

# Crossing extreme habitat boundaries: Jack-of-all-trades facilitates invasion but is eroded by adaptation to a master-of-one

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## Abstract

1. The invasion of new environments can be a key instigator of adaptive diversification, but the likelihood of such invasions succeeding can depend on the attributes of would-be invaders. Chief among these seems to be a generalist or 'jack-of-all-trades' phenotype.
2. Yet, despite the obvious link between habitat transitions and adaptation, we know surprisingly little about how phenotypes that might initially allow taxa to transition between habitats subsequently evolve or influence post-invasion differentiation.
3. We tested how a generalist phenotype of a broad diet and behavioural plasticity in marine blenny fish has facilitated the repeated invasion of extreme environments—particularly land—and how the conditions post-invasion have impacted that generalist phenotype and associated trophic morphology.
4. Our data show that a wide diet and plasticity in being able to shift between environments freely have been instrumental in the progressive invasion of land by amphibious blennies. Once established, however, terrestrial blennies have experienced strong stabilizing selection for a restricted diet, little to no plasticity and a highly specialized morphology. Instead of promoting diversification, the invasion of land appears to offer only a limited niche for survival, constraining descendent blennies to a specific adaptive phenotype.
5. While our study supports the view that generalism facilitates invasion and that habitat transitions instigate adaptation, it also shows a generalist strategy is not optimal for successful establishment and new environments may offer fewer (not more) opportunities for diversification. This has broad implications for how taxa might be expected to respond or adapt to abrupt environmental change more generally.

## KEYWORDS

Blenniidae, body size, contextual plasticity, diet, intertidal, land invasion, supralittoral, tooth morphology

## 1 | INTRODUCTION

It has long been recognized that the colonization of a new habitat is an event that can spur the evolution of adaptive evolution

(Schluter, 2000). Iconic radiations such as the Hawaiian silversword plants (Carr, 1985), anole lizards of the Greater Antilles (Losos, 2009) or the evolution of freshwater threespine sticklebacks from marine ancestors (McKinnon & Rundle, 2002) are all spectacular examples

of how invasions can result in new ecological opportunities that can prompt adaptive differentiation. There are also numerous phylogenetic comparative studies reporting a link between phenotypic diversification across closely related taxa and the diversity of habitats occupied by those taxa (Streelman & Danley, 2003; e.g. Collar, Schulte II, O'Meara, & Losos, 2010; Ord & Klomp, 2014), again implicating transitions in habitat as key in generating adaptive evolution. Yet explicit investigation of how taxa initially move into new habitats and then adaptively respond to the changed conditions in those habitats is rare. This is likely because it is often difficult to find the appropriate benchmarks that reflect pre- and post-invasion forms (but see Rosenblum, 2006; Taylor & McPhail, 2000) with the identification of transitional forms often required as well (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006).

Plant ecologists, and invasion biologist in particular, have made the best progress in this area, but have nevertheless focussed more on the attributes that make taxa successful invaders and establishers in new areas (Hayes & Barry, 2008; Jeschke & Strayer, 2006; Kolar & Lodge, 2001), rather than the implications of establishment for adaptive evolution (Brandenburger et al., 2018; Felker-Quinn, Schweitzer, & Bailey, 2013). Chief among such attributes seems to be a generalist strategy or a 'jack-of-all-trades' reflected by a wide niche or phenotypic plasticity that enables taxa to cope with the environmental stressors that might be experienced during (and following) colonization (Knop & Reusser, 2012; Richards et al., 2006). In the case of animals, a generalist strategy that includes a broad diet (e.g. DeMiguel, 2016; Gajdzik, Aguilar-Medrano, & Frederich, 2019) or reversible plastic shifts in behaviour ('behavioural flexibility' or 'contextual plasticity'; e.g. Ord, Charles, Palmer, & Stamps, 2016; Yeh & Price, 2004) are characteristics that could be behind many successful invasions (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005) and have the potential to subsequently facilitate adaptive diversification as taxa spread into new areas (Sol, Stirling, & Lefebvre, 2005).

Given the importance placed on concepts like ecological opportunity (or release) in how diversification is instigated (Stroud & Losos, 2016; Yoder et al., 2010), and given these clearly rely on taxa making transitions in habitat in the first instance, investigating both the cause and consequence of invasion is vital for not only understanding why some taxa are better invaders than others (e.g. generalists vs. specialists), but also what circumstances facilitate those transitions that go on to promote (or even constrain: e.g. Ord, Garcia-Porta, Querejeta, & Collar, 2020) diversification in some groups but not others (innovations or plasticity). In this study we examined how diet and behavioural plasticity have contributed to habitat transitions in a diverse fish group and how adaptive evolution has proceeded in key aspects of trophic morphology following these transitions. We define behavioural plasticity as the capacity of a fish to change its behaviour as a function of some external stimuli—for example environmental conditions—on a moment-to-moment basis (equivalent to 'contextual plasticity', Ord et al., 2016; Stamps & Groothuis, 2010, 'activational plasticity', Snell-Rood, 2013 or 'reversible phenotypic plasticity', Wright & Turko, 2016).

We focussed on a large family of marine fish—Blenniidae—that provided the rare opportunity to study the colonization of two extreme habitat types: the repeated invasion of the aquatic intertidal zone (Hundt, Iglesias, Hoey, & Simons, 2014) and the subsequent invasion of land in the supralittoral zone (Ord & Cooke, 2016). The constant fluctuation of the tide impacts conditions in both environments. In the aquatic intertidal zone, the water column retracts entirely at low tide to subtidal pools. Depending on the size and depth of these pools, the water can rapidly increase in temperature and leach dissolved oxygen resulting in hypoxic conditions (e.g. Giomi et al., 2014). In the aerial supralittoral zone, terrestrial blennies must remain moist in order to respire effectively through the skin and gills (Brown, Gordon, & Martin, 1992; Martin & Lighton, 1989), which means these species are subsequently restricted to the splash zone (Ord & Hsieh, 2011). This habitable area disappears at low tide forcing land-dwelling blennies to retreat from the exposed rocks into moist rock holes and crevices to await the incoming tide (Ord & Hsieh, 2011). Despite the dramatic physical and ecological challenges faced by blennies in both habitats, these fish have been hugely successful in making these transitions and are one of the most rapidly radiating families of spine-rayed fish (Near et al., 2013).

Part of this success could be attributed to the elongated cylindrical body form shared by most blennies (Hundt, Iglesias, et al., 2014; Ord & Cooke, 2016) and the lack of scales that enable cutaneous respiration to supplement that conducted via the gills (Martin & Bridges, 1999). More generally, however, the benefits conveyed by these characteristics are likely dependent on the modest body size of blennies (e.g. Knope & Scales, 2013), which should help these fish cope with the respiratory and thermoregulatory challenges of the wide fluctuations in temperature and oxygen in the aquatic intertidal habitat, while also facilitating terrestrial locomotion, desiccation resistance and respiration in the aerial supralittoral habitat (Gibb, Ashley-Ross, & Hsieh, 2013; Ord & Hsieh, 2011; Uchiyama et al., 2012).

Further to this general morphology, a key defining characteristic of blennies is their teeth, which is reflected in their colloquial name 'combtooth' blennies. This comb-like array of many long, thin teeth is used to scrape substrates for food and is clearly morphologically specialized compared to other closely related groups (Hundt & Simons, 2018). This unusual teeth morphology was assumed to reflect a similarly specialized diet of detritus (Bellwood, Hoey, Bellwood, & Goatley, 2014). Yet quantitative comparative analysis has since revealed considerable diversity in both diet and tooth morphology within the family (Hundt, Nakamura, & Yamaoka, 2014; Hundt & Simons, 2018). This implies that the diet, and diet breadth more specifically, of blennies and the seeming high adaptive potential of their otherwise unusual dentition (Hundt & Simons, 2018) could have been important factors driving the success of blennies in colonizing novel environments.

In the case of the supralittoral invasions, blennies offer an especially powerful means of examining how the process of colonization unfolds. This is because there is a range of species that exhibit varying degrees of amphibious behaviour: some taxa rarely if ever

emerge from water, others spend various amounts of time in and out of the water, while others still are highly terrestrial and spend their entire juvenile and adult life out of the water in the splash zone (Ord & Cooke, 2016). Comparison among these aquatic, amphibious and terrestrial lifestyles provides—what are in effect—ecological and evolutionary snapshots of the progressive colonization of land. But there is also considerable behavioural plasticity in the propensity for amphibious blennies to emerge from water within taxa (Ord & Cooke, 2016). This should help buffer against environmental stressors by allowing blennies to shift their time between the aquatic and aerial environments depending on the conditions experienced in those environments at any given time (Ord & Cooke, 2016; Ord, Summers, Noble, & Fulton, 2017).

For example, aquatic predation is one factor pushing blennies out of the water, with blennies spending more time on land during those times when the abundance of predatory fish in water is high (Ord et al., 2017). Conversely—and perhaps more importantly for the successful transition to land—some amphibious blennies vary their time out of the water depending on weather conditions and tide level (which again dictates the degree of splash and the danger of desiccation; Ord & Cooke, 2016; Ord & Hsieh, 2011). The propensity of some individuals to emerge even in favourable conditions could also depend on the availability of terrestrial refuges or nest options at a given site (rock holes or crevices; Ord & Cooke, 2016). Such plasticity in emergence behaviour as a means of flexibly responding to prevailing conditions experienced in water or on land (predation risk or aerial conditions respectively) is prominent within some amphibious species, while virtually absent in others (Ord & Cooke, 2016).

We began our study by reconstructing the evolutionary history of blenny diets to test whether a generalist diet has been associated with the repeated invasion of the aquatic intertidal habitat from an ancestral subtidal phenotype. This was then followed by a separate test of whether a generalist strategy, that included both a

wide diet and plasticity in amphibious behaviour, is currently facilitating the invasion of land in the supralittoral (splash) zone. Finally, we examined the evolution of dentition and gross body size in order to reveal the consequences of colonizing a novel environment (the aquatic intertidal or aerial supralittoral zones) for promoting adaptive evolution. Dentition has obvious links with diet (e.g. Hundt & Simons, 2018), while body size has ecological implications for resisting hypoxic conditions in water (e.g. Knope & Scales, 2013) and desiccation on land, while also impacting locomotor capacity in a terrestrial environment (Gibb et al., 2013).

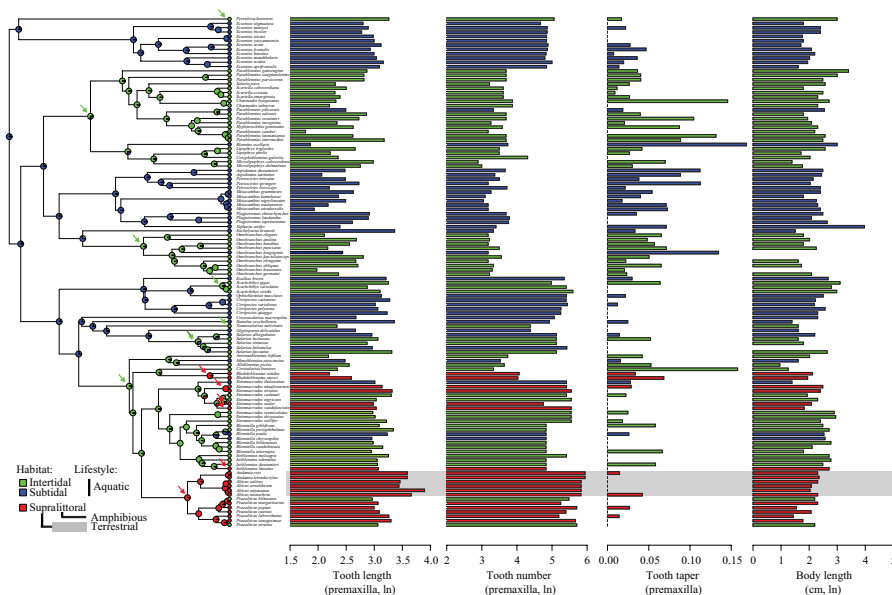
## 2 | MATERIALS AND METHODS

The Supporting Information accompanying this article provides other details on methodology not covered in the sections below.

### 2.1 | Data

#### 2.1.1 | Diet, tooth morphology and body size

Diet was quantified for 118 species (Figure 1) following procedures outlined in Hundt, Nakamura, et al. (2014; Hundt & Simons, 2018) and are described in detail in the Supporting Information SI. Briefly, we aimed to collect at least five individuals per species (median = 9, range = 1–21; see also supplementary table 2 from Hundt & Simons, 2018) and to dissect their gut contents fresh from collection in the field. These contents were classified into 13 food categories that were then grouped into three primary food types for analysis: detritus, plant and animal (see Supporting Information SI). We focussed on these food types because a previous meta-analysis across all living fish suggested potential associations between some of these food types and the propensity to emerge from water



**FIGURE 1** Reconstructions of habitat and lifestyle based on 1,000 stochastically mapped ancestor states presented alongside species data for three key tooth attributes (see also Table S3) and body size. Arrows highlight putative transitions between habitat types

(Ord & Cooke, 2016). We also computed a diet breadth score from the proportion of gut contents across the 13 initial food categories (see Supporting Information SI) using a transform of the Simpson index (1-D) in which larger values reflect a wider diet breadth. Data on tooth morphology were also obtained for the same fish following Hundt and Simons (2018; see Supporting Information SI), while species body size data were taken from 'Fishbase' ver 08/2019 (Froese & Pauly, 2019).

### 2.1.2 | Habitat and lifestyle

Habitat type was determined primarily through direct observation by the authors (76 species) or colleagues (1 species), supplemented with information for the remaining species (41) from Bell Museum collection notes, published literature (Bath, 2008; Springer, 1988; Springer & Williams, 1994) or FishBase (Froese & Pauly, 2019). Habitat was classified as subtidal, aquatic intertidal or aerial supralittoral, with the latter including any species with an average behavioural or 'lifestyle' score of  $\geq 1$ . Lifestyle was categorized as aquatic, amphibious or terrestrial using an established key (e.g. Ord & Cooke, 2016) to score the behaviour of adults for 36 species (504 individuals; median = 8 per species; see Supporting Information SI).

## 2.2 | Statistical analysis

We began our analyses by first investigating the role of diet and behavioural plasticity (in the case of supralittoral invasions) in instigating transitions in habitat. We then investigated how diet and behavioural plasticity changed following transitions and subsequently impacted adaptive evolution in trophic morphology (dentition, body size), including convergent evolution in cases of repeated, independent transitions into the same habitat. All analyses were conducted in R ver 3.5.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna) and were based on the phylogeny developed by Hundt and Simons (2018). This phylogeny included all species of interest and covered the same sampled populations from which phenotypic data had been collected. It was constructed using a Bayesian analysis of the partitioned concatenated dataset of five exons, thought to be well-conserved, single-copy markers (ENC1 822 bp, myh6 785 bp, ptr 759 bp, tbr1 762 bp and sreb2 975 bp) that was implemented in the program BEAST v. 1.7.4 (Drummond, Suchard, Xie, & Rambaut, 2012).

### 2.2.1 | Diet and the repeated colonization of the aquatic intertidal zone

Phylogenetic logistic Ornstein–Uhlenbeck (OU) regressions (Ives & Garland Jr., 2010) were used to test for an association between diet and occupying an intertidal versus subtidal habitat (coded as 1 and 0 respectively) and were implemented in the PHYLOLM package ver 2.6 (Ho & Ane, 2014). A model selection approach was used to rank

alternative models based on computed Akaike information criterion values that included a modification for sample size ( $AIC_c$ ). Two sets of analyses were applied. The first included all 118 species with supralittoral taxa grouped with other intertidal species, while the second excluded these taxa and included the remaining 100 fully aquatic intertidal and subtidal species.

Next, we tested whether diet was related to historic transitions from subtidal to intertidal habitats. This was done by examining the inferred diet at phylogenetic nodes at or immediately before reconstructed transitions in habitat were expected to have occurred. Reconstructions were made using the 'simmap' functions in the package PHYTOOLS ver 0.6–44 (Revell, 2012).

### 2.2.2 | Diet, behavioural plasticity and the colonization of the aerial supralittoral zone (land)

Phylogenetic OU regressions (Hansen, Pienaar, & Orzack, 2008) implemented using the PHYLOLM package were used to determine whether the propensity to emerge from water into the supralittoral zone (i.e. the degree of amphibious behaviour), or its plasticity, was predicted by diet or diet breadth. A model selection approach was again used to identify the most plausible predictor of emergence.

### 2.2.3 | Diet and evolutionary differentiation of tooth morphology

In order to evaluate potential adaptive differentiation in dentition following habitat transitions or changes in diet, we first established how tooth morphology and diet were related to one another, starting with a phylogenetic principal component analysis (pPCA) of tooth morphology implemented using PHYTOOLS. This analysis identified three key tooth attributes (see Supporting Information SI), and we then applied phylogenetic OU regression analyses to document how these tooth variables related to differences in diet among species.

### 2.2.4 | Habitat and evolutionary differentiation of tooth morphology and body size

There were multiple independent transitions into the intertidal zone, and then out of the water into the supralittoral zone. We tested for convergence in tooth morphology and body size as a function of these transitions using the Wheatsheaf index (Arbuckle, Bennett, & Speed, 2014) computed by the package WINDEX ver 1.0 (Arbuckle et al., 2014). We computed the Wheatsheaf index in two contexts, first to document potential convergence in dentition and body size as a function of repeated invasions of the aquatic intertidal zone, and second in relation to the repeated invasion of land in the supralittoral zone.

Finally, we tested for habitat-specific patterns of adaptive evolution in tooth variables and body size by fitting three alternative models of how these characteristics might have evolved as a function

of habitat: (a) a Brownian Motion (BM) null model in which dentition and body size have evolved stochastically (non-adaptively) and unrelated to habitat; (b) an OU model in which dentition and body size have evolved differently in subtidal, intertidal and supralittoral lineages and (c) an OU model in which dentition and body size have evolved differently in aquatic, amphibious and terrestrial lineages. These models were implemented using 'OUwie' ver 1.50 (Beaulieu, Jhwueng, Boettiger, & O'Meara, 2012) and compared using  $AIC_c$ . The best-supported model was used to interpret the rate of adaptation ( $\alpha$ ) pushing blenny phenotypes towards a lifestyle-specific optimum ( $\theta$ ), and the extent to which random fluctuations ( $\sigma^2$ ) have occurred during the process of evolutionary differentiation.

### 3 | RESULTS

#### 3.1 | Diet and the repeated colonization of the aquatic intertidal zone

No particular diet or diet breadth in extant species was associated with living in the intertidal zone (Table S1; Figure S1). Only one model was identified as being more credible than the null model and this was specific to analyses that only considered aquatic intertidals (Table S1b). This model included the proportion of detritus in the diet but the associated effect size for this variable was not

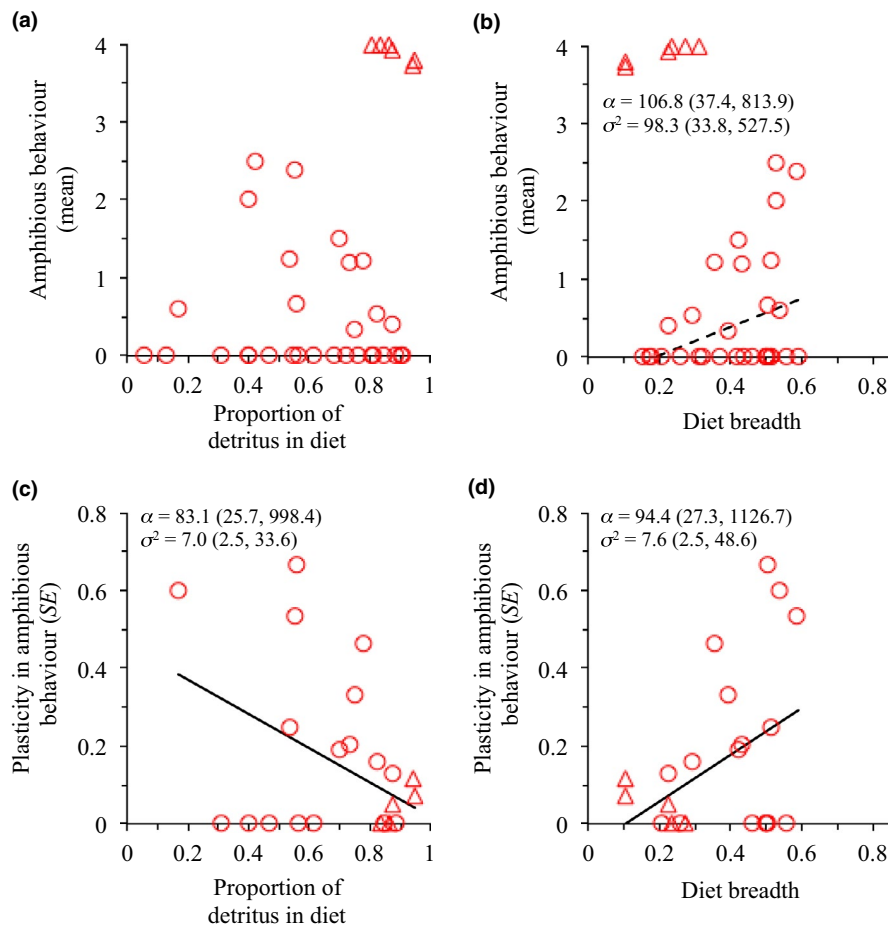
compelling ( $z < 2$ ; Table S1b). There also appeared to be a tendency for intertidal species to feed on a greater amount of plant material than subtidal species (i.e. 95% CIs did not overlap in Figure S1b), but this relationship was not robust in phylogenetic analyses (Table S1).

There was also no obvious relationship between historic diets and the invasion of the aquatic intertidal zone. Phylogenetic reconstructions uncovered seven independent invasions of the intertidal zone (Figure 1). These invasions were associated with a range of diet types and a modest breadth of diet more generally (Figure S2a). Ancestors immediately prior to these invasion events tended to have a greater proportion of detritus in their diets, but overall diet proportions and diet breadth were again unremarkable (Figure S2b).

#### 3.2 | Diet, behavioural plasticity and the colonization of the aerial supralittoral zone (land)

Terrestrial blennies were found to have a specialized diet heavily skewed to detritus, and this was unusual compared to the transitional amphibious blennies (Figure 2a,b). When terrestrial species were excluded from the analysis, diet breadth was marginally, positively correlated with mean amphibious behaviour (Table 1a ii): species with more diverse diets tended to be more amphibious (Figure 2b).

Plasticity in emergence behaviour was negatively correlated with the proportion of detritus in the diet (Table 1b), converging on



**FIGURE 2** Differences in amphibious behaviour among blenny species as a function of diet (a–d). Parameter estimates  $\alpha$  and  $\sigma^2$  infer the rate of adaptation and degree of stochasticity in the evolution process and are computed by phylogenetic Ornstein–Uhlenbeck regressions and equivalent to those reported in Figure 4 (NB: trend lines reflect continuous adaptive optima,  $\theta$ , whereas those shown in Figure 4 are stationary adaptive optima specific to a discrete habitat type). Values in parentheses are 95% confidence limits

**TABLE 1** Differences in amphibious behaviour among blenny species as a function of diet

Model applied	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	t <sub>detritus</sub>	t <sub>diet breadth</sub>
<b>(a) Amphibious behaviour (mean)</b>				
i. All species (N <sub>species</sub> = 36)				
Null	94.8	0.0		
Detritus	96.9	2.0	-0.76	
Diet breadth	96.4	1.6		0.98
Detritus + diet breadth	99.1	4.3	-0.13	0.64
ii. Terrestrials excluded (N <sub>species</sub> = 30)				
Null	68.2	1.2		
Detritus	69.8	2.8	-1.02	
Diet breadth	67.0	0.0		1.96 <sup>a</sup>
Detritus + diet breadth	69.9	2.9	0.10	1.65
<b>(b) Plasticity in amphibious behaviour (N<sub>species</sub> = 22)</b>				
Null	-3.62	0.9		
Detritus	-4.28	0.2	-1.98 <sup>b</sup>	
Diet breadth	-4.48	0.0		1.99 <sup>b</sup>
Detritus + diet breadth	-1.47	3.0	-0.61	0.72

<sup>a</sup>95% confidence interval marginally overlaps 0.

<sup>b</sup>95% confidence interval does not overlap 0.

virtually no plasticity in terrestrial species that were also almost exclusively detritivores (Figure 2c). In contrast, plasticity was positively correlated with diet breadth (Table 1b), with the most plastic amphibious species having the broadest diets (Figure 2d).

Taken together, these results are consistent with the notion that a generalist diet, and the ability to plasticly shift between the aquatic and land environment depending on the conditions occurring in those environments, have been important for the transition onto land. Once established in the supralittoral environment, however, species have become exclusively terrestrial (with little to no plasticity) and specialist detritivores.

### 3.3 | Diet and evolutionary differentiation of tooth morphology

Most aspects of blenny tooth morphology loaded predominantly on the first principal component axis in the pPCA, which accounted for 46% of the variation in dentition among species (Table S3). Tooth taper was a notable exception and was primarily associated with the fourth and fifth axes (7%–9% of the variation among species). Tooth number was also prominent on PC2 (17% of variation). In general, premaxilla and dentary tooth characteristics loaded on the same axes.

For subsequent analyses, we focussed on premaxilla teeth and selected the length of those teeth (prominent on PC1), their number (prominent on PC2) and taper (prominent on PC4–5).

Bivariate plots showed loose relationships between the three characteristics: a positive relationship between premaxilla tooth length and number, and negative relationships between premaxilla tooth length and taper, and between tooth number and taper (Figure S3). These plots, as well as tooth characteristics plotted against the phylogeny (Figure 1), implicated large shifts in both premaxilla tooth length and number in terrestrial species, but little relationship with habitat more generally.

All three tooth variables were heavily dependent on diet, but not on body size (Table 2). Both the proportion of detritus in the diet and diet breadth were strong predictors of differences in tooth length among species (Table 2a), with blennies that have a narrow diet specializing on detritus possessing the longest teeth (Figure 3a). Differences in the number and taper of teeth were specifically dependent on the proportion of detritus consumed (not diet breadth; Table 2b,c), with detritivores possessing the most teeth (Figure 3b) with little to no taper (Figure 3c).

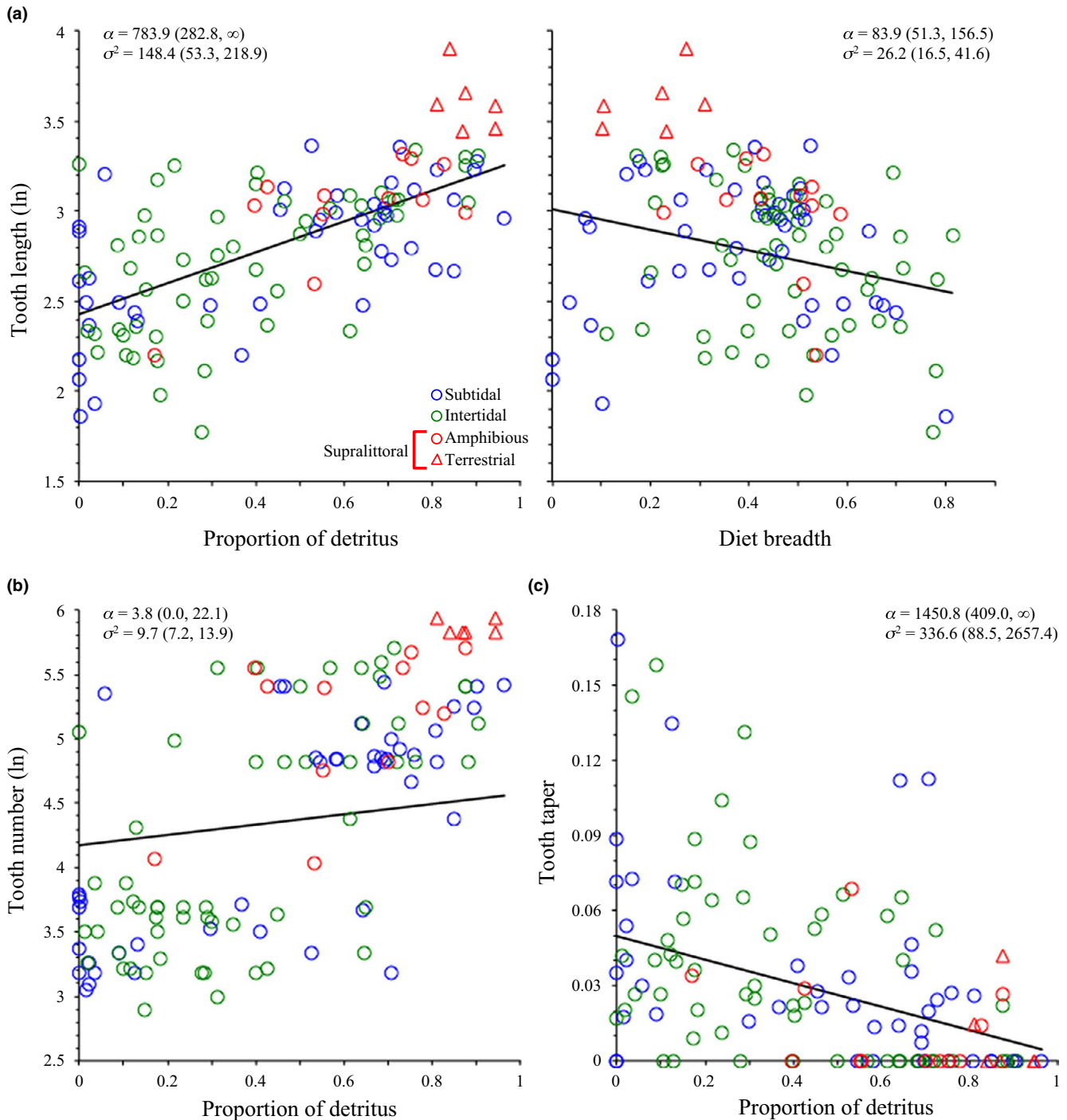
### 3.4 | Habitat and evolutionary differentiation of tooth morphology and body size

There was little evidence of convergence in tooth morphology or body size as a function of habitat. Although similarities in premaxilla tooth length, taper and number as well as body size were all

**TABLE 2** Differentiation of key aspects of dentition among blenny species as a consequence of diet or body size

Model applied	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	t <sub>body length</sub>	t <sub>detritus</sub>	t <sub>diet breadth</sub>
<b>(a) Tooth length (N<sub>species</sub> = 114)</b>					
Null	93.9	38.0			
Body length	96.0	40.0	0.29		
Detritus	60.1	4.1		8.41 <sup>a</sup>	
Diet breadth	82.9	26.9			-3.72 <sup>a</sup>
Detritus + diet breadth	56.0	0.0		7.92 <sup>a</sup>	-2.55 <sup>a</sup>
<b>(b) Tooth number (N<sub>species</sub> = 114)</b>					
Null	93.7	5.1			
Body length	92.5	3.9	1.84		
Detritus	88.6	0.0		2.72 <sup>a</sup>	
Diet breadth	95.9	7.3			-0.10
Detritus + diet breadth	90.7	2.1		2.72 <sup>a</sup>	0.23
<b>(c) Tooth taper (N<sub>species</sub> = 114)</b>					
Null	108.1	23.5			
Body length	110.2	25.7	0.02		
Detritus	84.6	0.0		-5.50 <sup>a</sup>	
Diet breadth	109.2	24.7			0.99
Detritus + diet breadth	86.6	2.0		-5.39 <sup>a</sup>	0.44

<sup>a</sup>95% confidence interval does not overlap 0.

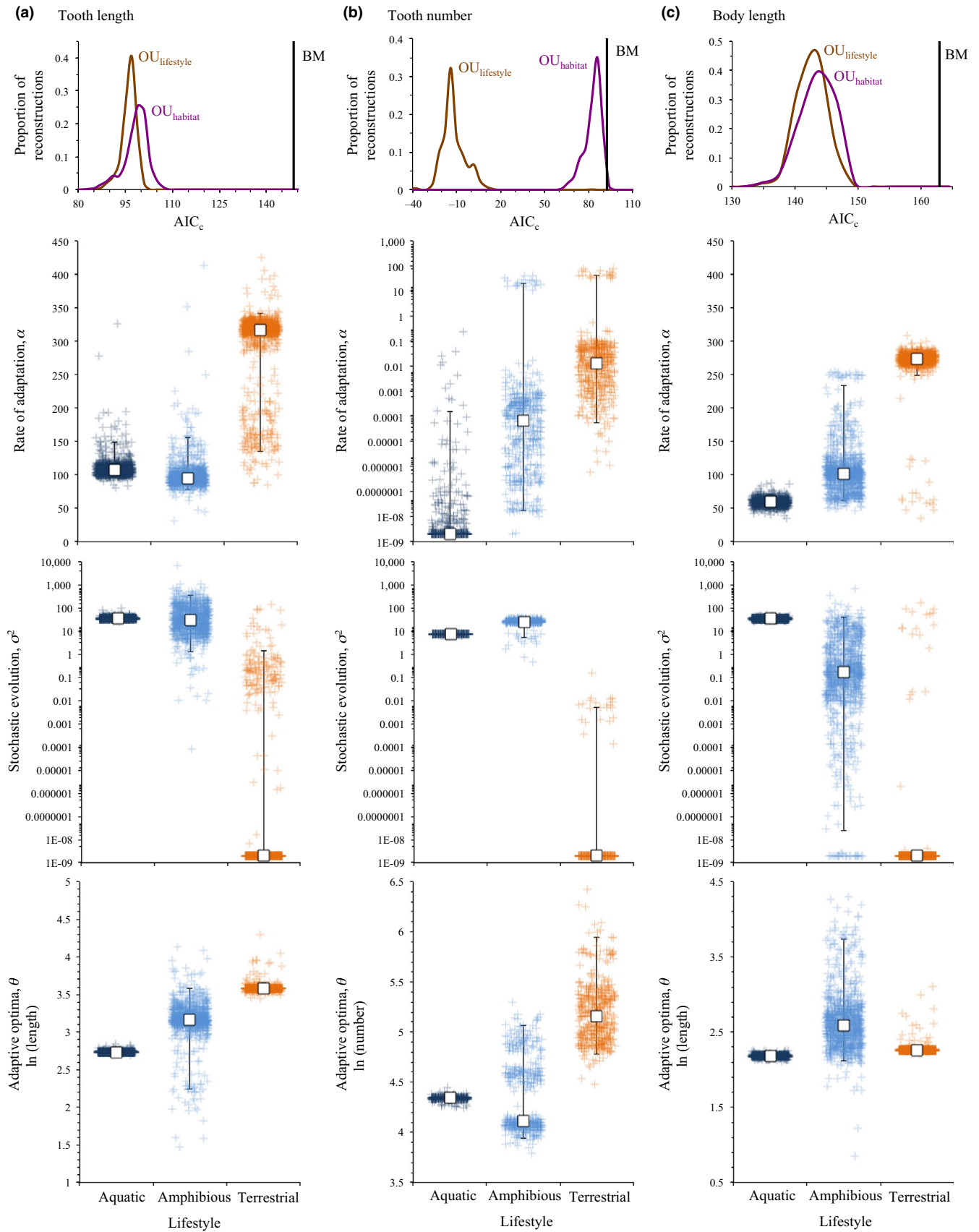


**FIGURE 3** Differentiation of key aspects of dentition among blenny species as a consequence of diet (a–c). See Figure 2 legend for explanation of inset parameter estimates

higher among aquatic intertidal species compared to other species, the magnitude of convergence was limited and similarities could have arisen by chance (Table S4a). Tooth length tended to be more similar among supralittoral species (amphibious and terrestrial blennies), while tooth number was especially so (Table S4b), but these similarities were quite limited (Wheatshaeaf values only just  $>1$ ) and could have either arisen by chance (tooth length) or were not compelling based on visually inspection of the data (tooth number; Figure 1).

We found it nearly impossible to fit any evolutionary model to tooth taper because of its low variability among species (e.g. tooth taper was largely regulated to the fourth or fifth axes in pPCA; Table S3). Power was quite low for tooth number for the same reason, but there was enough variability among species that this could be compensated for by increasing the number of runs used to compute evolutionary parameters (from 1,000 to 14,000).

The OU model in which the evolution of tooth length, tooth number and body size has been free to vary among aquatic, amphibious



**FIGURE 4** Tooth (a, b) and body size (c) evolution as a function of lifestyle. Upper most panel depicts the support for three alternative models. Lower panels illustrate the estimates from the best-supported model (in all cases 'lifestyle'). Coloured data points are individual estimates computed for 1,000 stochastically mapped reconstructions of lifestyle, which are summarized as a median and 95th percentile range overlay



and terrestrial lineages was the best supported of the three models applied (Figure 4, upper panel). Parameter estimates from this model showed the rate of adaptation ( $\alpha$ ) in all three variables has been highest in terrestrial blennies, with a very low rate of stochastic evolution ( $\sigma^2$ ; Figure 4). This is consistent with a history of strong stabilizing selection, which has tightly constrained terrestrial blennies to an inferred adaptive optimum ( $\theta$ ) of extremely long and numerous teeth, and to comparatively large body sizes (Figure 4, bottom panel).

## 4 | DISCUSSION

Diet does not appear to have played a pivotal role in facilitating the repeated invasion of the aquatic intertidal zone by subtidal blennies, although a detailed analysis of resource utilization more generally in these environments could provide better insight into this transition in the future. However, a wide diet breadth and behavioural plasticity in being able to cross the aquatic–aerial interface depending on the conditions experienced (in either environment) does seem to have been critical in allowing intertidal blennies to ultimately leave water for a life on land in the supralittoral zone. Once established in this terrestrial splash zone, the restrictive conditions experienced on land seem to have selected for a highly specialized diet of detritus, limited (to no) plasticity and modest body size. Rather than promoting adaptive diversification among terrestrial taxa more broadly, the transition into this novel aerial environment has resulted in strong stabilizing selection on both tooth morphology and body size for all terrestrial blennies. This almost certainly reflects the shift from a generalist to specialist diet post-invasion (in relation to teeth specialization: this study) and the likely constraints imposed on fish locomoting and respirating in a terrestrial, aerial environment (in relation to the limits on body size: e.g. Knope & Scales, 2013).

These findings provide new insight into how phenotypic characteristics that might facilitate invasion are in themselves shaped by conditions post-invasion and, vice versa, how characteristics found to differentiate adaptively in a novel environment might have initially contributed to the invasion of that habitat in the first instance. This perspective is rare. Documenting such links requires a system that is actively undergoing an environmental transition and where clear examples of pre- and post-transition phenotypes can be readily identified. Invasion fronts of species undergoing range expansions offer potential for such investigations, but tend to be regulated to comparisons across environmental gradients for contiguous populations of a single species (e.g. bluebirds: Duckworth & Badyaev, 2007; cane toads: Pettit, Greenlees, & Shine, 2016). Other examples might include prey that have shifted between environments differing dramatically in background colour, which has selected for prominent changes in dorsal colour in order to maintain prey crypsis (walking-stick insects: Nosil, Crespi, & Sandoval, 2002; lizards of white sands: Rosenblum, 2006; beach mice: Mullen, Vignieri, Gore, & Hoekstra, 2009). The pre- and post-invasion phenotypes in these systems are obvious and have allowed detailed study of the underlying genetic changes associated with

adaptation (Linnen et al., 2013; Rosenblum, Römpler, Schöneberg, & Hoekstra, 2010; Soria-Carrasco et al., 2014). Nevertheless, transitional forms are harder to identify and this makes it difficult to uncover the ecological attributes that facilitated transitions and how those attributes differentiated following (or contributed to) establishment. For these reasons, blennies are an unusual system in which the process and consequence of habitat transitions can be examined from both an ecological and evolutionary standpoint, with multiple species representing clearly defined stages of the invasion process between two drastically different environments.

Being a generalist has often been considered a key attribute of a successful invader (reviewed by Clavel, Julliard, & Devictor, 2011; Richards et al., 2006). However, our findings go further and reveal the advantages conveyed by a generalist strategy are transitional and specific to the process of invasion itself, becoming a target of selection post-invasion to produce a specialist ‘master of one’ phenotype more suited to permanently occupying the narrow habitable zone on land. Transitions from generalist to specialist are probably widespread throughout the tree of life (e.g. Clavel et al., 2011; Colles, Liow, & Prinzing, 2009; see also Kassen, 2002) and are also perhaps implicit in the process of adaptive radiation more generally in which a generalist descendent species differentiate through specialization to fill a range of new ecological niches: that is, a ‘jack-of-all-trades’ ancestor diversifies into many ‘master of one (or some)’ phenotypes. Examples include the putative generalist origins of the specialist ecomorphs of the Greater Antillean *Anolis* lizards (Losos, 1992), threespine sticklebacks (Taylor & McPhail, 2000) and Darwin finches (Grant & Grant, 2008). In the case of terrestrial blennies, however, the available niche in the supralittoral zone appears limited and descendent species have instead evolved towards a singular specialist phenotype rather than proliferated into many new forms.

The area available for survival out of the water for blennies is limited and intimately dependent on the tides (see Section 1). Terrestrial blennies continue to rely on respiration through the gills and skin (Brown et al., 1992; Martin & Lighton, 1989) and must remain moist to avoid asphyxiation. This necessarily restricts them to the splash zone (Ord & Hsieh, 2011). But there are other, more general, reasons why a transition into a novel habitat might not open the door to the evolution of many new forms. New environments can bring new enemies and this can restrict the areas that might be available to colonizers. In the case of marine blennies, while the transition to land has alleviated predation pressure (Ord et al., 2017), this benefit is confined to the exposed rocks of the splash zone, where the body colour and patterning of blennies remains cryptic (Morgans & Ord, 2013). In other terrestrial habitats (e.g. adjacent beaches), this crypsis is broken and blennies become conspicuous targets to visually oriented predators (Morgans & Ord, 2013). Competition from other taxa already established in an area can be another constraining force, and if not excluding colonizers outright (i.e. via competitive exclusion; e.g. Losos, Marks, & Schoener, 1993), it can restrict the available niches that might be available within a new environment (e.g. Ord et al., 2020). It is unclear what ecological competitors blennies might face beyond (or even within) the splash zone, but resource competition from other

taxa could be an additional factor limiting the niche of blennies on land (e.g. crabs are potential rivals for rock holes and crevices).

The initial plasticity that allowed blennies to shift freely across the aquatic–aerial interface is also broadly consistent with the scenario often discussed by invasion biologists (Richards et al., 2006) in which plasticity emerges as part of the invasion process itself (e.g. Knop & Reusser, 2012). However, once establishment occurs, plasticity could become costly and this appears to have been the case for amphibious blennies. There is a performance trade-off that reflects morphological and behavioural factors associated with effective locomotion in or out of the water (e.g. Hsieh, 2010; see also Gibb et al., 2013), but not both. In order to make a successful transition to a terrestrial environment, blennies must therefore adapt in a manner that almost certainly renders them poorly suited for effective locomotion in water (e.g. see Hsieh, 2010; note too the differences in optimal body size between aquatic and terrestrial blennies; Figure 4, bottom panel), and this in turn has eroded their capacity to freely (plasticly) move between environments.

Baldwin (1896) classically noted how plasticity in behaviour might allow animal populations to successfully invade new environments, but it took over a century before documented examples of this would begin to appear (e.g. Yeh & Price, 2004). Baldwin also noted that post-invasion, behaviours that were initially plastic would ultimately become genetically assimilated; that is, plasticity would be eroded by selection to an adaptive phenotype most suited to the conditions experienced in the new environment. The behaviour of blennies offers a rare empirical example of just this outcome.

Specialism more broadly has been argued to present an important constraint to the prospects of taxa being able to cope with future environmental change (Clavel et al., 2011; Colles et al., 2009). In particular for animal taxa, there is often an association between dietary specialization and extinction risk (Colles et al., 2009). This has become especially pertinent with the increasing impacts of the climate crisis being documented across the globe and the debate over whether taxa will be able to track or adapted to environmental changes quickly enough to avoid extinction. While the trajectory of generalists differentiating into specialists appears common in nature (Colles et al., 2009)—and our data are certainly consistent with this—the extent to which specialists readily evolve back to more generalist phenotypes is unclear (Colles et al., 2009). On the one hand, our data illustrate just how effective a generalist strategy can be in allowing taxa to make dramatic environmental transitions (fish leaving water for a life on land), but on the other hand it also shows this to be a transitional phenotype that is ultimately lost as an outcome of the colonization process. Captive experiments on these fish could provide a tractable system for assessing the impact of specialization on the ability of animals to cope with abrupt environmental changes that (for example) push their diets or habitable zone to the edge or outside their current specialized niche.

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## AUTHORS' CONTRIBUTIONS

T.J.O. designed the study; P.J.H. and T.J.O. collected the data; P.J.H. developed the phylogeny; T.J.O. analysed the data and wrote the paper with P.J.H. contributing to revisions.

## DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rn8pk0p6r> (Ord & Hundt, 2020).

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## SUPPORTING INFORMATION

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

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