

# Interspecific and interpopulation variation in individual diet specialization: Do environmental factors have a role?

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**Abstract.** Individual diet specialization (IS) has important community- and population-level implications and its ecological drivers are actively investigated. Here, to test the hypothesis that local environmental conditions may influence IS in wild populations, we analyzed the stomach contents of 395 individuals from eight populations of five allopatric species of European cave salamanders (genus *Hydromantes*). We assessed whether their degree of individual diet specialization (1) scaled positively with the respective niche widths, in agreement with Van Valen's niche variation hypothesis (NVH), and (2) could be predicted by satellite-derived climatic and vegetation characteristics of the sites where the populations live. Consistent with the NVH, the degree of individual diet specialization increased with the populations' total niche width. Furthermore, two variables describing local nonarborescent vegetation cover and habitat heterogeneity successfully predicted the variation in individual specialization across the eight populations. Climatic factors had a generally low predictive power, with individual specialization in low- and high-elevation populations showing contrasting patterns of co-variation with air temperature in the warmest quarter of the year. However, independently from elevation, specialization peaked under conditions of high nonarborescent vegetation cover and high precipitation regimes. We discussed the results against two mutually nonexclusive scenarios hypothesizing different mechanisms linking environmental factors to salamanders' trophic strategy at an individual and population level. We concluded that satellite-derived climatic and vegetation variables to date generally adopted to model Grinnellian niches might also be useful in predicting spatial variations in dietary habits of populations, that is, their Eltonian niches.

*Key words:* cave salamanders; climate; dietary specialization; habitat heterogeneity; *Hydromantes*; trophic niche width; vegetation.

## INTRODUCTION

Interindividual trait variability is widespread in wild populations, and there is an increasing recognition of its contribution to mediating species interactions, ecosystem functions, and coevolutionary dynamics (Melián et al. 2014, Des Roches et al. 2018). In this context, individual diet specialization (IS hereafter) has long received

attention for its consequences on population stability, strength of interspecific interactions, and food web structure (Bolnick et al. 2011 and literature cited therein, Layman et al. 2015). IS occurs when individuals, independently from their size, sex, or ontogenetic stage, only use a subset of prey types included in the trophic niche of the population to which they belong (Bolnick et al. 2002, 2003). Under these circumstances, the total niche width of the population reflects both the variability of prey types in the diet of different individuals and the average intraindividual dietary diversity (Roughgarden 1972, 1974).

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Multiple ecological drivers may influence, independently or in concert, the degree of individual diet specialization in wild populations (Araújo et al. 2011 and literature cited therein, Cloyd and Eason 2016, Costa-Pereira et al. 2018). In general, ecological release (sensu Wilson 1961) from heterospecific competitive or predatory interactions has been indicated to affect IS, with both positive and negative effects on individual specialization (Bolnick et al. 2010, Araújo et al. 2011). Intraspecific competition has traditionally been assumed to exert the strongest effects on IS: positive density compensation effects (sensu MacArthur et al. 1972) may stimulate intraspecific resource competition, in turn determining a frequency-dependent selection for specialist phenotypes (e.g., Svanbäck and Bolnick 2005, 2007, Sheppard et al. 2018, Costa-Pereira et al. 2019). Increased individual specialization may ultimately lead to an expansion of the population's niche width: this hypothesis, known as the niche variation hypothesis (NVH; Van Valen 1965), has received support from a number of dietary studies on both vertebrate and invertebrate taxa (Bolnick et al. 2007, Bison et al. 2015, Cloyd and Eason 2017, Maldonado et al. 2017).

It is worth noting that the concepts of ecological release and density compensation are strictly related to ecological opportunity, here broadly defined in terms of accessibility to unoccupied niche space (Yoder et al. 2010, Sjödin et al. 2018) thus including both resource availability and diversity. Ecological opportunity may promote specialization by increasing the foraging options available to individuals, and allowing their trophic niche to widen (Roughgarden 1974, Cloyd and Eason 2016). Hetero- and intraspecific interactions per se can alter ecological opportunity by changing optimal foraging mechanisms (Stephens and Krebs 1986, Svanbäck and Bolnick 2005, Svanbäck et al. 2015). In addition, ecological opportunity can vary along ecological gradients such as climate and habitat diversity (Nosil and Reimchen 2005, Parent and Crespi 2009, Schriever and Williams 2013, Dermond et al. 2018).

Increases in ecological opportunity often positively affect IS at the local scale (Nosil and Reimchen 2005, Darimont et al. 2009, Cloyd and Eason 2016, Marklund et al. 2018) and correspond to variation in total niche width consistent with the NVH (Bison et al. 2015, Cloyd and Eason 2017, Costa-Pereira et al. 2017). At larger spatial scales, variation in ecological opportunity has been suggested to affect individual specialization in marine mammals (Yurkowski et al. 2016), and in multiple taxa across tropical and temperate regions (Araújo and Costa-Pereira 2013). Remarkably, both studies used latitude as a proxy for ecological opportunity.

Compared to only using latitudinal positioning, satellite-derived environmental data can provide more accurate information on the actual biotic and abiotic conditions experienced by individuals in the wild; indeed, this is the founding assumption of current investigative efforts using correlative approaches to study the

influence of environmental factors on species' distributions (i.e., their Grinnellian niche: Peterson et al. 2011). Besides the aforementioned exceptions, the influence of environmental drivers on IS variation across multiple species or populations distributed over a spatial scale encompassing different biotopes or climatic conditions remains largely unexplored.

Here we analyzed the stomach contents of 395 individuals from eight allopatric populations of European cave salamanders belonging to five *Hydromantes* species (Plethodontidae) distributed across Sardinia island (Italy). Salamanders of the genus *Hydromantes* are nonobligate cave dwellers endemic to Italy and France, using subterranean environments for shelter as they offer a combination of abiotic conditions suitable for their cutaneous respiration (Spotila 1972, Lanza et al. 2006). They prey upon invertebrates in the neighborhood of the cave's entrance (Salvidio et al. 2015, Lunghi et al. 2018a); accordingly, their trophic activity is strongly influenced by epigeic climatic conditions (Lunghi et al. 2015, 2018c). Moreover, *Hydromantes* populations are characterized by a high site fidelity and restricted home ranges (<80 m: Lanza et al. 2006) to the point that populations from different caves can be considered isolated (Salvidio 2013, Lunghi and Bruni 2018).

We preliminarily tested the null hypothesis of no individual specialization, that is, that the eight populations were actually made up by generalists with resource use probabilities equal to those of the whole population (as in, e.g., colonial seabirds: Wiley et al. 2019). Subsequently, we verified whether populations with a greater degree of individual specialization exhibited wider trophic niches in agreement with the NVH. Both biotic interactions and ecological opportunity can induce a positive co-variation in populations' individual specialization and niche width; a rejection of the hypothesis may thus indicate that other mechanisms regulate the trophic strategy of salamanders at a population and individual scale (e.g., individual or parallel release: Bolnick et al. 2010).

Finally, we assessed if local environmental factors—as defined by satellite-derived climatic and vegetation cover variables—predicted the degree of dietary specialization in *Hydromantes* populations. To this end, a correlative procedure conventionally used in environmental niche modeling was used to identify a minimum adequate predictive model of IS by means of a heuristic multiple regression approach. Local temperature and precipitation conditions together with vegetation cover have been shown to affect the distribution, abundance, and body condition of *Hydromantes flavus* populations in northern Sardinia (Lunghi et al. 2018c). On this basis, we tested two nonmutually exclusive scenarios (summarized in Fig. 1) relying on different assumptions on how climate, vegetation cover, and habitat heterogeneity may potentially affect individual diet specialization and total niche width of the populations under analysis. In the first scenario, suitable bioclimatic conditions positively

affect the epigeal abundance and foraging activity of salamanders, promoting intraspecific competitive interactions, an increase in individual specialization and ultimately, an expansion of the niche. In the second scenario, vegetation cover and/or habitat heterogeneity positively affect local ecological opportunity by increasing invertebrate prey diversity and abundance and by promoting the expansion of the populations' niche (in agreement with the resource diversity hypothesis: Lawton 1983) achieved through an increase in individual diet specialization (Bolnick et al. 2010).

## METHODS

### *Study species and dietary data*

Analyses were based on the data set published by Lunghi et al. (2018b) providing quantitative information on the stomach contents of cave salamanders belonging to six *Hydromantes* species occurring in allopatry in peninsular and insular Italy. Here we focused on the species distributed on Sardinia Island, namely, *Hydromantes flavus*, *Hydromantes supramontis*, *Hydromantes imperialis*, *Hydromantes sarrabusensis*, and *Hydromantes genei*.

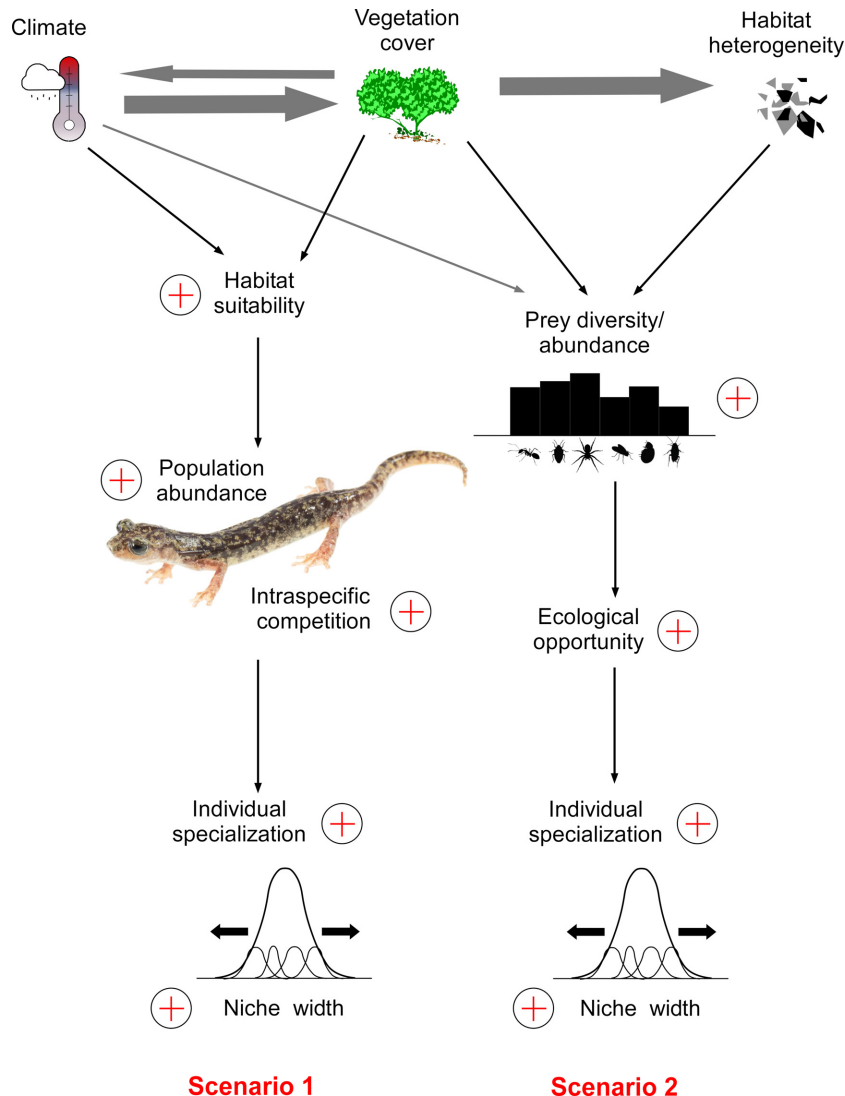


FIG. 1. Hypothesized scenarios regarding the potential effects of climate, vegetation cover, and heterogeneity on the degree of individual diet specialization and total niche width among *Hydromantes* populations. In the first scenario, climate and vegetation cover increase habitat suitability for salamanders, positively affecting their epigeal abundance and foraging activity, a condition promoting intraspecific competitive interactions and ultimately determining an expansion of the populations' trophic niche achieved through an increase in individual specialization. In the second scenario, vegetation cover and habitat heterogeneity promote an increase in ecological opportunity in terms of prey diversity and abundance, in turn reflecting on an expansion of populations' trophic niche and increase in the proportion of specialized individuals. Gray arrows refer to interactions between climate/microclimate, vegetation cover, and prey diversity and abundance, which are not explicitly addressed in the present study. see Introduction for further details.

Sardinia is located in the Western Mediterranean Sea, between 38°51' N and 41°15' N latitude and between 8°8' E and 9°50' E longitude. It is the second-largest island in the Mediterranean, with an area of approximately 24,090 km<sup>2</sup>. The topography is complex, with plain, hill, and mountainous biotopes extending over a variety of lithologies of volcanic, metamorphic, and sedimentary origin dating back to the early Paleozoic (Carmignani et al. 2016).

The sites surveyed during the study (i.e., caves and other subterranean environments; Appendix S1: Fig. S1) were located over an area of about 5,800 km<sup>2</sup> in the southwestern (*H. genei*), southeastern (*H. sarrabusensis*), and central-eastern (remaining species) parts of the island. Sites were generally located in hilly and mountainous areas, with elevations ranging from 164 to 1,033 m above sea level (asl; Appendix S2: Table S1); climatic conditions and vegetation cover varied accordingly, with thermomediterranean thermotypes and Mediterranean shrubs dominating at low elevations, and mesomediterranean thermotypes and evergreen broad-leaved woodland characterizing higher elevations (Appendix S2: Table S1 and Appendix S1: Fig. S1 for two contrasting examples; see also Results and Appendix S2: Table S5).

Stomach flushing was used to assess the diet of individual salamanders captured from 2015 to 2017. During this period, we surveyed each site twice in fall (2015 and 2016) and twice in spring (2016 and 2017). For each salamander, the ontogenetic stage (juvenile vs. adult), sex, and body size (snout–vent length, in millimeters) were assessed. Prey found in stomachs were classified to the lowest possible taxonomic level, discriminating between life stages when relevant, and identifying a total of 41 prey categories.

For each season, we pooled data from different years, and we analyzed only those populations where at least 15 individuals with recognizable prey in their stomachs and a minimum of three individuals per season. For *H. sarrabusensis*, we pooled data from “cave 1” and “cave 2,” as the two populations were located at a distance of approximately 35 m and likely nonindependent. Overall, we retained data representing the occurrence of 31 identified prey items in 395 individuals from eight populations belonging to five *Hydromantes* species (Appendix S2: Table S2). The minimum interpopulation distance was 1,382 m, largely exceeding the known dispersal distance of *Hydromantes* (Lanza et al. 2006, Lunghi and Bruni 2018); in addition, they were located in different grid cells of the climatic layers used in subsequent analyses (see further in this section and Appendix S2: Table S5). Accordingly, the eight populations were assumed to be isolated groups (sensu Bolnick et al. 2007).

#### Niche metrics

For each population, we calculated the index of individual specialization as

$$IS = \frac{\sum_i PS_i}{N}$$

(Bolnick et al. 2002) where  $N$  = number of  $i$  individuals in a population and  $PS_i$  values were estimated using the revised version of Schoener's (1968) proportional similarity index (PS) proposed by Bolnick et al. (2002):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where  $p_{ij}$  is the frequency of a prey category  $j$  in the individual  $i$ 's diet, and  $q_j$  is the frequency of prey category  $j$  in the entire population. For the sake of clarity, we used the index  $V = 1 - IS$  proposed by Bolnick et al. (2007), where values close to 1 indicate a high proportion of specialized individuals in a considered group or population, and values approximate 0 when there is no individual specialization.

In addition, we estimated the populations' total niche width (TNW) using the measure proposed by Roughgarden (1979), based on the Shannon-Weaver diversity index:

$$TNW = - \sum_j q_j \ln q_j$$

where  $q_j$  is the frequency of prey category  $j$  in the population's niche. TNW equals zero when the entire population concentrates on a single prey category, and increases with both the number of prey categories and the evenness with which they are consumed. Noticeably, both IS and TNW are calculated using  $q_j$  values—the proportion of the  $j$ th prey category in the population's diet—and may thus be nonindependent. Alternatively, the total niche width of the eight *Hydromantes* populations was also calculated using Levins' (1968) measure  $B$  of niche breadth:

$$B = \sum_j w_j \log w_j$$

where  $w_j$  is the proportion of individuals within a population feeding on the  $j$ th prey category. A preliminary comparison indicated a significant correlation between TNW and  $B$  (Pearson  $r = 0.85$ ,  $P = 0.007$ , 6 df); accordingly, TNW values were assumed to be reliable estimates of populations' total niche width and used in further analyses.

#### Climatic and vegetation variables

Climatic variables obtained from the WorldClim v2 data set<sup>11</sup> (approximate spatial resolution 0.92 × 0.70 km within the study area) were used to predict variation in  $V$  among *Hydromantes* populations. The lungless condition and cutaneous respiration of Plethodontid salamanders make air temperature and humidity crucial factors influencing their physiology and ecology (Feder 1983). Accordingly, together with annual mean temperature, temperature

<sup>11</sup> <http://www.worldclim.org/>

seasonality, annual precipitation, and precipitation seasonality used in Lunghi et al. (2018c), we included five supplementary temperature and precipitation variables characterizing the hottest/driest quarter of the year, because dietary data were collected in spring and fall (Appendix S2: Table S3). In addition, two vegetation variables—that is, percentage of arboreal and nonarboreal habitat cover—were extracted from the Terra MODIS Vegetation Continuous Field (VCF) product (available as MOD44B v006<sup>3</sup>, 250-m spatial resolution). Percentage of arboreal cover included all forest types and age classes, while percentage of nonarboreal vegetation cover included meadows, regeneration areas, and clear-cut areas. Data were extracted from MODIS tiles of the study area for the years 2015, 2016, and 2017 and averaged.

### Statistical analyses

All statistical analyses were performed in the R statistical environment (R Development Core Team 2019); specifically, the package *RInSp* (v. 1.2.3; Zaccarelli et al. 2013) was used for niche metric analyses and related resampling procedures.

We first assessed whether individual diet specialization within populations was affected by seasonality or by other intrapopulation characteristics related to sex, body size, and ontogeny (e.g., Bolnick et al. 2003, de Camargo et al. 2014). Individual proportional similarity values ( $PS_i$ ) were calculated for each population and analyzed by a two-way permutational ANOVA (PERMANOVA hereafter) with Factor 1 = season (fixed, two levels, “spring” and “autumn”), Factor 2 = ontogenetic stage (fixed, two levels, “adult” and “juvenile”) and the snout–vent length of individual salamanders as a covariate. We repeated the analyses for adults only, to test the influence of sex. In addition, for each population, spring and fall distributions of  $PS_i$  values were smoothed using a kernel density estimation with a normal optimal bandwidth, and compared by a permutation test of equality (Bowman and Azzalini 1997). Comparisons were limited to populations with >8 analyzed individuals per season, twice the minimum sample size required for monodimensional data sets (Silverman 1998).

Bootstrapping was adopted to perform a test of no individual specialization, hypothesizing that individuals were generalist foragers with resource use probabilities equal to those of their population. To this end, for each population, diet matrices were generated in which each individual  $i$  was assigned the observed number of diet items, but each item was placed in resource categories with probabilities determined from the whole population resource utilization. The procedure was repeated 9,999 times, and probabilities were estimated as the proportion of simulated  $V$  values higher than the observed value.

Regression analysis was used to verify the correlation between the individual specialization index ( $V$ ) and the

TNW values of populations. A Monte Carlo resampling procedure (described in Bolnick et al. 2007) was adopted to test whether the slope observed for the  $V$ –TNW relationship could be generated by an artifact determined only by stochastic sampling. Briefly, the procedure requires each individual having  $n$  prey items in its stomach to sample  $n$  items randomly from the diet frequencies of the population it belongs to via multinomial sampling. After 9,999 resampling replicates, a mean  $IS_{null}$  measure was estimated and used to calculate a  $V_{null}$  value. Populations'  $V_{null}$  values were regressed against the observed TNW to evaluate the null hypothesis of a randomly generated negative relationship between the two metrics, considering that the niche variation hypothesis is supported if the empirical slope of the  $V$ –TNW relationship is significantly steeper than the null slope (Bolnick et al. 2007). Conversely, an empirical slope equal or lower than the null slope indicates that similar or higher degrees of specialization occur in the studied populations only by stochastic sampling effects.

The coordinates of the locations (Appendix S2: Table S1) were used to extract climatic and vegetation data from environmental layers. The MODIS Vegetation Continuous Field product is not well resolved below 30% arboreal cover, and does not differentiate for ranges <10% of the variable (Staver and Hansen 2015); in addition, here percent of arboreal and nonarboreal vegetation cover were characterized by a highly significant correlation ( $r = -0.94$ ,  $P = 0.0005$ , 6 df). Consequently, only the latter vegetation variable was included in further analyses. The percent nonarboreal vegetation cover was used to estimate a first-order measure of habitat heterogeneity according to the procedure described in Tuanmu and Jetz (2015). In brief, the value of the variable was extracted from 2015, 2016, and 2017 MODIS tiles for the pixel containing the location as well as for the eight neighboring pixels, thus covering an area of  $750 \times 750$  m. The coefficient of variation was calculated over the 27 extracted pixels and used to presume the spatial–temporal habitat heterogeneity (HH in Appendix S2: Table S3). Subsequently, the 11 climatic and vegetation variables (Appendix S2: Table S3) were log-transformed and z-scaled to reduce skewness and improve linearity. A principal components analysis followed by a one-way PERMANOVA was used to highlight statistically significant groups of salamander populations characterized by similar environmental conditions.

We identified a minimum adequate model (MAM; i.e., the model that contains the minimum number of predictors that satisfy some statistical criterion: Whittingham et al. 2006) linking the variation of populations' specialization index values with the predictor variables using a heuristic generation of alternative regression models. Model selection was performed adopting an information theoretic criterion (Burnham and Anderson 2002, Hegyi and Garamszegi 2011). To this end, the second-order Akaike information criterion  $AIC_c$  (Akaike 1974, Sugiura 1978), corrected for small sample sizes, was

<sup>3</sup> <https://lpdaac.usgs.gov/products/mod44bv006/>

calculated for each combination of  $n$  explanatory variables (max  $n = 2$  given the relatively low number of populations) and used to identify the best MAM among the alternative regression models generated by the procedure. For model comparison,  $AIC_c$  values were used to estimate a set of positive Akaike weights  $w_i$  summing to 1 (Burnham and Anderson 2002). The model containing predictors significant at  $P < 0.05$  and showing the highest  $w_i$  was considered the best candidate (e.g., Mancinelli 2010); model building and statistical analyses were performed following Fox and Weisberg (2011).

## RESULTS

The proportional similarity index  $PS_i$  of individual salamanders varied significantly across the studied populations independently from season, sex, ontogenetic stage, or multifactor interactions (Appendix S2: Table S4). In addition, nonsignificant differences occurred between the spring and fall distributions of  $PS_i$  values for the five populations tested (Appendix S1: Fig. S2).

The degree of individual diet specialization  $V_{emp}$  varied considerably among the eight populations (Fig. 2A), independently from the number of individuals having prey in their stomachs or the total number of sampled individuals (Appendix S2: Table S2;  $r = 0.02$ ,  $P = 0.97$ , and  $r = 0.01$ ,  $P = 0.98$ , respectively; 6 df). With only two exceptions, the majority of the populations showed  $V_{emp}$  values significantly different from those obtained assuming a random prey sampling ( $V_{null}$ ; Fig. 2A). The highest and lowest degrees of specialization were observed for *H. genei* (pop2) and *H. flavus* (pop3), respectively, the former characterized by a proportion of specialized individuals four times higher than the latter ( $V_{emp} = 0.69$  vs. 0.16; see Fig. 2B for examples of the respective bipartite networks).

Populations with a higher degree of individual diet specialization had wider niche widths (Fig. 2A), varying from a minimum of 0.44 to a maximum of 2.2 (*H. flavus* [pop3] and *H. genei* [pop2], respectively). Noticeably, the general pattern was confirmed at the intraspecific scale for those species for which multiple populations were analyzed (i.e., *H. flavus*, *H. genei*, and *H. supramontis*). Total niche width scaled positively also with  $V_{null}$  values (Fig. 2A); however, the linear regression model (after log transformation of total niche width values) showed a slope significantly lower than that determined for empirical  $V$  values (slope  $\pm$  SE:  $V_{emp} = 0.71 \pm 0.06$ ;  $V_{null} = 0.59 \pm 0.09$ ;  $F_{2,12} = 12.1$ ,  $P = 0.002$ ).

The heuristic search procedure identified a MAM based on the two explanatory variables VEG and HH, that is, percent of nonarboreal vegetation and habitat heterogeneity (Fig. 3A; adjusted  $r = 0.83$ ,  $P = 0.02$ ,  $df = 2, 5$ ). The MAM was characterized by the lowest  $AIC_c$  value, and by an Akaike weight  $w_i$  more than 10 times larger than the second and third best candidate MAMs, based uniquely on percent of nonarboreal vegetation and habitat heterogeneity, respectively (Table 1).

The two variables were not significantly correlated ( $r = 0.53$ ,  $P = 0.18$ , 6 df) and both provided positive, significant contributions to variation in individual specialization across populations (Table 1 and Appendix S1: Fig. S3; VEG:  $b = 0.49 \pm 0.16$  [mean  $\pm$  SE],  $t = 2.81$ ,  $P = 0.037$ , HH:  $b = 0.58 \pm 0.18$ ,  $t = 3.31$ ,  $P = 0.021$ ).

Climatic variables showed a generally low predictive power, with annual precipitation and precipitation seasonality, contributing with HH only to the fourth-best MAM (Table 1;  $w_i$  weights approximately 58 and 78 times smaller than the best candidate). Noticeably, a principal-components analysis performed on predictor variables indicated that the eight populations separated along the first component axis (62.3% explained variance) into two significantly distinct groups, with temperature and precipitation variables specific to the driest/warmest quarter providing a major contribution (Appendix 1: Fig. S4 and Appendix 2: Table S6). The first group comprised four populations living at high elevations (i.e., between 708 and 1,033 m asl: *H. flavus* [pop2] and [pop3], *H. imperialis* [pop2], and *H. sarrabusensis* [pop1]), and the second group included four low-elevation (164–339 m) populations (*H. supramontis* [pop2] and [pop3], *H. genei* [pop2] and [pop3]). Depending on the group, two distinct patterns of variation in individual specialization were observed (Fig. 3B): for high-elevation populations,  $V$  values showed a significantly negative relationship with the mean temperature of the warmest quarter ( $r = -0.99$ ,  $P = 0.008$ , 2 df after log–log data transformation), reaching maximum values at sites characterized by relatively high precipitations in the driest quarter and nonarboreal vegetation cover. Conversely, individual specialization in low-elevation populations increased significantly with temperature ( $r = 0.96$ ,  $P = 0.04$ , 2 df), even though, as observed for high-elevation populations, maximum  $V$  values were observed at sites characterized by high precipitations and vegetation cover (Fig. 3B).

## DISCUSSION

Individual diet specialization (IS) has been repeatedly investigated in terrestrial amphibians focusing on both single and multiple populations/species (e.g., Araújo et al. 2009, Costa et al. 2015, Salvidio et al. 2015, Costa-Pereira et al. 2018, 2019). To our knowledge, however, no previous studies have explored the potential relationships between environmental factors and IS variation among multiple allopatric populations or species of amphibians over a geographical scale comparable to that of the present investigation (but see also Cloyed and Eason 2016). Here we verified that dietary specialization across the eight populations of cave salamanders from Sardinia scaled positively with the respective niche width. Furthermore, we indicated that remotely sensed environmental variables were successful in predicting among-population variations in individual specialization; specifically, populations living under conditions of

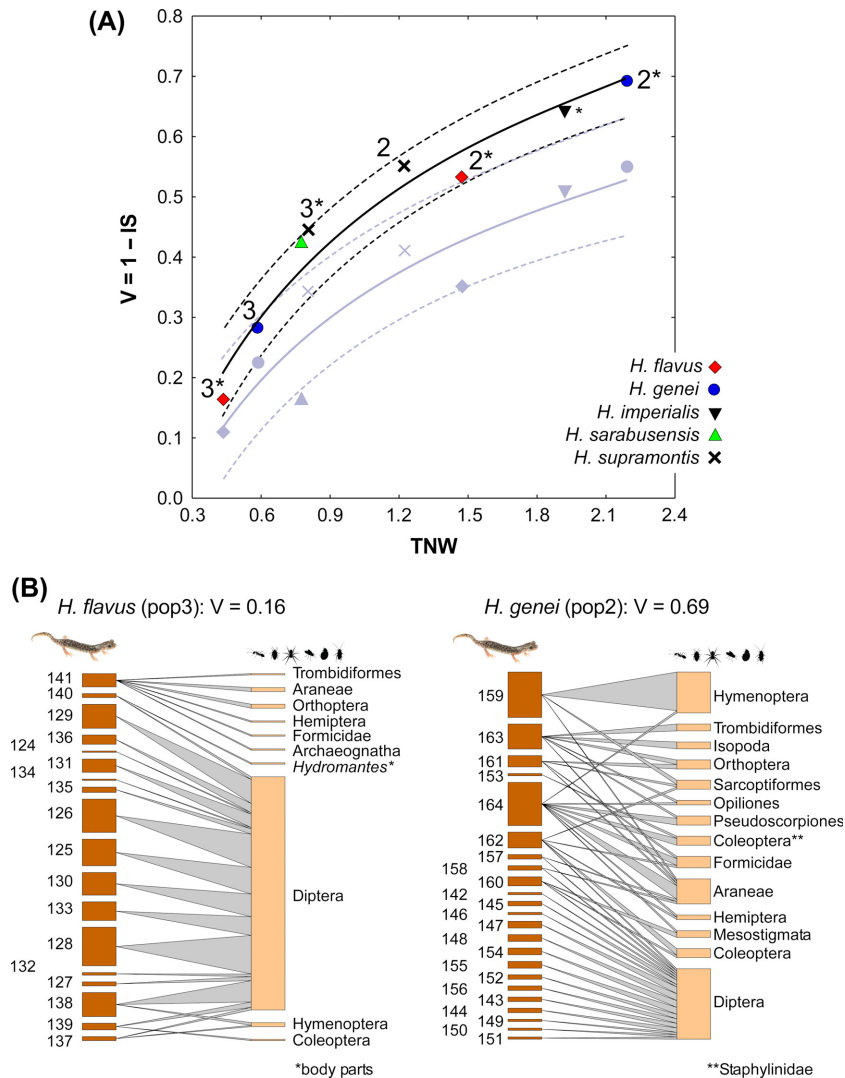


FIG. 2. (A) Degree of individual diet specialization (IS,  $V$ ) of *Hydromantes* populations and their respective niche width (TNW). Empirical results ( $V_{emp}$ ) are in black; gray symbols indicate simulated values ( $V_{null}$ ) obtained through a null model assuming diet specialization to emerge only from individuals sampling a shared prey distribution ( $H_0$ ) stochastically. Asterisks identify populations characterized by significant differences between  $V_{emp}$  and  $V_{null}$  (see Results). Logarithmic curves are fitted to  $V_{emp}/null$ -TNW relationships after a test based on an Akaike information criterion indicating that a logarithmic model was the best fit for the  $V_{emp}$ -TNW relationship as compared with a linear ( $\Delta AIC_c = -9.1$ ,  $P = 0.001$ ) and power model ( $\Delta AIC_c = -6.4$ ,  $P = 0.03$ ). Dashed lines are 95% confidence intervals. (B) Two contrasting examples of bipartite individual-prey networks of the two *Hydromantes* populations characterized by the highest ( $V = 0.69$ , *H. genei* [pop2]) and lowest ( $V = 0.16$ , *H. flavus* [pop3]) degrees of individual diet specialization, respectively. Link thickness represents the number of prey items found in the stomach of each salamander, the numerical code refers to that assigned in the original data set (see Results for further details).

high nonarboreal vegetation cover and high habitat heterogeneity showed a higher degree of dietary specialization as compared with those from locations characterized by lower values of both these variables.

The interpretation of the results requires some preliminary methodological considerations. Studies on individual diet specialization based on stomach contents generally necessitate complementary data provided by longitudinal sampling procedures or stable isotope analyses to corroborate the temporal consistency of foraging

strategies (Bolnick et al. 2002). All Sardinian *Hydromantes* species are included in the European Community Habitat Directive 43/92/EEC (European Community 1992) and are listed as “vulnerable” or “threatened” in the IUCN Red List of Italian vertebrate species (reported as *Speleomantes* spp.; Rondinini et al. 2013). Accordingly, only stomach flushing and marking of a limited number of individuals were authorized, and no collection of tissue samples was allowed. The low recapture rate observed for *H. flavus* (approx. 0.045; Lunghi

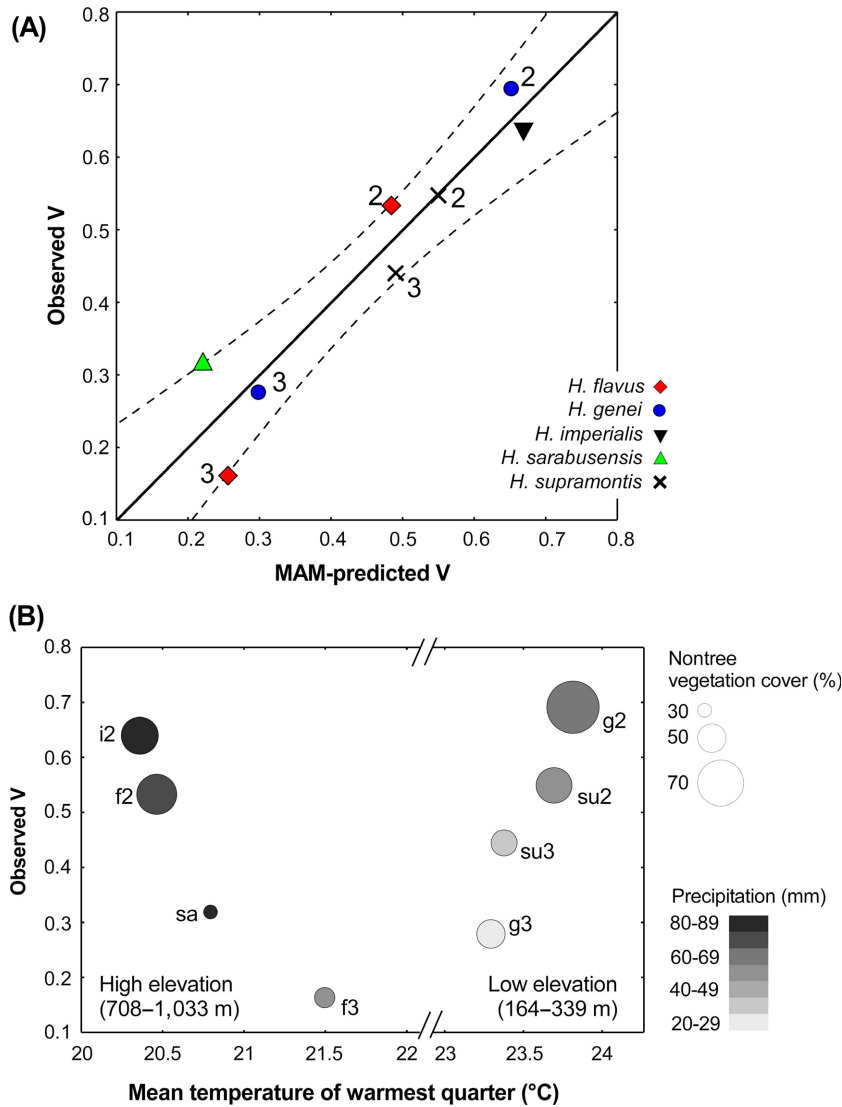


FIG. 3. (A) Degree of individual diet specialization ( $V$ ) in *Hydromantes* populations plotted against the values predicted by the best minimum adequate model (MAM) including % of nonarboreal vegetation cover and habitat heterogeneity (VEG and HH in Appendix S2: Table S3) as bioclimatic predictors. The second and third-best candidate MAMs, including VEG and HH as single predictors, are shown in Appendix S1: Figure S3. The biplot data are fitted by a linear regression model (continuous lines); dashed lines are 95% confidence intervals. (B)  $V$  values in high elevation (>708 m; left) and low-elevation *Hydromantes* populations (<339 m; right) are plotted against the mean temperature of the warmest quarter. The diameter of the circles scales with the degree of nonarboreal vegetation cover, the shades of grey indicate different precipitation regimes in the driest quarter, and the codes refer to the different populations (i.e., f2 = *H. flavus* [pop2]; f3 = *H. flavus* [pop3]; g2 = *H. genei* [pop2]; g3 = *H. genei* [pop3]; i2 = *H. imperialis* [pop2]; sa = *H. sarabusensis* [pop1]; su2 = *H. supramontis* [pop2]; su3 = *H. supramontis* [pop3]).

and Veith 2017) coupled with the generally high incidence of empty stomachs (on average 49% of the total number of sampled individuals in this study: Appendix S2, Table S2) prevented us from using mark-recapture approaches to verify the temporal consistency of individuals' foraging strategy. Alternatively, we opted for maximizing the number of analyzed populations and individuals per population while explicitly testing the consistency of dietary habits across different seasons. In fact, the results of the PERMANOVA performed on

individual proportional similarity indices ( $PS_i$ ) showed that the mean individual specialization of the eight populations was independent from season, as well as from sex, age, and size-related effects (Appendix S2: Table S4). Furthermore, at least in five populations (those with >8 individuals) the frequency distribution of  $PS_i$  values showed nonsignificant seasonal differences (Appendix S1: Fig. S2). Noticeably, this happened despite considerable seasonal changes in the taxonomic structure of the prey community (Lunghi et al. 2018a).



TABLE 1. Summary of the heuristic multiple regression analysis followed by a parsimonious selection procedure of the minimum adequate model (MAM) predicting individual diet specialization ( $V$ ) by means of bioclimatic variables; only the first five best MAMs are reported.

$K$	Predictors	$AIC_c$	$w_i$
2	% of nonarboreal vegetation cover (VEG +); habitat heterogeneity (HH +)	-26.11	0.783
1	% of nonarboreal vegetation cover (VEG +)	-21.42	0.075
1	Habitat heterogeneity (HH +)	-21.37	0.073
2	Habitat heterogeneity (HH +); precipitation seasonality (BIO15 -)	-17.97	0.013
2	Habitat heterogeneity (HH +); annual precipitation (BIO12 -)	-17.54	0.011

Notes: For each variable, we also report the sign of the contribution of the predictor to the model in parentheses.  $AIC_c$ , second-order Akaike information criterion;  $K$ , number of predictors included in the model;  $w_i$ , Akaike weight.

In the best minimum adequate candidate model, nonarboreal vegetation cover and habitat heterogeneity predicted the variation of individual diet specialization across *Hydromantes* populations (Fig. 3, Table 1), supporting a scenario where the salamanders' trophic strategy is influenced by ecological opportunity (Fig. 1). Indeed, high vegetation cover and habitat heterogeneity may indirectly promote ecological opportunity by increasing invertebrate prey diversity and abundance (among others, Tews et al. 2004 and literature cited, Schaffers et al. 2008, Ebeling et al. 2018), determining an expansion of the populations' niche in agreement with the resource diversity hypothesis (Lawton 1983). Noticeably, this hypothesis does not explicitly address potential effects on individual diet specialization. Optimal foraging theory predicts that population niche expansion may imply a decrease in specialization (Roughgarden 1972, Stephens and Krebs 1986, parallel release in Bolnick et al. 2010); alternatively, functional trade-offs may limit individuals' niche width (because of, e.g., behavioral or physiological constraints), with the population's niche expanding through an increase in individual diet specialization in agreement with the niche variation hypothesis (Bolnick et al. 2010). Our results provide support to this hypothesis, even though they should be taken with caution, as they should be corroborated by quantitative, field-determined microhabitat information on the abundance and diversity of local arthropod assemblages (e.g., Costa et al. 2015, Cloyd and Eason 2016). In addition, the procedure herein adopted is acknowledged to provide more detailed information on habitat heterogeneity than previously available metrics (Tuanmu and Jetz 2015), yet further confirmation is needed, based on a more accurate estimation of environmental heterogeneity at a microhabitat scale (see Stein and Kreft 2015 for a recent review of methods).

Climatic variables did not contribute significantly to the best candidate models (Table 1). Indeed, the underlying null hypothesis of this study was that the explanatory power of bioclimatic variables was generally negligible, as their spatial resolution is too coarse to capture Eltonian trophic niche-related processes taking place at microhabitat scale (Soberón 2007; see also Mancinelli et al. 2019). The spatial (approx.  $0.92 \times 0.70$  km within the study area) and temporal resolution (data averaged over the period 1970–2000) of the WorldClim climatic layers are coarser compared with the MODIS vegetation layers (250 m, data averaged over the period 2015–2017; Appendix S2: Table S3) and may provide less ecologically meaningful information. However, Fig. 3 suggests that climatic variables might have a less straightforward and nonlinear effect on populations' individual specialization, partially supporting the first hypothesized scenario (Fig. 1) and confirming that multiple ecological factors may simultaneously affect the degree of individual diet specialization in wild populations (Cloyd and Eason 2016, Costa-Pereira et al. 2017, 2018). Among others, precipitation can exert a positive indirect effect on the abundance and diversity of soil arthropod communities in temperate environments (Sweet et al. 2015, Pan et al. 2018). Second, vegetation cover generally provides suitable microclimatic conditions of temperature and humidity to Plethodontids, positively affecting populations' abundance (Peterman and Semlitsch 2013, O'Donnell et al. 2014, Cosentino and Brubaker 2018). Water loss, in particular, represents a critical physiological challenge: Plethodontids are lungless, and respiration takes place through their skin (Whitford and Hutchison 1967). A narrow range of suitable habitat temperature and humidity combinations controls their eco-physiological performance, in turn influencing their activity, distribution, and abundance, with vegetation exerting an important effect in buffering climatic extremes at a microhabitat scale (Spotila 1972, Lunghi et al. 2015, 2016, Ficetola et al. 2018, Lunghi et al. 2018c). Figure 3 indicates that *Hydromantes* populations showing a higher degree of specialization generally occurred under conditions of high nonarboreal vegetation cover and high precipitation regimes in the driest quarter. Intriguingly, depending on the elevation these conditions corresponded with different temperature regimes: in high elevation populations (located at  $>708$  m a.s.l., and including *H. flavus*), characterized by temperate mesomediterranean thermotypes (Appendix S2: Table S1), individual specialization peaked at relatively low temperatures in the warmest quarter. Lunghi et al. (2018c) showed that low temperatures and high precipitation regimes maximize habitat suitability for *H. flavus*, with corresponding positive variations in population range distribution and abundance. Hence, a high habitat suitability may have triggered a positive population density compensation and an increase in intraspecific competition, in turn determining higher individual specialization and larger niche

widths in agreement with the niche variation hypothesis. At low-elevation sites (<339 m a.s.l.), generally characterized by harsher Mediterranean conditions (Appendix S2: Table S1), individual specialization (and niche width) increased progressively with nonarboreal vegetation cover and precipitation and peaked at relatively high temperatures (Fig. 3B). This spectrum of environmental conditions may have maximized habitat suitability for salamanders at low elevations, increased populations' abundance, and induced a mechanism of niche expansion and increase in individual specialization in line with the NVH. Species-specific physiological requirements may have contributed in determining the observed patterns, as distinct *Hydromantes* species show significant differences in preferred microhabitats in terms of temperature and humidity (Ficetola et al. 2018). Individual physiological adaptations may have provided a further, important contribution: Plethodontids readily acclimatize metabolic and ingestion rates to habitat temperature and humidity to maintain a positive energy balance (Clay and Gifford 2017, Riddell et al. 2018b), the latter being likely regulated by intrapopulation trade-offs in physiological traits (Riddell et al. 2018a). The potential effects that different physiological phenotypes promoted by climatic conditions have on the proportion of specialist salamanders in a population, is to date an unexplored field and merits to be addressed in future investigations.

The previously described scenario relies on the assumption that higher habitat suitability causes a density compensation-related increase in intraspecific competition, and that no other biotic interactions influence their trophic strategies. Indeed, *Hydromantes* species are allopatric; thus interspecific competition with other ecologically equivalent amphibians can be ruled out. On the other hand, heterospecific interactions with spiders or other potential predators are possible (Manenti et al. 2016, Lunghi et al. 2018d). Here, population abundances were not estimated, and the strength of competition among *Hydromantes* conspecifics needs to be thoroughly assessed in the future (see e.g., Costa-Pereira et al. 2018) given also the scant and contradictory information available to date (Salvidio and Pastorino 2002, Ficetola et al. 2013).

In conclusion, our analysis on Sardinian *Hydromantes* provided evidence that satellite-derived climatic and vegetation variables are not only useful in modeling species occurrence, but may also capture the complex nature of Eltonian processes acting at both individual and population levels. The study identified robust background hypotheses for future investigations on urodeles, a group threatened worldwide and acknowledged to play a key functional role in forest-floor food webs (Catenazzi 2015, e.g., trophic cascades in detrital food webs: Mancinelli and Mulder 2015 and literature cited). In addition, the two scenarios explored suggest hypothesized mechanisms that can be tested in future ecologically realistic models predicting how interindividual variability in wild populations will mediate community-scale impacts

determined by climate changes (Bolnick et al. 2011, Des Roches et al. 2018).

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## SUPPORTING INFORMATION

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