GENERAL WETLAND SCIENCE

On the Topologies of micro/macrohabitats in the Mollusca-Sciomyzidae Taxocene

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Abstract

A new perspective on habitat is presented, which considers the topological relationships among macrohabitats of adults and the sub-set microhabitats of eggs and other juvenile stages. A model of seven topologies is presented using the snail-killing flies (Sciomyzidae: Diptera) as an exemplar; four of these topologies are drawn on a hydrological continuum from aquatic through shoreline to terrestrial, and three are presented as stand-alone specialized feeding groups. Colonisation-extinction dynamics are discussed in relation first to macrohabitat dynamics and then microhabitat structure. The topological perspective has wide application outside the Mollusca-Sciomyzidae taxocene e.g. in parasitoid wasp-host taxocenes, in phytophagous insect-host communities, for freshwater macro-invertebrates and even, in the context of a "landscape of fear", for bird and mammal populations. The perspective taken is more "autecological" than the traditional "biotope" or resource view of habitats, yet is broad enough to encompass many different behavioural groups as shown for the Sciomyzidae.

Introduction

Taxocenes

Taxocenes have been defined by Hutchinson (1978) as collections of individuals representing a monophyletic group and found in a given area. More recently, the term has implied a particular trophic affinity e.g. Miller (1995) and Nabozhenko et al. (2016). In this piece, I deal with the mollusc-Sciomyzidae (snail-killing flies) taxocene in terms of what I call the micro/macrohabitat topologies. Although this appears fairly limited in scope, the implications of topological thinking have wide applications for how we view other macro/microhabitat associations e.g. in parasitoid wasp-host taxocenes, in phytophagous insect-host communities, for freshwater macro-invertebrates and even, in the context of a landscape of fear[1] (Brown et al. 1999), for bird and mammal populations.

Existing Biological Assessment Paradigms

There is a long history of habitat classification for animal communities. Elton and Miller (1954) classified the habitat of animals according to the physiognomy of the dominant plant communities. Prior to this, Shelford (1932) argued against such a scheme due to the fact that animals move between strata. Shelford notes three types of classification with respect to animal communities: (1) based on the family and its guests as in many social insects; (2) those developed by limnologists and hydrobiologists and (3) those based on wider formations and biomes. For the "small communities" with which this paper is concerned, there have historically been many eco-taxonomic approaches to the habitat question (Dibb 1948). These concepts are all part of the *biotope* habitat paradigm.

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1 The landscape of fear is where habitat utilization is affected by the fear of predators e.g. re-introduction of woolves in Yellowstone National Park caused elk to avoid certain dangerous locations and subsequently aided the recovery of vegetation like aspen.

Modern views of habitat assessment rely heavily on *compositional* definitions whereby habitats are defined according to the similarity among sites based on a site by site similarity matrix. This is done either by a divisive or agglomerative dendrogram production and ordination e.g. for Ground Beetles (Luff et al. 1989). These groups are then interpreted ecologically by *a posteriori* analysis. Another modern approach is to perform a direct ordination i.e. an ordination whereby the graphing of community similarity is constrained by dominant environmental variables, such an analysis was performed on Odonata data by Schindler et al. (2003). Although based on a constrained ordination, the interpretation of Schindler et al. is still *a posteriori*; highlighting different assemblages in man-made and natural water bodies.

A priori classifications of habitat also exist. For example, Shreeve et al.'s (2004) resource view of habitats and Walter and Hengeveld's (2000) autecological view of habitats whereby, habitat refers to specific neurophysiological and behavioural interactions between individual and environment (Walter and Hengeveld 2000) The topological view of habitats has some resemblance to Shreeve et al.'s (2004) resource view of habitats, but is more autecological in nature. The topological view has the advantage of summarizing the relations among many divergent behavioural groups as will be shown for the Sciomyzidae.

Snail-killing Flies (Sciomyzidae)

With 38% of the taxonomically described species with lifecycles deduced (Knutson and Vala 2011; Murphy et al. 2012), the snail-killing flies (Sciomyzidae) are one of the biologically most well-known families of true fly (Diptera). This, together with their obligate malacophagy (Berg 1953) in patchy mollusc communities makes the family both spatially tractable and ecologically well-known. The snail-killing flies are one of the dominant higher Diptera in wetlands (Keiper et al. 2002; Whiles and Goldowitz 2001) and have been suggested as suitable wetland bioindicators as long ago as the 1980s (Speight 1986). Recent studies on turloughs (temporary lakes) by Williams et al. (2009a, b) and the Shannon callows (unregulated river flood plains) by Maher et al. (2014) have demonstrated the qualitative and quantitative response to hydrology and management. Furthermore, Carey et al. (2017a; b) highlighted their use as biodiversity surrogates with compositional changes in parataxonomic units of nine fly families being highly correlated with compositional changes in snail-killing flies ($r^2 = 0.84$ $P = 0.002$). Recent work by Ahmed et al. (2021) has shown their use as indicators of farm intensity and field margin type. For all these reasons snail-killing flies have a lot to teach us about wetland habitats.

Knutson and Vala (2011) have noted that Sciomyzidae adults occupy a rather broad range of macrohabitats whereas eggs, larvae and puparia occupy various microhabitats nested within the broader adult macrohabitat. It is the topologies of these microhabitats, and their differences among behavioural groups defined by Knutson and Vala (2011), within the macrohabitat, which are our concern here. It has long been known that both aquatic and terrestrial Mollusca exhibit "patchy" distributions in what appear to be uniform environments (Macan 1950). It appears as though adult Sciomyzidae communities track well the hydrological conditions of their habitat whether this be in temporary lakes (turloughs) or flood meadows (Shannon callows) – See Williams et al. (2009a; b) and Maher et al. (2014) – with some overlap in communities between different hydroperiods. Also, Williams et al. (2010) showed, using mark-recapture, limited movement of adults within a sedge-dominated turlough habitat.
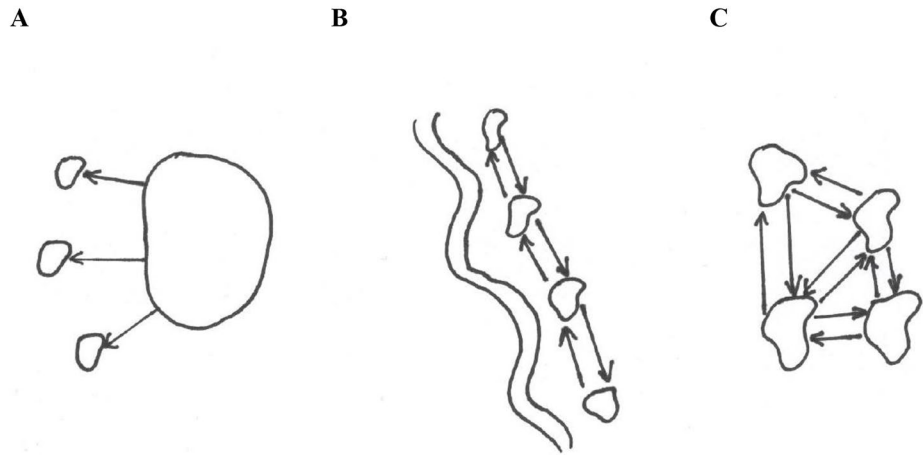
Adult Macrohabitats

Before dealing with the topologies of micro/macrohabitats, I will deal with the macrohabitat and how this may relate to landscape features. Then I will consider how microhabitat processes may impact upon these macrohabitat extinction-colonisation dynamics, before presenting a model of micro/macrohabitat topologies according to behavioural group classification.

Sciomyzidae macrohabitats can exhibit three possible (or a mixture of more than one) dynamics according to landscape features – all are metapopulations. They can either exhibit source-sink dynamics as in a central core habitat such as a fen and outlying seepages (Fig. 1A), or they can exhibit stepping-stone dynamics as one might find in a river floodplain (Fig. 1B). Of course, at a wider landscape scale, fluvial communities may exhibit dendritic metapopulations (Fagan 2002) something that can most easily be ascribed by comparing geographical, river network and genetic distances. Finally, they can exhibit a classical metapopulation dynamics as exemplified by a number of lakes (temporary or otherwise) in a lowland area (Fig. 1C).

We can consider egg, larval and puparial microhabitats nested within each larger adult macrohabitat patch. The persistence of a metapopulation does not necessarily require large numbers of propagules (adults or puparia in our case) to move between adult macrohabitats, Stacey et al., (1997) have noted that some simulation models have shown that only five or six immigrants per year are necessary to prevent extinctions even in stochastic environments. Very large populations of Sciomyzidae were studied at a temporary lake by Williams et al. (2010). These populations exhibited very

Figure 1 Three models of Sciomyzidae adult macrohabitats. A) shows a fen with bordering seepages concurring with a source-sink metapopulation. B) shows a river floodplain with patchy distributions concurring with a stepping stones model. C) shows temporary wetlands in the landscape concurring with a classical metapopulation.

limited within-habitat movement. We may presume that movement between macrohabitats will be more likely when adult movements within macrohabitats are high.

Taking the simplest metapopulation dynamics:

$P = 1 - e/m$.

Where P = the proportion of macrohabitats occupied.

e = extinction rate i.e. the rate at which macrohabitats become locally extinct.

m = migration rate i.e. the rate at which empty macrohabitats become successfully colonized.

Any factor that increases m and decreases e will increase the proportion of macrohabitats occupied.

1) **Area and abundance of resources**: This will tend to be, for aquatic and shore-line species, areas of appropriate hydrology and vegetation structure around lentic bodies of water (Fig. 1C) – see Williams et al. (2009) and Maher et al. (2014). For terrestrial species there may be a number of critical ecosystem elements in the matrix (*sensu* Hunter Jr., 2005) such as proximity to hedgerows and tall, dead and moribund vegetation (Bistline-East et al. 2020). Other critical ecosystem elements in a farmed landscape are drainage ditches (Ahmed et al. 2021). Area can be conceived as the traditional "biotope" area on a GIS and resources can be quantified within these patches. Greater area will tend to decrease e. Ouin et al. (2006) demonstrated this for forest-specialist hoverflies (Syrphidae). A greater total abundance of larval and adult resources will tend to support a higher population of Sciomyzidae, and experience lower demographic stochasticity (drift), lowering the chance of local extinction. Dunn et al. (2020) note, again with respect to Syrphidae, that the numbers of syrphid larvae and eggs were positively correlated to aphid (larval resource) abundance. Area *per se* is unlikely to affect m, though it may do so in certain

circumstances e.g. if inter-macrohabitat migration is active, m may be density-dependent. Moerkens et al. (2009) proposed density-dependent migration as a factor that may explain local crashes in populations of the earwig (*Forficula auricularia*). Perimeter/area would tend to decrease with increasing area thereby acting against m (see below). There is some theoretical evidence to support perimeter-dependent migration (Hambäck and Englund 2005), but no empirical evidence that this is the case for Sciomyzidae.

2) **Distance between macrohabitat patches**: Again, this can be conceived as a typical biotope habitat in a landscape (see Fig. 1A–C). Increased distance between macrohabitat patches would tend to decrease m, but would have little effect on e (See Shulman and Chase [2007] who demonstrate steeper declines of predators compared to prey with increased isolation). For active migration, the chance of not detecting suitable patches is increased with distance. For passive dispersal, the colonization rate of a patch varies inversely as a function of 2π.distance between patches (MacArthur and Wilson 1963).

3) **Perimeter/Area**: Drawing up a habitat suitability model on a GIS can allow this metric to be easily calculated. Increased perimeter/area would tend to increase m – any individual would be more likely to be near a boundary of the focal macrohabitat and hence subject to passive movement beyond it. Edge effects associated with the perimeter may increase e. However, this is an edge effect in the traditional sense. A few papers have noted that there is no general edge effect and species responses to habitat edges is often species-specific e.g. *Phytomyza ilicis* (Agromyzidae: Diptera) populations are affected by natural enemies, microclimate, adult movement and host-plant quality at boundaries (McGeoch and Gaston 2000). Some edge effects may actually increase a focal

species' populations either by differentially affecting a superior competitor (Nee and May 1992) or by directly aiding the species by increasing the fractal dimension of the landscape, as appears to be the case for some Syrphidae (Haslett 1994). Williams et al. (2010) and Carey et al. (2017b) both suggest that Sciomyzidae are somewhat sedentary as adults, responding to local patch-level factors in the main. In order to assess the degree to which neighboring A patches are colonized genetic analysis is needed to establish Fst values. This is a pressing need for both pure and applied studies.

Microhabitats

The effects of microhabitat structure and extent will now be considered on e and m of the macrohabitat in a landscape ecological context.

1) **Egg (*E*) and Larval/Puparial (*L/P*) microhabitats and adult resource patches**: Optimal foraging models predict movement of larvae between patches of L micohabitats (if possible), but it is unlikely that larval movements would result in migration between adult macrohabitats. Nevertheless, movement of gravid females between E microhabitat patches and adults, in general, between resource patches may be critical. It is relevant to mention here that Bistline-East et al. (2018) have demonstrated the importance of aphid honey-dew as an adult nutritional resource.

2) **Area**: Greater total area of E and L/P microhabitats would tend to decrease e as would greater total adult resource patch area. High E and adult resource area may decrease m, if adults can confine themselves to one oviposition / foraging patch. This may be what is happening on Irish turloughs (temporary lakes) and the flood plains of the Shannon Callows (see Williams et al. 2009, 2010 and Maher et al. 2014).

3) **Distance between E and L/P microhabitats and adult resource patches**: Increased distance between L/P microhabitats may increase e if each patch does not support the whole development of larvae and migration of larvae (within adult macrohabitats but between L microhabitats) is necessary. There is a possible increase in m with increasing distance between E microhabitats as females are "on the wing" more often and subject to possible air currents and passive dispersal. Extensive searches of the entomological literature found no empirical evidence for this effect and so it must remain a theoretical supposition.

4) **Perimeter/Area**: Increasing perimeter/area may increase e if edge effects act on larvae in a similar way

to "traditional" edge effects. See above for exceptions to this.

Topological Models of Sciomyizdae

Figure 2 provides seven topological models for the Mollusca-Sciomyizdae taxocene. The first four models are arranged on a hydrological continuum from the fully aquatic species (**a**) through shoreline species (**b**) to terrestrial species (**c**). The special case of univoltine species on temporary wetlands is denoted as (**d**). It will be noted that adult macrohabitats tend to overlap quite a bit and there is good empirical evidence for this – see Maher et al. (2014) who presents a graphical representation of the hydrological niche of all Sciomyzidae found on the Shannon callows (unregulated flood plain). The three remaining topologies do not fit into a hydrological scheme. They are: highly intimate parasitoids (**e1**), snail egg-killers (**e2**) and clam killers (**e3**).
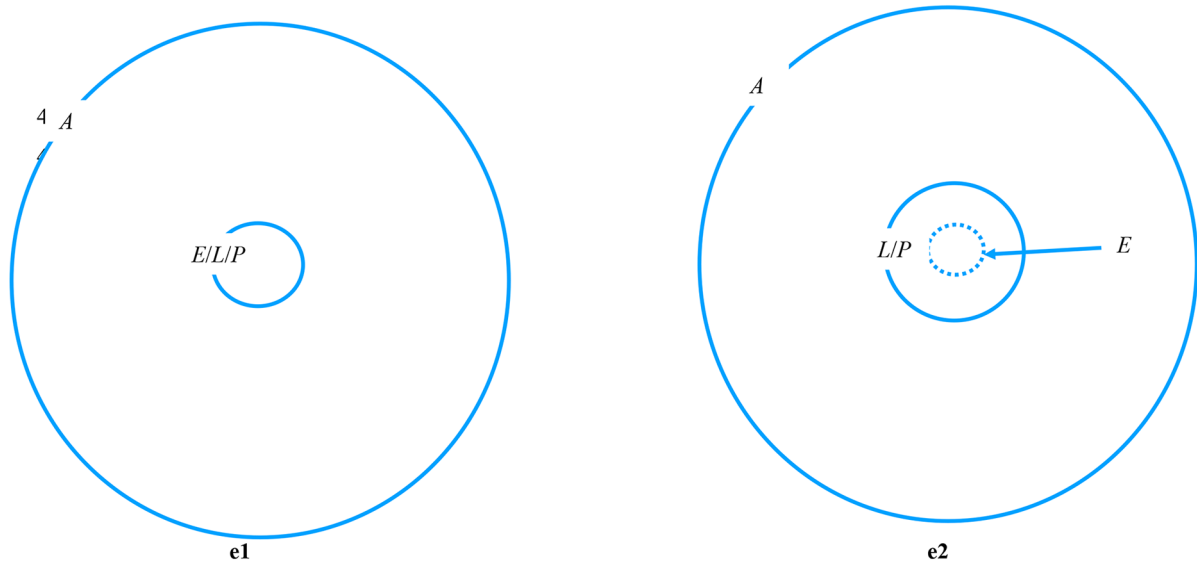
For both aquatic (**a**) and shoreline (**b**) species, gravid females oviposit on vegetation so that the extent of the egg micro-habitat is not much less than that of the adult. Since larvae swim and dive in aquatic species, but are more-or-less confined to the shoreline in shoreline species, this is shown by the relative smaller sub-set of larval microhabitats in (**b**) as compared to (**a**). Puparia in (**a**) are floating so are coterminous sets with larval microhabitat (i.e. quite extensive) whereas in (**b**) they pupariate typically in the shell of the gastropod host/prey and so are more restricted than the larval microhabitat (i.e. in (**b**) puparial microhabitats are a subset of larval microhabitats). In terrestrial situations, egg microhabitats are more restricted and the more parasitoidal larvae and puparia form coterminous sets, which are a subset of the egg microhabitat. For highly intimate parasitoids (**e1**), egg, larval and puparial microhabitats are a single coterminous set (i.e. the host snail). For snail egg feeders (**e2**) larval and puparial microhabitats are broader than the egg microhabitat since after first instar, larvae feed on stranded snails. The relationship between habitat topology, behavioural group (according to Knutson and Vala, 2011), a brief description of the behavioural group and also some example taxa are shown in Table 1.

Wider Applications

The topological perspective may aid in a lot of basic and applied ecology. We may talk about coincidence and non-overlapping sets of immature and adult resources (e.g. Lepidoptera) as represented by various degrees of intersecting sets. This occurs when larval resources may occur outside of adult macrohabitat patches. Such situations although
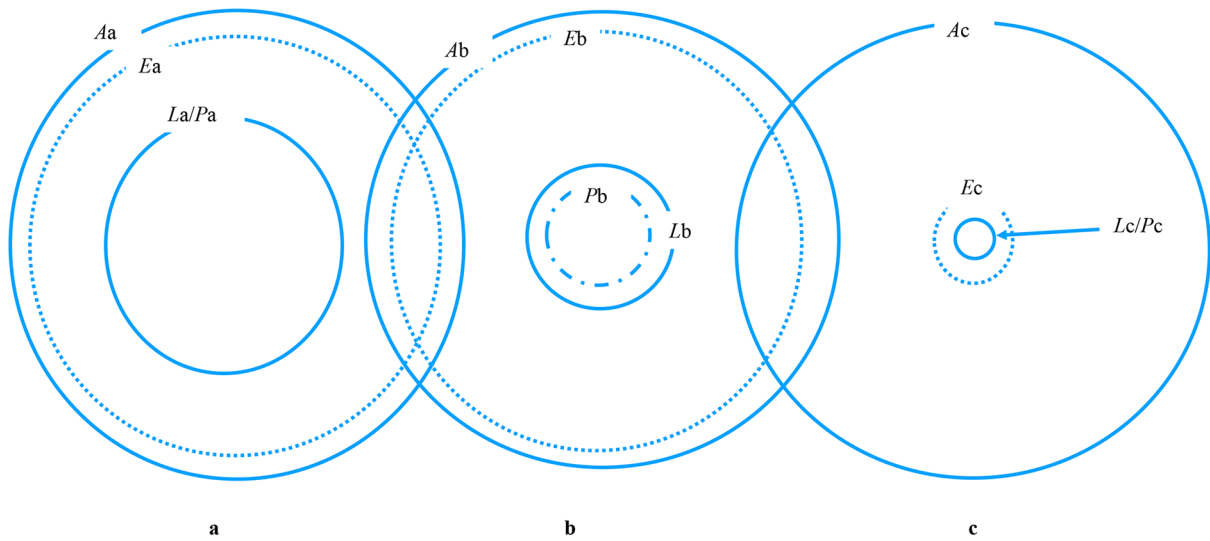
d as in **a** & **b**, but univoltine

e3 as a, but first istar larvae feed below the water surface on clams.

a = Permanent aquatic

b = Shoreline predators

c = Terrestrial

d = Temporary aquatic specialist

e = Special behavioural groups : **e1** = Highly intimate parasitoids, **e2** = Snail egg-feeders, **e3** = Clam killers

Figure 2 Topological models of Sciomyzidae micro/macrohabitats. There is a gradient of hydrology going from **a** to **b** to **c**, from fully aquatic through shoreline to fully terrestrial. **a** encompasses the behavioural groups, of Knutson and Vala (2011), 11 and 12; **b** encompasses behavioural group 4; **c** encompasses groups 1, 7, 8, 9 and 10; **d** encompasses group 13; **e1** encompasses groups 3 (shoreline), 4 (semi-terrestrial) and 6 (terrestrial); **e2** encompasses group 5 and **e3** encompasses group 14. Behavioural groups 12 and 15 are not covered by the model. For details on the autecology of different behavioural groups see Table 1

Table 1 Behavioural groups according to Knutson and Vala (2011), descriptions of the groups, example taxa and habitat topology (see Fig. 2) to which each belong

Behavioural group	Description of Behavioural group	Example taxa in each group	Habitat topology
1	Facultative, opportunistic, predators/parasitoids/ saprophages that can feed on dead, moribund, or living snails.	*Salticella fasciata* (terrestrial) *Atrichomelina pubera* (moist surfaces)	c
2	Predators/saprophages of non-operculate, primarily freshwater snails exposed on moist surfaces by receding or fluctuating water levels.	*Colobaea americana, C. pectoralis, C. punctata, Pteromicra* spp., *Sciomyza simplex, Hydromya dorsalis.*	b
3	Parasitoids or parasitoids/predators more or less intimately associated with non-operculate freshwater snails exposed in temporary freshwater habitats	*Colobaea bifasciella, Sciomyza varia,* some *Pherbellia* spp.	e1
4	Parasitoids or parasitoids/predators more or less intimately associated with hygrophilous, semi-terrestrial Succineidae snails.	*Pherbellia s. schoenherri, P. s. maculata, Pteromicra anopla, Sciomyza aristalis, S. dryomyzina, S. testacea.*	e1
5	Obligate parasitoids/predators of exposed egg masses of freshwater Lymnaeidae or *Aplexa* (Physidae) or semi-terrestrial Succineidae snails during early larval life, followed by predation on juvenile snails on damp surfaces.	*Anticheta* spp.	e2
6	Parasitoids intimately associated with terrestrial non-operculate snails.	*Oidematops ferrugineus, Pherbellia* spp., *Pteromicra steyskali, Tetanura pallidiventris.*	e1
7	Predators/saprophages of non-operculate terrestrial snails	*Pherbellia cinerella, Coremacera marginata, Trypetoptera punctulata.*	c
8	Predators/ saprophages opportunistic on both terrestrial snails and slugs.	*Limnia unguicornis, L. paludicola,* some *Tetanocera* spp.	c
9	Obligate ecoparasitoids/predators of slugs.	*Tetanocera clara, T. elata, T. plebeja.*	c
10	Obligate mesoparasitoids of slugs.	*Euthycera chaerophylli, E. arcuata.*	c
11	Predators of non-operculate snails at or just below the water surface on emergent vegetation, and occasionally those exposed on moist surfaces	Most *Dictya* spp., *Dichetophora biroi, D. hendeli, Dictyodes dictyodes, Elgiva* spp.	a/b
12	Predators and predators/parasitoids of exposed and neustonic operculate aquatic snails.	*Hoplodictya setosa, Dictya lobifera, Pherbellia prefixa, Dictya fontinalis, Neolimnia tranquilla.*	-
13	Predators of non-operculate snails under the water surface.	*Hedria mixta, Ilione albiseta, I trifara.*	d
14	Predators/parasitoids of fingernail clams.	*Eulimnia philpotti, Ilione lineata.*	e3
15	Predators of freshwater oligiochaete worms	*Sepedonella nana, Sepedon knutsoni.*	-

A B C

unusual at the moment could become more common with climate change. With climate change or habitat modifications, if microhabitat sets become separated from the macrohabitat set then it is likely that there will follow local extinction of the organism. As an exemplar, we may consider *Hydromya dorsalis*. This species is a typical shoreline predator of aquatic snails. Figure 3 shows an infographic of the likely changes to the habitat topology of *H. dorsalis* given either the impacts of climate change or extensive land reclamation at a landscape scale. Firstly, adult macrohabitats become more restricted causing lower populations, but critically, also, the larval microhabitats become much more reduced in extent meaning that the already lower adult populations are less viable. We may also look at restriction of habitat extent within versus outside a landscape of fear (Brown et al. 1999) for mammals and birds. The topology of habitats may vary quantitatively (and even qualitatively) in a landscape of fear compared to "control" situations. Ecological release either in different zoogeographical realms, as is the case for invasive species, may show a fundamental change in micro/macrohabitat topology. For a contemporary issue, how habitat topology changed during COVID
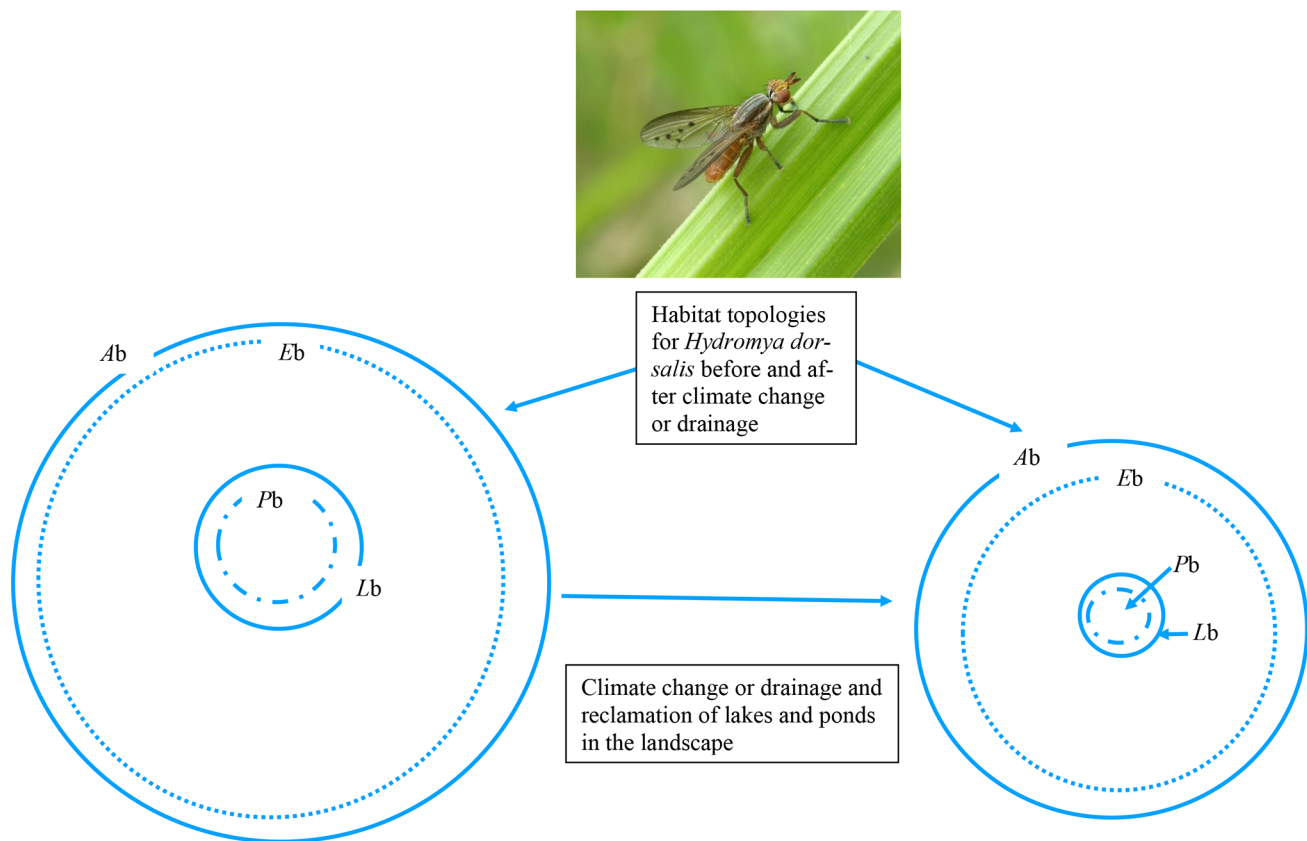
Figure 3 Infographic showing the effects of climate change or drainage of lakes and ponds inthe landscape on the habitat topologies of *Hydromya dorsalis*, a typical shoreline predator of aquatic snails

lockdowns for some carnivores (Wilmers et al. 2021) is an interesting case in point.

Declarations

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