

## SPECIAL FEATURE

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# Idea paper: Elucidation of the long-term properties of food webs based on the intraspecific genetic diversity of hub species populations

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## Abstract

Organisms interact across time and space; collectively, these interactions constitute webs that drive energy and material cycles. Classical ecological studies have tested the hypothesis that complex food webs are less stable in closed systems and have thus focused mainly on internal, local drivers of interspecific interactions in food webs. Recently, theories relating to food webs and ecosystems have been expanded to larger spatial scales through the concept of meta-communities (i.e., metawebs and metaecosystems), whose properties are driven by climatic conditions. However, these concepts have been limited to short-term phenomena observable on ecological time scales, while long-term historical processes have rarely been considered. In addition, the components of food webs have not been considered as determinants of food web persistence, even though species' persistence is determined by factors other than interspecific interactions within local food webs. Here, I emphasized the potential utility of intraspecific genetic diversity of hub species as a metric for evaluating the long-term persistence of local food webs. I also proposed a method for calculating this new metric, expressed as the sum of all metaweb level centrality and intraspecific genetic diversity values for each species. Furthermore, I discussed hypothetical patterns in food web properties as determined from both food web structure and intraspecific genetic structure along geographical and climatic gradients; these patterns have yet to be verified empirically. Finally, I summarized recent developments in molecular methods for collecting genetic data, which may support the empirical study of the concepts presented here.

## KEYWORDS

food web structure, macroecology, metabarcoding, multitrophic comparative phylogeography, population genetics

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## 1 | RESEARCH QUESTION

How do the long-term properties of local food webs change along geographical and climatic gradients? Specifically, do food webs in more isolated and/or lower-productivity areas have lower long-term persistence?

## 2 | VALUE

Elucidating the mechanisms related to the persistence of food webs and ecosystems is a long-standing issue (Kondoh, 2003; May, 1972). Trophic interactions are considered primarily from two distinct perspectives, the ecological perspective (i.e., local processes) and the evolutionary perspective (i.e., historical processes), but there are substantial gaps between the two (Nakadai, 2017). Until around 2000, the structure of food webs was studied as a short-term, local phenomenon in closed systems (Holt & Hoopes, 2005). Since then, the importance of broader spatial processes (e.g., metacommunity processes) in the dynamics of local food webs has gradually gained attention, although there is still a focus on short-term trends. In nature, food-web collapses have not been observed frequently (e.g., loss of large apex consumers, reviewed in Estes et al., 2011), and the persistence of food webs might not coincide with ecological time scales (defined here as time frames observable by humans, which may range from decades to centuries, e.g., monitoring surveys). Therefore, detecting patterns in the long-term properties of food webs will help elucidate the biogeographical formation processes underlying food webs at regional scales (e.g., the Japanese archipelago). Here I define “long-term” as the typical focal period of phylogeographic studies (e.g., since the Last Glacial Maximum, approximately 21,000 years ago).

## 3 | RELEVANT HYPOTHESES

Traditional approaches to food web studies assume a closed system (Kondoh, 2003; May, 1972). Classical ecological theory suggests that complexity destabilizes food webs (May, 1972). Thus, it follows that food web structure determines the persistence of populations and, consequently, the stability of food webs, but the opposite is not true (Kondoh, 2003). However, food webs and ecosystems are generally open and interconnected, and components of food webs can move among systems, as recent studies of food webs have also recognized (Holt & Hoopes, 2005). Therefore, long-term population persistence in local food webs should be driven by geographic factors (e.g., geographic isolation) as well as by climatic

conditions and interspecific interactions in local food webs, although the importance of those processes has not been well-integrated into the concept of species persistence within food webs.

Recent increases in the amount of available information on species occurrences and interactions have allowed scientists to explore large-scale patterns (Gravel et al., 2019). Recent studies have attempted to apply these patterns to wider spatial scales (i.e., metawebs: Dunne, 2006). Metawebs can represent the potential interactions among all species in a given area (Dunne, 2006; Gravel et al., 2019). Gravel et al. (2019) hypothesized that the co-occurrence of and interaction among species, and by extension the food web structure, may be driven by climatic factors, and they modeled the food web structure in tri-trophic interactions among willows, sawfly wasps, and parasitoid wasps based on climatic variables. Their focus was on short-term food web structures, (i.e., on ecological time scales) and did not discuss how the web and its components have persisted to the present. The effects of population persistence on the long-term properties of food webs were therefore not considered in their study.

## 4 | NEW RESEARCH IDEA

Here, I propose a new conceptual framework that combines comparative phylogeography with the study of food webs to elucidate the long-term properties of food webs. In particular, I emphasize the importance of intraspecific genetic diversity of hub species as a metric for evaluating the long-term persistence of local food webs.

## 5 | HOW TO SOLVE THE QUESTION THROUGH THE NEW IDEA

Ecologists have long sought to understand species in the context of their biotic environment, that is, the Eltonian niche (Elton, 1927), and have developed methods for describing the roles of different species in food webs (e.g., degree, trophic level, motif, and centrality; reviewed in Cirtwill et al., 2018). In this paper, I define hub species as species that are in key positions of the topological space of predator–prey interactions; thus, species that exhibit high centrality (Jordán, Benedek, & Podani, 2007). The loss of hub species would exert stronger effects on the persistence of food webs than would the loss of low-centrality species (Jordán et al., 2007). However, the long-term persistence of populations of hub species in food webs has not been well studied.

The proposed idea using the phylogeographic diversity as the persistence of food web stems from the existing ideas in the field of comparative phylogeography. Genetic information is now readily accessible for many species and can be represented spatially, particularly in the context of comparative phylogeography. Smith, Seeholzer, Harvey, Cuervo, and Brumfield (2017) collected genetic data for 210 New World bird species distributed across a broad latitudinal gradient and developed a suite of metrics characterizing their phylogeographic history. They found that lower-latitude species had, on average, greater phylogeographic diversity than higher-latitude species. Higher intraspecific genetic diversity has been interpreted as evidence of the long persistence of local populations in comparative phylogeography. Therefore, the patterns of intraspecific genetic diversity in birds provided evidence of greater persistence of the population of each species in the tropics, suggesting that the latitudinal gradient in species richness originates, at least in part, from population-level processes within species (Smith et al., 2017). However, their discussion was somewhat limited; they did not make inferences or predictions regarding comparative phylogeography at the multi-trophic level.

Integrating the concepts of comparative phylogeography into food web ecology should provide new insights. I propose a statistical approach to exploring genetic structure and predator–prey patterns, using a combination of metaweb network centralities and local intraspecific genetic diversity. This approach can be used to test the association between species centrality and species persistence. The test statistic ( $T$ ) generated represents the sum of all centrality and intraspecific genetic diversity values for each species:  $T = \sum_i C_i G_i$ .  $C_i$  represents the centrality of species  $i$  at the metaweb level, while  $G_i$  indicates the local intraspecific genetic diversity of species  $i$ . There are many different metrics for both centrality (reviewed in Lai, Liu, & Jordán, 2012; Toju et al., 2017) and intraspecific diversity (reviewed in Hughes, Inouye, Johnson, Underwood, & Vellend, 2008); I do not recommend any specific metric here, as the suitability of various metrics needs to be assessed through additional studies. In brief, centrality ( $C$ ) is related to the importance of a species to food-web persistence, and local intraspecific genetic diversity ( $G$ ) is related to the long-term persistence of species. The multiple values of  $C$  and  $G$  for each species should be interpreted as its contribution to the long-term persistence of the food web.  $T$  should be correlated with species richness ( $S$ ) in the local food web, so  $P = T/S$  can be used as a standardized metric of the persistence of local food webs.  $P$  represents the average of the potential persistence of species populations in each local food web, where high values indicate a

stable food web. Patterns in  $P$  can be explored along geographical and climatic gradients, for example, to predict food web stability in geographically well-connected areas to other food webs by individual migration or in high-productivity systems (e.g., where temperatures and precipitation are high). Also, the test statistic  $T$  can be compared with a null model in a randomization test to determine the effect size for any given dataset. If hub species (i.e., species with high centrality) have greater intraspecific genetic variation within a local food web, which is indicative of a more centered and stable web, the above statistic is expected to be larger than that under the null model, and vice versa. Thus, it can be used to test for a significant concentration of intraspecific genetic diversity toward either the hubs or other nodes of the food web. A similar randomization method was used by Barraclough, Segraves, Hogan, and Vogler (1999) and Nakadai and Kawakita (2016).

In addition, differences between local and metaweb centralities may indicate the potential flexibility of different species. If metaweb-level hub species with high potential flexibility show high average genetic similarity among local food webs, we expect the whole system to be more stable and persistent. High genetic similarity of hub species among food webs would indicate that the persistence of hub species is driven by dispersal processes. By contrast, low genetic similarity of hub species among food webs would suggest that the persistence of hub species is driven by local processes, such as climate and interspecific interactions. Therefore, the relationship between species centrality and intraspecific genetic diversity has broad utility.

Recent developments in molecular methods, specifically metabarcoding, facilitate the collection of data on local biodiversity, species interactions, and intraspecific genetic variation for multiple species (Elbrecht, Vamos, Steinke, & Leese, 2018). In addition, studies using multiple loci increase the information available for population genetics (Marquina, Esparza-Salas, Roslin, & Ronquist, 2019). Metabarcoding methods are being developed that focus on local biodiversity (Marquina et al., 2019; Miya et al., 2015) and predator–prey interactions (Leray, Meyer, & Mills, 2015; Nakadai & Kawakita, 2017). Sequencing and amplicon errors present challenges to the application of metabarcoding methods in population genetics studies, but recent denoising methods address these challenges by allowing researchers to exclude errors from sequence outputs (e.g., Divisive Amplicon Denoising Algorithm 2: DADA2, Callahan et al., 2016). These methodological advances will allow for simultaneous collection of data on predator–prey interactions and intraspecific genetic variation.

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## CONFLICT OF INTEREST

The author declares no competing interests.

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