized by homogenously mountainous landscapes (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Dataset

The dataset includes the majority of extant (6) and Plio-Holocene (15) insular bovids (Table S1). Linear measurements (recorded to the tenth of a millimetre) of distal limb elements were used to estimate shortening and degree of robustness (see below and Tables S1 and S2). Additional specimens were used for morphological comparisons. The sources for these data and a complete list of specimens (780), stored in 13 European and American museums, are reported in Table S3. In three cases (*Myotragus balearicus*, *Ovibos moschatus wardi*, and *Nesogoral cenisae*), estimates were based on additional data given in publications (Table S1). In addition to these measurements, we recorded 10 predictor variables (see below) describing topographic and ecological conditions of the focal taxa or islands (see Table S4, for characterization of 11 focal islands).

2.2 | Description of main variables associated with 'low gear' locomotion

We calculated mean robustness indices (RI; transverse diameter at midshaft/total length) of metacarpals (RI Mc) and metatarsals (RI Mt) (Tables S1 and S2, and a few examples in Figure 2). Because stout metapodials are not necessarily short and vice versa, we also defined species average shortening index (SI) of metacarpals (SI Mc; length of metacarpal/length of radius) and metatarsals (SI Mt; length of metatarsal/length of tibia) (see Tables S1 and S2, and a few examples in Figure 3). Evaluating changes in relative proportions of limb elements of fossil insular bovids is extremely difficult because remains belonging to a single individual are rare. Accordingly, we measured bones with matching epiphyseal articulation of comparable size recovered from the same site. Furthermore, because living insular bovids do not exhibit significant sexual size dimorphism (see e.g. Jass & Mead, 2004; Martin & Barboza, 2020; Rozzi, 2017, 2018; Rozzi & Palombo, 2014 and references in those papers), robustness and shortening indices based on specimens of male and female individuals were averaged together to obtain reference mean values.

We performed a correlation analysis of these morphometric variables in R ver. 3.5.0 (R Core Team, 2013) using the function *ggpairs* in the package 'GGally' (Schloerke et al., 2018). Hindlimb and forelimb shortening and robustness indices are positively correlated ($r = 0.633$ and 0.953; see Figure S1). Therefore, we selected as our response variables the two indices associated with the highest numbers of observations in the dataset (SI Mt and RI Mc).

2.3 | Description of predictor variables: body size and S_i, ecology, topography

To test whether the most common morphological features associated with 'low gear' locomotion (i.e. shortening and thickening of metapodials) are dependent on body size and body size change (prediction 1), we took body mass values from the literature (Rozzi, 2018). We also included estimates of S_i (= insular body size divergence, sensu Lomolino, 1985, 2005), that is the mass of the insular taxon divided
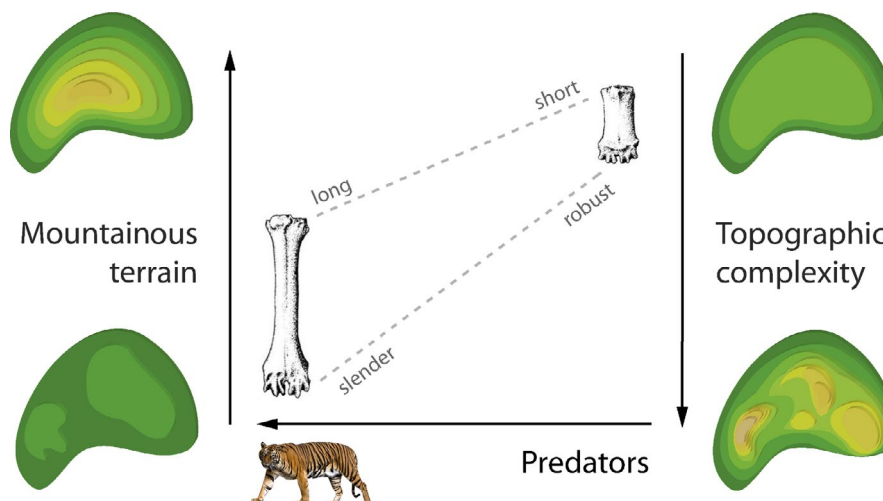

FIGURE 1 Conceptual model illustrating the contextual nature of selective forces hypothesized to influence shortening and/or thickening of metapodials in insular ruminants. Drafts of metacarpals from Sondaar (1977). Image of Sumatran tiger modified from Wikimedia Commons: https://upload.wikimedia.org/wikipedia/commons/e/e1/Sumatran_Tiger_Berlin_Tierpark.jpg?uselang=de by Captain Herbert, licensed under CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)
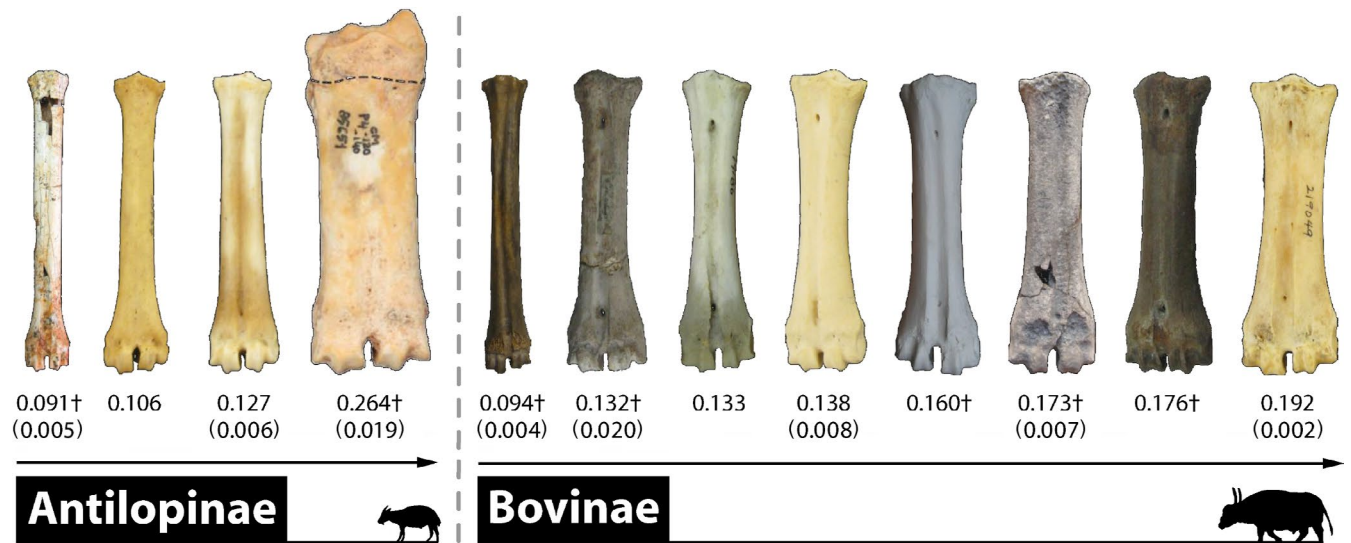
FIGURE 2 Selection of metatarsals of extant and fossil insular bovids arranged in order of increasing RI and by subfamily. Mean and standard deviation values of RI Mt (if available) are reported under each bone. All the specimens are figured with the same total length in order to highlight their different RI Mt values. Antilopinae, from left to right: *Nesogoral* sp., *Capricornis crispus*, *C. swinhoei*, *Myotragus balearicus*. Bovinae, from left to right: *Duboisia santeng*, *Bos primigenius siciliae*, *Bubalus quarlesi*, *Bubalus depressicornis*, *Bubalus cebuensis*, *Bubalus palaeokerabau*, *Bison priscus siciliae*, *Bubalus mindorensis*

FIGURE 3 Selection of radii and metacarpals of extant and fossil insular bovids. Metacarpals are arranged in order of decreasing shortening index and by subfamily. Mean and standard deviation values of SI Mc (if available) are reported under each bone. All radii are figured with the same total length in order to highlight different SI Mc values. Antilopinae, from left to right: *Nesogoral* sp., *Capricornis crispus*, *C. swinhoei*, *Myotragus balearicus*. Bovinae, from left to right: *Duboisia santeng*, *Bibos palaesondaicus*, *Bubalus depressicornis*, *Bubalus mindorensis*. Images of metacarpals of *Myotragus balearicus*, *Bibos palaesondaicus* and *Nesogoral* sp. were flipped horizontally to match corresponding left radii of comparable size

by that of its putative mainland relative, the latter based on geographic proximity and taxonomic designation (see Table S1).

Variables describing ecological conditions of the focal insular communities (see prediction 2) included species richness of large mammals and number of predators or competitors likely to directly interact with the focal insular taxa. Values were taken from

Rozzi (2018) and were estimated by first developing a list of all other mammals co-occurring on each island, and then consulting references on the diet and habitats of those species to assess which ones were likely to be predators or competitors of the focal taxa (see Materials and Methods and Supporting Information in Rozzi, 2018 for details).

To examine the role that habitat selection had on each island either in driving the acquisition of 'low gear' locomotion or in maintaining/increasing a cursorial aptitude (prediction 3), we obtained island (palaeo) area from different published sources (Table S4) and we calculated different topographic indices (see e.g. Yu et al., 2015). We took maximum elevation values for each island (= range of elevation sensu Yu et al., 2015) from the UN Island database (Table S4). Although maximum elevation of focal islands might have fluctuated in response to Plio–Pleistocene sea-level changes, tectonics and volcanic activity (see e.g. Champagnac, Molnar, Sue, & Herman, 2012), present values likely provide an idea of the presence of mountainous areas on each island over time. To calculate other topographic indices, we first obtained altitude information for each island by using ETOPO1 (Amante & Eakins, 2009), an 1 arc-minute global relief model of Earth's surface, and the 'raster' package in R (Hijmans, 2018). To obtain the perimeter of each island in the present we used a global land-mask shapefile downloaded from https://www.naturalearthdata.com/downloads/10m-physical-vectors/, and selected our islands with QGIS (QGIS Development Team, 2020, ver. 2.18.20). To quantify the irregularity of the terrain, we used a roughness index that measures the degree of irregularity of the surface by estimating the largest inter-cell difference of the central pixel and its eight surrounding cells using QGIS. We then reclassified the roughness map into a binary map identifying mountainous areas, that is pixels with a roughness index larger than 100, indicating a difference of over 100 m in a circle of a ~2 km ratio (at the equator). Finally, we used these physiographic data and the (palaeo) area of island size (see above and Table S4) to calculate the following indices: mean roughness, accumulated roughness (= total roughness of each island) and mountainous terrain (= percentage of mountainous areas on each island). We used R (ver. 3.5.0), with the packages 'raster' (Hijmans, 2018), 'maptools' (Bivand & Lewin-Koh, 2017) and 'rgdal' (Bivand, Keitt, & Rowlingson, 2017). Code available in https://github.com/macroecology/islands.

Finally, to assess the role of bauplan—or phylogenetic conservatism of body plan (see e.g. Harvey & Pagel, 1991; Losos, 2008)—in influencing the acquisition of 'low gear' locomotion, we also included subfamily of the focal taxa (Antilopinae or Bovinae) as a predictor variable in the analyses.

2.4 | Data analysis

We fitted multiple linear regression models to investigate the relationship between response variables (SI Mt and RI Mc) and predictor variables describing life history, ecological, and topographic conditions of the focal taxa and islands. We scaled selected predictor variables with a Z-transformation and we verified model assumptions by inspecting diagnostic plots of the residuals. For both dependent variables, we tested the effects of each predictor separately, and we fitted a 'maximal' model with all predictors, three models including variables associated with the focal predictions (see above; body size and S_i, ecology, topography), and a null model (intercept-only).

In all models, we included subfamily as a fixed effect to account for phylogenetic dependence (see Table 1). Furthermore, we tested the interaction between subfamily and each predictor (differences in slopes between the groups). We followed this approach and did not fit linear mixed models with subfamily as a random effect to avoid singularity, which commonly occurs with small numbers of random-effect levels (e.g. <5; see Bates, Kliegl, Vasishth, & Baayen, 2018; Gelman, 2006; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017) and which we observed in a preliminary analysis (subfamily includes only two levels). Phylogenetic trees are unavailable for most of the species in our dataset, precluding the use of more complex modelling techniques (e.g. Phylogenetic generalized least squares). To detect collinearity between the predictors in the most complex models we calculated variance inflation factors (vifs) (see e.g. Thompson, Kim, Aloe, & Becker, 2017). We used Akaike information criterion scores for small sample sizes (AICc) to rank our models and selected two 'top model sets' (one for each response variable) containing models with ΔAICc between 0 and 6 (Harrison et al., 2018). All statistical analyses were conducted in R ver. 3.5.0 (R Core Team) using the following packages: 'lme4' (Bates et al., 2019), 'dplyr' (Wickham, François, Henry, Müller, & RStudio, 2020), 'ggplot2' (Wickham et al., 2019), 'ggfortify' (Horikoshi et al., 2019), 'GGally' (Schloerke et al., 2018), 'AICcmodavg' (Mazerolle, 2019), 'car' (Fox et al., 2019), 'jtools' (Long, 2020), 'RColorBrewer' (Neuwirth, 2014) and 'gridExtra' (Auguie & Antonov, 2017).

To further assess the most important predictors influencing the evolution of 'low gear' locomotion in the focal taxa, we ran a regression tree analysis on the RI Mc dataset (which encompasses the highest number of observations; $n = 19$). Although regression trees—as all other machine learning methods—do not assume data independence (Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009; Lomolino et al., 2012; Melo, Rangel, & Diniz-Filho, 2009; Rozzi, 2018; Westoby, Leishman, & Lord, 1995), we decided to include subfamily of the focal taxa as a predictor variable in the analysis to further control for the effects of phylogenetic affinities. The main product of regression tree analysis is a branching tree that describes the contextual relationships between the response variable (here RI Mc) and a subset of predictors (life history, ecological and topographic variables) (see e.g. Durst & Roth, 2012, 2015; Lomolino et al., 2012; Lyons et al., 2016; Rozzi, 2018; Van der Geer, Lomolino, & Lyras, 2018). We adopted a holdout validation approach (split ratio = 75:25) and built a regression tree using *MSE* (mean squared error) splitting criterion. To prevent overfitting we pruned the tree by setting a maximum depth of two. In other words, given the small sample size, we focused only on the first split to interpret our results. Furthermore, we assessed the importance of predictors across many different possible trees by performing a random forest analysis. Random forests fit a number of decision trees on various subsamples of the dataset and use averaging to control overfitting and improve predictive accuracy (Prasad, Iverson, & Liaw, 2006). Accordingly, they do not overfit as easily as decision trees and deal well with high-dimensional feature spaces and small sample sizes (Biau & Scornet, 2016; Breiman, 2001). We created a random forest with 100 trees and used *MSE* (mean squared error) splitting criterion to build

TABLE 1 Results of regression analyses of the relationships among response and predictor variables in the study. *P*-values < 0.05 are in bold. For additional statistical details, see Tables S5, S6, S7

Regression model	Predictor variables	RSE	R^2	p
$Y = b_0 + b_1X_1 + b_2X_2 + b_{12}(X_1X_2)$	Y = RI Mc; X_1 = Mammal richness; X_2 = Subfamily	0.08404	0.4068	**0.01233**
	Y = RI Mc; X_1 = Competitors; X_2 = Subfamily	0.05785	0.719	**5.395e−05**
	Y = RI Mc; X_1 = Mountainous terrain; X_2 = Subfamily	0.1085	0.01087	**3.37e−04**
	Y = SI Mt; X_1 = Competitors; X_2 = Subfamily	6.575	0.4007	0.0562
$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + ...$				
All	Y = RI Mc; X_1, X_2,..., X_{11} = All predictor variables	0.03443	0.9004	**6.591e−04**
Ecology	Y = RI Mc; X_1 = Mammal richness; X_2 = Predators; X_3 = Competitors; X_4 = Subfamily	0.07039	0.5839	**0.002131**
Topography	Y = RI Mc; X_1 = Island area; X_2 = Maximum elevation; X_3 = Mean roughness; X_4 = Accumulated roughness; X_5 = Mountainous terrain; X_6 = Subfamily	0.1087	0.006951	0.4426
Body size and S_i	Y = RI Mc; X_1 = S_i; X_2 = Body size; X_3 = Subfamily	0.1133	−0.07712	0.6431
All	Y = SI Mt; X_1, X_2,..., X_{11} = All predictor variables	7.268	0.2678	0.4783
Ecology	Y = SI Mt; X_1 = Mammal richness; X_2 = Predators; X_3 = Competitors; X_4 = Subfamily	7.399	0.2411	0.195
Topography	Y = SI Mt; X_1 = Island area; X_2 = Maximum elevation; X_3 = Mean roughness; X_4 = Accumulated roughness; X_5 = Mountainous terrain; X_6 = Subfamily	4.908	0.6661	**0.03567**
Body size and S_i	Y = SI Mt; X_1 = S_i; X_2 = Body size; X_3 = Subfamily	9.166	−0.1646	0.7335

the trees. To visualize the most important features of the dataset, we reported feature importance scores for both the regression tree and random forest models. Furthermore, we used the test data to calculate R^2 and *MSE* and validate the models' performance. All machine learning analyses were performed using PYTHON 3.7.3 and the packages 'scikit-learn' (Pedregosa et al., 2011), 'pandas' (McKinney, 2011), 'seaborn' (Waskom et al., 2020), 'matplotlib' (Caswell et al., 2020), 'numpy' (Oliphant, 2006) and 'graphviz' (Bank, 2019).

3 | RESULTS

Results of regression analyses show significant relationships between RI Mc and richness of large mammals, number of competitors and amount of mountainous terrain (Figure 4, Tables 1 and S5). We observed a negative relationship between RI Mc and richness of large mammals, but we found no evidence for an interaction between the latter and subfamily ($F_{1,15}$ = 0.4397, p = 0.52, Figure 4a). Conversely, slopes of the relationships between number of competitors and RI Mc and amount of mountainous terrain and RI Mc are significantly different between the two subfamilies Antilopinae and Bovinae ($F_{1,15}$ = 22.985, p < 0.001, Figure 4b; $F_{1,15}$ = 23.5885, p < 0.001, Figure 4c). In particular, while a negative relationship between amount of mountainous terrain and RI Mc can be observed within Antilopinae, a slightly positive slope characterizes this relationship within Bovinae (slope = 0.000323; Figure 4c). No correlation between RI Mc and all other predictors—including number of predators, mean roughness and accumulated roughness—was found. Model selection based on ΔAICc

revealed that number of competitors (AICcWt = 0.91) and amount of mountainous terrain (AICcWt = 0.09) are particularly important to explain the acquisition of robust metapodials in the focal taxa (Table S7). A more complex model, with all ecological independent variables, although statistically significant (see Table 1) and including non-collinear predictors (vifs < 4; Hair, Black, Babin, Anderson, & Tatham, 1998), received a higher (i.e. worse) AICc score (AICc$_{ecology}$ = −33.73; Table S7). Results of regression tree analyses and random forest analyses confirm the importance of large mammal richness and number of competitors, but they also suggest that body size and S_i might have played a role in influencing the evolution of stout metapodials in insular bovids. In fact, richness of large mammals, body size, number of competitors and S_i contribute the most to the predictive accuracy of the obtained random forest model (Figure 4e), and richness of large mammals provides the first split in the regression tree generated from analysis of the RI Mc dataset (Figure S2).

A negative relationship between the number of competitors and SI Mt can be observed in Figure 4d, but it is not statistically significant (p = 0.056, Table 1) and does not vary across subfamilies (intercepts and slopes are not significantly different between Antilopinae and Bovinae; Table S6). However, the effect of competitors within the model is statistically significant per se (p = 0.02). No significant relationships between SI Mt and other predictors were found and none of our models—including the 'maximal' model—received a better AICc score than the null model (Table S7). Nevertheless, model selection based on ΔAICc suggested that number of competitors (AICcWt = 0.18) contributes, albeit marginally, to influence the evolution of short limbs in island bovids (Table S7).
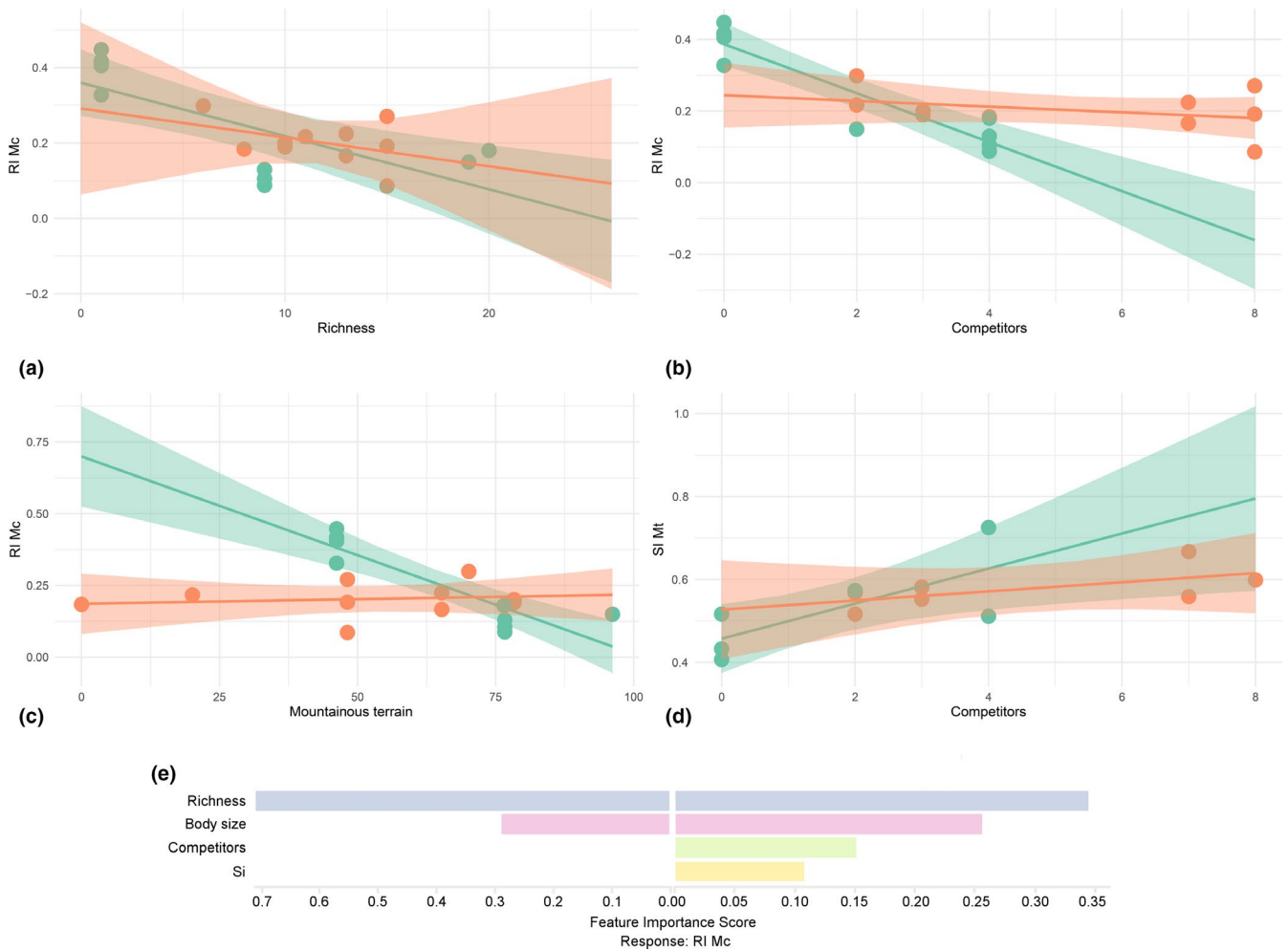
FIGURE 4 Results of regression analyses between mean robustness index of metacarpals (RI Mc) and richness of large mammals (a), number of competitors (b) and amount of mountainous terrain (c); and between metatarsal shortening index (SI Mt) and number of competitors (d). Representatives of Antilopinae are depicted in green, while representatives of Bovinae are depicted in orange. Shaded area represents 95% confidence interval of a linear regression. For detailed statistical results, see Tables 1, S5, S6 and S7). (d) Report showing the importance of features included in regression tree (on the left) and random forest (on the right) models and how much they contribute to their predictive accuracy. All importance scores are rescaled to have values between 0 and 1 and only predictors with scores higher than 0.05 are included

4 | DISCUSSION

4.1 | Allometry and phylogenetic conservatism of bauplan

Our assessment of causal explanations influencing the acquisition of 'low gear' locomotion suggests that the evolution of short and robust metapodials in insular ruminants does not parallel the direction and magnitude of their island rule pattern, that is, it cannot be explained by a simple allometric downscaling of the animals (prediction 1; see also Rozzi & Palombo, 2014). In fact, no significant relationships were found between our response variables—RI Mc and SI Mt—and body size of the island species or S_i (Table 1), and multiple models that included these two predictors received worse AICc scores than null models (Table S7). On the other hand, the role of bauplan (and subfamily, as a surrogate) in the evolution of robust

metapodials in the focal species is not negligible, as it seems to act as a constraint on their different responses to some ecological and topographic predictors (see Figure 4b,c). In particular, not only intercepts and slopes of the relationships between RI Mc and some predictors are significantly different between the two focal subfamilies, but the subfamily Bovinae is characterized by less extreme slopes (Figure 4a–d). Insular Antilopinae maintain a caprine-like bauplan (i.e. weighing less than 70 kg, with a slender chest), while insular Bovinae maintain a bovine/bubaline-like bauplan (i.e. weighing more than 70 kg, with a broader barrel chest) suggesting taxonomic constraints of phylogenetic conservatism. Accordingly, differences in limb proportions and shape in larger and more robust species (i.e. Bovinae) are likely less dependent on habitat and interspecific interactions, as already suggested by Scott (1985). For instance, large bovids do not depend on flight or crypsis as a defence against predators, but rely mainly on size and group defence (Scott, 1985). The presence of

body size among the features contributing to the predictive accuracy of regression tree and random forest models (Figure 4e) might also reflect the significant effect of subfamily in influencing the evolution of robust metapodials in the focal taxa.

Assessing whether insular bovids exhibit a shortening of limb length and an increase of limb bone robustness relative to their ancestors or closest mainland relatives is challenging because of the dearth of available fossil and phylogenetic information (see e.g. Bover et al., 2019; Rozzi & Palombo, 2013b, 2014). However, our results suggest that short and stout metapodials are traits of convergent evolution, in that 'low gear' has evolved multiple times on different islands across phylogenetic clades (see also Bover et al., 2019; Bover et al., 2010; Palombo et al., 2013; Rozzi & Palombo, 2014). In fact, although the effect of subfamily on some of the patterns that we observed is significant, a variety of trait combinations characterizes metapodials of insular bovids, with taxa exhibiting different degrees of robustness and shortening within the same clade (see e.g. Figures 2 and 3). Accordingly, unveiling the role of habitat selection and interspecific interactions in driving the evolution of those traits is essential.

4.2 | Ecology

The most extreme cases of 'low gear' locomotion evolved in the absence or scarcity of predators (e.g. *Myotragus balearicus*, *Bubalus mindorensis*, *Bubalus cebuensis*; see also Rozzi & Palombo, 2014). This has led many authors to hypothesize that predator release on islands would be one of the main factors driving the acquisition of this peculiar suite of traits (e.g. Bover et al., 2010; Caloi & Palombo, 1994; Palombo & Rozzi, 2013; Rozzi & Palombo, 2013b; Sondaar, 1977; Van der Geer et al., 2011, cf. prediction 2 and Figure 1). Results obtained here challenge this view, as we did not find any significant relationships between number of predators and our response variables (Tables 1, S5, S6 and S7) and number of predators is not a relevant predictor in the regression tree and random forest models (Figure 4d). However, our results suggest that ecological release from competitors in species-poor insular communities is the most important factor in triggering the acquisition of 'low gear' locomotion (Figure 4, Tables 1, S5, S6 and S7). In species-rich communities, niche partitioning, competition dynamics and ecological displacement favour diversification and might prevent the loss of climbing and cursorial aptitudes and manoeuvrability. Conversely, these advantages are lessened in typical, low-biodiversity island communities and insular ruminants may invest in increasing their stability and developing a slow and powerful locomotion. Fossil Caprini from Sardinia and the Balearic islands are good examples of these opposite trends. Sardinian representatives of the genus *Nesogoral* likely originated by adaptive radiation (Palombo et al., 2013; Rozzi & Palombo, 2013b), occupied different niches and preserved long and slender metapodials and a cursorial aptitude in the presence of mammalian competitors and predators (e.g. *Asoletragus gentryi*, *Sus sondaari*, *Macaca majori*, *Chasmaporthetes melei*; Palombo & Rozzi, 2014). On the other

hand, *Myotragus* was the only large mammal on Mallorca and chronospecies of this lineage underwent drastic morphological changes since the Pliocene and evolved a highly specialized locomotion (see above and Bover, 2004; Bover & Fornós, 2005; Bover et al., 2019; Bover et al., 2010; Palombo et al., 2013; Rozzi & Palombo, 2014).

4.3 | Topography

Topographic complexity is a well-known measure of habitat heterogeneity and available niches and has been linked to species richness in many ecological communities (see e.g. Hutchinson, 1959; Owen, 1990; Yu et al., 2015 and references in those papers). Thus, we expected taxa that inhabited or are still living on islands characterized by relatively complex physiographies to display long and slender metapodials and maintain a less specialized gait (cf. prediction 3 and Figure 1). This hypothesis garnered some indirect support from our assessment of the importance of ecological predictors in the evolution of 'low gear' locomotion (large mammalian richness and the number of competitors in the focal communities likely reflect habitat heterogeneity of the respective islands; see above). Nevertheless, we did not find significant relationships between RI Mc and SI Mt and proxies for topographic complexity (mean roughness and accumulated roughness).

Animals from rugged-mountainous areas—including humans and ruminants—tend to exhibit relatively robust and short lower limb bones (see Figure 1 and e.g. Higgins, 2014; Rozzi & Palombo, 2013a,b; Scott, 1985 and references in those papers). However, much variation exists, even within the same family. For instance, a few mountainous Antilopinae, such as the Japanese serow, *Capricornis crispus* and the Appennine chamois, *Rupicapra pyrenaica ornata*, exhibit long and slender metapodials (see also Rozzi & Palombo, 2013b, 2014). Moreover, some Bovinae reported as inhabiting flat terrains (Higgins, 2014)—i.e. the muskox, *Ovibos moschatus*—are actually characterized by short and robust metapodials (Bover et al., 2019; Rozzi & Palombo, 2014). Results obtained seem to reflect this variation. The amount of mountainous terrain on each island is an important factor triggering the evolution of robust metapodials in the focal taxa, as highlighted by results of regression analyses (Figure 4c, Tables S5 and S7). Nevertheless, while Bovinae that occurred or still live on mountainous islands tend to display slightly stouter metapodials—in agreement with our initial hypothesis (cf. prediction 3 and Figure 1), Antilopinae are characterized by the opposite trend (see Results and Figure 4c). This variation in the magnitude and direction of responses to the amount of mountainous terrain on the focal islands may be explained in light of the influence of bauplan on habitat selection (see also above). In fact, Bovinae—with their plump bodies and heavy rumps—might be more prone to acquire a higher degree of stability by evolving robust metapodials. This would be especially true in mountainous areas, where stability might play an even more important role in increasing the survival of these species by reducing the risk of traumatic injuries (e.g. the tamaraw, *Bubalus mindorensis*,

on Mindoro; RI Mt: 0.192 (0.002); mountainous terrain: 70.15%; see Figure 2 and Table S1). Conversely, Antilopinae of mountainous islands would often retain relatively slender metapodials and a climbing and cursorial aptitude, especially in the presence of mammalian predators and competitors (e.g. *Capricornis crispus* on Honshu, Shikoku, and Kyushu; RI Mt: 0.106; mountainous terrain: 96.17%; see Figure 2 and Table S1). In this regard, the evolution of 'low gear' locomotion and the loss of adaptation to mountain climbing in *Myotragus* would reflect its great body mass in relation to body height (Bover & Fornós, 2005) and should be regarded as a unique case within Antilopinae. Furthermore, this low-speed and clambering locomotion must have been advantageous, in the absence of mammalian predators, on an island such as Mallorca, characterized by a relatively uniform physiography (mean roughness: 169.37; standard deviation of roughness: 182.18) and extensive flat areas (mountainous terrain: 46.2%).

5 | CONCLUSIONS

The evolution of 'low gear' locomotion in insular ruminants does not simply result from phyletic dwarfing and from the absence or scantiness of predators in the focal communities. Competitive release on species-poor islands plays an essential role in prompting adaptations for this peculiar type of gait, such as shortening and thickening of metapodials. Given that predator diversity is the main factor influencing body size evolution of insular bovids (Rozzi, 2018), different traits associated with the island syndrome may evolve in response to varied drivers, even within the same taxonomic group (see also Rozzi & Palombo, 2014; Van der Geer, 2014a). Furthermore, island topography is not as relevant as interspecific dynamics in influencing the evolution of the focal morphological traits, although the amount of mountainous terrain occurring on each island seems to significantly affect the evolution of robust metapodials in insular bovids.

Short and stout metapodials are traits of convergent evolution for insular ruminants, in that they evolved multiple times on different islands across Antilopinae and Bovinae. The marked variation in the responses to ecological and topographic predictors that we observed within Bovidae supports the idea that the evolution of 'low gear' locomotion would be the product of a complex interplay of biotic and abiotic factors, and calls for caution in drawing conclusions on this phenomenon on the basis of isolated, albeit significant cases (e.g. *Myotragus*). All in all, investigations on other large herbivores, especially cervids and graviportal taxa (e.g. elephants, hippopotamuses), might be crucial to provide further insights into the mechanisms triggering the acquisition of such a peculiar locomotion or promoting the maintenance of a more generalistic gait.

DATA AVAILABILITY STATEMENT
The authors declare that the data supporting the findings of this study are available within the paper and its Supporting Information file.

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BIOSKETCH

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Author contributions: R.R. designed the study, collected the data and performed the statistical analyses. S.V. described and quantified topographic variables. All authors contributed to interpretation of the results and writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.