Chapter 15
Ecomorphology

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Abstract The goal of ecomorphology is to identify morphological variation that is related to ecology (e.g., dietary preference or locomotor habits), with the aim of inferring ecological traits from morphological traits. This chapter reviews the basic principles of ecomorphology and provides many examples of ecomorphic studies in a range of taxa, with an emphasis on bovids (antelope and relatives). The focus of this chapter is on "applied" ecomorphology, which refers to studies that use ecomorphology as a tool to reconstruct environments. The chapter summarizes some of the strengths and weaknesses of the applied ecomorphic approach, and discusses future directions for studies using this methodology.

Keywords Functional morphology • Environmental reconstruction • Functional traits • Bovidae • Phylogenetic signal

Background

The aim of ecomorphology is to link morphological form with function in a particular ecological context (Bock and von Wahlert 1965; Bock 1989). Ecomorphology can be an end unto itself for understanding the autecology (sensu Wing et al. 1992) of extinct organisms, or it can be a means towards the end of characterizing entire extinct communities and the habitats supporting them. The distinction between ecomorphology and traditional functional morphology is not always clear-cut. The term "ecomorphology" is broader than "functional morphology" as the latter term generally refers explicitly to biomechanics, such as the ratio of force and resistance arms in skeletal lever systems and the resulting functional outcomes (Dunn 2018). Ecomorphology builds upon functional morphology but encompasses a broader view of how biomechanical functions are put to use in ecological contexts in ways that are adaptive for organisms (Bock 1994).

"Applied" ecomorphology is a term that is useful for describing studies employing ecomorphic techniques to reconstruct the proportions of organisms in a community with different adaptations, usually in an effort to understand some aspect of the sampled habitat (e.g., vegetation structure). Applied ecomorphology is primarily concerned with inferences about habitat structure rather than the adaptations of individuals or species, although inferences about individuals and species form the foundation of applied studies. Because the focus of this volume is on methods for reconstructing past environments, the examples used in this chapter are heavily biased towards applied ecomorphology studies rather than more classic examples of ecomorphic analysis (see Wainwright and Reilly 1994). Applied ecomorphic studies based on bovids (antelopes and relatives) have been particularly common (Kappelman 1991; Plummer and Bishop 1994; Scott et al. 1999; DeGusta and Vrba 2003; Kovarovic and Andrews 2007; Plummer et al. 2008; White et al. 2009; Barr 2014) and have served as important sources of evidence for the environmental context of human evolution.

Types of Ecomorphic Analyses

Dietary Ecomorphology

Many different ecomorphic methods have been used to reconstruct dietary preferences of extinct animals. I begin by discussing the most commonly used characteristic –

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hypsodonty – and then address other characteristics useful for relating craniodental form with diet. Examples from a variety of taxonomic groups are discussed, but the primary focus is on ungulates (hoofed mammals), particularly bovid artiodactyls.

Ungulates are often categorized either as grazers, which mostly subsist on monocot grasses, or browsers, which preferentially select dicot leaves and stems from bushes and trees (Janis 2008; Damuth and Janis 2011; Cerling et al. 2015). Mixed-feeders form a third group and typically consume significant amounts of vegetation from both categories (Hofmann and Stewart 1972). These gross categories tend to conflate the type of food acquired (grasses vs. dicots) with the method of food acquisition (i.e., bulk consumption vs. selective feeding; see Spencer 1995). Furthermore, additional factors, especially feeding height relative to the ground, often strongly influences dental form due to variation in the amount of exogenous grit in the diet, regardless of the type of food consumed (Damuth and Janis 2011). Nonetheless, the browser/grazer dichotomy persists and is a useful generalization that is applicable to characterizing the diets of fossil and modern ungulates (Gordon and Prins 2008; Cerling et al. 2015).

One of the most salient features related to dietary function is a tooth's mechanical resistance to wear. A variety of factors influence wear resistance (Van Valen 1960), but by far the most important factor is the quantity of enamel present in a tooth. While some organisms, like hominoids (Martin 1985), tend to increase wear resistance by increasing enamel thickness, ungulates tend to increase wear resistance by increasing tooth height (Fortelius 1985). The term "hypsodont" is used to describe teeth that have high crowns, allowing an organism's dentition to remain functional for a long period of time in the face of extreme wear (see Fig. 15.1). In contrast to low-crowned (brachydont) teeth, hypsodont teeth often have tall enamel pillars that are buttressed by cementum. Unworn teeth in hypsodont ungulates with complex crown morphology are capable of very little functional shearing but quickly wear to expose enamel ridges. Hypsodont teeth continue to erupt from the jaw during much of the lifespan of the animal, exposing fresh enamel ridges that preserve tooth function even as an abrasive diet quickly wears down teeth (Janis and Fortelius 1988; Damuth and Janis 2011). Traditionally, hypsodonty was often discussed as an adaptation to grazing (Simpson 1951; Stebbins 1981; Jacobs et al. 1999), and phytoliths (literally "plant rocks," structural silica incorporated into the tissues of many plants, especially grasses; see Strömberg et al. 2018) were thought to be the dominant source of abrasive particles (Baker et al. 1959). However, recent studies suggest that exogenous environmental grit may be a major source of abrasive particles contributing to tooth
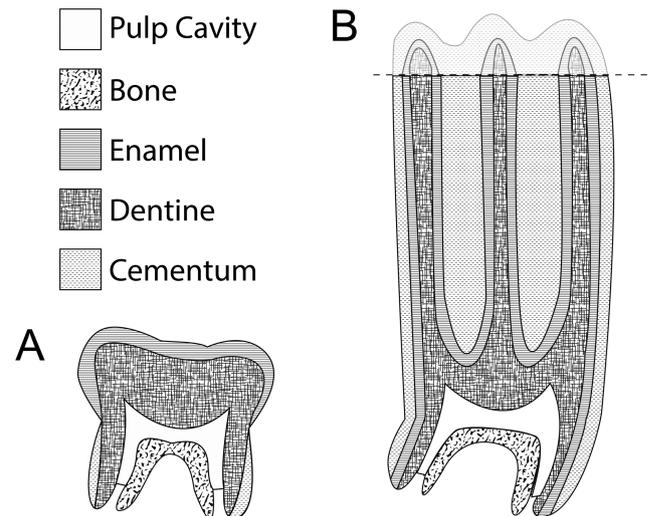
Fig. 15.1 Idealized coronal sections through: A, brachydont human molar; and B, hypsodont horse molar. Dotted line on hypsodont molar indicates wear level. A hypsodont molar retains functional enamel ridges even as abrasive wear reduces the height of the tooth crown during the life of the organism. Redrawn after Janis and Fortelius (1988, their Figure 8)

wear (Hoffman et al. 2015 and references therein; but see Spradley et al. 2016). Therefore, it is critical to emphasize that hypsodonty is adaptive for resisting dental wear, not for eating grass per se (Damuth and Janis 2014).

Many distantly-related mammalian groups have evolved hypsodonty to cope with high rates of wear. Janis and Fortelius (1988: Table 2) detail a wide range of groups with hypsodont species including; suids (pigs and relatives), rhinocerotids, equids (horses and kin), proboscideans (elephant relatives), notoungulates (extinct South American ungulates), macropodoid marsupials (wallabies and kangaroos), xenarthrans (sloths, armadillos, and relatives), lagomorphs (rabbits and pikas), and many rodent groups. Hypsodonty is a reliable ecomorphic indicator of an abrasive diet that has evolved convergently in many mammalian lineages.

The relationship between tooth crown height and diet is complicated by the occurrence of hypselodonty: teeth that grow and erupt continuously throughout an animal's lifespan. Among the groups noted above, hypselodonty has evolved in notoungulates, xenarthrans, lagomorphs, and rodents. In effect, ever-growing teeth are infinitely tall, because the tooth crown continues to form throughout life as teeth are worn, even if the crown is not necessarily tall at any given point in an organism's lifespan. Therefore, linking the height of the tooth crown with diet or habitat can be difficult in hypselodont species (Bargo et al. 2006a).

For ungulates, Janis (1988) showed that a simple hypsodonty index (HI), calculated as M3 height divided by M3 buccolingual width, effectively differentiates between extant

browsers and grazers. Exclusive browsers generally have HI values < 2, and exclusive grazers typically show HI values > 4.5 (Damuth and Janis 2011). HI is commonly used to infer the diet of newly described species (e.g., Faith et al. 2012) and for broader paleoecological studies to predict diet in a taxonomically diverse array of species (e.g., Reed 1997; Janis et al. 2000; Flynn et al. 2003; Croft et al. 2008). In taxa with highly modified dentitions, such as rodents, other hypsodonty metrics may be more appropriate. Williams and Kay (2001) used a hypsodonty metric of M1 height scaled to M1 crown area because M1 is the largest tooth in many rodent lineages and rodent molars vary in shape to a greater degree than those of ungulates.

Efforts have been made to link hypsodonty to measureable aspects of climate at broad geographic scales and through geological time (Fortelius et al. 2002). So-called "ecometric" studies (see Vermillion et al. 2018) have demonstrated that the geographic distribution of mean hypsodonty values for large mammals in a community correlates with mean annual precipitation (MAP) (Eronen et al. 2010a; Polly et al. 2011). This approach seeks to characterize the distribution of an ecomorphic trait (hypsodonty) in a community and correlate this community value with underlying climate variables. As such, this type of approach is a promising way forward for "applied" ecomorphology because it provides a means of connecting the morphology of individuals with habitat variables that may be understood with reference to modern analogue habitats. The analysis of dental traits other than hypsodonty is discussed elsewhere in this volume (Evans and Pineda-Munoz 2018).

Craniodental Dietary Ecomorphology

Craniodental morphology has been linked to dietary ecology in a wide array of animals and has been particularly well-studied in ungulates (Mendoza et al. 2002; Clauss et al. 2008; Raia et al. 2010). In ungulates, one of the best-understood craniodental differences between grazing and browsing forms is the overall shape of the muzzle (Janis and Ehrhardt 1988; Solounias and Moelleken 1993; Pérez–Barbería and Gordon 2001; Tennant and MacLeod 2014). Modern grazing taxa such as equids (horses), warthogs (*Phacochoerus* spp.), the white rhinoceros (*Ceratotherium simum*), and alcelaphin bovids (wildebeest and relatives) tend to have wide (blunt or U-shaped) muzzles, reflecting a non-selective feeding strategy of cropping grasses. Browsers, such as black rhinoceros (*Diceros bicornis*) and cephalophin bovids (duikers), have narrower (pointed or V-shaped) muzzles that reflect their more selective browsing habits (see Fig. 15.2). Spencer (1995, 1997) identified several additional craniodental features related to dietary and habitat preferences in bovids. Grazers are characterized by flexed braincases, deep and wide mandibles, and generally long faces, whereas browsing taxa tend to have the converse (Spencer 1995). Spencer (1995) also showed that premolar row length differentiates taxa that inhabit secondary grasslands, which have relatively short premolar rows, from those dwelling in edaphic grassland, which have longer premolar rows. These established relationships between craniodental morphology and diet/habitat preference make it possible to confidently characterize the autecology of fossil bovids when adequate craniodental evidence is available.

The correlations between craniodental morphology and diet described above are general relationships that are not specific to ungulates. For instance, grazing macropodoid marsupials are convergent with grazing ungulates in having broad incisors, deep and wide mandibular angles, and acute basicranial angles (Janis 1990). Similarly, extinct South American ground sloths appear to exhibit the same relationship between muzzle shape and dietary selectivity as ungulates, with wide-muzzled sloths inferred to be
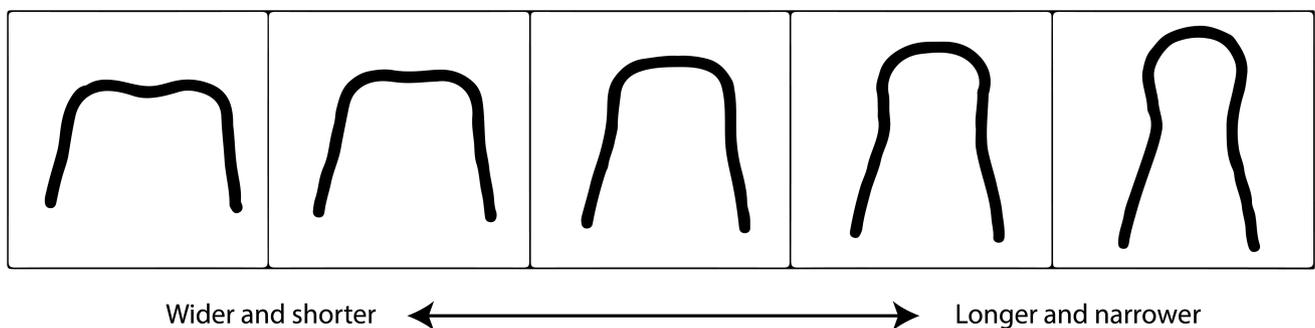
Fig. 15.2 Diagrams illustrating the first principal component of shape variation in the snouts of extant ruminants, from Tennant and MacLeod (2014). The left side of the figure shows snouts more typical of grazers, while the right side shows snouts more typical of browsers. These diagrams illustrate shape change across a dietary spectrum and none corresponds with a particular taxon

Wider and shorter ⟷ Longer and narrower

non-selective bulk feeders and narrow-muzzled forms inferred to be more selective (Bargo et al. 2006b; Bargo and Vizcaíno 2008; Shockey and Anaya 2011). Similar dietary trends in muzzle and mandible shape have been shown for extinct equids (Raia et al. 2010; Bernardes et al. 2013) and have also been inferred for extinct South American relatives of armadillos known as glyptodonts (Vizcaíno et al. 2011).

Various aspects of craniodental morphology have been linked to broad dietary categories in rodents (Samuels 2009). For example, carnivorous rodents have elongate incisors and reduced cheek tooth areas, insectivorous rodents have elongate snouts and degenerate dentitions, and herbivorous rodents have elongate molar tooth rows and a wider skull and rostrum (Samuels 2009). These characterizations apply to rodents from diverse phylogenetic groups, indicating convergence in these morphological features as dietary adaptations. Furthermore, some characteristics such as wide rostra in herbivorous rodents parallel differences in rostrum shape seen among ungulate dietary groups (discussed above) and thus point to general biomechanical principles driving these shape differences.

Craniodental ecomorphology has been well studied in carnivorans (members of order Carnivora, such as cats, dogs, and bears) with respect to feeding style and prey capture and how these traits have changed through evolutionary time (e.g., Radinsky 1981; Van Valkenburgh 1988, 1989; Lewis 1997; Wesley-Hunt 2005; Werdelin and Wesley-Hunt 2010, 2014; Figueirido et al. 2011; Meloro 2011a, b; Meloro and O'Higgins 2011; Meloro et al. 2015). Carnivorans can be classified into broad dietary categories ranging from hyper-carnivores that specialize on flesh consumption to meat/bone eaters to omnivores that have broad diets (Van Valkenburgh 1989). As might be expected, species in these categories possess distinctive craniodental adaptations related to their diet. Hypercarnivores (e.g., lions and tigers) tend to have extremely well-developed carnassial teeth (specialized for shearing flesh) and little to no tooth area devoted to grinding (Van Valkenburgh 1989). Meat/bone eaters (e.g., hyenas) have somewhat less well-developed carnassials and are characterized by extremely large and robust premolars for crushing bones (Van Valkenburgh 1989). Omnivorous car-nivorans (e.g., bears and raccoons) have weakly developed carnassial teeth and a relatively large proportion of tooth area devoted to grinding (Van Valkenburgh 1989).

Canine tooth morphology is related to killing behaviors in predatory carnivorans. Felids (cats and relatives) have long, strong canines that are used to kill prey with deep bites that often contact bone (Van Valkenburgh and Ruff 1987). Canids (dogs and relatives) kill prey with shallower bites

that do not penetrate deeply and less frequently result in canine-bone contact (Van Valkenburgh and Ruff 1987). Thus, canids and other carnivorans that kill with shallow slashing wounds exhibit mediolaterally compressed canines characterized by lower bending strengths than felids (Van Valkenburgh and Ruff 1987).

Locomotor Ecomorphology

A large proportion of the fossil record consists of isolated postcranial fossils, which often cannot be precisely identified taxonomically (e.g., to genus or species). However, such specimens can be analyzed using "taxon-free" (Andrews and Hixson 2014) ecomorphological methods. In general, loco-motor ecomorphology aims to link morphological traits with habitat-specific locomotor performance. This link may be based on habitual substrate use, as in studies of cercopithe-coid primate (Old World monkey) ecomorphology, which have focused on distinguishing terrestrial, semi-terrestrial, and arboreal forms (Gebo and Sargis 1994; Elton 2001, 2002; Gosselin-Ildari 2013; Elton et al. 2016). Studies of carnivoran postcranial ecomorphology have focused both on substrate use (fossorial, terrestrial, arboreal) and locomotor speed (Van Valkenburgh 1987; Polly 2010; Walmsley et al. 2012; Meloro et al. 2013). A recent study of rodent postcranial ecomorphology focused on distinguishing loco-motor categories based on substrate use (Samuels and Van Valkenburgh 2008).

For ungulates, the link between morphology and loco-motion has been made with regard to habitat-specific modes of predator avoidance. Ungulate taxa living in open, grassland-type habitats face intense pressure from cursorial (fast-running) carnivorans. Many open-country taxa rely on running speed to out-pace these predators (Jarman 1974) and thus have adaptations for rapid locomotion over flat sub-strates. Cursorial adaptations include elongate distal limb elements (Scott 1985) and joint adaptations that restrict joint motion to the parasagittal plane (Kappelman 1988). How-ever, it is important to note that not all cursorial adaptations are the result of selection for increased running speed. In camelids, cursorial adaptations may have arisen for efficient long-distance dispersal rather than to outpace cursorial car-nivorans (Janis et al. 2002).

Ungulate taxa that occupy dense forests with closed canopies are faced with complicated three-dimensional substrates that include undergrowth, fallen trees, and other obstacles. Cursoriality is a less effective predator-avoidance strategy in these environments, and forest-dwelling taxa tend

to rely more on crypsis (hiding) to avoid predation. Thus, cursorial adaptations are less pronounced in forest-adapted taxa, and adaptations towards joint mobility are emphasized. In bovids, locomotor ecomorphology has been used to predict habitat preferences based on the morphology of femora (Kappelman 1988, 1991; Kappelman et al. 1997; Janis et al. 2012), metapodials (Plummer and Bishop 1994; Scott et al. 1999), astragali (DeGusta and Vrba 2003; Plummer et al. 2008, 2015; Barr 2014, 2015), phalanges (DeGusta and Vrba 2005; Louys et al. 2013), and a variety of other skeletal elements (Kovarovic and Andrews 2007). Similar methods linking postcranial morphology to predator avoidance have also been applied to suids (pigs; Bishop et al. 1999, 2006) and cervids (deer; Curran 2012, 2015).

Steps in an Applied Ecomorphic Analysis

This section details the steps in a typical applied ecomorphic analysis. As a practical example, this will be based on my own ecomorphic study of bovid astragali.

First, traits to be measured or observed are identified, ideally with reference to specific functional hypotheses linking each trait to the ecological variable of interest (e.g., dietary preference or locomotor category). These traits may be typical linear measurements or composite variables derived from an ordination of geometric morphometric data (e.g., Curran 2012, 2018). In my analysis of bovid astragali, I mined the literature of previous ecomorphic work on astragali (DeGusta and Vrba 2003; Weinand 2007; Plummer et al. 2008) as well as the functional morphology literature on artiodactyl ankle joints (Schaeffer 1947, 1948; Alexander and Bennett 1987) in order to obtain a candidate list of traits.

It is advisable to restrict the number of traits used in an ecomorphic analysis, as using too many traits can lead to "over-fitting," which produces artificially high classification accuracies (Kovarovic et al. 2011). One approach to deal with this issue is to use phylogenetic comparative methods in order to identify the traits that are most closely related to the ecological category of interest (Barr and Scott 2014). Traits that are less clearly related to ecology can then be removed from further analyses (Barr 2014). Other approaches exist for dealing with this problem (Louys et al. 2013; Elton et al. 2016), and this is also discussed further below.

The next step is to use relevant comparative species to determine how well the measured variables reflect the ecological categories of interest. Comparative species are often chosen among closely-related taxa, but this may not always be possible, especially when studying the ecomorphology of extinct species with no modern relatives (Chen and Wilson 2015). Comparative species must be classified into one of several ecological categories of interest. For instance, in bovid locomotor studies (e.g., Kappelman 1991; Plummer and Bishop 1994; Kappelman et al. 1997; Scott et al. 1999; DeGusta and Vrba 2003; Kovarovic and Andrews 2007), species are typically classified as occupying one of several habitat types such as open grassland, closed forest, or montane habitat. For studies relating to diet, the classification scheme reflects dietary categories, such as hypercarnivore, meat/bone, or omnivore in the case of carnivorans (Van Valkenburgh 1989).

Once variables are measured and extant species are classified into categories, Discriminant Function Analysis (DFA) (Manly 2004) is frequently used to quantify the relationship between the traits and the ecological categories of interest. Wilk's lambda (Manly 2004: 46) and its associated p-value can be used to determine whether a DFA is statistically significant. If a DFA is shown to be statistically significant, a variety of metrics can be used to judge the accuracy of its classifications. The simplest metric is termed "resubstitution" (DeGusta and Vrba 2003; Plummer et al. 2008). Resubstitution involves making categorical predictions for each specimen with DFA equations derived from the original dataset and computing the percent accuracy of these predictions. However, making "predictions" for specimens using equations derived from those specimens is problematic and results in overestimation of predictive success (Kovarovic et al. 2011). Cross-validation gets around this problem by withholding each specimen of the dataset one-by-one and recalculating the DFA each time. Classifications for each specimen are thus made using equations that do not include that particular specimen. Cross-validation offers a more realistic picture of DFA prediction success (Kovarovic et al. 2011).

Finally, the same measurements can be taken from fossils and added to the DFA equations derived from the extant comparative study in order to predict their most likely ecological category. These categorical predictions can then be used to infer distribution of the ecological trait of interest in the community. In my study of the bovids from the Shungura Formation in Ethiopia (Barr 2015), I measured 234 fossil astragali using the same measurement scheme I had previously validated in extant species (Barr 2014). I used the DFA predictions generated from these fossils to demonstrate that the Shungura Formation bovid community was dominated by individuals adapted to closed environments at 3.4 Ma, while the community at 2.4 Ma included more open-adapted individuals. These kinds of results can

be used to infer changes in ecological communities and environmental conditions through geological and evolutionary time.

Strengths of Ecomorphology

A widely-cited strength of ecomorphology is that the method is "taxon-free" (Andrews and Hixson 2014), meaning that ecomorphic inferences do not rely on taxonomic identifications; rather, they are based on functional morphological traits. The taxon-free nature of ecomorphology is a strength in two ways. First, because it is taxon-free, ecomorphology does not require the assumption of taxonomic uniformitarianism; i.e., that a fossil species must have had the same ecological characteristics as modern representatives of the same taxonomic group (e.g., tribe or subfamily). This assumption often underlies paleoenvironmental interpretations of faunal lists, for instance. To take a hypothetical example: tragelaphin bovids (bushbuck and relatives) may be identified at a site based on horn core evidence, and this may be taken to indicate the presence of woodland habitats because modern tragelaphins are browsing taxa, and several modern species occupy dense woodland and forest environments. This assumption may be problematic if there is within-lineage evolution in ecological characteristics because fossil species may differ from their modern relatives. In contrast to this uniformitarian approach, the ecomorphic approach infers ecological information for each specimen based directly on functional links between morphology and ecology. In an applied ecomorphic study, a site would only be interpreted as reflecting a woodland environment if fossil remains showed functional traits that could be functionally linked to a browsing diet or locomotion adapted for woodland habitats.

Secondly, the taxon-free nature of ecomorphology means that much larger samples are available for ecological characterizations. In many cases, only relatively complete craniodental specimens, which are rare in the fossil record, can be identified to species and analyzed via taxonomy-based methods. Fossil limb bones and other less-complete material that can only be identified to a higher taxonomic level (e.g., to family) can still be used for ecomorphic reconstructions. Moreover, as alluded to above, taxonomic identification in bovids relies heavily on horn cores, which in some taxa are only found in males. By contrast, both sexes have limb bones and teeth, common targets of ecomorphic studies. Furthermore, molar teeth and some postcranial elements (e.g., astragali) are extremely durable and tend to be well represented in all paleontological collections. Thus, studying postcranial elements and teeth may provide a clearer picture of the relative abundances of bovids with different ecological characteristics as compared to taxonomy-based analyses that rely preferentially on horn cores and cranial material.

Shortcomings of Ecomorphology

One of the major shortcomings of ecomorphology is related to the categorization schemes used in ecomorphic studies (e.g., browser vs. grazer for diet, or forest vs. grassland for habitat). Some species are easily assigned unambiguously to categories on the extremes of ecological continua (e.g., committed grazers or dedicated browsers), but many others are intermediate with respect to these continua (e.g., mixed-feeding species). Species assigned to such intermediate ecological categories can show significant variation. For instance, some mixed-feeding species might prefer grass while others prefer browse even though all mixed feeders consume both vegetation types. This heterogeneity within ecological categories is the result of parsing continuous ecological variation into discrete analytical units. Assigning taxa to a particular category is almost always an oversimplification, but more precise methods of ecological characterization are possible. For example, GIS analysis of species distributions with respect to ecological gradients can be used to achieve a more quantitative picture of a species' habitat preferences (Meloro et al. 2013).

Although the "taxon-free" nature of ecomorphology has been discussed as a strength of the method, there are several ways in which taxonomy (and phylogeny) can influence the results of an ecomorphic study. First, ecomorphology is not completely taxon-free because specimens must generally be identified at least to family, as many ecomorphic predictive equations apply within families (Andrews and Hixson 2014). Secondly, the taxonomic composition of the comparative sample can influence the outcome of a DFA (Klein et al. 2010). For instance, if a modern comparative sample is heavily dominated by alcelaphin bovids (committed grazers) and cephalophin bovids (committed browsers), the DFA will produce very high classification accuracies and will appear to succeed very well in predicting diet. However, the same DFA may not perform nearly as well for mixed-feeding taxa that were not well represented in the extant sample. This problem can be mitigated to some extent by careful selection of the extant comparative sample.

Even if all modern species were to be included in a comparative sample, the phylogenetic relationships of extant taxa would need to be carefully considered. This is because phylogenetic signal can cause a DFA to produce high classification

accuracies that are easy to over-interpret in terms of the functional link between morphological traits and ecological categories (Barr 2014). This problem stems from the fact that species are related in a hierarchical phylogeny, with some species in the extant sample more closely related to one another than to other species in the sample. Since closely-related species tend to resemble each other in morphology as well as ecology, each species in the data set may not represent a separate instance of adaptation for a particular diet or locomotor strategy. This can raise issues of what is known as phylogenetic pseudo-replication; closely related species are not statistically independent, and it is inappropriate to treat them as such (Felsenstein 1985).

The issue is illustrated in Fig. 15.3, which shows two hypothetical phylogenetic relationships for woodland and grassland-adapted bovids. In Fig. 15.3A, woodland and grassland taxa are scattered across the two clades, and there is a perfect correspondence between the morphological trait and the habitat category. This implies a very strong functional relationship between the trait represented by the green circles and woodland habitats, because species in different clades have adapted convergently to the same habitat several times. Therefore, extrapolating outside this sample (i.e., predicting habitat preference based on trait values in fossils) could be done with relative confidence; there are multiple instances of convergent morphological adaptation to habitat supporting this ecomorphic linkage.

In Fig. 15.3B, the woodland taxa comprise a phylogenetic group to the exclusion of the grassland-adapted taxa. There is still a perfect correspondence between morphological traits and habitat preference, but there are no instances of convergence (independent evolution of the same trait). Adaptation to habitat occurred in ancestral taxa (green and yellow triangles), and descendant taxa within each clade share habitat preferences and morphological traits because they inherited them from their common ancestor. Traits that have a distribution that tracks phylogenetic topology in this way are said to have high phylogenetic signal (Münkemüller et al. 2012). Clearly, the morphological traits in the extant taxa in Fig. 15.3B must be functionally compatible with the taxon's habitat preference; otherwise, these taxa would either go extinct or adapt morphologically. Thus, traits with high phylogenetic signal are not necessarily uninformative for ecomorphology. Nevertheless, when traits have high phylogenetic signal, extrapolating ecomorphic predictions to taxa outside of the comparative sample may be more difficult, because the functional relationship between traits is confounded by phylogenetic relatedness.

Figure 15.3 presents extreme cases for purposes of illustrating the issue. In practice, morphological traits tend to
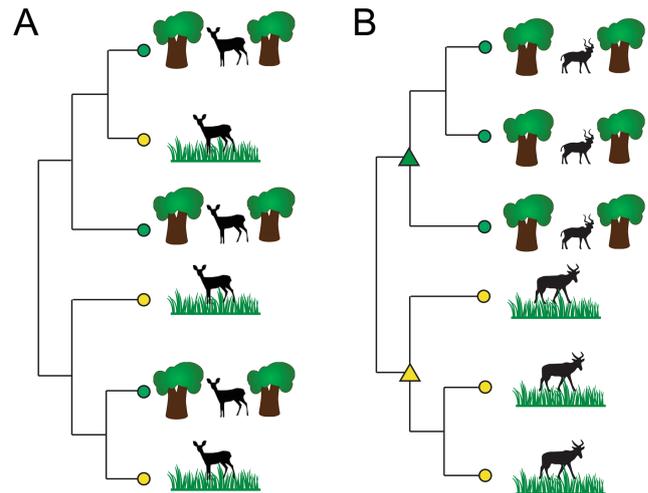
Fig. 15.3 Two hypothetical scenarios showing different relationships between morphological traits (colored circles) and habitat preferences (grassland or woodland). Colored triangles represent morphological traits in extinct ancestral taxa. In scenario A, there is a perfect correspondence between morphology and habitat, and there are several instances of convergent evolution of the same morphological trait in a particular habitat. In scenario B, there is still a perfect correspondence between habitat and morphology, but there are no examples of convergent evolution of morphological traits. Rather, each species inherited morphological traits and habitat preferences from a common ancestor. Scenario A offers the strongest possible evidence for a functional link between morphology and habitat, while the evidence for a functional link in scenario B is not as well supported because it lacks evidence of convergent evolution

have more subtle and complex relationships to both phylogenetic and ecological groupings. Traits that exhibit some level of phylogenetic signal often also exhibit a functional signal above and beyond that predicted based on phylogenetic relationships (Scott and Barr 2014). Thus, the presence of phylogenetic signal by no means precludes the use of a trait in an ecomorphic study, but it does argue for careful consideration about what factors drive variation in that trait. One approach to dealing with the issue of phylogenetic signal is to screen traits for a significant functional relationship using phylogenetic comparative methods and to exclude traits that do not have strong functional signals exceeding that expected based on phylogenetic relationships (Barr 2014). A different approach is to perform DFA first and subsequently search for examples of morphological convergence among distantly-related species in the same ecological category as well as morphological divergence among closely-related species in different ecological categories (Louys et al. 2013). The benefits and limitations of these and other methods for dealing with phylogeny in applied ecomorphic studies continues to be discussed (Elton et al. 2016).

Future Prospects

The biggest challenge facing applied ecomorphic studies is understanding what results mean in terms of interpretable ecological variables. Take, for example, a bovid fossil assemblage for which postcranial ecomorphology indicates that 85% of the bovids are open-country adapted and 15% are light-cover adapted. These proportions provide critical primary data regarding the adaptations of the bovid community. However, these proportions are not straightforward to interpret in terms of what they reveal about inferred habitats in the past, even if we assume perfect fidelity (i.e., 100% accuracy) in habitat predictions for each fossil.

What is the likelihood that the hypothetical sample above could be drawn from the bovid community in an open-arid environment such as the Etosha National Park in Namibia, a habitat dominated by grassland and low-density mopane savanna (du Plessis 1999)? What is the likelihood of drawing the same sample from a grassland community in the Serengeti ecosystem? Both systems have extensive grasslands, but the Serengeti receives more precipitation than Etosha, and the two areas likely present distinct ecological challenges and affordances. The methods currently used in ecomorphology do not offer a formal way of excluding or including either of these possible modern analogs based on the relative proportions of bovid adaptations in the fossil sample. One clear path forward is to examine the proportions of bovids with different adaptations in modern ecosystems to link these proportions to potential modern analogues. This type of analysis has been done only on a limited basis with bovid locomotor categories (Plummer and Bishop 1994). Taxonomically broader community structure analysis has been more successful in linking the distribution of ecological traits with environmental variables and/or modern analogues (Andrews et al. 1979; Reed 1997, 1998; Flynn et al. 2003; Kovarovic et al. 2018). In the future, a major focus in applying ecomorphic methods should be in establishing rigorous ways of interpreting the results of these methods. So-called "ecometric" methods, which link community values of ecomorphic traits with climatic correlates (Fortelius et al. 2002; Eronen et al. 2010a, b; Polly et al. 2011; Vermillion et al. 2018) may offer a way forward.

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