

Colonization of a novel depauperate habitat leads to trophic niche shifts in three desert lizard species

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In a novel, depauperate ecosystem, colonizing species may experience changes in their trophic niche as a result of a new resource base and fewer competitors and predators. To examine trophic niche shifts of recent colonists, we focused on three ecologically and phylogenetically divergent lizard species that inhabit both the geologically distinctive depauperate habitat of White Sands and the surrounding Chihuahuan ‘dark soil’ desert in New Mexico. In White Sands the three species comprise the entire lizard community, whereas in the dark soils habitat, they constitute less than half of the lizard community abundance. As a result, we hypothesized that the three focal species would collectively represent a greater variety of trophic positions in the White Sands habitat than in the dark soils habitat. We hypothesized that the extent of shifts in each species’ trophic position would parallel diet and ecomorphology differences between habitats. To test these hypotheses, we combined analysis of lizard stomach contents with carbon and nitrogen stable isotopes in the context of previously published ecomorphology measurements. Stable isotope data indicated that as predicted, species were more different from one another in White Sands than in dark soils, suggesting community-wide ecological release. Overall, all species were lower on the White Sands food chain; however, only one species decreased trophic level significantly, one increased trophic level variance, and one did not change significantly. Furthermore, stomach content data paralleled both stable isotope and ecomorphological data, showing different degrees of dietary overlap between habitats, depending on the species. That species’ differences in trophic ecology also correspond with ecomorphological differences suggests that these factors are either causally linked or collectively responding to similar ecological pressures, such as competition. By examining diet, trophic position, and ecomorphology of three colonist species, we demonstrate both species-specific and community-wide trophic differences in adjacent, but distinct habitats.

Species often experience drastic trophic niche changes in novel, depauperate ecosystems as a result of a new resource base and fewer competitors and predators (Losos and De Queiroz 1997, Yoder et al. 2010). Although most research focuses on the dietary ecology of colonists of oceanic islands (Crowell 1962, Lister 1976, Case et al. 1979), similar patterns may be observed in other distinctive and depauperate habitats. For these “habitat islands,” (reviewed by Gilbert 1980) ecological distinctiveness from the neighbouring habitat may be important in determining colonization history (Brown and Dinsmore 1988) and therefore species composition and community organization (Schoener 1974, Cohen and Newman 1991, Holt 1996, Takimoto et al. 2008, Harvey and MacDougall 2014). In any novel habitat, fewer species will have had time to colonize, establish and adapt (Larsen et al. 2005, Losos and Ricklefs 2009).

Young habitat islands, which contain fewer species, typically have shorter food chains and fewer trophic interactions than more complex, diverse ecosystems (Post 2002a). Therefore, colonists may often experience changes in diet and trophic position. For example, because depauperate ecosystems have fewer predators and competing species

(Post 2002a), successful colonists may experience ecological (Crowell 1962) or competitive (Persson and Hansson 1999) release. In addition, they may have a more important ecological function than they did in their ancestral habitat because they consume a greater variety of available prey across different trophic levels (Case et al. 1979). Additionally, differences in resource availability (Grant and Grant 1989) and the trophic level of prey species could lead to changes in diet and trophic position (Matthews et al. 2010). Despite these expectations, the association between variation in diet and trophic position is inconsistent throughout the literature (Bolnick et al. 2003) and evidence for changes in trophic level following colonization of habitat islands and depauperate ecosystems is lacking (Persson and Hansson 1999).

To investigate differences in diet and trophic position of species in a novel, depauperate habitat, we focused on three lizard species that inhabit the geologically unique ecosystem of White Sands and the surrounding ‘dark soil’ Chihuahuan desert scrubland in southwestern New Mexico. In many ways, White Sands can be considered a habitat island. Although the 650 square kilometers of white gypsum dune habitat is nested within the dark soil desert, it is

geologically young (less than 7000 years old, Kocurek et al. 2007) and ecologically distinctive, being relatively depauperate of plants (Emerson 1935, Parsons 1976) and animals (Dice 1930, Bugbee 1942, Des Roches et al. 2011). Reptile diversity is high outside White Sands (up to 41 lizard species and 45 snake species in New Mexico, Degenhardt et al. 2005), however, there are only three lizard species that are ubiquitous throughout the gypsum dunes. The species, the little striped whiptail *Aspidoscelis inornata*, the lesser earless lizard *Holbrookia maculata* and the southwestern fence lizard *Sceloporus cowlesi* have established dense local populations within White Sands and represent the entire lizard community (Des Roches et al. 2011). Despite being distantly related to one another (Wiens et al. 2010), they exhibit striking convergence in blanched colouration (Rosenblum 2006, Rosenblum and Harmon 2011) and various morphological characteristics including body size, head size and limb length (Rosenblum and Harmon 2011, Des Roches et al. 2014, 2015a).

There is much support for close links among resource availability, diet and ecomorphology in lizards (Herrel et al. 2008) and other reptiles (Herrel and O'Reilly 2006), however, research rarely extends to analysis of trophic position (but see Takimoto et al. 2008). In White Sands, previous work has found that both prey availability and trophic ecomorphology differ between White Sands and the surrounding dark soil habitat (Des Roches et al. 2015a). Differences in prey availability between the two habitats are reflected in lizard diet as indicated by stomach contents, indicating parallel responses to shared environments (Des Roches et al. 2015a). Specifically, all three White Sands lizard species tend to consume harder-bodied prey, and two of the three species have larger head size and stronger bite force than their dark soils counterparts (Des Roches et al. 2015a). The fact that the same species have different diets and trophic ecomorphology in two divergent habitats suggests that their trophic niches may also differ with their surroundings.

In our current study, we combine analysis of lizard stomach contents with carbon ($\delta^{13}\text{C}/\delta^{12}\text{C}$) and nitrogen ($\delta^{15}\text{N}/\delta^{14}\text{N}$) stable isotope data to determine differences in the trophic niche of lizards in White Sands and dark soils habitats. While stomach contents give a detailed cross-section of recent diet at one point in time (Warburton et al. 1998, Araújo et al. 2007), stable isotope levels in tissue provide a long-term average of diet (Peterson and Fry 1987, Hesslein et al. 1993, Post 2002b, Araújo et al. 2007) and may reflect physiological (Reich et al. 2008, McCue and Pollock 2008) or environmental (Peterson and Fry 1987) conditions. Because carbon stable isotope ratios of a consumer reflect those of its food change only marginally with trophic level (Warne et al. 2010), they provide information about which primary producers are at the base of a particular food chain (Barrett et al. 2005). On the other hand, consumer tissues become increasingly enriched with heavy nitrogen at each trophic level (Peterson and Fry 1987) and thus reflect trophic position (Ehleringer et al. 1986).

We predict that differences in community composition between White Sands and dark soils will be reflected in trophic structure and variation in stomach contents among the three species in the White Sands and dark soils habitats as measured by the species' carbon and nitrogen isotopic signatures.

Specifically, we expect expansion of overall variation in lizard diet in the depauperate ecosystem of White Sands, where the three species represent the entirety of the lizard community. We predict that expansion of trophic niche across the three species will reflect species-specific shifts in diet and trophic position. Furthermore, we predict that trophic position of each species will parallel previously documented differences in mean and variance of diet and ecomorphological traits in the two habitats (Des Roches et al. 2015a).

Material and methods

Sampling

We collected lizards from dark soils and White Sands habitats in New Mexico from 12 May to 9 July 2010. We captured lizards from three different collection sites in each habitat. Our dark soils sites included a blue-gramma grassland and a yucca-mesquite scrubland, both located in the Jornada Long-Term Ecological Research Station, Doña Ana County, and a similarly vegetated Bureau of Land Management site northeast of the White Sands Missile Range, Otero County. Within the dark soils habitat, we collected 19 dark *Aspidoscelis inornata*, 15 dark *Holbrookia maculata* and 20 dark *Sceloporus cowlesi*. The broad distribution of our dark soils collection sites reflects the disjunct and non-overlapping populations of the three species outside of White Sands. Our White Sands sites were all located at the White Sands National Monument, Otero County and included alkali flatlands with plant communities consisting primarily of soap tree yucca, sumac, saltbrush, and rosemary mint. Here, we collected 18 white *A. inornata*, 15 white *H. maculata* and 18 white *S. cowlesi*. Although trophic differences may exist between the sexes and across ages, we focused on only adult male lizards to control for variation in developmental stage and sexual dimorphism while focusing on habitat and species-level shifts. We captured all lizards by hand or with pole and slipknot noose, with the exception of two dark *A. inornata* that we obtained from pitfall traps. We collected each species one at a time during a 12 to 15 day period, alternating between collection at dark soils and White Sands habitats. We returned all lizards to the site of capture the following day.

We collected plant tissue from the dark soils and White Sands sites at the same time and location that we sampled lizards. We randomly sampled leaf and stem tissue at both dark soils and White Sands habitats from abundant plant species known to experience arthropod herbivory, including soap tree yucca *Yucca elata*, rosemary-mint *Poliomintha* sp., *Ephedra* sp., Indian ricegrass *Oryzopsis hymenoides* and honey-mesquite *Prosopis glandulosa*. We collected samples from 12 different plant species from dark soils sites, and 13 from White Sands sites and froze them at -4°C for storage.

Stable isotopes and trophic position

We obtained muscle tissue from a total of 97 lizard tails (about 10 mm from tip) and 25 plant stems and leaves to be used in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis. After storing the tissue at -80°C , we dissected

muscle tissue from the tail samples, removing skin and bone. After freeze-drying the tissue, we manually ground the samples to a powder by agitating a small metal ball in the sample capsule until a fine powder was produced. We analyzed two samples of approximately 2 mg each from each lizard tail as biological replicates. We used an average of these two measurements for subsequent analyses. For plants, we freeze-dried the tissue, and then manually ground each sample as described previously. Finally, lizard and plant tissue were analyzed at the Univ. of Idaho stable isotopes laboratory using an isotope ratio mass spectrometer.

We calculated trophic position using an isotopic baseline from primary producers (Vidal and Sabat 2010) in the two habitats using the formula (Post 2002b):

$$\text{trophic position} = \lambda + (\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n$$

Where λ is the trophic position of the organism used to estimate $\delta^{15}\text{N}_{\text{base}}$, in this case, for primary producers $\lambda = 1$, $\delta^{15}\text{N}_{\text{secondary consumer}}$ and $\delta^{15}\text{N}_{\text{base}}$ are measured directly, (pooled mean $\delta^{15}\text{N}_{\text{base}}$ for dark soils = 1.31; White Sands = 2.18) and Δ_n is the enrichment of $\delta^{15}\text{N}$. In this case, $\Delta_n = 3.4\%$, following averages calculated across various food chains (Post 2002b) commonly used in comparable lizard studies (Barrett et al. 2005, Fariña et al. 2008, Takimoto et al. 2008). We considered fractionation of $\delta^{13}\text{C}$ to be 0‰ (Post 2002b, Takimoto et al. 2008).

Stomach contents

To obtain samples of lizard diet, we stomach flushed all caught individuals according to standard methods (Legler and Sullivan 1979). Our flushing instrument consisted of a 75 mm \times 16 g curved stainless steel dosing cannula attached to a 5 ml plastic syringe. We stimulated each lizard to open its jaws, which we propped open with a small plastic ring cut from a pasteur pipette. While securing the animal in one hand, we slowly inserted the metal cannula through the digestive tract. We flushed the entire stomach contents with room temperature (20–22°C) tap water and stored stomach contents in ethanol.

To obtain a rough estimate of diet composition, we identified whole and partially digested arthropods to order in each sample. We identified and separated samples into the following orders: Coleoptera, Hymenoptera, Hemiptera, Orthoptera, Lepidoptera and Isoptera. Because we were unable to identify larvae to order, we grouped larvae of all species in the separate group, 'larvae'. We grouped unidentified matter with rare orders (including Diptera, Araneae, Neuroptera, Thysanoptera, Chilopoda, Scorpiones and Solifugae), which never comprised more than 10% of any given stomach content, and included these in the category 'other'. We subsequently dried sorted arthropod groups from each sample in a drying oven for approximately 24 h at 37°C and weighed them to the nearest 0.001 grams. We recorded total stomach content sample weight for each lizard as the summed weights across each order. To obtain a rough estimate of morphospecies richness, we recorded the number of morphologically distinct species in each sample (see also Des Roches et al. 2015a). To evaluate potential changes in the variability of prey, we used niche breadth values for each

individual based on their stomach contents (calculated as the inverse of Simpson's diversity index from arthropod orders, Edwards et al. 2013) from Des Roches et al. (2015a), which used the same individuals as in the current study.

We used morphological measurements of snout–vent length (SVL), adjusted head size (adj. HS), and adjusted bite force (adj. BF) from Des Roches et al. (2015a) to examine potential relationships with stable isotope and stomach content data. We performed a principal component analysis on residuals from a linear model of each of the three measures of head shape (width, length, depth) and SVL, and used the first principal component as a representation of adjusted head size. We similarly calculated adjusted bite force as the residuals of a linear model of bite force and SVL.

Statistical analysis

To evaluate the effect of habitat (dark soils versus White Sands) and species on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes, and arthropod proportions, we used two-way ANOVAs and MANOVAs, respectively. For the latter analysis, we first obtained axes using non-metric multidimensional scaling (NMDS) using a Bray–Curtis similarity index from raw of stomach contents. We ran an NMDS first on all species at once, from which we tested the effects of both species and habitat. We then ran separate NMDS analyses for each species to detect specific differences between habitats. For all pairwise comparisons between lizards from different habitats, we performed Welch's t-tests (to test for differences in means) and Levene's tests (to test for differences in variance) within each species. We examined potential relationships among ecomorphological traits (SVL, adjusted head size, adjusted bite force), habitat (dark soils, White Sands) and trophic response variables (stable isotopes, stomach content composition, and arthropod order proportions) using generalized linear models with a Gaussian link function. We performed all analyses in R (< www.r-project.org >).

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.cr764> > (Des Roches et al. 2015b).

Results

Trophic differences in lizard communities

Our results show significant differences in the trophic structure and stomach contents of the focal lizard communities of dark soils and White Sands habitats in both stable isotopes and stomach contents. Specifically, $\delta^{13}\text{C}$ was affected by habitat, species, and the interaction between habitat and species whereas $\delta^{15}\text{N}$ was affected by habitat and the interaction between habitat and species (two-way ANOVA: all $p < 0.0001$). Pairwise comparisons on combined stable isotope data for all three species revealed a higher $\delta^{13}\text{C}$ for lizards in the dark soils habitat compared to those in the White Sands habitat (Welch's t-test: $p < 0.0001$), however, there were no significant differences in mean $\delta^{15}\text{N}$ (Welch's t-test, $p > 0.05$, Table 1, Fig. 1). Furthermore, $\delta^{13}\text{C}$ was more variable in the dark soil lizard community (Levene test: $p < 0.05$), but $\delta^{15}\text{N}$ was more variable in the White Sands lizard community (Levene test: $p < 0.001$, Table 1, Fig. 1).

Table 1. Results of pairwise comparisons for mean (Welch's t-test) and variance (Levene test) of morphology, performance, stable isotopes and stomach content characteristics between dark soils and White Sands habitats for the three species. Larger mean or variance is denoted by 'DS' (dark soils) or 'WS' (White Sands). Non-significant comparisons are indicated by '-'. Significance is denoted by '**' ($p < 0.05$), '***' ($p < 0.01$), or '****' ($p < 0.001$).

y			<i>A. inornata</i>		<i>H. maculata</i>		<i>S. cowlesi</i>	
			Welch's t-test	Levene test	Welch's t-test	Levene test	Welch's t-test	Levene test
Morphology	SVL ¹		WS****	-	WS**	-	-	DS**
	HS ¹	raw	WS****	-	WS***	-	-	DS*
Performance		adj.	DS**	-	WS**	-	-	-
	BF ¹	raw	WS*	-	WS***	-	-	DS*
Stable isotopes		adj.	-	-	WS**	-	-	-
	$\delta^{13}C$		WS****	-	WS***	-	WS**	WS**
	$\delta^{14}N$		DS****	-	-	WS*	WS****	-
Diet composition	trophic position		DS****	-	-	WS**	-	-
	morphospecies richness		WS****	-	-	-	WS*	WS*
Proportion in diet	niche breadth ¹		-	-	WS**	-	-	-
	Coleoptera		WS**	WS*	-	-	-	-
	Hymenoptera		-	-	WS*	WS****	-	-
	Hemiptera		-	-	-	-	-	-
	Orthoptera		-	-	-	-	DS*	DS*
	Larvae		WS**	WS****	-	-	-	-
	Isoptera		DS****	DS****	-	-	-	-
	Lepidoptera		-	-	WS*	WS*	WS*	WS*

¹data is taken from Des Roches et al. 2014.

As with stable isotopes, diet as assessed from stomach contents varied with both habitat and species. The full model retaining two NMDS axes of variation (stress score = 0.19) showed an effect of habitat, species, and the interaction between habitat and species (MANOVA using Wilks' lambda: all $p < 0.05$). Our analysis of raw proportions of arthropod orders in stomach contents demonstrated differences between habitats for all three species collectively. Again, the full model showed an effect of habitat, species, and the interaction between habitat and species on the proportion of arthropod orders in stomach contents (MANOVA: all

$p < 0.0001$). In general, Orthoptera and Isoptera were more common in the diets of all dark soils lizard species (both $p < 0.01$); whereas Lepidoptera were more common in the diets of White Sands lizard species ($p < 0.001$). Finally, proportions of Hymenoptera, Hemiptera, larvae and Isoptera in stomach contents were affected by the interaction between species and habitat (all $p < 0.05$). Below, we outline species-specific differences in stomach contents between White Sands and dark soils habitats.

Trophic differences in lizard species

Of the three species, *A. inornata* demonstrated the most extreme directional differences in stable isotopes, trophic position, and stomach contents between the two habitats. Both $\delta^{13}C$ and $\delta^{15}N$ were significantly higher in dark soils *A. inornata* than in their White Sands counterparts, but were not more variable (Fig. 2, Table 1). Correspondingly, *A. inornata* had a significantly higher mean trophic level in dark soils than White Sands, but again did not differ in variance (Fig. 3, Table 1). *Aspidoscelis inornata* also demonstrated the least overlap between dark soils and White Sands in terms of NMDS axes (MANOVA: $p < 0.0001$, Fig. 4), and White Sands lizards had a higher morphospecies richness in their diets than dark soils lizards. Furthermore, the proportions of Coleoptera and larvae were higher and more variable in the stomachs White Sands *A. inornata* compared to the same species in dark soils whereas the proportion of Isoptera was higher and more variable in dark soils lizard stomachs (Fig. 5). Extreme directional differences in stable isotopes and stomach contents in *A. inornata* correspond with similar differences in ecomorphological traits, such as larger SVL, absolute head size, and absolute bite force in White Sands lizards (Des Roches et al. 2015a).

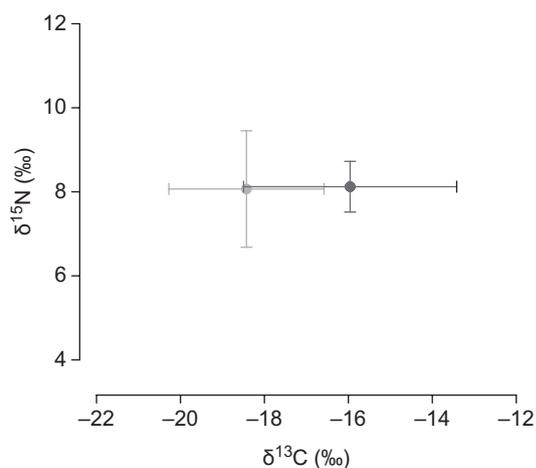


Figure 1. Plot showing pooled means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for all of the three species in both dark soils (dark grey shading) and White Sands (light grey shading) habitats. The figure shows higher mean and greater variation in $\delta^{13}C$ in the dark soils habitat, and greater variation in $\delta^{15}N$ in the White Sands habitat.

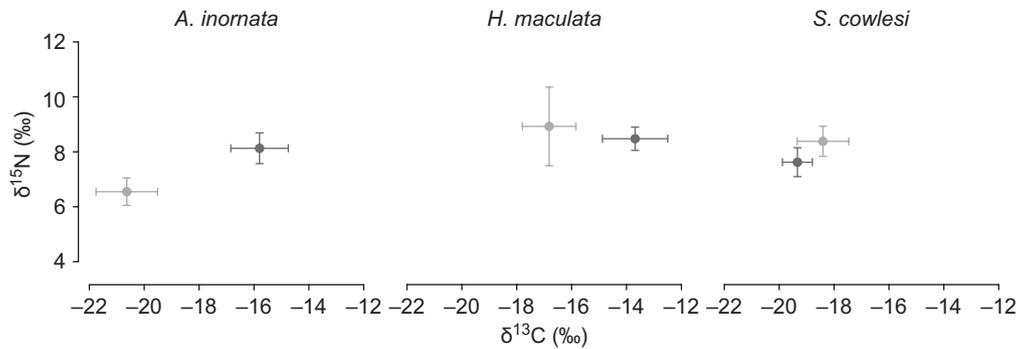


Figure 2. Plots showing the same $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data as in Fig. 1 split by species in dark soils (dark grey shading) and White Sands (light grey shading) habitats. The figures show no overlap in the isotopic ratios of *A. inornata* from the two habitats, minimal overlap in *H. maculata*, and moderate overlap in *S. cowlesi*.

Compared to the other two species, *H. maculata* showed the greatest evidence of trophic niche expansion in White Sands versus dark soils. As with *A. inornata*, $\delta^{13}\text{C}$ was higher in dark soils *H. maculata* than in their White Sands counterparts, but was not more variable (Fig. 2, Table 1). Although mean $\delta^{15}\text{N}$ did not differ between habitats for *H. maculata*, only in this species was $\delta^{15}\text{N}$ significantly more variable for White Sands lizards than for dark soils lizards (Fig. 2, Table 1). Mean trophic level of *H. maculata* did not differ significantly between the habitats, but the variance of trophic level in White Sands lizards was larger than in dark soils lizards for this species (Fig. 3, Table 1). *H. maculata* demonstrated moderate overlap between dark soils and White Sands in terms of NMDS axes (MANOVA: $p > 0.05$, Fig. 4), however, in this species, White Sands individuals had a higher niche breadth in their diets than dark soils individuals. In terms of stomach contents, proportions of Hymenoptera and Lepidoptera were higher and more variable in *H. maculata* in White Sands than in dark soils. Directional differences also existed in ecomorphological traits, such as larger SVL, raw and absolute head size, and raw and absolute bite force in White Sands *H. maculata* (Des Roches et al. 2015a).

The final species, *S. cowlesi* showed the most overlap in isotopic signature, trophic position and stomach contents

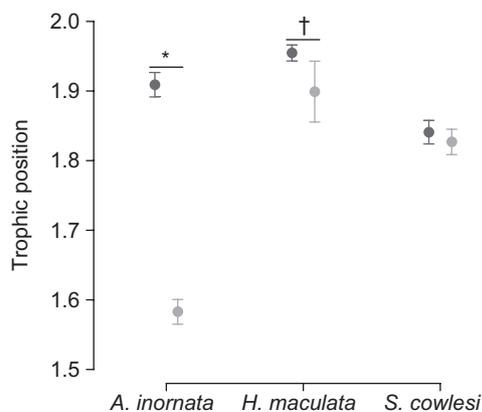


Figure 3. Trophic position of the three species of lizards in both dark soils (dark grey shading) and White Sands (light grey shading) habitats as represented by means and standard errors. Significant differences in mean trophic position (in *A. inornata*) are denoted by ‘*’ ($p < 0.0001$), whereas significant differences in variance (in *H. maculata*) are denoted by ‘†’ ($p < 0.05$).

between the two habitats. However, White Sands *S. cowlesi* still had higher and more variable $\delta^{13}\text{C}$ than their dark soils counterparts (Fig. 2, Table 1). While $\delta^{15}\text{N}$ was higher in White Sands *S. cowlesi* than in their dark soils counterparts, it was not more variable (Fig. 2, Table 1). Trophic level of *S. cowlesi* did not differ significantly in mean or variance between individuals in the two habitats (Fig. 3, Table 1). Although NMDS axes overlapped considerably between *S. cowlesi* from White Sands and dark soils (Fig. 4), morphospecies richness was both higher and more variable in the stomach contents of White Sands lizards. Finally, stomach content analysis revealed that the proportion of Orthoptera was higher and more variable in dark soils lizards but the proportion of Lepidoptera was higher and more variable in White Sands lizards (Fig. 5). Overlap in stable isotope and stomach content data corresponds with minimal directional differences in ecomorphological traits (Des Roches et al. 2015a).

Trophic differences and ecomorphology

General linear models revealed that while habitat was the main determinant of differences in stomach content composition and stable isotopes (especially for *A. inornata*), ecomorphological traits such as SVL, head size, and bite force also affected trophic ecology to a certain extent (Table 2). In particular, $\delta^{14}\text{N}$ was affected by SVL, habitat, and their interaction for *A. inornata*, indicating that $\delta^{14}\text{N}$ increases in the dark soils, but not the white sands habitat. Various aspects of diet composition and proportion of arthropod orders were also influenced by ecomorphological traits. For example, in *H. maculata*, proportion of Coleoptera in the diet increased and proportion of Hemiptera decreased significantly with increasing adjusted head size, but were not affected by habitat. In *S. cowlesi*, proportion of Orthoptera increased with adjusted head size and bite force.

Discussion

Our results illustrate important shifts in the trophic ecology of the entire lizard community, and individual focal species between the depauperate White Sands habitat and the ancestral dark soils habitat. Specifically, we found evidence that ecological release has occurred on a community

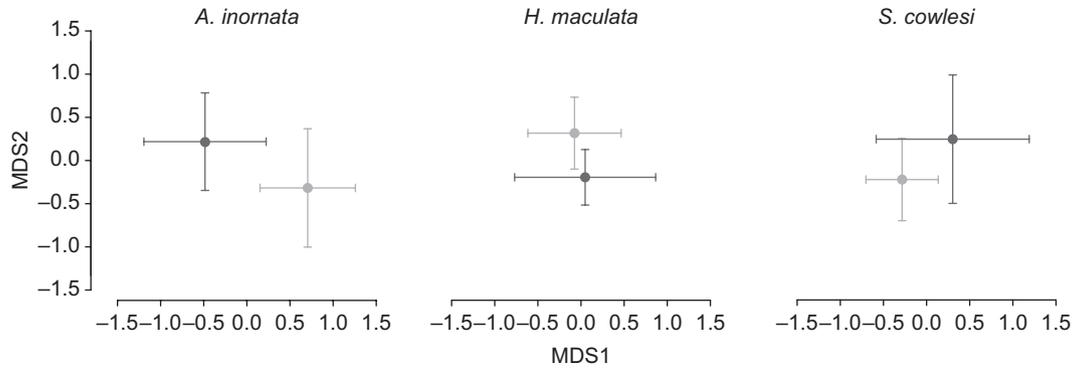


Figure 4. Plots showing means and standard deviations of values calculated from an NMDS analysis of arthropod proportions in stomach contents within each of the three species in dark soils (dark grey shading) and White Sands (light grey shading) habitats. The figures demonstrate the least overlap in the diets of *A. inornata* from the two habitats, moderate overlap in *H. maculata*, and nearly complete overlap in *S. cowlesi*.

level. Furthermore, in each species, shifts in trophic position paralleled the extent of changes in diet, as indicated by stomach contents, and ecomorphology. Our findings demonstrate the early stages of community composition and

trophic structure. Together with our previous work (Des Roches et al. 2015a) they also provide a complete and comparative perspective of the relationship among morphology, diet, trophic position and habitat in three separate species.

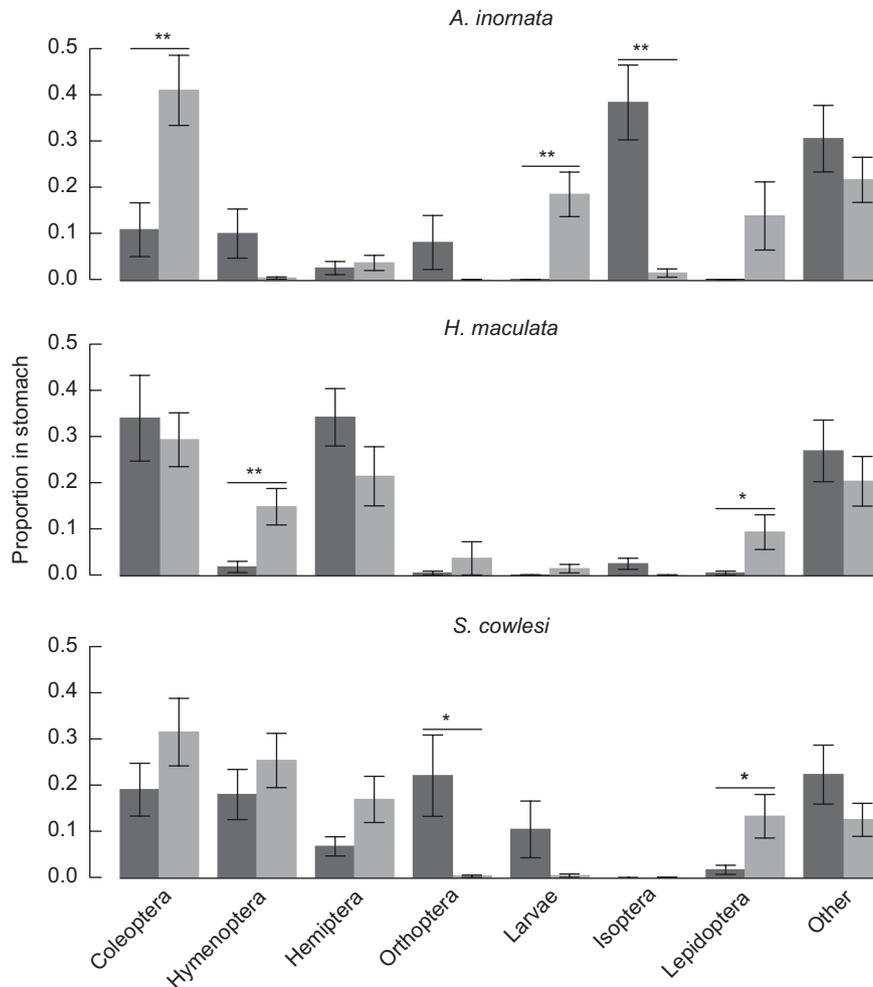


Figure 5. Proportions of different arthropod orders and groups in the stomach contents of the three species of lizards in dark soils (dark grey bars) and White Sands (light grey bars) habitats. ‘Other’ includes unidentified arthropod parts, as well as Diptera, Neuroptera, Aranae, Chilopoda, Solacea, Scorpiones and Thysanoptera orders, which each represent < 10% of any given stomach content. Insignificant differences are greyed out while significant differences in mean proportions are denoted by ‘*’ ($p < 0.05$) or ‘**’ ($p < 0.01$). All significant pairwise comparisons also differed in variance in the same direction. Error bars represent standard error of the mean.

Table 2. Results of generalized linear models examining the relationship between ecomorphology (e, including morphology and performance), habitat (h), and the interaction (e × h) with stable isotopes and stomach content characteristics for the three species. Trophic level is not included as it is directly related to $\delta^{14}\text{N}$ and produces identical results. Non-significant comparisons are indicated by '-'. Significance is denoted by * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$).

x	y		<i>A. inornata</i>			<i>H. maculata</i>			<i>S. cowlesi</i>		
			e	h	e × h	e	h	e × h	e	h	e × h
SVL	stable isotopes	$\delta^{13}\text{C}$	-	-	-	-	**	*	-	-	-
		$\delta^{14}\text{N}$	**	*	*	-	-	-	-	-	-
	diet composition	morphospecies richness	-	*	*	-	-	-	-	-	-
		niche breadth	-	*	-	-	-	-	-	-	-
	proportion in diet	Coleoptera	-	-	-	-	-	-	-	-	*
		Hymenoptera	*	-	-	-	-	-	-	-	-
		Hemiptera	-	*	-	-	-	-	-	-	-
		Orthoptera	-	-	-	-	-	-	-	-	-
		Larvae	-	-	-	-	-	-	*	-	-
		Isoptera	-	-	-	-	-	-	-	-	-
Lepidoptera		-	-	-	-	-	-	-	-	-	
Adj. HS	stable isotopes	$\delta^{13}\text{C}$	-	***	-	-	***	-	-	***	-
		$\delta^{14}\text{N}$	-	-	-	-	-	-	-	***	-
	diet composition	morphospecies richness	-	*	-	-	-	-	-	-	-
		niche breadth	*	-	-	-	-	-	-	-	-
	proportion in diet	Coleoptera	-	-	-	***	-	-	-	-	-
		Hymenoptera	-	-	-	-	**	-	-	-	-
		Hemiptera	-	-	-	**	-	-	-	-	-
		Orthoptera	-	-	-	-	-	-	**	-	-
		Larvae	-	**	-	-	-	-	-	-	-
		Isoptera	-	**	-	-	-	-	-	-	-
Lepidoptera		-	-	-	-	-	-	-	*	-	
Adj. BF	stable isotopes	$\delta^{13}\text{C}$	-	***	-	-	***	-	-	*	-
		$\delta^{14}\text{N}$	*	***	-	-	-	-	-	**	-
	diet composition	morphospecies richness	-	**	-	*	*	-	-	*	-
		niche breadth	-	*	-	-	-	-	-	-	-
	proportion in diet	Coleoptera	-	**	*	-	-	-	-	-	-
		Hymenoptera	-	-	-	-	***	-	-	-	-
		Hemiptera	-	-	-	-	-	-	-	-	-
		Orthoptera	-	-	-	-	-	-	**	*	-
		Larvae	-	***	-	-	-	-	-	-	-
		Isoptera	-	***	-	-	-	-	-	-	-
Lepidoptera		-	-	-	-	**	-	-	-	-	

Trophic differences in lizard communities

Community-wide ecological release in White Sands was supported by the collective increase in variance in $\delta^{15}\text{N}$ of all three species when pooled together (Fig. 1) and their parallel shifts to lower trophic levels in the White Sands habitat compared to dark soils habitat (Fig. 3). In addition, in the dark soils habitat, the three species all occupied around the third trophic level (i.e. they consume primary consumers), however, in White Sands each species shifted to consume between the second and third trophic level. Surprisingly, this shift was not corroborated by stomach content data and thus may reflect changes in dietary preferences throughout the activity season. Expansion of the White Sands species trophic positions may have contributed to, or occurred simultaneously with previously documented (Des Roches et al. 2011) lizard community-wide density compensation (MacArthur et al. 1972). Although it is impossible to determine differences in food chain length between the two habitats from our data, future work that explores the trophic position of other dark soils species could elucidate whether

there are fewer trophic levels in White Sands as is the case for other depauperate ecosystems like lakes (Vander Zanden et al. 1999) and islands (Takimoto et al. 2008).

Differences between dark soils and White Sands lizards' $\delta^{15}\text{N}$, and therefore trophic levels, may also indicate several non-mutually exclusive ecological and physiological dissimilarities between the two habitats. First, dietary changes (Des Roches et al. 2015a) may have led to changes in trophic position (Peterson and Fry 1987, Post 2002b, Araújo et al. 2007). For instance, the fact that all three species consume lower on the food chain and at more disparate trophic levels in White Sands might be a direct result of changes in resource availability or an indirect result of release from interspecific competition (Takimoto et al. 2008, Matthews et al. 2010). Second, dark soils lizards may be more likely to undergo starvation as a result of interspecific competition for food (Hairston et al. 1960), leading to increased enrichment of $\delta^{15}\text{N}$ and higher apparent trophic level (McCue and Pollock 2008). Future work that disentangles the complex physiological and ecological factors in stable isotope analysis in an experimental setting would help elucidate

the relationship between starvation and trophic position (Oelbermann and Scheu 2002).

As predicted, stomach content analyses, which provides a cross-section of diet in time (Warburton et al. 1998, Araújo et al. 2007), showed similar trends to stable isotopes. Like stable isotopes, stomach contents also differed between habitat and among species. Significant differences in diet among species and between habitats were supported by both models of both raw proportions of arthropod orders in lizard stomachs and of NMDS outputs. Although our study was unable to resolve the specific dietary mechanisms that tie shifts in stable isotopes to shifts in stomach contents, both results demonstrate corresponding changes in the magnitude and variation of trophic niche of lizards in the two habitats. Similar parallels between stable isotopes and stomach contents have been found in fish (Bolnick et al. 2007) and frogs (Araújo et al. 2009) suggesting that niche expansion may be characterized by multiple aspects of diet across diverse clades. To better elucidate the relationships among stable isotope ratios, stomach contents, and ecomorphology we examine species-specific differences between lizards from the dark soils and White Sands habitats below.

Trophic differences in lizard species

Our prediction that the three focal species would have more different trophic roles from each other in White Sands than in dark soils was supported by our data. There was a trend for all species to have lower trophic positions in White Sands compared to dark soils, however, the magnitude of this shift varied across species. Specifically, only in *Aspidoscelis inornata* was the decrease significant, whereas in *Holbrookia maculata* trophic niche breadth increased, and in *Sceloporus cowlesi* there was no significant change resulting in increased spread in trophic level across species at White Sands. Overlap between White Sands and dark soils lizards in stable isotope levels and stomach contents ranged from minimal for *A. inornata*, to moderate for *H. maculata*, to almost complete for *S. cowlesi* (Fig. 2). Stable isotope and stomach content results parallel previously published diet niche breadth and morphological results (Des Roches et al. 2015a) with *A. inornata* at one extreme demonstrating the largest differences in morphology and diet between habitats, and *S. cowlesi* showing the smallest differences.

Results from stable isotopes (Fig. 2), trophic position (Fig. 3), stomach contents (Fig. 4, 5), and ecomorphological data (Des Roches et al. 2015a) all suggest that *A. inornata* has undergone the most extreme trophic shift between habitats. Differences in $\delta^{13}\text{C}$ (Fig. 2) in *A. inornata* probably reflect differences in the producer community between the two habitats, while lower $\delta^{15}\text{N}$ and thus trophic position in White Sands *A. inornata* may have been driven by dietary shifts or lower baseline $\delta^{15}\text{N}$ levels. Low trophic level in White Sands *A. inornata* (Fig. 3) indicates that this species might be consuming plant matter. Surprisingly, we found no plant matter in White Sands *A. inornata* stomach contents, as well as few herbivorous Isoptera, and more omnivorous Coleoptera than lizards from dark soils. Inconsistencies between stomach content and stable isotope data often reflect fluctuating diet over time because the former reveals only the most recent prey and the latter represent a

long-term average of diet (Peterson and Fry 1987, Hesslein et al. 1993, Post 2002b, Araújo et al. 2007). Both stable isotope results and the fact that other whiptails have been known to shift to partial herbivory in depauperate island ecosystems (Paulissen and Walker 1994) suggest that White Sands *A. inornata* may consume plant matter at an earlier point in the activity season.

That *A. inornata* exhibited the most extreme shifts in trophic ecology is not surprising given that it is the most ecologically and ecomorphologically distinctive species of the three species. Divergence in ecomorphology, stable isotopes, and stomach contents between dark soils and White Sands *A. inornata* suggests that these factors may be either causally linked, or responding similarly to ecological pressures. Both are supported by our data (e.g. body size and adjusted bite force correlate with $\delta^{15}\text{N}$, and adjusted head size correlates with niche breadth Table 2) and findings in fish (Matthews et al. 2010, Svanbäck and Eklöv 2003) and lizards (Losos 1990). One explanation for extreme shifts in stable isotopes, diet, and ecomorphology is that as the only active forager in White Sands, *A. inornata* has fewer ecologically similar, con-generic competitors (Des Roches et al. 2011). Release from competition may lead to increased access to resources, a higher growth rate (Lister 1976), and lower incidence of starvation (McCue and Pollock 2008), all leading to reduced $\delta^{15}\text{N}$ enrichment and even larger body size (Des Roches et al. 2015a).

Next to *A. inornata*, *H. maculata* showed the second most extreme differences in stable isotopes (Fig. 2), trophic position (Fig. 3), stomach contents (Fig. 4, 5), and ecomorphology (Des Roches et al. 2015a) between habitats. Although mean trophic position and mean $\delta^{15}\text{N}$ were not significantly different between *H. maculata* in the two habitats, both were more variable in White Sands. Increase in the variance of $\delta^{15}\text{N}$ and trophic position may correspond to *H. maculata* dietary niche expansion (Bolnick et al. 2003, 2007) in White Sands, where it has a higher niche breadth and consumes a greater richness of arthropod morphospecies than its dark soils counterparts (Table 1, Des Roches et al. 2015a). Although White Sands *H. maculata* consumed significantly more Hymenoptera and Lepidoptera than their dark soils counterparts (Fig. 5), increased variance in morphospecies richness in the White Sands individuals seemed to reflect consumption of a greater number of morphospecies across all orders (Des Roches et al. 2015a), rather than consuming specific orders with higher richness. In general, concordance between $\delta^{15}\text{N}$, trophic position and stomach contents indicated increased variation in both the short term and long term diet of White Sands *H. maculata*.

Although not as extreme as *A. inornata*, trophic differences in *H. maculata* between habitats indicated an association between ecomorphology and diet. Like *A. inornata*, White Sands *H. maculata* were significantly larger than their dark soils counterparts with larger head size and bite force even after correcting for body size (Table 1, Des Roches et al. 2015a). Some of these ecomorphological changes were associated with diet. For example, proportion of Coleoptera increased significantly with adjusted head size, suggesting that they might be an important component of diet in White Sands *H. maculata* (Des Roches et al. 2015a). Being able to consume a diversity of prey sizes might well have

contributed to the increase in variation of arthropods consumed by White Sands *H. maculata* as larger individuals with stronger bite force can include both small and large prey in their diets (Peters 1983). Indeed, increase in trophic niche breadth corresponds with increased body size in other lizards such as *Anolis* (Lister and McMurtrie 1976) and insects (Novotny and Basset 1999), with longer bills in passerine birds (Brändle et al. 2002), and with stronger bite force in phyllostomid bats (Aguirre et al. 2002).

Of the three species, *S. cowlesi* showed the most minimal differences in stable isotopes (Fig. 2), trophic position (Fig. 3), stomach contents (Fig. 4, 5), and ecomorphology (Des Roches et al. 2015a) between habitats. Unlike the other two species, *S. cowlesi* had both a higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 2) in White Sands than in dark soils, but did not differ significantly in trophic position. Stable isotope trends may reflect our sampling of a greater number of younger *S. cowlesi* in dark soils, which likely had higher growth rates and thus lower fractionation of stable isotopes (Reich et al. 2008). That high $\delta^{15}\text{N}$ in White Sands *S. cowlesi* did not translate into a significantly higher trophic position (Fig. 3) suggests that differences may be related to variation in plant baseline $\delta^{15}\text{N}$. Stable isotope and trophic position results were again in agreement with stomach contents, showing high overlap and little difference between *S. cowlesi* in the two habitats (Fig. 4). As expected, pairwise differences in raw proportions of arthropod orders between habitats were not as pronounced in *S. cowlesi* diet as for the other two species; however, *S. cowlesi* did consume fewer Orthoptera and more Lepidoptera in White Sands compared to dark soils (Fig. 5). Perhaps that *S. cowlesi* shift from consuming one predominantly herbivorous insect order to another explains their minimal change in trophic position between habitats.

As expected, similarities in trophic ecology between *S. cowlesi* in the two habitats is consistent with this species exhibiting the smallest changes in ecomorphology of the three species (Table 1, Des Roches et al. 2014, 2015a). However, the proportion of larvae in stomach contents decreased with decreasing body size and the proportion of Orthoptera increased with increasing adjusted head size and bite force (Table 2), indicating that relationships between diet and ecomorphology might exist, but do not correspond with the different habitats. Minor detectible differences in trophic ecology of *S. cowlesi* between habitats may be a result of its generalist insectivore habits (Stebbins 1985) and minimal selection for trophic specialization.

By examining stomach contents and trophic position of three ecologically different species we gain insight into both community-wide and species-specific differences in distinct ecosystems, one of which is a depauperate, habitat-island. As predicted based on evidence from our previous work (Des Roches et al. 2015a) and results from other studies of colonists in depauperate systems (Crowell 1962, Lister 1976), our data demonstrated both broad shifts the trophic structure of the lizard community and individual differences in the trophic position and stomach contents between dark soils and White Sands. More dissimilar trophic positions of the three lizard species in White Sands may be a response to the depauperate ecosystem and is consistent with other evidence of ecological release in White Sands (Des Roches et al. 2011, 2015a, Refsnider et al. 2015). Furthermore, general

concordance between stable isotopes, stomach contents, and ecomorphology for each species suggest a direct relationship between long and short-term diet in each habitat, which has been found in other systems (Bolnick et al. 2003); however, is only rarely explored in colonists of novel habitats (but see Matthews et al. 2010). Future work, which examines food chain length and trophic position of interspecific competitors in the dark soils habitat, and documents stomach contents of the same individuals through time, could reveal the mechanistic links among ecomorphology, resource use and community structure in these two distinct desert ecosystems.

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