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Niche Diversification and Differentiation as Exemplified by the Snail-killing Flies (Sciomyzidae: Diptera)

Wetlands (2025) 45:113
https://doi.org/10.1007/s13157-025-01999-5

SHORT COMMUNICATIONS

Niche Diversification and Differentiation as Exemplified by the Snail-killing Flies (Sciomyzidae: Diptera)

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Received: 13 August 2025 / Accepted: 20 October 2025

Abstract
New definitions of "niche diversification" and "niche differentiation" are proposed. The former is the opening up of new adaptive zones through major changes in the environment or though internal changes that allow a range of new resources to be exploited. The latter is the lowering of competition (both intra- and interspecific) within existing adaptive zones through partitioning of resources. These definitions are discussed with respect to Hutchinson's n-dimensional concept of the niche. The snail-killing flies (Sciomyzidae: Diptera), one of the biologically best known and most species rich higher flies in wetlands, are used as exemplars of this concept.

Keywords Niche diversification · Niche differentiation · Sciomyzidae · Marsh flies · Snail-killing flies

Introduction

The terms "niche diversification" and "niche differentiation" are in widespread use in the ecological and evolutionary sciences (including wetland ecology). A google scholar search[1] of the terms resulted in about 362,000 results for "niche diversification" and about 1,440,000 results for "niche differentiation". Despite this widespread use, after an examination of some of the papers resulting from the search, it is apparent that the terms are used almost synonymously.

It is the modest proposal of the present paper that these two terms be defined and used in a distinct way. The following definitions are proposed:

1) **Niche diversification** is the opening up of new adaptive zones through major changes in the environment of a taxon or through internal changes that allow a range of new resources to be exploited.

2) **Niche differentiation** is the lowering of competition within an existing adaptive zone through partitioning of resources.

These definitions can be thought of in a different, but complementary, way. In 1957 G. Evelyn Hutchinson defined the ecological niche as an n-dimensional hypervolume within which a species can maintain a viable population. In isolation this gave rise to the fundamental niche and with other competing species this gave rise to the smaller, or at most equally voluminous, realised niche (Hutchinson 1957). Hutchinson's model of the ecological niche did not take into account facilitation or succession, but it has become a meaningful way to examine the niche relations of flora and fauna. The present definition of "niche diversification" can be thought of as the adding of a new dimension to Hutchinson's model and "niche differentiation" as splitting species along an existing dimension.

What follows in the present brief paper, is an attempt to apply these two definitions to the biology of one of the most species rich Higher flies in wetlands – the Snail-killing flies of the family Sciomyzidae (Keiper et al. 2002). Following a brief introduction to the family, I will look at its early evolution followed by the major episodes of diversification of their niche. Following this, episodes of niche differentiation will be highlighted.

[1] Google scholar was searched on the 4th August 2025 in two separate searches: the first was with the term "niche diversification" and the second with the term "niche differentiation".

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Published online: 07 November 2025

Background to the Snail-killing Flies (Sciomyzidae: Diptera).

The Snail-killing flies, or Marsh flies (Sciomyzidae: Diptera) are one of the biologically most well-known family of the true flies (Diptera) with the biology known of 225 of the 549 species (41%) (Murphy, *in lit*[2]). Although Sciomyzidae have been described since the dawn of modern taxonomy e.g. see *Musca rufipes* Scopoli 1798 (now known as *Sepedon sphegea* [Fabricius, 1775]), studies of their life cycles are quite recent, following the seminal work of Berg (1953) who discovered the almost obligate malacophagy[3] in the family. For a recent overview of the family, see Murphy et al. (2012).

Knutson and Vala (2011) hypothesised that the Sciomyzidae arose during the early Upper Cretaceous and were derived from saprophagous species that were already feeding on dead snails. Berg et al. (1959), Foote et al. (1960) and Berg (1964) suggested *Atrichomelina* Cresson, 1920 as a model for the early feeding behaviour of Sciomyzidae. This monotypic genus has a rather labile feeding behaviour, feeding as a saprophage/predator/parasitoid on exposed semi-aquatic and aquatic non-operculate snails. From this early state, it was just a small step to leave the saprophagic lifestyle behind and specialise as either a predator or parasitoid on living non-operculate snails. This scenario has led to a diversity of feeding behavioural groups with different topologies of immature microhabitats within the larger adult macrohabitat (Williams 2023). The retention of behavioural groups that include the saprophagous (whether obligately or facultatively) habit strengthens the case of the evolutionary scenario outlined above.

The habit of feeding on live snails, in effect, saw the Sciomyzidae entering a largely vacant niche-space, which subsequently allowed for rapid adaptive radiation. It is in this framework that we now consider the various instances of niche diversification followed by niche differentiation, as defined above.

Niche Diversification in the Snail-killing Flies (Sciomyzidae: Diptera)

Following the evolution of the habit of killing live snails, probably in shore-line situations, the Sciomyzidae added extra dimensions to their niche by specialising on different snail species to reduce interspecific competition (Beaver 1974). Each new snail species (or group of species) attacked can be thought of as a new dimension in niche-space. Within each of these dimensions there was additional niche differentiation (e.g. size of snails attacked, adaptive differences in phenology etc. – see below).

The next major event in niche diversification in the Sciomyzidae came with a series of aquatic-terrestrial transitions and even secondary reversions to aquatic habitats. Eric Chapman's important work on this subject includes a detailed look at co-adaptations and inferred transitions from a genetic phylogeny, firstly in the genus *Tetanocera* Duméril, 1800 (Chapman et al. 2006) and then in the Sciomyzidae more generally (Chapman et al. 2012). The first terrestrial transition, similarly to the initial evolution of the snail-killing habit, opened up a vast array of potential prey in an essentially vacant niche.

Terrestrial Species

Within the terrestrial habitat, niche diversification took place and gave rise to a number of distinct behavioural groups (Knutson and Vala 2002, 2011), which differ in the prey that they exploit or in feeding habit i.e. saprophagy versus predatory versus parasitoidal traits. *Salticella fasciata* Meigen, 1830 has the most eurytopic of niches in the terrestrial habitat and acts as a facultative, opportunistic predator/parasitoid/saprophage. It feeds on dead, moribund or living snails or clams.

Mollusca, in general, have rather "patchy" distributions (Macan 1950). In aquatic situations, given the added buoyancy of the habitat, predatory "cruise foraging" is more easily achieved than in the terrestrial sphere. This is probably why many terrestrial species are parasitoidal. *Oidematops ferrugineus* Cresson, 1920, *Pteromicra steyskali* Foote, 1959 and *Tetanura pallidiventris* Fallén, 1820, along with at least six *Pherbellia* Robineau-Desvoidy, 1830 species are all parasitoids intimately associated with terrestrial non-operculate snails.

Nevertheless, the predatory habit is exhibited amongst terrestrial species, though this is usually combined with a rather labile feeding as saprophages, when the opportunity arises e.g. in *Pherbellia cinerella* (Fallén, 1820), *Coremacera marginata* (Fabricius, 1775) and *Trypetoptera punctulata* (Scopoli, 1763). Another diversification of the terrestrial niche was the shift to slug-killing and feeding. In fact, there exists a near continuous differentiation of the niche axis from predatory or saprophagic species, which

[2] Mr Murphy keeps a referenced list of known biological studies of Sciomyzidae, which he kindly sent to me.

[3] "Almost" because Vala et al. (2000) discovered a species of Oligochaete-feeding *Sepedon* Latreille, 1804 and in 2002 reported a second species of *Sepedon* feeding in this way (Vala et al. 2002).

feed opportunistically on both terrestrial snails and slugs (e.g. *Euthycera cribrata* [Rondani, 1868] and *Limnia unguicornis* [Scopoli, 1763]) through obligate ectoparasitoids/predators of slugs (e.g. *Tetanocera elata* [Fabricius, 1781] and *Tetanocera plebeja* Loew, 1862) to obligate mesoparasitoids of slugs (e.g. *Euthycera chaerophylli* [Fabricius, 1798]).

As noted earlier, there was also a transition from moist strand-line habitats to truly aquatic habitats. This diversification, similarly, gave rise to vacant niche axes around which further diversification occurred. It is to this aquatic habitat that we now turn.

Aquatic Species

In the aquatic realm, lots of behavioural groups are concerned with either exposed surfaces (e.g. *Hydromya dorsalis* [Fabricius, 1775]), temporary wetlands (e.g. *Colobaea bifasciella* [Fallén, 1820] and *Sciomyza varia* [Coquillett, 1904]– see below) or semi-aquatic Succineidae snails (e.g. *Pherbellia s. schoenherri* [Fallén, 1826]). This range of species includes diversification of the niche from predatory/saprophagy (*H. dorsalis*) to parasitoids (*C. bifasciella* and *S. varia* and *P. s. schoenherri*). In the case of *C. bifasciella* and *S. varia*, these two species, which evolved quite distantly from each other (Marinoni and Mathis 2000; Tóthová et al. 2013) in separate zoogeographical realms (*C. bifasciella* is Palearctic whereas *S. varia* is Nearctic), show a striking convergent evolution with adult females laying eggs directly on the shells of aquatic species and the puparium undergoing torsion when laid down inside the shell hosts. This may be an adaptation to parasitoid avoidance (Williams et al. 2025).

One group has further diversified the aquatic niche by focusing on exposed egg masses of Mollusca (e.g. *Anticheta* spp.). Truly aquatic predators have also evolved (e.g. *Sepedon spinipes* Scopoli, 1763). Another quite extreme diversification is the focus by *Renocera pallida* (Fallén, 1820) and *L. unguicornis* on fingernail clams (Foote and Knutson 1970).

Another, more extreme diversification, is the transition to halophytic habitats like salt marshes. *Hoplodictya setosa* (Coquillett, 1901) feeds on the operculate (another extreme diversification) marine littoral species *Littorina littorea* (L. 1758). Less extreme are the species that feed on freshwater operculates (e.g. *Pherbellia prefixa* Steyskal, 1967, which feeds on the freshwater operculate *Valvata* spp.).

Perhaps the most extreme example of niche diversification is in the derived genus *Sepedon* Latreille, 1804, two African species of which have been found to feed on oligochaete worms (Vala et al. 2000, 2002). There could be very many more species of *Sepedon*, unknown to science, that are feeding in this way. Or, alternatively, this could be the beginning of a new adaptive radiation for the family.

Having considered the major terrestrial and aquatic events of niche diversification, it is now time to turn to the question of how these diversified niches are differentiated along their axes.

Niche Differentiation in the Snail-killing Flies (Sciomyzidae: Diptera)

It is important to set out at the beginning that niche differentiation, unlike niche diversification, which is a primarily interspecific concept, can occur both intra- and interspecifically. One of the most obvious ways in which diversified niches have become differentiated is through size choice of prey. Mc Donnell et al. (2014) reared different sized larvae of *S. spinipes* (different instars) on differently sized lymnaeid snails. The many other rearings (summarised in Knutson and Vala 2011) have shown the same phenomenon. Thus, especially for multivoltine species with overlapping cohorts of larvae, different cohorts from the same species limit intraspecific competition through specialising in different sized prey for each instar. This is also likely to be true in certain circumstances, interspecifically. For example, *Pherbellia nana* (Fallén, 1820) is a diminutive Sciomyzini, which shares a behavioural group (group 2 – see Knutson and Vala [2011] for details) with many other larger species. It is likely that *P. nana* exploits smaller prey thus, differentiating its niche axis from that of other competing species by lowering interspecific competition in this way.

Another way in which interspecific competition can be reduced via niche differentiation is through adaptive differences in phenology (Berg et al. 1982). The timing of life-history stages, the stage at which overwintering takes place, and the distinction between univoltine and multivoltine species all act to reduce competition among species, which may be sharing the same habitat and even the same host/prey species. The different timings of life stages mean that early eclosing larvae feed on the first small generation of molluscs while later eclosing larvae feed on either another generation or larger molluscs of the same generation. Group 1 phenology species are multivoltine and overwinter as a pupa. Group 2 phenology species reduce the time to emerge as adults, mate and lay eggs, by overwintering as adults, they can thus, exploit molluscan hosts/prey earlier in the season. Group 3 phenology flies are univoltine and overwinter in the egg membrane, thus exploiting even earlier cohorts of Mollusca. Group 4 phenology flies take this to the ultimate extreme by overwintering as partly grown larvae. They are also univoltine. They not only take molluscan hosts/prey earlier in the season, but as they are partly grown, they presumably take large prey, thus further differentiating their niche – though this of course depends on the relative size of the different fly species. Group 5 phenology species are univoltine but overwinter as pupae. This is thought to be a specialised adaptation to ephemeral water bodies, and this was confirmed by Williams et al. (2009a, b) on Irish Winter lakes (turloughs). It could be argued that phenology group 5 is in fact a new dimension to the niche-space and so is really, niche diversification rather than niche differentiation. However, Williams et al. (2009a) recorded seven species sharing a transect at Skealoghan turlough and in a wider study across ten sites, recorded 19 species (Williams et al. 2009b) sharing this temporary lake habitat. The same is true for ephemeral lotic habitats. Maher et al. (2014) recorded 22 species of Sciomyzidae in river flood meadows (Callows) on the Shannon. It is likely that Whiles and Goldowitz's (2001) study on the central Platte river wetlands (Sloughs) similarly collected many Sciomyzidae species in their sampling though they only reported family abundance. Therefore, whereas group 5 phenology puts these species at an advantage – in the cases above *Ilione albiseta* (Scopoli, 1763) was dominant – it is not really a "new" habitat since other phenology group species also exploit these ephemeral wetlands. This argues against niche diversification and for niche differentiation.

It should be noted that niche differentiation can occur at all life stages. Eggs, for example can be laid either on aquatic vegetation, on terrestrial vegetation or directly on the shell of the snail (see above for a discussion of the convergently evolved habits of *C. bifasciella* and *S. varia*). Vala and Ghamizi (1992) showed that females of *P. s. schoenherri* will oviposit multiple times on the shell of *Oxyloma* (*Succinea*) *elegans* (Risso, 1826) when they are at low density, but will oviposit only single eggs when densities of the snail are high. Thus, adults can gauge the optimal level of intraspecific competition to maximise their fitness returns.

It is likely that many Sciomyzidae exhibit trail following behaviour. Trelka and Berg (1977) showed that third instar *T. plebeja* will follow fresh slug trails. Mc Donnell et al. (2007) showed that both *S. spinipes* and *Dictya montana* Steyskal, 1954 neonates will also follow lymnaeid snail trails. Critically, for aged trails, Mc Donnell et al., showed that the trail following behaviour does not last to the end of the Y maze meaning that the larvae exhibit an adaptive optimal foraging response. Trail following will lead predaceous larvae to fresh, presumably unparasitized, prey and so has the effect of differentiating the prey niche.

Slug killers like *T. elata* minimise competition intraspecifically by exhibiting a mixed foraging strategy. Neonates act as parasitoids in an "ambush foraging strategy" (Griffin 2012). Neonates sit and wait on vegetation and then "latch on" (Hynes et al. 2014). In the later instars the species adopts a "cruise foraging strategy" and actively pursues and feeds on multiple slug individuals. Thus, there is niche differentiation between instars.

Conclusion

This paper makes the modest proposal to define and use the terms niche diversification and niche differentiation in two distinct ways. The first term adds dimensions to the n-dimensional hypervolume of the environment in which the species maintains a viable population – this usually acts to lower interspecific competition. The second term denotes a splitting of resources along existing dimensions and can act both intra- and interspecifically. I have outlined, in this brief paper, examples of the two processes in the Sciomyzidae an important member of the Higher Diptera, especially in wetlands. Of course, this scheme is not just restricted to the Sciomyzidae. There are lots of fly families which exploit different taxocenes e.g. the Pipunculidae regularly exploit Hemiptera. The scheme is not even restricted to insects and could be valuably applied to marine mammals and birds, or island endemics like Darwin's Finches.

Acknowledgements I thank Mr William L. Murphy for providing unpublished information and permission to cite him.
I thank two anonymous referees for *Wetlands*, whose comments improved this paper.
This paper is dedicated to Professors Michael J. Gormally and Rory J. Mc Donnell, who first introduced me to the wonderful world of Sciomyzidae biology more than 21 years ago, in 2004.

Author Contributions This work was completed in its entirety by the sole author, apart from where acknowledgements are made.

Funding No Funding was received to research or write this paper.

Data Availability No data are associated with this paper as it is largely a theoretical piece of work.

Declarations

Competing Interests The author has no relevant financial or non-financial interests to disclose.

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