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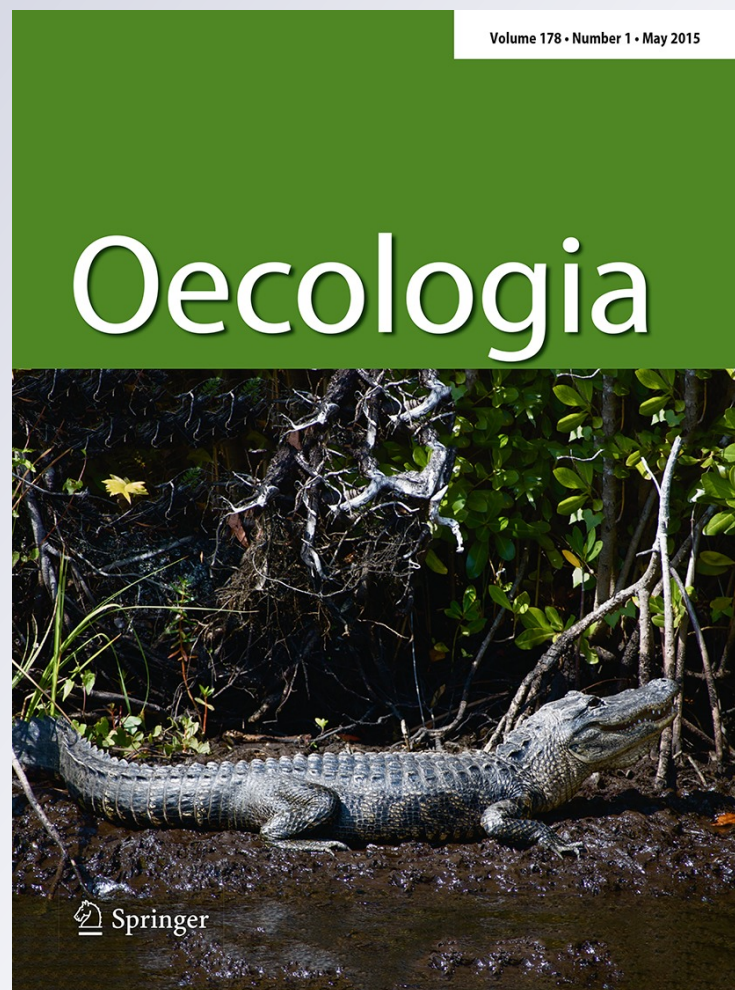
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# Individual-level niche specialization within populations: emerging areas of study

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## Introduction

Charles Darwin would likely question the novelty of a special section on intraspecific variation 156 years after publication of *On the Origin of Species*. Not only was phenotypic variation fundamental to the theory of evolution by natural selection, Darwin argued it was a challenge in classifying individuals to particular species. He wrote in chapter 2: "... but I could show by a long catalogue of facts, that parts which must be called important, whether viewed under a physiological or classificatory point of view, sometimes vary in the individuals of the same species. I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure..." (Darwin 1859).

Yet during the historical development of many sub-disciplines in the ecological sciences, inter-individual differences were typically subsumed to coarser levels of classification. In community ecology, species served as the nodes in food web models; ecosystem ecologists focused on energy/nutrient flow through systems with little consideration of how individuals mediate ecosystem processes.

A shift in thinking emerged with acknowledgment of the apparently widespread, but often overlooked, occurrence of "individual specialization" (IS) (Bolnick et al. 2003), which built on earlier observations and theory regarding the role that between-individual variation plays in niche expansion (Van Valen 1965; Roughgarden 1972). Following conventions described in Roughgarden (1972), Bolnick et al. (2003) defined an individual specialist as an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age, or discrete morphological characteristics. Since the Bolnick et al. (2003) review, research on IS has burgeoned and emerged as a primary framework for exploring individual-level variation within populations.

Recent reviews summarized the state of research in this area and identified remaining gaps in our understanding of the causes and consequences of IS (Araújo et al. 2011; Bolnick et al. 2011; Dall et al. 2012). In this special issue, we feature empirical studies that fill some of these knowledge gaps. In doing so, we outline several developing areas of inquiry in the field, helping guide future empirical studies regarding IS.

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## Drivers of IS: ecological opportunity

Araújo et al. (2011) reviewed the widespread occurrence of IS, and suggested means by which ecological mechanisms (e.g., competition, predation) may mediate its incidence or magnitude. At that time, ecological opportunity—broadly defined as resource diversity, distribution and availability/accessibility for consumers—was a mechanism with relatively little empirical study. Several contributions in this special issue suggest that ecological opportunity is an essential consideration when quantifying IS. Rosenblatt et al. (2015)

suggest that American alligator populations inhabiting lakes exhibit a lower degree of IS than coastal populations, primarily due to the greater diversity of resources available in the latter. Elliott Smith et al. (2015) link behavior to ecological opportunity, specifically by showing that differences in movement patterns, and thus access to resources, depend on sex-based differences in sea otter foraging ranges. Robertson et al. (2015) posit access to farmland foraging habitats is a primary determinant of IS in European badgers. Newsome et al. (2015b) relate ecological opportunity to prey functional roles, and suggest that sea otters living in habitats dominated by prey from a single functional group have reduced ecological opportunity and thus lower potential for IS. In sea otters, specialized foraging tactics and prey handling skills are needed to efficiently process prey from particular functional groups (Estes et al. 2003), which suggests a link between ecological opportunity and individual-level foraging.

### Temporal scale of study

Perhaps the most challenging aspect of quantifying the degree of IS within populations is identifying the time-scale over which it is manifest (or assessed). Novak and Tinker (2015) show that analyses of feeding observations in sea otters over short time frames (e.g., hours) overestimate the degree of IS. Fodrie et al.'s (2015) conclusions parallel those of Novak and Tinker (2015), emphasizing how time scales of study, as well as number of independent observations, can greatly influence assertions regarding the degree of niche specialization. Notably, Fodrie et al. (2015) utilize data along a less commonly used niche axis, i.e., habitat use, highlighting that theory and tools used to analyze trophic data can likewise be applied to other types of resource use.

### How should resource categories be defined?

Newsome et al. (2015b) draw attention to the ways we classify resource categories, another factor which can affect analysis of IS. They suggest that prey functional groupings, not taxonomic categories, might be a more appropriate means to quantify IS in sea otters. For instance, an otter that feeds on many species of infaunal bivalve may be considered a generalist, yet the search image and extraction technique for each species of bivalve would be quite similar. Conversely, an individual that feeds in habitats that contain prey belonging to a wide variety of functional groups requires a more complex set of foraging tactics, conditions that likely promote IS. Also examining sea otter foraging patterns, Novak and Tinker

(2015) suggest that simply considering incidence versus frequency of prey categories can affect conclusions regarding IS. The methodological perspectives provided in these studies, as well as the two cited in the previous section, are helpful reminders that designation of specialists within a population is a construct we use to simplify complex ecological patterns and dynamics. As such, quantification of IS is rather sensitive to the methodological approaches employed.

### Variables used to predict incidence of diet variation: morphology

Snowberg et al. (2015) explore whether intrapopulation diet variation is correlated with intrapopulation morphological variation, and thus whether morphology can be used as a proxy for dietary patterns. They found evidence that this was the case across 12 lacustrine populations of three-spine stickleback, but they caution that this was apparent only because they measured an entire suite of morphological traits. Any singular trait lacked strong predictive power. As such, although correlations may be informative, caution must be taken in inferring diet variation based on morphological variation.

### Variables used to predict incidence of diet variation: trophic position

Svanbäck et al. (2015) used size classes of Eurasian perch to explore if the degree of IS varies predictably across trophic levels. They found evidence that IS was strongest at intermediate trophic levels, likely because of increased omnivory, i.e., intermediate-sized perch may feed on resources at multiple trophic levels (resources ranging from zooplankton to carnivorous fishes). Such patterns in the incidence of IS allow for specific, testable, predictions across study systems and taxa.

### Roles of humans in mediating IS

Human activities have resulted in heterogeneous landscapes, creating conditions that may favor individual specialists within populations. Newsome et al. (2015a) explored this possibility with coyotes in the greater Chicago area. The reliance of individual coyotes on natural (primarily mammalian prey in nature preserves) and anthropogenic food items was highly variable, even among individuals with overlapping territories. This variability suggests a potentially high degree of IS within the urban landscape. Likewise, Robertson et al. (2015) show that landscape mosaics created by human land



use provide the background context for patterns of IS in badgers. The roles of humans in altering degrees of specialization in animal populations are largely unknown, and these studies provide important advances in this area.

### Integrating insights from behavioral ecology

Dall et al. (2012) pointed out similarities in the study of niche specialization across three sub-disciplines in the biological sciences: trophic niche variation in population and community ecology, division of labor within insect societies, and animal “personality” variation from the perspective of behavioral ecology. Each has different motivations for the study of individual-level variation, yet provide for potentially complementary insights in terminology, methods and theoretical constructs. Some of these similarities are apparent in the contribution of Urszán et al. (2015). They explore consistency in behavior within and across life stages of agile frog tadpoles. Although trends were variable across responses, they did find evidence for consistency in some behaviors and were able to link these behaviors to individual-level life history variation. This finding parallels observations in other studies of this volume, e.g., consistency in habitat use of three-spine stickleback (Snowberg et al. 2015).

### Revisiting the original definition of an “individual specialist”

Bolnick et al. (2003) defined an “individual specialist” as an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete morphological group. This specific definition served to exclude obvious categorical classifications where intraspecific diet variation would be likely, such as in cases of extreme sexual dimorphism. But papers in this issue illustrate how subtle differences between sexes or morphological variants may fall within the original scope of the IS definition. For instance, Elliott Smith et al. (2015) show that in sea otters, differences in reproductive effort between sexes are an important determinant in the strength of IS. Snowberg et al. (2015) show that morphological variation among individuals can be related to diet; yet the morphological differences do not amount to discrete morphological sub-groups.

### Synthesis

The papers in this volume represent a growing body of literature that asks: what has been overlooked by the

prominent population-level perspective in ecology, and how might ecological systems and evolutionary processes be better understood by more explicit recognition of variation among individuals? These studies suggest that previously described population-level means may be more appropriately viewed as emergent properties than principal entities of interest. As new analytical approaches allow for advances regarding individual-level ecological variation, these studies suggest that it is critical that we carefully define the spatial and temporal scales of IS. The challenge moving forward is to further refine IS theoretical frameworks (Bolnick et al. 2003, 2011; Araújo et al. 2011) by identifying which ecological contexts lead to the promotion and maintenance of IS within populations. Charles Darwin surely would have agreed that this is a worthy pursuit.

**Author contribution statement** All authors contributed equally in writing this manuscript.

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