Inter-specific and inter-population variation in individual diet specialization: do bioclimatic factors have a role?

Running Head: Bioclimate and individual specialization

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Abstract

Individual diet specialization (IS) is to date recognized to have important community- and population-level implications and its ecological drivers are actively investigated. Here, to test the hypothesis that bioclimatic factors may successfully predict 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 *i*) scaled positively with the respective niche widths, in agreement with Van Valen’s niche variation hypothesis (NVH), and *ii*) could be predicted by the bioclimatic conditions 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 non-tree vegetation cover and habitat heterogeneity successfully predicted the variation in individual specialization across the eight populations. Climatic factors showed 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 hottest quarter of the year. However, independently from elevation, specialization peaked under conditions of high non-tree vegetation cover and high precipitation regimes. We discussed the results against two mutually non-exclusive scenarios hypothesizing different mechanisms linking bioclimate with salamanders’ trophic strategy at an individual and population level. We concluded that bioclimatic variables, to date generally adopted to model Grinnellian niches, might also be useful in predicting spatial variations in dietary habits of populations, i.e. their Eltonian niches.

Keywords: dietary specialization, trophic niche width, bioclimate, cave salamanders, *Hydromantes*

Introduction

Inter-individual trait variability is widespread in wild populations, and there is an increasing recognition of its contribution in mediating species interactions, ecosystem functions, and eco-evolutionary 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, Layman et al. 2015). IS occurs when individuals, independently from their size, sex, or ontogenetic stage, use only 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 intra-individual dietary diversity (Roughgarden 1972, 1974).

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, Cloyed and Eason 2016, Costa-Pereira et al. 2018). In general, ecological release (*sensu* Wilson 1961) from heterospecific interactions has been indicated to affect IS, with positive or negative effects on individual specialization depending on how population and individuals' niches respond to heterospecifics (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, Mateus et al. 2016, Sheppard et al. 2018, Costa-Pereira et al. 2019). Increased specialization may ultimately reflect on an expansion of the population's niche width: this hypothesis, known as the Niche Variation Hypothesis (NVH hereafter; Van Valen 1965), has been repeatedly supported by dietary studies on a number of vertebrate and invertebrate taxa (Bolnick et al. 2007, Araújo et al. 2009, Bolnick et al. 2010, Bison et al. 2015, Cloyed and Eason 2017, Maldonado et al. 2017).

It is worth noting that the concepts of ecological release and density compensation are strictly related with that of 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 has long been suggested to promote specialization by increasing the foraging options available to individuals, allowing their trophic niche to widen (Roughgarden 1974). Hetero- and intraspecific interactions *per se* alter ecological opportunity through optimal foraging mechanisms (Stephens and Krebs 1986, Svanbäck and Bolnick 2005, Svanbäck et al. 2015). In addition, ecological opportunity can vary along ecological gradients as affected by extrinsic factors such as climate heterogeneity, habitat diversity and environmental stability (Nosil and Reimchen 2005, Parent and Crespi 2009, Schriever and Williams 2013, Algar and Mahler 2016, Dermond et al. 2018).

Increases in ecological opportunity have been repeatedly indicated to positively affect IS at a local scale (Nosil and Reimchen 2005, Tinker et al. 2008, Darimont et al. 2009, but see Parent et al. 2014 for a counterexample, Cloyed and Eason 2016, Marklund et al. 2018, Balme et al. 2019) and to correspond with variations in total niche width consistent with the NVH (Bison et al. 2015, Cloyed and Eason 2017, Costa-Pereira et al. 2017). At larger spatial scales, variations in ecological opportunity have been suggested to determine remarkable IS differences in marine mammals (Yurkowski et al. 2016), and in multiple taxa between tropical and temperate regions (Araújo and Costa-Pereira 2013). Remarkably, both studies used latitude as a proxy for ecological opportunity. Satellite-derived bioclimatic variables can provide more accurate information on the actual environmental 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' distribution (i.e., their Grinnellian niche: Peterson et al. 2011, Fletcher and Fortin 2018). Besides the aforementioned exceptions, however, it is apparent that the influence of bioclimatic drivers on IS variation across multiple species or populations over large spatial scales remains virtually unexplored.

In the present study, we analyzed the stomach contents of 395 individuals from eight allopatric populations of European cave salamanders belonging to five *Hydromantes* species (Plethodontidae) distributed in the Sardinia Island (Italy). Salamanders of the genus *Hydromantes* are non-obligate 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 a wide spectrum of arthropods and other epigean invertebrates captured in the neighborhood of the caves entrance (Vignoli et al. 2006, Salvidio et al. 2015, Lunghi et al. 2018b); accordingly, their trophic activity is strongly influenced by external bioclimatic conditions (Lunghi et al. 2015, 2018c). Moreover, *Hydromantes* populations are characterized by a high site fidelity and restricted home ranges (< 80m: Salvidio 2013 and literature cited), to the point that populations from different caves can be considered isolated (Lanza et al. 2006, Lunghi and Bruni 2018).

Here we addressed two main questions. First, we tested whether populations with a greater degree of individual diet specialization exhibited wider trophic niches, in agreement with NVH. As previously described, both intraspecific competition and ecological opportunity are expected to 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 *Hydromantes* salamanders populations (e.g., parallel release: Bolnick et al. 2010). Second, we verified whether local bioclimate - as defined by satellite-derived vegetation cover and climatic variables - predicted the degree of dietary specialization in *Hydromantes* populations, reflecting on their niche width in a way consistent with NVH. Lunghi et al. (2018c) indicated that local vegetation cover together with temperature and precipitation regimes significantly affected the distribution, abundance, and body condition of *H. flavus* populations in northern Sardinia. On this basis, we identified two potential non-mutually exclusive scenarios (summarized in Fig. 1) relying on different assumptions on how climate, vegetation cover, and habitat heterogeneity may potentially affect the degree of individual diet specialization and total niche width of *Hydromantes* populations.

In the first scenario, suitable bioclimatic conditions positively affect the epigean 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 in terms of invertebrate prey diversity and abundance, 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).

To verify which scenarios is the most probable, we adopted a correlative procedure conventionally used in environmental niche modelling, identifying a minimum adequate predictive model for IS variability across *Hydromantes* populations by means of a heuristic multiple regression approach.

Methods

Study species and dietary data

Analyses were based on the dataset published by Lunghi et al. (2018a) providing quantitative information on the stomach contents of cave salamanders belonging to six *Hydromantes* species distributed in allopatry in peninsular Italy and in the Sardinia Island. Here we focused on species located in Sardinia; surveyed sites (i.e., caves and other subterranean environments) were located throughout the island over an area of about 5,800 km^2 (Fig. S1 in supporting online information). Their elevations varied remarkably by approximately 870 m, ranging between 164 and 1033 m a.s.l. (Tab. S1); bioclimatic 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 (Tab. S1 and Fig. S1 for two contrasting examples; see also Results and Tab. 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 mm) 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 plus unidentified items.

For each season, we pooled data from different years, and we considered only those populations where at least 15 individuals with recognizable prey in their stomachs were analyzed, with a minimum of three individuals per season. For *H. sarrabusensis,* we pooled data from "cave 1" and "cave 2", as the two populations distance were not considered independent given the distance between the two sites (35 m). Overall, we retained data related to the occurrence of 31 identified prey items in 395 individuals from eight populations belonging to five *Hydromantes* species (Table S2). The minimum inter-population distance was 1,382 m, largely exceeding the dispersal distance charactering *Hydromantes* individuals (Lanza et al. 2006, Lunghi and Bruni 2018); accordingly, the eight populations were assumed as isolated groups (*sensu* Bolnick et al. 2007), with no exchange of individuals.

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, while PS_i values were estimated using the revised version of Schoener's (1968) proportional similarity index PS proposed by Bolnick et al. (2002):

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

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, while 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 non-independent. Alternatively, the total niche width of the eight *Hydromantes* populations were 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 d.f.); accordingly, TNW values were assumed to be reliable estimates of populations' total niche width and used in further analyses.

Bioclimatic variables

Bioclimatic variables obtained from the WorldClim v2 dataset (http://www.worldclim.org/) were used to predict the variation in the V measure among *Hydromantes* populations. Together with annual mean temperature, temperature 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, since dietary data were collected in spring and fall (Table S3). In addition, two vegetation variables - i.e., percent tree covered habitats and percent non-tree covered habitats - were extracted from the Terra MODIS Vegetation Continuous Field (VCF) product (available as MOD44B v006 at https://lpdaac.usgs.gov/products/mod44bv006/). Percent tree cover included all forest types and age classes, while percent non-tree 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

We preliminary assessed whether individual diet specialization within populations was affected by seasonality or by other intra-population characteristics related to sex, body size and ontogeny (e.g., Bolnick et al. 2003, de Camargo et al. 2014). Individual PS_i values were calculated using the R package *RInSp* (see further in this section) and analyzed using a two-way permutational ANOVA 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 (Factor 3). We repeated the analyses for adults only, verifying the influence of sex. In addition, for each population spring and fall distributions of PSi 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 individuals per season, twice the minimum sample size required for mono-dimensional datasets (Silverman 1998).

We used regression analysis to verify the correlation between populations’ V and TNW values. 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 artefact 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 *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 NVH 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 can be determined in the studied populations only by stochastic sampling effects.

The coordinates of the locations (Table S1) were used to extract climatic and vegetation data from environmental layers. the MODIS VCF product is not well-resolved below 30 % tree cover, and does not differentiate for ranges < 10% of the variable (Staver and Hansen 2015); in addition, here % tree cover and % non-tree vegetation cover were characterized by a highly significant correlation (r = - 0.94, P = 0.0005, 6 d.f.). Consequently, only the latter vegetation variable was included in further analyses.

% non-tree vegetation cover was used to estimate a first-order measure of habitat heterogeneity according with 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 neighbouring pixels, thus covering an area of 750 × 750 m; the coefficient of variation was calculated over the 27 extracted and used to express the spatial-temporal habitat heterogeneity (HH in Tab. S3).

Subsequently, the 11 bioclimatic variables (Tab. S3) were log-transformed and z-scaled to reduce skewness and improve linearity. The identification of a minimum adequate model, i.e., the model that contains the minimum number of predictors that satisfy some statistical criterion (MAM; Whittingham et al. 2006). linking the variation of populations' V values with the selected bioclimatic variables was based on the heuristic generation of alternative regression models. Model selection adopted an Information Theoretic criterion (Burnham and Anderson 2002, Hegyi and Garamszegi 2011). The second-order Akaike Information Criterion AICc (Akaike 1974, Sugiura 1978) corrected for small sample sizes was 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 models comparison, AICc values were used to estimate a set of positive Akaike weights w_i summing 1. 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).

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

Results

Individual specialization and niche width

The proportional similarity index PS_i of individual salamanders varied across the studied populations independently from season as well as from sex, ontogenetic stage, or multi-factor interactions (Table S4). In addition, non-significant differences occurred between the spring and fall distributions of *PSi* values for the five populations tested (Fig. S2).

The degree of individual diet specialization V_{emp} varied considerably among the eight populations (Fig. 2), independently from the number of individuals having prey in their stomachs or the total number of sampled individuals (Table S2; $r = 0.02$, $P = 0.97$, and $r = 0.01$, $P = 0.98$, respectively; 6 d.f.). 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. 2). The highest and lowest degrees of specialization were observed for *H. genei* (pop 2) and *H. flavus* (pop3) respectively, the former characterized by a proportion of specialized individuals 4 times higher than the latter ($V_{emp} = 0.69$ *vs.* 0.16; see Fig. 2 for examples of the respective bipartite networks).

Populations with a higher degree of individual diet specialization had wider niche widths (Fig. 2), the latter varying by one order of magnitude 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 intra-specific scale for those species for which multiple populations were analyzed (i.e., *H. flavus*, *H. genei*, and *H. supramontis*). TNW scaled positively also with V_{null} values (Fig. 2); however, the linear regression model (after log-transformation of TNW) showed a slope significantly lower than that determined for empirical V values (slope ± SE: $V_{emp} = 0.71 \pm 0.06$; $V_{null} = 0.59 \pm 0.09$; $F_{2,12} = 12.1$, $P = 0.002$).

Bioclimatic variables and individual specialization

The heuristic search procedure identified a Minimum Adequate Model (MAM) based on the two explanatory variables VEG and HH (Fig. 3; adjusted $r = 0.83$, $P = 0.02$, d.f. = 2, 5). The MAM was characterized by the lowest AICc value, and by an Akaike weight w_i more than 10 times larger than the second and third best candidate MAMs, based uniquely on the variables VEG and HH, respectively (Tab. 1).

The two variables were not correlated ($r = 0.53$, $P = 0.18$, 6 d.f.) and both provided positive, significant contributions to V variation across populations [Tab. 1 and Fig. 3; VEG: $b = 0.49 \pm 0.16$ (mean ± SE), $t = 2.81$, $P = 0.037$, HH: $b = 0.58 \pm 0.18$, $t = 3.31$, $P = 0.021$], testifying that populations living under conditions of high % non-tree vegetation cover and high habitat heterogeneity were characterized by a higher degree of individual specialization.

Noticeably, climatic variables showed a generally low predictive power, with BIO12 and BIO15 (annual precipitation and precipitation seasonality, respectively) contributing with HH only to the fourth best MAM (Tab. 1; w_i weights approx. 58 and 78 times smaller than the best candidate). An in-depth scrutiny of the effects of climatic variables on V variation across the eight populations did not highlight any significant pattern; the only exceptions were provided by variables specific to the driest/warmest quarter, as two distinct patterns of variation in individual specialization were observed (Fig. 3). For populations living at elevations between 708 and 1033 m a. s. l. [i.e., *H. flavus* (pop2) and (pop3), H. *imperialis* (pop2), and H. *sarrabusensis* (pop1)], V values scaled negatively with temperature, reaching maximum values at sites characterized by high precipitation and vegetation cover. Conversely, individual specialization in low-elevation populations [i.e., *H. supramontis* (pop2) and (pop3), H. *genei* (pop2) and (pop3)] increased with temperature, even though showing maximum values at sites characterized by relatively high precipitation and vegetation cover (Fig. 3).

Discussion

Individual diet specialization 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, Carvalho-Rocha et al. 2018, Costa-Pereira et al. 2018, 2019). To our knowledge, however, no previous studies, with the partial exception of Cloyed and Eason (2016), 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. Here we verified that dietary specialization in eight populations of cave salamanders from Sardinia scaled positively with the respective niche width; in addition, we indicated that satellite-derived variables describing the degree of vegetation cover and habitat heterogeneity of the sites where the populations live could predict their degree of individual specialization. Before addressing these results, some methodological considerations are necessary. In general, studies on individual diet specialization based on stomach contents analysis necessitate complementary data provided by e.g. 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 (EC 1992), and are listed as “vulnerable” or “almost threatened” in the IUCN Red List of Italian vertebrate species (reported as Speleomantes spp.; Rondinini et al. 2013). Consequently, authorizations to carry out the present investigation (see Acknowledgements) allowed for stomach flushing and mark-recapture of a limited number of individuals, and no tissue sampling. Given the low recapture rates previously observed for *H. flavus* (approx. 12%: Lunghi and Veith 2017) and the high incidence of empty stomachs [Lunghi, personal observation; on average 49% of the total number of sampled individuals in this study (Tab. S2)] we opted for maximizing the number of analyzed populations and individuals per population and explicitly testing the consistency of dietary habits across two different seasons. In fact, the results of the PERMANOVA performed on individual PS_i values showed that the mean individual specialization of the eight populations was independent from season, as well as from sex, age, and size-related effects (Tab. S4). Furthermore, at least for the five populations tested the frequency distribution of *PSi* values showed non-significant differences between fall and spring (Fig. S2). Noticeably, this happened notwithstanding considerable seasonal changes in the taxonomic structure of the prey assemblage (Lunghi et al. 2018b). Thus, we are confident that, even without the support of complementary data, the observed IS variation across the eight populations was actually determined by temporally consistent differences in the occurrence of “true” individual specialists (*sensu* Bolnick et al. 2003) within the populations themselves.

The best MAM including % non-tree vegetation cover and habitat heterogeneity (VEG and HH, Table S3) successfully predicted the degree of individual diet specialization in *Hydromantes* populations, providing full support to a scenario hypothesizing that salamanders' trophic strategy might be influenced by ecological opportunity (Fig. 1). Specifically, in the best candidate MAM both variables positively co-varied with individual diet specialization (Fig. 3, Tab. 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, Schuldt et al. 2008, Ebeling et al. 2018), determining an expansion of the populations' niche in agreement with the "resource diversity hypothesis" (Lawton 1983). The 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, in agreement with the NVH, functional trade-offs may limit individuals' niche width (due to e.g., behavioral or physiological constraints), with the population's niche expanding through an increase in individual diet specialization (Bolnick et al. 2010). The results provide support to this hypothesis, suggesting that vegetation cover may exert a stronger effect as compared with habitat heterogeneity, given the nearly significant contribution provided by the latter to the best MAM. However, these results should be taken with caution given the rather simplified approach used for estimating habitat heterogeneity. Even though the procedure herein adopted is acknowledged to provide more detailed information on habitat heterogeneity than previously available metrics (Tuanmu and Jetz 2015), further confirmations are needed, based on a more accurate estimation of the actual microhabitat heterogeneity by field measurements (see Stein and Kreft 2015 for a recent review).

Climatic variables did not contribute significantly to the best candidate MAMs (Tab. 1). Indeed, the underlying null hypothesis of this study was that the predictability power of bioclimatic variables was generally negligible, as their spatial resolution is too low to capture Eltonian trophic niche-related processes taking place at e.g., at a microhabitat scale (Soberón 2007, Rosado et al. 2016, see also Mancinelli et al. 2019). The spatial (approx. 0.92 × 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; Tab. S3), and may provide less ecologically meaningful information. The patterns showed in Figure 3 actually suggest that climatic variables might have a less straightforward and non-linear effect on populations' individual specialization, partially supporting the first hypothesized scenario (Fig. 1). First, precipitation can exert a positive, indirect effect on the abundance and diversity of soil arthropod communities in temperate environments (Fig. 3; 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 (Homyack and Haas 2009, O'Donnell et al. 2014, Cosentino and Brubaker 2018). In particular, water loss represents a physiological challenge for Plethodontids: they are lungless, and respiration takes place through their cutaneous membrane (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 (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 vegetation cover and high precipitation regimes in the warmest 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 (Tab. 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 elevations sites (< 339 m a.s.l.), generally characterized by harsher thermomediterranean thermotypes (Tab. S1), individual specialization (and niche width) increased progressively with % non-tree vegetation cover and precipitation and peaked at relatively high temperatures (Fig. 3). 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 Sardinian *Hydromantes* species show significant differences in preferred microhabitats in terms of temperature and humidity (Ficetola et al. 2018); in addition, 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 likely to be regulated by intra-population trade-offs in physiological traits (Riddell et al. 2018a). How climatic selection on specific physiological phenotypes may reflect on an increase in dietary specialists within salamander populations is to date unexplored and merits to be addressed in future investigations.

It is apparent that the previously described scenario relies on the assumption that higher habitat suitability indirectly generates intraspecific competition in salamanders by increasing their abundance, and that no other biotic interactions may influence the trophic strategies of salamanders. Indeed, the allopatry characterizing *Hydromantes* populations in the Sardinia island excludes interspecific competition; interactions with spiders or other predators are possible (Pastorelli and Laghi 2006, Manenti et al. 2016, Hickerson et al. 2018, Lunghi et al. 2018d) yet unlikely, given the salamanders' toxic skin (Brizzi and Corti 2007). Here, population abundances were not estimated; thus, the strength of competition among *Hydromantes* conspecifics necessitates 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* populations provided evidence that satellite-derived bioclimatic variables are not only useful in modeling species occurrence, but they may also capture the complex nature of Eltonian processes acting both at an individual and population level. The present study, even though manifestly exploratory in nature, highlighted the potential role of a spectrum of environmental factors acting at different spatial scales to be thoroughly scrutinized in future investigations on Urodeles, a group of species threatened worldwide and acknowledged to exert significant ecosystem-scale effects (Catenazzi 2015, e.g., trophic cascades in detrital food webs: Mancinelli and Mulder 2015 and literature cited). It is worth emphasizing that the two scenarios herein proposed are not mutually exclusive, and provide a simplified representation of the ecological drivers determining the degree of individual niche variation in *Hydromantes* populations and, most importantly, of the interactions occurring among the drivers themselves. Recent studies have started to indicate that under natural conditions, populations are usually responding to multiple ecological factors simultaneously and that the effects of these factors may not be independent (Cloyed and Eason 2016, Costa-Pereira et al. 2017, 2018). Yet, they provided a useful basis to cast our results within a theoretical framework based on general ecological theories, thus allowing the hypothesized mechanisms to be widely tested in future investigations not limited to amphibians. Therefore, the present work offers an original contribution to the identification of ecologically-realistic models predicting how inter-individual variability in wild populations will mediate impacts on community dynamics determined by climate changes (Bolnick et al. 2011, Des Roches et al. 2018, Raffard et al. 2019).

Acknowledgements

Fieldwork was authorized by the Italian Ministry of Environment (Prot. 9384/PNM - 12/05/2015 and Prot. N. 20624/PNM - 30/09/2016) and by the Regione Autonoma della Sardegna (n° 6312 of 27/03/2017). E. Lunghi is supported by the Chinese Academy of Sciences President's International Fellowship Initiative for postdoctoral researchers.

Data availability

Data are freely available in: Lunghi E., Cianferoni F., Ceccolini F., Mulargia M., Cogoni R., Barzaghi B., Cornago L., Avitabile D., Veith M., Manenti R., Ficetola G. F. and Corti C. (2018). Field-recorded data on the diet of six species of European *Hydromantes* cave salamanders. Scientific Data 5: 180083 DOI: 10.1038/sdata.2018.83.

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control **19**:716-723.

Algar, A. C. and D. L. Mahler. 2016. Area, climate heterogeneity, and the response of climate niches to ecological opportunity in island radiations of Anolis lizards. Global Ecology and Biogeography **25**:781-791.

Araújo, M. S., D. I. Bolnick, L. A. Martinelli, A. A. Giaretta, and S. F. Dos Reis. 2009. Individual-level diet variation in four species of Brazilian frogs. Journal of Animal Ecology **78**:848-856.

Araújo, M. S., D. L. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters **14**:948-958.

Araújo, M. S. and R. Costa-Pereira. 2013. Latitudinal gradients in intraspecific ecological diversity. Biology Letters **9**:20130778.

Balme, G. A., N. le Roex, M. S. Rogan, and L. T. B. Hunter. 2019. Ecological opportunity drives individual dietary specialization in leopards. Journal of Animal Ecology **in press, https://doi.org/10.1111/1365-2656.13109**.

Bison, M., S. Ibanez, C. Redjadj, F. c. Boyer, E. Coissac, C. Miquel, D. Rioux, S. Said, D. Maillard, P. Taberlet, N. G. Yoccoz, and A. Loison. 2015. Upscaling the niche variation hypothesis from the intra- to the inter-specific level. Oecologia **179**:835-842.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution **26**:183-192.

Bolnick, D. I., T. Ingram, W. E. Stutz, L. K. Snowberg, O. Lee Lau, and J. S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society B **277**:1789-1797.

Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences of the United States of America **104**:10075-10079.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist **161**:1-28.

Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. Ecology **83**:2936-2941.

Bowman, A. W. and A. Azzalini. 1997. Applied Smoothing Techniques for Data Analysis: the Kernel Approach with S-Plus Illustrations. OUP Oxford.

Brizzi, R. and C. Corti. 2007. Cutaneous antipredatory secretions and pheromones in anurans and urodeles. Marine and Freshwater Behaviour and Physiology **40**:225-231.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, NY.

Carvalho-Rocha, V., L. B. Cortês, and S. Neckel-Oliveira. 2018. Interindividual patterns of resource use in three subtropical Atlantic Forest frogs. Austral Ecology **43**:150-158.

Catenazzi, A. 2015. State of the World's Amphibians. Annual Review of Environment and Resources **40**:91-119.

Clay, T. A. and M. E. Gifford. 2017. Population level differences in thermal sensitivity of energy assimilation in terrestrial salamanders. Journal of Thermal Biology **64**:1-6.

Cloyed, C. S. and P. K. Eason. 2016. Different ecological conditions support individual specialization in closely related, ecologically similar species. Evolutionary Ecology **30**:379-400.

Cloyed, C. S. and P. K. Eason. 2017. Feeding limitations in temperate anurans and the niche variation hypothesis. Amphibia-Reptilia **38**:473-482.

Cosentino, B. J. and K. M. Brubaker. 2018. Effects of land use legacies and habitat fragmentation on salamander abundance. Landscape Ecology **33**:1573-1584.

Costa-Pereira, R., M. S. Araújo, F. L. Souza, and T. Ingram. 2019. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. Proceedings of the Royal Society B **286**:20190369.

Costa-Pereira, R., V. H. W. Rudolf, F. L. Souza, and M. S. Araújo. 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology **87**:1452-1464.

Costa-Pereira, R., L. E. R. Tavares, P. B. de Camargo, and M. S. Araújo. 2017. Seasonal population and individual niche dynamics in a tetra fish in the Pantanal wetlands. Biotropica **49**:531-538.

Costa, A., S. Salvidio, M. Posillico, G. Matteucci, B. De Cinti, and A. Romano. 2015. Generalisation within specialization: inter-individual diet variation in the only specialized salamander in the world. Scientific Reports **5**:13260.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology **78**:126-133.

de Camargo, N. F., J. F. Ribeiro, A. J. A. de Camargo, and E. M. Vieira. 2014. Intra- and inter-individual variation show distinct trends as drivers of seasonal changes in the resource use of a neotropical marsupial. Biological Journal of the Linnean Society **111**:737-747.

Dermond, P., S. M. Thomas, and J. Brodersen. 2018. Environmental stability increases relative individual specialisation across populations of an aquatic top predator. Oikos **127**:297-305.

Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A. Schweitzer, and E. P. Palkovacs. 2018. The ecological importance of intraspecific variation. Nature Ecology & Evolution **2**:57-64.

Ebeling, A., J. Hines, L. R. Hertzog, M. Lange, S. T. Meyer, N. K. Simons, and W. W. Weisser. 2018. Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. Basic and Applied Ecology **26**:50-63.

EC. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Union **L 206/7**:1-44.

Ficetola, G. F., E. Lunghi, C. Canedoli, E. Padoa-Schioppa, R. Pennati, and R. Manenti. 2018. Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. Scientific Reports **8**:10575.

Ficetola, G. F., R. Pennati, and R. Manenti. 2013. Spatial segregation among age classes in cave salamanders: habitat selection or social interactions? Population Ecology **55**:217-226.

Fletcher, R. and M. J. Fortin. 2018. Species Distributions. Pages 213-269 *in* R. Fletcher and M. J. Fortin, editors. Spatial Ecology and Conservation Modeling. Springer.

Fox, J. and H. S. Weisberg. 2011. An R Companion to Applied Regression, Second Edition. Sage Publications, Inc., Thousand Oaks, CA.

Gaudio, N., X. Gendre, M. Saudreau, V. Seigner, and P. Balandier. 2017. Impact of tree canopy on thermal and radiative microclimates in a mixed temperate forest: a new statistical method to analyse hourly temporal dynamics. Agricultural and Forest Meteorology **237-238**:71-79.

Hegyi, G. and L. Garamszegi. 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. Behavioral Ecology and Sociobiology **65**:69-76.

Hickerson, C. A. M., C. D. Anthony, and A. M. Figura. 2018. Behavioral interactions between terrestrial salamanders and spiders: competition or intraguild predation? Ethology Ecology & Evolution **30**:285-296.

Homyack, J. A. and C. A. Haas. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation **142**:110-121.

Kawabata, A., K. Ichii, and Y. Yamaguchi. 2001. Global monitoring of interannual changes in vegetation activities using NDVI and its relationships to temperature and precipitation. International Journal of Remote Sensing **22**:1377-1382.

Lanza, B., C. Pastorelli, P. Laghi, and R. Cimmaruta. 2006. A review of systematics, taxonomy, genetics, biogeography and natural history of the genus *Speleomantes* Dubois, 1984 (Amphibia Caudata Plethodontidae). Atti del Museo Civico di Storia Naturale di Trieste **52**:5-135.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology **28**:23-39.

Layman, C. A., S. D. Newsome, and T. G. Crawford. 2015. Individual-level niche specialization within populations: emerging areas of study. Oecologia **178**:1-4.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N. J.

Lunghi, E. and G. Bruni. 2018. Long-term reliability of Visual Implant Elastomers in the Italian cave salamander (*Hydromantes italicus*). Salamandra **54**:283-286.

Lunghi, E., F. Cianferoni, F. Ceccolini, M. Mulargia, R. Cogoni, B. Barzaghi, L. Cornago, D. Avitabile, M. Veith, R. Manenti, G. F. Ficetola, and C. Corti. 2018a. Field-recorded data on the diet of six species of European *Hydromantes* cave salamanders. Scientific Data **5**:180083.

Lunghi, E., F. Cianferoni, F. Ceccolini, M. Veith, R. Manenti, G. Mancinelli, C. Corti, and G. F. Ficetola. 2018b. What shapes the trophic niche of European plethodontid salamanders? PLoS ONE **13**:e0205672.

Lunghi, E., R. Manenti, G. Canciani, G. Scarì, R. Pennati, and G. F. Ficetola. 2016. Thermal equilibrium and temperature differences among body regions in European plethodontid salamanders. Journal of Thermal Biology **60**:79-85.

Lunghi, E., R. Manenti, and G. F. Ficetola. 2015. Seasonal variation in microhabitat of salamanders: environmental variation or shift of habitat selection? PeerJ **3**:e1122.

Lunghi, E., R. Manenti, M. Mulargia, M. Veith, C. Corti, and G. F. Ficetola. 2018c. Environmental suitability models predict population density, performance and body condition for microendemic salamanders. Scientific Reports **8**:7527.

Lunghi, E., C. Mascia, M. Mulargia, and C. Corti. 2018d. Is the Sardinian grass snake (*Natrix natrix cetti*) an active hunter in underground environments? Spixiana **41**:160.

Lunghi, E. and M. Veith. 2017. Are Visual Implant Alpha tags adequate for individually marking European cave salamanders (genus *Hydromantes*). Salamandra **53**:541-544.

MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. **53**:330-342.

Maldonado, K., F. Bozinovic, S. D. Newsome, and P. Sabat. 2017. Testing the niche variation hypothesis in a community of passerine birds. Ecology **98**:903-908.

Mancinelli, G. 2010. Intraspecific, size-dependent variation in the movement behaviour of a brackish-water isopod: a resource-free laboratory experiment. Marine and Freshwater Behaviour and Physiology **43**:321-337.

Mancinelli, G., S. Mali, and G. Belmonte. 2019. Species richness and taxonomic distinctness of zooplankton in ponds and small lakes from Albania and North Macedonia: the role of bioclimatic factors. Water **11**:2384.

Mancinelli, G. and C. Mulder. 2015. Detrital dynamics and cascading effects on supporting ecosystem services. Advances in Ecological Research **53**:97-160.

Manenti, R., E. Lunghi, C. Canedoli, M. Bonaccorsi, and G. F. Ficetola. 2016. Parasitism of the leech, *Batracobdella algira* (Moquin-Tandon, 1846), on Sardinian cave salamanders (genus *Hydromantes*) (Caudata: plethodontidae). Herpetozoa **29**:27-35.

Marklund, M. H. K., R. Svanbäck, Y. Zha, K. Scharnweber, and P. Eklöv. 2018. The influence of habitat accessibility on the dietary and morphological specialisation of an aquatic predator. Oikos **127**:160-169.

Mateus, L., J. Ortega, A. Mendes, and J. Penha. 2016. Nonlinear effect of density on trophic niche width and between-individual variation in diet in a neotropical cichlid. Austral Ecology **41**:492-500.

Melián, C. J., F. Baldó, B. Matthews, C. Vilas, E. González-Ortegón, P. Drake, and R. J. Williams. 2014. Individual trait variation and diversity in food webs. Advances in Ecological Research **50**:207-241.

Nosil, P. and T. E. Reimchen. 2005. Ecological opportunity and levels of morphological variance within freshwater stickleback populations. Biological Journal of the Linnean Society **86**:297-308.

O'Donnell, K. M., F. R. Thompson III, and R. D. Semlitsch. 2014. Predicting variation in microhabitat utilization of terrestrial salamanders. **70**:259-265.

Pan, C., Q. Feng, J. Liu, Y. Li, Y. Li, and X. Yu. 2018. Community structure of grassland ground-dwelling arthropods along increasing soil salinities. Environmental Science and Pollution Research **25**:7479-7486.

Parent, C. E., D. Agashe, and D. I. Bolnick. 2014. Intraspecific competition reduces niche width in experimental populations. Ecology and Evolution **4**:3978-3990.

Parent, C. E. and B. J. Crespi. 2009. Ecological opportunity in adaptive radiation of Galapagos endemic land snails. The American Naturalist **174**:898-905.

Pastorelli, C. and P. Laghi. 2006. Predation of *Speleomantes italicus* (Amphibia: Caudata: Plethodontidae) by *Meta menardi* (Arachnida: Araneae: Metidae). Pages 45-48 Atti del 6° Congresso Nazionale della Societas Herpetologica Italica (Roma, 27.IX-1.X.2006), Roma.

Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, M. Nakamura, E. Martinez-Meyer, and M. B. Araújo. 2011. Ecological Niches and Geographic Distributions. Princeton University Press, Princeton, NJ.

R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Last accessed September 18, 2019.

Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. **94**:648-661.

Riddell, E. A., J. McPhail, J. D. Damm, and M. W. Sears. 2018a. Trade-offs between water loss and gas exchange influence habitat suitability of a woodland salamander. Functional Ecology **32**:916-925.

Riddell, E. A., J. P. Odom, J. D. Damm, and M. W. Sears. 2018b. Plasticity reveals hidden resistance to extinction under climate change in the global hotspot of salamander diversity. Science Advances **4**:eaar5471.

Rondinini, C., A. Battistoni, V. Peronace, and C. Teofili. 2013. Lista Rossa IUCN dei Vertebrati Italiani. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma.

Rosado, B. H. P., M. S. L. Figueiredo, E. A. de Mattos, and C. E. V. Grelle. 2016. Eltonian shortfall due to the Grinnellian view: functional ecology between the mismatch of niche concepts. Ecography **39**:1034-1041.

Roughgarden, J. 1972. Evolution of niche width. The American Naturalist **106**:683-718.

Roughgarden, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. The American Naturalist **108**:429-442.

Roughgarden, J. 1979. Theory of Population Genetics and Evolutionary Ecology. Macmillan Publishing Company, New York.

Salvidio, S. 2013. Homing behaviour in *Speleomantes strinatii* (Amphibia Plethodontidae): a preliminary displacement experiment. North-Western Journal of Zoology **9**:429-433.

Salvidio, S., F. Oneto, D. Ottonello, A. Costa, and A. Romano. 2015. Trophic specialization at the individual level in a terrestrial generalist salamander. Canadian Journal of Zoology **93**:79-83.

Salvidio, S. and M. V. Pastorino. 2002. Spatial segregation in the European plethodontid *Speleomantes strinatii* in relation to age and sex. Amphibia-Reptilia **23**:505-510.

Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. F. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology **89**:782-794.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology **49**:704-726.

Schriever, T. A. and D. D. Williams. 2013. Ontogenetic and individual diet variation in amphibian larvae across an environmental gradient. Freshwater Biology **58**:223-236.

Schuldt, A., N. Fahrenholz, M. Brauns, S. Migge-Kleian, C. Platner, and M. Schaefer. 2008. Communities of ground-living spiders in deciduous forests: does tree species diversity matter? Biodiversity and Conservation **17**:1267-1284.

Sheppard, C. E., R. Inger, R. A. McDonald, S. Barker, A. L. Jackson, F. J. Thompson, E. I. K. Vitikainen, M. A. Cant, and H. H. Marshall. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecology Letters **21**:665-673.

Silverman, B. W. 1998. Density Estimation for Statistics and Data Analysis. Chapman & Hall, Boca Raton, FL.

Sjödin, H., J. Ripa, and P. Lundberg. 2018. Principles of niche expansion. Proceedings of the Royal Society B **285**:20182603.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters **10**:1115-1123.

Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecological Monographs **42**:95-125.

Staver, A. C. and M. C. Hansen. 2015. Analysis of stable states in global savannas: is the CART pulling the horse? - a comment. **24**:985-987.

Stein, A. and H. Kreft. 2015. Terminology and quantification of environmental heterogeneity in species-richness research. Biological Reviews **90**:815-836.

Stephens, D. W. and J. R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, N.J.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory and Methods **A7**:13-26.

Svanbäck, R. and D. I. Bolnick. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evolutionary Ecology Research **7**:993-1012.

Svanbäck, R. and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B **274**:839-844.

Svanbäck, R., M. Quevedo, J. Olsson, and P. Eklöv. 2015. Individuals in food webs: the relationships between trophic position, omnivory and amongindividual diet variation. Oecologia **178**:103-114.

Sweet, S. K., A. Asmus, M. E. Rich, J. Wingfield, L. Gough, and N. T. Boelman. 2015. NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. Ecological Applications **25**:779-790.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography **31**:79-92.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences **105**:560-565.

Tuanmu, M.-N. and W. Jetz. 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. Global Ecology and Biogeography **24**:1329-1339.

Van Valen, L. 1965. Morphological variation and width of ecological niche. The American Naturalist **99**:377-390

Vignoli, L., F. Caldera, and M. A. Bologna. 2006. Trophic niche of cave populations of *Speleomantes italicus*. Journal of Natural History **40**:1841-1850.

Whitford, W. G. and V. H. Hutchison. 1967. Body size and metabolic rate in salamanders. Physiological Zoology **40**:127-133.

Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? Journal of Animal Ecology **75**:1182-1189.

Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. The American Naturalist **95**:169-193.

Wise, D. H. and J. R. Lensing. 2019. Impacts of rainfall extremes predicted by climate-change models on major trophic groups in the leaf litter arthropod community. Journal of Animal Ecology **88**:1486-1497.

Yoder, J. B., E. Clancey, S. Des Roches, J. M. Eastman, L. Gentry, W. Godsoe, T. J. Hagey, D. Jochimsen, B. P. Oswald, J. Robertson, B. A. J. Sarver, J. J. Schenk, S. F. Spears, and L. J. Harmon. 2010. Ecological opportunity and the origin of adaptive radiations. Journal of Evolutionary Biology **23**:1581-1596.

Yurkowski, D. J., S. Ferguson, E. S. Choy, L. L. Loseto, T. M. Brown, D. C. G. Muir, C. A. D. Semeniuk, and A. T. Fisk. 2016. Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecology and Evolution **6**:1666-1678.

Zaccarelli, N., D. I. Bolnick, and G. Mancinelli. 2013. RInSp: an R package for the analysis of individual specialization in resource use. Methods in Ecology and Evolution **4**:1018-1023.

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 5 best MAMs are reported. K: number of predictors included in the model; AICc: second-order Akaike Information Criterion; w_i: Akaike weight. For each variable, we also report the sign of the contribution of the predictor to the model in brackets.

K	**Predictors**	**AICc**	w_i
2	% non-tree vegetation cover (VEG +); Habitat heterogeneity (HH +)	-26.11	0.783
1	% non-tree 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

Figure captions

Figure 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 epigean 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 expansion of both populations' trophic niche and proportion of specialized individuals, achieved through an increase in ecological opportunity in terms of prey diversity and abundance. Grey arrows refer to interactions between climate and vegetation cover (e.g., Kawabata et al. 2001) as well as between vegetation cover and local microclimate (e.g., Gaudio et al. 2017) or climate and prey diversity and abundance (e.g., Wise and Lensing 2019) not explicitly addressed in the present study. See the text for further details.

Figure 2. (A) Degree of individual diet specialization (V) of *Hydromantes* populations and their respective niche width (TNW). Empirical results (V_{emp}) are in black; grey symbols indicate simulated values (V_{null}) obtained through a null model assuming diet specialization to emerge only from individuals sampling stochastically a shared prey distribution (H_0). Asterisks identify populations characterized by non-significant differences between V_{emp} and V_{null} (see text). Logarithmic curves are fitted to $V_{emp/null}$ - TNW relationships after a test based on an IT selection criterion indicated that a logarithmic model was the best fit for the V_{emp}-TNW relationship as compared with a linear (ΔAICc = -9.1, $P = 0.001$) and power model (ΔAICc = -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, whose numerical code refers to that assigned in the original dataset (see text for further details).

Figure 3. (A) Degree of individual diet specialization (V) in *Hydromantes* populations plotted against the values predicted by the best Minimum Adequate Model (MAM) including % non-tree vegetation cover and habitat heterogeneity (VEG and HH in Table S3) as bioclimatic predictors. The second and third best candidate MAMs, including VEG and HH as single predictors, are showed in figure S3. In the bi-plot 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 non-tree vegetation cover, the shades of grey indicate different precipitation regimes, while 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. sarrabusensis* (pop1); su2 = *H. supramontis* (pop2); su3 = *H. supramontis* (pop3)].

Figure 1

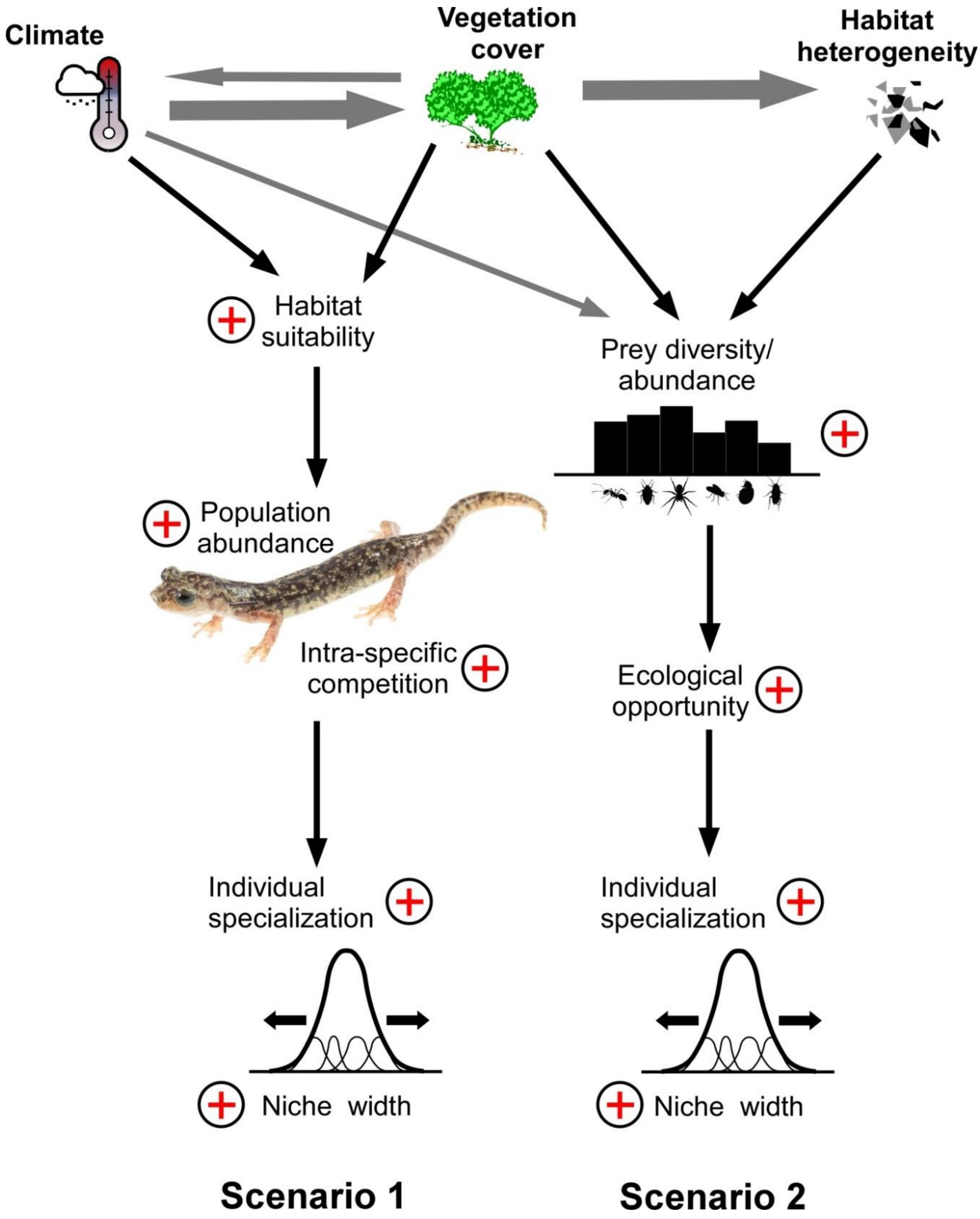

Climate
Vegetation cover
Habitat heterogeneity
+ Habitat suitability
Prey diversity/ abundance +
+ Population abundance
Intra-specific competition +
Ecological opportunity +
Individual specialization +
Individual specialization +
+ Niche width
+ Niche width
Scenario 1
Scenario 2

Figure 2

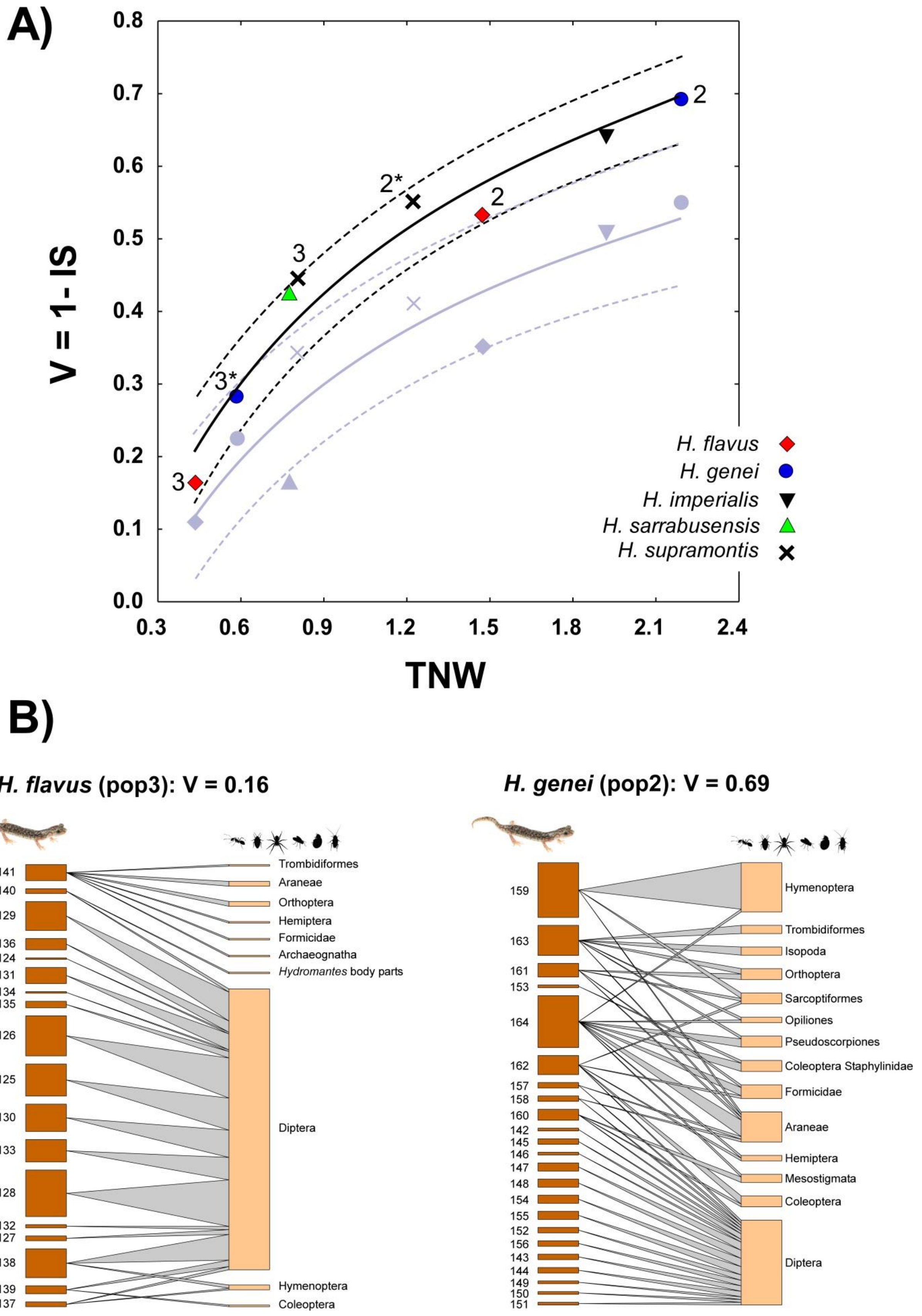
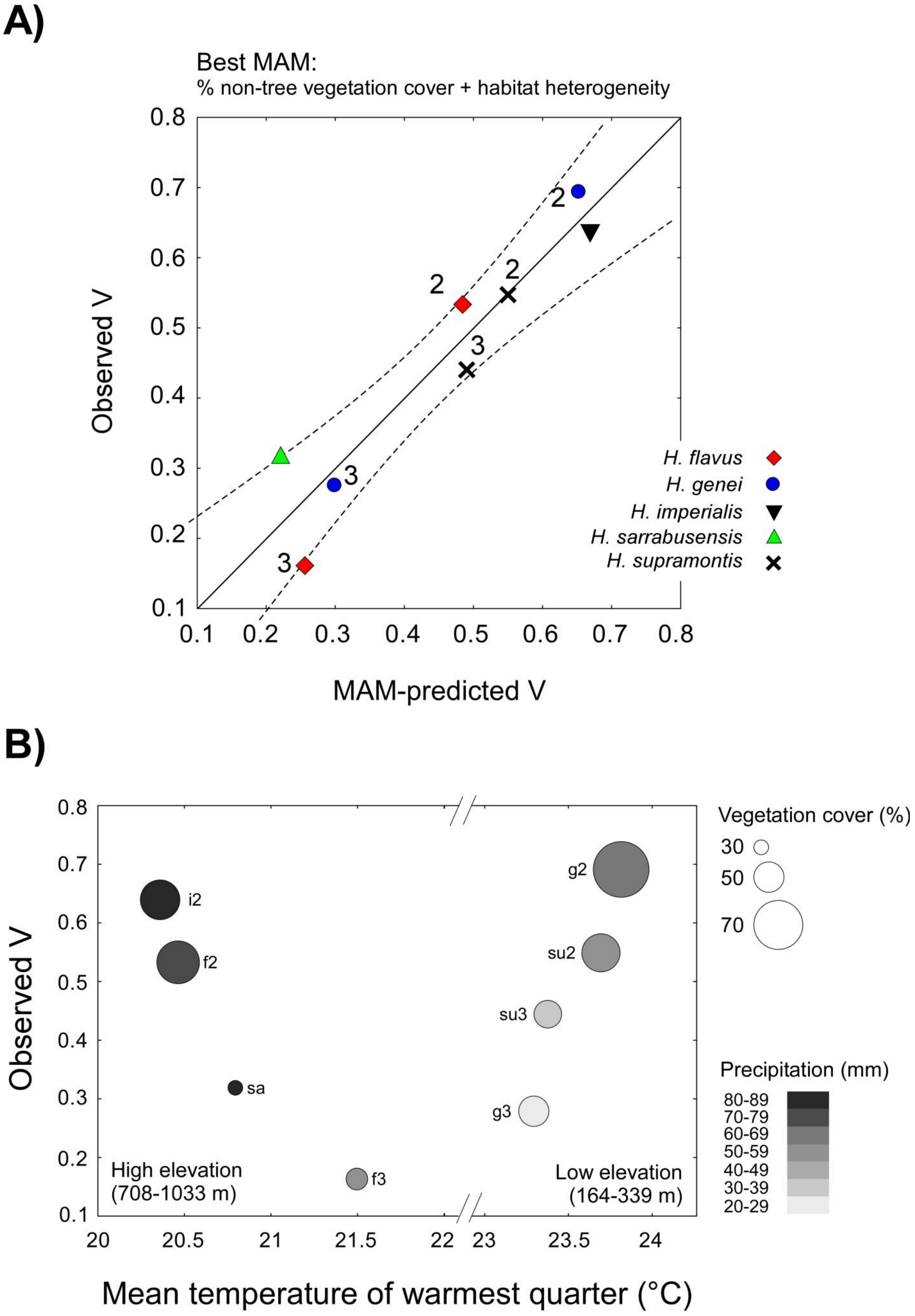

A)
V = 1- IS
TNW
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.3
0.6
0.9
1.2
1.5
1.8
2.1
2.4
2
2*
2
3
3*
3
H. flavus
H. genei
H. imperialis
H. sarrabusensis
H. supramontis
B)
H. flavus (pop3): V = 0.16
H. genei (pop2): V = 0.69
141
140
129
136
124
131
134
135
126
125
130
133
128
132
127
138
139
137
Trombidiformes
Araneae
Orthoptera
Hemiptera
Formicidae
Archaeognatha
Hydromantes body parts
Diptera
Hymenoptera
Coleoptera
159
163
161
153
164
162
157
158
160
142
145
146
147
148
154
155
152
156
143
144
149
150
151
Hymenoptera
Trombidiformes
Isopoda
Orthoptera
Sarcoptiformes
Opiliones
Pseudoscorpiones
Coleoptera Staphylinidae
Formicidae
Araneae
Hemiptera
Mesostigmata
Coleoptera
Diptera

Figure 3


A)
Best MAM:
% non-tree vegetation cover + habitat heterogeneity
Observed V
MAM-predicted V
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
2
3
H. flavus
H. genei
H. imperialis
H. sarrabusensis
H. supramontis
B)
Observed V
Mean temperature of warmest quarter (°C)
20
20.5
21
21.5
22
23
23.5
24
i2
f2
sa
f3
g2
su2
su3
g3
High elevation
(708-1033 m)
Low elevation
(164-339 m)
Vegetation cover (%)
30
50
70
Precipitation (mm)
80-89
70-79
60-69
50-59
40-49
30-39
20-29