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Research article

Community composition of invasive, outbreak, and non-pest snail species along a source spring-to-fishpond gradient in a spatially structured aquacultural region

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ABSTRACT

Agricultural lands are integrated into and interact with natural areas. Such is the case of Emek HaMa'ayanot, northern Israel, comprising a springs-rich area characterized by multiple land-uses, including spring-water-based aquaculture, recreational springs, and nature reserves. Aquacultural farms suffer from pest snails that carry fish disease; in the study region, these species are invasive (*Thiara scabra, Tarebia granifera, Pseudosuccinea columella*) and outbreak endemic (*Melanoides tuberculata*). Previous snail control efforts have focused on individual fishponds without considering management on larger environmental scales in the waterways from the source springs to the fish farms. To broaden our understanding of the status of the pest snail problem in the study area prior to suggesting environmental managerial solutions, we quantified changes in the community composition of snail species along the springs-to-fishponds gradients in a spatially explicit system. We found a remarkable increase in pest snail abundances along these gradients, indicating that pest snails might be invading upstream towards the springs. There were always nearly 100% pest snails in the endpoint sites for water tracks that ended in fishponds. Moreover, pest snails dominated the site when it was used as a fishpond, even though the site was also a spring. In contrast, in a water track that does not end in a fish farm, the relative abundances of non-pest snail species was similar between the source spring and the downstream endpoint, in spite of an increase in pest snail abundance at a midpoint site. These results suggest that invasive pest snails are actively moving upstream and that the fishponds have a marked upstream effect on the ability of non-pest snails to resist pest species invasions. We suggest further investigation of possible strategies for biocontrol of the observed invasion of the snails into natural areas as a basis for environmental management efforts. Finally, the observations made during this study could have practical global implications for snail management in aquaculture and agriculture, and for the control of snails and snail vectors implicated in animal and human diseases.

1. Introduction

Freshwater snails embedded in freshwater and aquacultural systems as water-quality bioindicators, grazers, and prey for other organisms (Elder and Collins, 1991; Okumura and Rocha, 2020), are considered essential parts of those systems (Lysne et al., 2008; Oloyede et al., 2017). However, freshwater snails are also disease vectors for various species of trematode, including those with complex life cycles (Bartoli and Boudouresque, 2007; Lysne et al., 2008; Oloyede et al., 2017; Routtu et al., 2014), found in numerous agroecological and aquacultural systems (Garchitorena et al., 2017; Haggerty et al., 2021; Roll et al., 2009). The enormous potential damage caused by certain species of freshwater snails as disease vectors include veterinary and economic damage due to the loss of fish crops (Bartoli and Boudouresque, 2007; Yizhar et al., 2009) and the spread of

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disease to other animals (Szuroczki and Richardson, 2009) and to humans (Garchitorena et al., 2017; Ozretich et al., 2022; Simon and Ben-Ami, 2014; Sokolow et al., 2016; Thieltges and Poulin, 2016). To date, the widely accepted strategy to control diseases caused by trematodes with complex life cycles is to target the snail as the intermediate host (Ben-Ami and Heller, 2001; Garchitorena et al., 2017; Haggerty et al., 2021; Rascalou et al., 2012; Sokolow et al., 2014; Yizhar et al., 2009), affecting aquaculture and conservation goals through snail control.

In addition to the above-described potential harm, snails that are introduced into ecosystems can also cause ecological damage to natural areas and aquacultural systems by invading, competing with, and changing ecosystem structure and function (Cianfanelli et al., 2007; Gherardi, 2007; Haggerty et al., 2021; Lysne et al., 2008). Thus, mapping snails in agroecological landscapes is crucial for controlling diseases affecting humans, animals, and crops, for the study of invasion dynamics, and for ecological conservation.

1.1. The model system

The selected model system of Emek HaMa'ayanot (Valley of the Springs), located in northeastern Israel, is an ideal area for aquacultural-ecological studies. The Valley is rich in natural springs used for recreation, tourism, agriculture, and aquaculture. A diverse land-use mosaic characterizes the area, alongside a unique and relatively closed hydrological system (personal communication, Ran Ben-Nun, CEO, Afikei Maim Ltd, Emek HaMa'ayanot). The aquaculture crops are mainly freshwater fish, such as carp, bass, and tilapia (Leventer, 1981; Savaya et al., 2020). Since the Valley is rich in independent freshwater sources, many natural springs have been harnessed for aquaculture by diverting the water through trenches that crisscross the Valley, eventually spilling into fish farms with hardly any external water supply, as is found in other aquacultural regions such as in Africa (Makherana et al., 2022; Oloyede et al., 2017; Sokolow et al., 2015). The between-farm waterways vary within the region, ranging from natural springs flowing directly into farms to man-made trenches supplied with pumped water. For this region, in many of the waterways both the start and endpoints are known since each farm uses the water of a particular spring or a small number of springs. This set-up, with a known inlet and a known outlet, simplifies the study of the water tracks.

The regional water system facilitates the connectivity of invasive, outbreak and overabundant snail populations and their dispersal into fishponds. Understanding the snail community composition along entire waterways will shed light on different snail control options for the area, not only for aquacultural purposes, but also for snail-borne disease control associated with a variety of high anthropogenic activity (Oloyede et al., 2017; Sokolow et al., 2015). Past studies have focused only on the springs (Cohen et al., 2020; Heller et al., 2014), only on the fishponds or farms (Ben-Ami and Heller, 2001; Leibowitz et al., 2019; Leventer, 1981), or only on water tracks between sources and endpoints, but in a more natural landscape (Ben-Ami and Heller, 2007; Heller et al., 2005; Yizhar et al., 2009). In contrast to this set-up, past studies worldwide have examined anthropogenic gradients in large water reservoirs or recreational lakes that do not have a clear source or outlet (Leighton et al., 2000; Makherana et al., 2022). Some past surveys were generalized over vast areas [see examples (Facon et al., 2005; Facon and David, 2006; Glaubrecht et al., 2009; Glöer and Pešić, 2012; López-López et al., 2009; Roll et al., 2009):]. Others were done for entire river systems, similar to the proposed study area, but nearly 30 years ago (Pointier et al., 1998) or in non-agricultural areas (Tolley-Jordan and Owen, 2008). Hence, to the best of our knowledge, our study is the first to explore changes in the composition of the snail communities along a spring-to-fishpond gradient in an aquacultural-agroecological landscape, which can also shed light on similar anthropogenically disturbed inland water landscapes suffering from snail related disturbances (Oloyede et al., 2017; Sokolow et al., 2015). In this study, we set out to close the knowledge gap of snail community compositions between sources and fishponds in waterways situated in combined natural/-agroecological landscapes.

By mapping the snail communities, we will have a solid foundation to plan large-scale environmentally friendly snail control management that is not simply confined to the endpoints or the fishponds. Some snails, which are agricultural pests, are currently treated by farmers at the individual fishpond level with non-specific biocides that may eliminate or harm all the organisms in the fishpond (Al-Akel and Suliman, 2012; Haggerty et al., 2021; Mitchell et al., 2007; Pingali and Roger, 1995; Savaya et al., 2020). Environmentally based and more sustainable alternatives rely on various biocontrol agents, such as introduction of the giant freshwater prawn *Macrobrachium rosenbergii* as a species that preys on snails (Garchitorena et al., 2017; Savaya et al., 2020; Sokolow et al., 2014, 2015). This solution could be implemented in connective trenches or water sources as well as in fishponds [Ran Ben-Nun, personal communication (Al-Akel and Suliman, 2012; Leventer, 1981);].

1.2. The snail species

In this study, we classified snails as "pests" or "non-pests". Snails were classified as pests if they fell into all three categories taken from the following literature: 1) intermediate hosts for trematodes, 2) previously defined as agricultural pests known to be present in commercial fishponds in the study area in very high densities, and 3) invasive or outbreak species, in which outbreak species were defined as "species that undergo unsustainable population growth" (Anderson, 2016). The snails that were defined as pests according to this classification were: *Melanoides tuberculata* (Müller, 1774) (Ben-Ami & Heller, 2001, 2005; Savaya et al., 2020; Simon and Ben-Ami, 2014), *Thiara scabra* (Müller, 1774) (Roll et al., 2009; Savaya et al., 2020; Simon and Ben-Ami, 2014; Yizhar et al., 2009), *Tarebia granifera* (Lamarck, 1816; Cañete et al., 2004; Facon and David, 2006; Roll et al., 2009; Simon and Ben-Ami, 2014; Yizhar et al., 2009), and *Pseudosuccinea columella* (Ben-Ami and Heller, 2001; Cañete et al., 2004; Ebbs et al., 2018; Gutiérrez et al., 2011; Roll et al., 2009). The snails that did not fall into the above three categories and were thus considered non-pests were *Theodoxus* and species of the family Melanopsidae (Monfort, 1810). For further detailed description of the snail species, see Supplementary material, section 1.1. Any other molluscan species found were considered as "other".

1.3. Working hypotheses

We hypothesized that the snail community composition in the source springs differs from that in the fishponds. More specifically, we expected, based on previous studies of the fishponds in the area, that the snail community in the source springs would be dominated by local non-pest species (Cohen et al., 2020; Heller et al., 2005), while the fishpond communities would be dominated by pest species (Ben-Ami and Heller, 2001; Leventer, 1981; Savaya et al., 2020). We also predicted that the snail community composition would change gradually between the source and the fishpond since snails would have to actively move upstream from the fishponds to reach the sources, as shown in previous surveys of water sources of the study area (Cohen et al., 2020; Simon and Ben-Ami, 2014) and in similar surveys in the Caribbean (Facon and David, 2006; Pointier et al., 1998). This composition gradient would be due to the snails' upstream movement and the expected spread of invasive species, which are included in the pest group (Cañete et al., 2004; Facon and David, 2006; Heller et al., 2014; Pointier et al., 1998). We further hypothesized that the proximity to the aquaculture industry (exhibiting lower water quality, i.e., higher levels of NO_2^- and NH_4^+) would correlate to the snail community composition. Thus, even if a source spring is used as a fishpond, we posit that the site will exhibit a species composition similar to other fishponds rather than to source springs due to the lower water quality expected in fishponds.

2. Materials and methods

2.1. Waterways (tracks) – natural experiment design

Waterways (tracks) from water sources to fishponds in the study region were chosen to cover a variety of waterway characteristics (Fig. 1A, Table S1.1). The tracks were considered suitable for the study if the endpoint received water from a trackable water source via various water-transport systems (on the assumption that water from a pumping station does not change between the pump entrance and exit) with as few underwater areas as possible. In this study, we focused on three representative tracks with different characteristics: track A, which has a source spring but no fishpond; track B, which has source springs and a fishpond; and track C, which is a source spring and is also used as a fishpond (Fig. 1B).

2.2. The tracks and sites

For site ranking (used for analyses), see Supplementary material, section 1.2. For detailed summary of representative tracks see Table S1.1 in the Supplementary material.

Track A. Sachne (Fig. 1, Table S1.1): This track was taken as the reference track because water from the Sachne source spring and water track is not used for fish farming. The source, A1, is located in a popular national park (Sachne, also known as Gan HaShlosha), in a 4 m deep pool. The second site, A2, is the only intermediate point in this track, in which the water is diverted from natural flow through an underground pipe to an open concrete trench. The site was chosen because it was the closest available spot for sampling after the water transport system changed from natural flow to a concrete trench; sampling at this site is from the concrete trench. The last site on the track, A3, is approximately 15 m before the Shluhot pumping and mixing station; it is located in a concrete trench lined with plastic. In the pumping station, the water from the Sachne source spring is mixed with other water sources for agriculture.

Track B. Ein HaNatziv (Fig. 1, Table S1.1): This track was chosen because it serves as an example of an almost direct track from a water source to a fishpond. Track B is fed by two sources, creating two legs to the track, of water of good quality, according to the Israel Nature and Parks Authority (INPA). The water from the sources is mixed in an underground pipe and pumped into a small, isolated section of a fish farm immediately across the road from the mixing point. The first leg begins with site B1, the Ein Yehuda spring, which is situated in close vicinity to the village of Ein HaNaziv, making it a popular swimming spot for residents and hikers. During the sampling period, the spring was declared a future national park by the INPA and had since gone under construction. The water flows naturally from the pool to site B2, which is the point where the water is pumped underground. The second leg begins in site B3, in Naftali spring, an independent source in the track which is located in a nature reserve immediately beyond the southern border of the Ein HaNaziv village. The end point for the track, site B4, is the soil-bottomed southern fishpond of the Upper Ein HaNaziv fish farm.

Track C. Tirat Zvi (Fig. 1, Table S1.1): In this track, the source itself is used by the local farm as a fishpond. The source is the Avraham spring, site C1. The source/fishpond is protected with a bird net, aerated, and usually stocked with bass fishlings (*Moronidae*). Since the site is populated with fish, it was treated in the analysis as all other fishponds, even though it is a source; this corresponded with our working hypothesis that the snail species composition at site C1 would be closer to that of a fishpond than to that of a source.

Two more tracks, track D and track E, were chosen to complete the picture of the Valley, as described below, and were included in some of the analyses (Fig. 1A, Table S1.1).

Track D. Muda (Fig. 1, Table S1.1): This track was chosen because it has many water-transport changing points compared to other tracks in the Valley. It begins at the Muda spring, D1, and pools into a man-made rock pool that is a popular tourist attraction. The water then flows naturally from the spring to a small pumping station. Immediately before the pumping station is sample site D2. Water from this site is pumped up a hill to the Muda reservoir, which covers an area of 1.7 km^2.

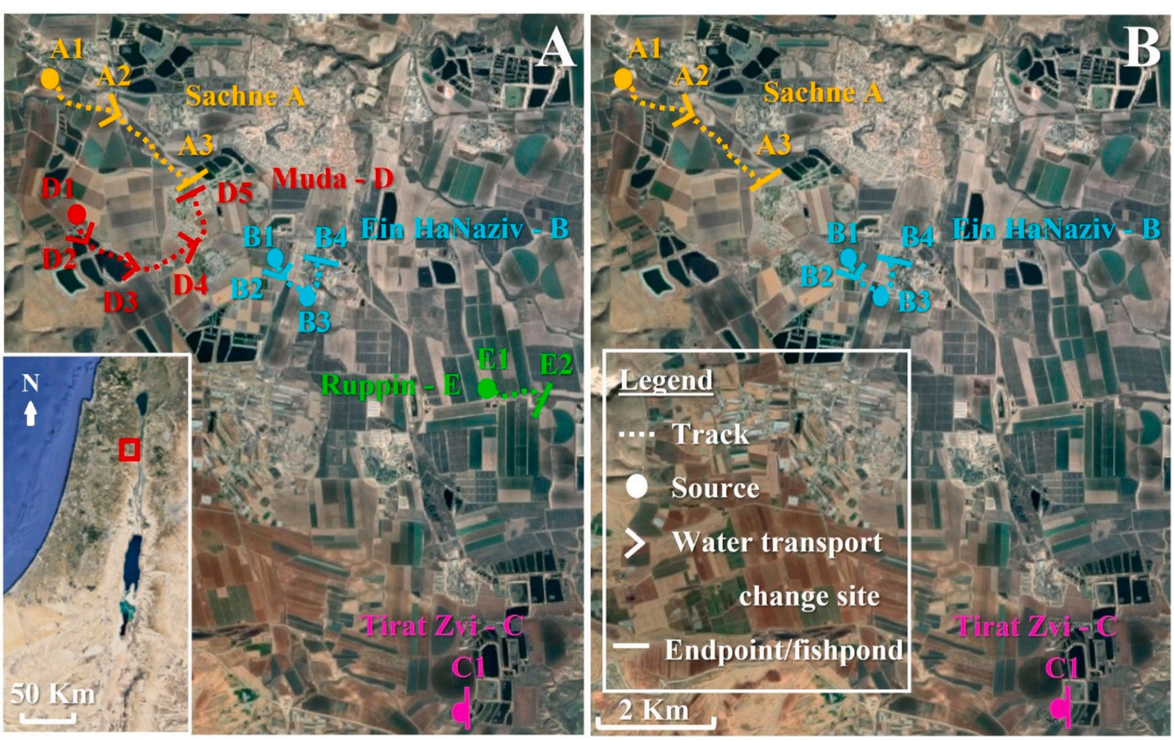

Fig. 1. Representative waterways (tracks) in Emek HaMa'ayanot. (A) The map shows five complete typical tracks in the study area. Insert: Map of Israel showing the study area as a red square. (B) The three most characteristic tracks in the study area constituting the main focus of the study.

The reservoir is used by local fish farmers (personal communication, Ran Ben-Nun, CEO, Afikei Maim Ltd, Emek HaMa'ayanot). Since the reservoir acts as a fishling storage pond during sporadic times of the year and is not continuously treated as a fishpond (not regularly oxidized or fed with fish feed), it was not considered as a fishpond in this study. The reservoir is 16–18 m deep, and the greater part is lined with very slippery plastic, making deep sampling dangerous and beyond our sampling abilities. However, we were able to sample from the top 1.5 m of the reservoir, and for every sampling event during the sampling period (Table S1.2), no snails were found. Instead, the outlet of the reservoir was chosen as site D3, which is situated in a trench 10 m from the reservoir exit; that site was selected because there the water flow changes from a reservoir to a concrete trench. The next site, D4, was selected because the track continues through a village and is, therefore, likely to be disturbed and hence different from site D3, which is in an agricultural area. The endpoint for track D, site D5, was located in the same place as site A3, a few meters upstream from the pumping station. The site was chosen since the water is pumped from there to endpoints throughout the Valley. The water from this source is usually mixed with other sources downstream for aquaculture farms in the Valley (personal communication, Ran Ben-Nun, CEO, Afikei Maim Ltd, Emek HaMa'ayanot). Under the working assumption that the snail population in the pipes is the same as that at the pumping site, site D5 was a proxy for the fishponds supplied by the water from this track. We note that the trench belonging to track A is separated from that belonging to track D by a third trench, 1.5-m wide, that carries water from a different source—the Homa spring (Fig. 2).

Track E. Ruppin (Fig. 1, Table S1.1): The Ruppin track was chosen because it is a natural flow track from the source directly to the fish farm and is the best example of direct natural flow in the Valley. It begins in a fenced nature conservation area, where the terrain is rough and covered with tall shrubs, which prevents visitors from continuously disturbing the track. Site E1 on this track is located in the Saharon nature reserve, which was built in 2014 as part of a conservation plan for the local endangered fish, the stone loach (*Oxynoemacheilus insignis)*. Since the source is quite difficult to access due to the dense vegetation, site E1 is located approximately 40 m downstream from the source, at the most accessible point in the creek. The water flows naturally through the creek until it reaches Ruppin fish farm. Because the farm was inactive during the year of the experiment, the end point for this track, site E2, was located in a connecting soil trench close to the water entry point to the farm which connects the creek to the fishponds, thus regarded as a proxy for a fishpond.

2.3. Sample collection

Samples were collected from each site three times in total during the late spring and summer of 2021 (Table S1.2). Because sampling from all five tracks usually took longer than a single working day, the samplings were sometimes a few weeks apart due to logistical constraints. It is noteworthy that the average temperatures were similar over the different sampling dates (Israel Meteorological services website, https://ims.gov.il/en). It is to be further noted that the first sampling of tracks B, C, and E was performed from dusk to dark due to time constraints, which resulted in bias due to poor vision. This problem was understood only during the sample analysis, so the correction of the event led to a time gap between the first sampling date of tracks B, C, and E and tracks A and D.

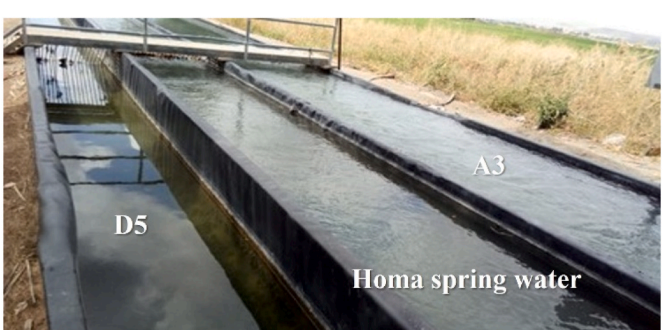

Fig. 2. Sites A3 and D5 and the trench separating them.

Snail samples were taken from each site in triplicate. To obtain each snail sample, a 0.25-m^2 frame was placed on the bottom of the water body or when not feasible (e.g., site A1, which is 4 m deep, and A3, where the rapid water speed presumably prevented snails from clinging to the bottom of the trench) the frame was placed on a wall or rock at an approximate depth of 0.5–1 m to match the depth of the water at the other sites. The snails and sediment were collected from the frame by skimming off the top of approximately 3 cm of sediment with a trowel or by hand when using a trowel were not possible, in a similar fashion to previous work in the area (Savaya et al., 2020). The locations for the triplicate samplings were selected randomly at each site.

2.4. Sample analysis

Each sample triplicate was analyzed individually. The snails were washed clean of sediment and sludge and sieved through a series of three metal sieves, 6-, 4-, and 2-mm mesh. The snails were thus separated into three size categories, >6 mm, 4–6 mm, and 2–4 mm, respectively. In each size category, the snails were segregated according to species following their morphological characteristics (Milstein et al., 2012) and counted. Due to morphological similarity, there may have been a few errors in distinguishing between *Thiara scabra* and *Tarebia granifera* in the 2- to 4-mm size grade. Relative abundances were calculated using PRIMER v.6 of the Plymouth Marine Laboratory (Clarke et al., 2014; Clarke and Gorley, 2007) standardized option.

Abiotic factors were sampled once at each site at every sampling event. NH_4^+ (in $mg\ L^{-1}$) and NO_2^- (in $mg\ L^{-1}$) were determined colorimetrically with the Merck MColorset Ammonium and Nitrite test kits, respectively.

2.5. Statistical analyses

Multivariate analyses were performed using PRIMER v.6 of the Plymouth Marine Laboratory (Clarke et al., 2014; Clarke and Gorley, 2007). Relative abundances were square-root transformed. Permutational MANOVA (PERMANOVA), based on the Bray-Curtis dissimilarity matrix supplemented with a dummy variable of 1 to eliminate the relative abundances with the value 0, was performed. PERMANOVA tests were performed under a reduced model to test the effects of the sampling event, the track, and the site name or the site rank or the site rank category (the last three nested in the track) on the snail species composition when all factors are random, tested against 999 permutations. This analysis was followed by a non-metric multi-dimensional scaling (nMDS) ordination to visually assess the snail community composition between the triplicates under the effects of the sites and the site ranks. The next step comprised pairwise comparisons (ANOSIM) (Clarke et al., 2014; Clarke and Gorley, 2007) adjusted for a two-way crossed factor with replicates to examine the comparisons between the sampling events and the sites or site ranks or site rank categories. This process was performed for data for tracks A, B, and C and for all five tracks, for data division of snail species, snail species and size grades, and according to snail species aggregated into groups of pests, non-pests, or other. Pearson correlations were set to >0.5, unless stated otherwise.

In the results presented below, we focus mainly on tracks A, B, and C and the snail species division into pest or non-pest groups. All other analyses are available in the Supplementary information.

3. Results

A summary of all the results is presented in the Supplemental results, Table S1.3. Detailed analyses and descriptions of the results for the different snail species along the source-spring-to-fishpond gradients as well as analyses that take into consideration the snail species and their size grades, are available in the Supplementary results in sections 3 and 4.

3.1. Abiotic factors

Generally, water quality decreased along the source-spring-to-fishpond gradient (Table S1.4). In tracks B, C, and E, the endpoints had higher levels of NO_2^- and NH_4^+ than in the source. In contrast, for tracks A and D, levels of NO_2^- and NH_4^+ remained constant along the tracks, from the source to the endpoint, with levels of both being lower than 0.175 mg L^{-1} and 0.17 mg L^{-1}, respectively. It should be noted that site C1 (a source spring serving as a fishpond) appears twice with the same values (Fig. S1), once grouped with the source springs and once grouped with the fishponds, for comparison. The levels at site C1 resembled those of the endpoints of tracks B and E, and thus abiotically, site C1 is more "typical" of a fishpond than a source spring.

3.2. Segregation of snails according to pest and non-pest species

3.2.1. Snails segregated into pest and non-pest species along the tracks in the Valley

Generally, the closer the site to a fishpond, the higher the proportion of pest snails in all the tracks, and the closer the site is to the source spring, the higher the proportion of the non-pest snails. In addition, a general increase in snail abundances were evident closer to the fishponds (Fig. 3, Fig. S2.1).

In track A, the proportion of non-pest snails was 99.7% at the source and 100% at the endpoint, with a high number of snails in general (nearly 10-fold higher than A1 and A3) at the A2 midpoint. Of the snails sampled at site A2, there were about 900 non-pest snails (on average, making up 60% of the sample), and almost 600 pest snails (making up the other 40% of the sample). This high snail count was found only at site A2, and not upstream or downstream at sites A1 and A3.

In track B, the proportion of the non-pest snails was high, although there was a minor presence of pest snails downstream at site B2 and site B3 (a source), i.e., 7% and 5% pest snails, respectively. There was a similarity in the general increase in snail abundance in the two downstream sites, B2 and A2. Site B4 showed a striking 100% pest snail population in the fishpond.

Similarly to site B4, at site C1, there were nearly 97% pest snails in the sample, showing that even though the site is a source spring, the snail population resembled that of a fishpond, as seen at site B4 and in other endpoints (Fig. 3, Fig. S2.1). Site C1 displayed a very high density of snails, with an average of 3500 snails per quadrant, when compared to the sites with a high proportion of pests, such as B4 and A2, which showed, on average, 400 and1600 snails per quadrant respectively.

An examination of Fig. 3 reveals the striking observation that in track A, for which there is no fishpond anywhere along the track, the endpoint of the track showed a population composition of 100% non-pest snails (even with the pest snail disturbance at site A2), as opposed to tracks ending with fishponds, which showed almost 100% pest snail community.

Snail community composition varied significantly between the sites (PERMANOVA, $F_{5,10} = 483.98$, $p = 0.001$), and this pattern was consistent for the different sampling events (Site × Sampling event interaction: PERMANOVA, $F_{10,48} = 0.84$, $p = 0.543$, Table S2.1A). This pattern was also evident in the nMDS ordination showing clearly that the sources, intermediate points, and fishponds are aggregated among each site type by 80% similarity, and that the sources and intermediate points show 40% similarity, while the fishponds do not (Fig. 4). Notably, site A3 is aggregated with the sources rather than with the other fishponds. Furthermore, site C1 is aggregated with 40% and 80% similarity with the fishpond at site B4 rather than with the sources A1, B1, and B3. Further ordinations supporting the significance of the site effect on the snail species composition for all five tracks may be seen in Fig. S2.2. All other factors (sampling event, track) and their interactions were not significant for tracks A, B, and C (Table S2.1A).

When all five tracks were examined together (Table S2.1B), the site effect was significant (PERMANOVA, $F_{10,20} = 80.7$, $p = 0.001$), but this pattern was not consistent among sampling events (Site × Sampling event interaction: PERMANOVA, $F_{8,20} = 2.59$, $p = 0.01$). This seasonal variation in snail community composition (Fig. S2.3) was observed to some extent in track A, with a decrease in the absolute abundance of snails at site A2. In track B, there were fluctuations in the relative abundances of pest snails at site B2 throughout the summer, first decreasing (in the second sampling event) and then increasing (in the third). At sites B3 and B4, there was also an increase in the absolute abundance of both pest and non-pest snails. At site C1, there was an increase in the absolute snail abundance, with a decrease in absolute and relative abundances of the non-pest snails from 7.7% at the first sampling event to 1% at the third sampling event. For track D, the snail population composition changed through the summer as follows: at site D1, there was no observed change in either pest or non-pest absolute and relative abundances; at site D2, there was an increase, and then a decrease in the proportion of the non-pest snails; at site D3, there was a general decrease in the absolute abundances of both pest and non-pest snails, while the relative abundances of both groups remained similar; at site D4, there was a decrease and then increase in the absolute abundances of the pest and non-pest snail groups, while the relative abundances of both groups remained similar; and at site D5 there was an increase in the absolute abundances of both pest and non-pest snail groups. In track E, there was a general decrease in the absolute abundances of pest and non-pest snails throughout the summer at both sites in the track, and an increase and then a decrease in non-pest relative abundance at site E1.

Qualitatively similar PERMANOVA results were obtained when the sites were aggregated into ranks for tracks A, B, and C alone (Table S2.2A) and for all five tracks (Tables S2.2B). When sites were aggregated into site rank categories (Table S2.3), the results were qualitatively similar to the results for tracks A, B and C alone, with a significant effect of the site on the snail composition, which was consistent throughout the sampling events.

Additional results supporting the effect of the site and resolution-dependent seasonality on the snail community composition were obtained from pairwise ANOSIM tests, as detailed in the supplementary results in section S2.2. These tests were performed for: sampling events and for the sites of tracks A, B, and C (Table S2.4A) and for all five tracks (Table S2.4B); for sampling events and site ranks for tracks A, B, and C, and for all five tracks (Tables S2.5A and B, respectively); and for sampling events and site rank categories when the sites were aggregated into rank categories for all five tracks (Table S2.6).

3.2.2. Overview of the snail population segregated into pest and non-pest species at the sources and endpoints/fishponds for tracks A, B, C, D, and E

General trends showed that source springs contained mainly (>90%) non-pest snails while fishponds contained 100% pest snails. In comparison, the endpoint that did not have a fishpond (A3) still contained 100% non-pest snails due to the absence of a fishpond (Fig. 5). It should be noted that site C1, due to its unique characteristics, is presented both in the source-springs and at the endpoints and fishponds for clear characteristic comparison, since it is both a source spring and a fishpond (see section *2. Materials and methods*).

The source springs as a whole showed lower absolute abundances of snails, with the snail community in most source springs comprising mainly non-pest snails: in the source springs, A1, B1, B3, and D1, the proportion of non-pest snails was nearly 100%. The exceptions were

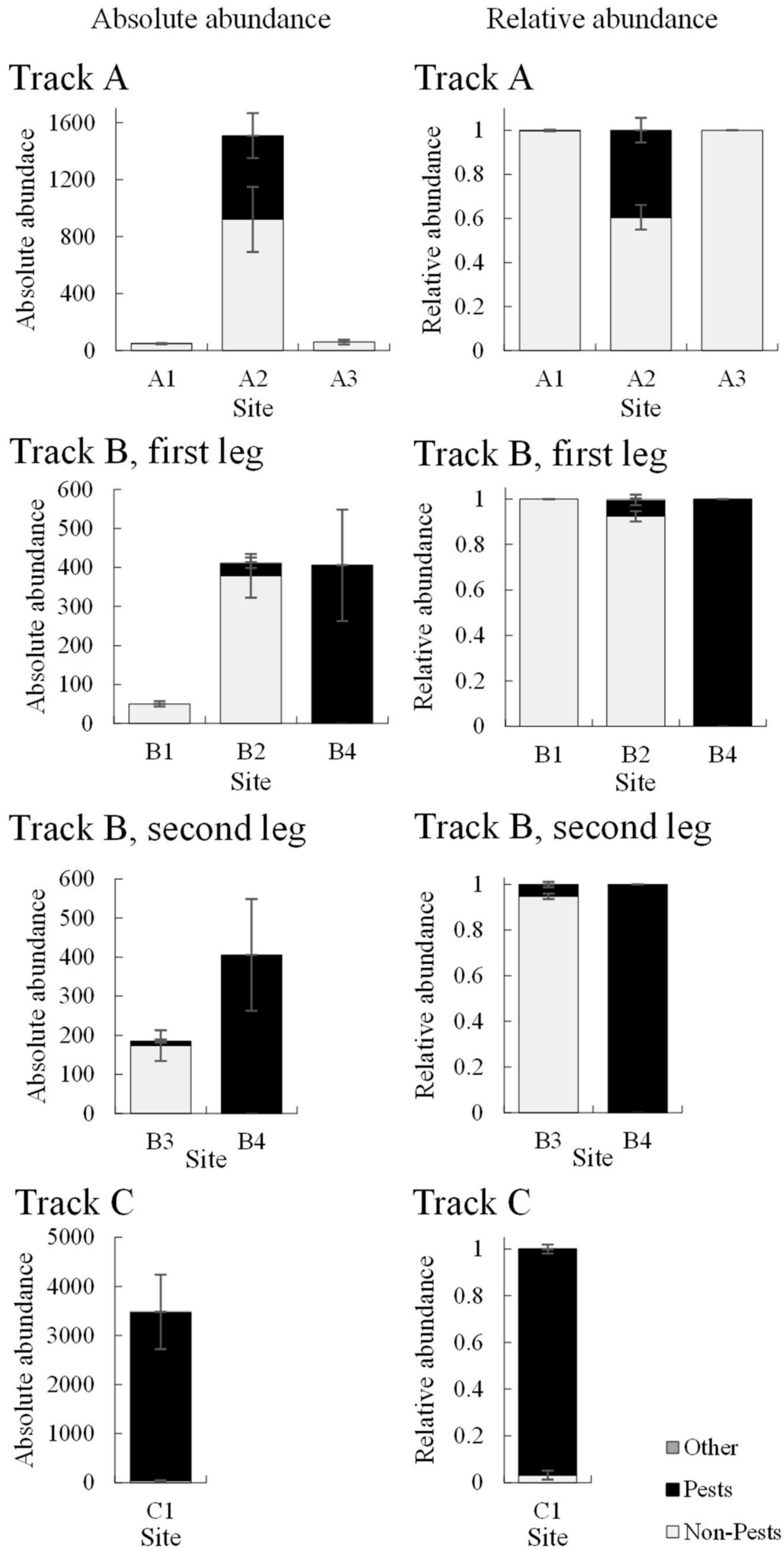

Fig. 3. Absolute and relative abundances (proportion) (mean±1SE) of snails in tracks A, B, and C segregated into pest and non-pest species. The direction of water flow is from left to right; site names are presented on the x-axis, and absolute or relative snail abundance, is on the y-axis.

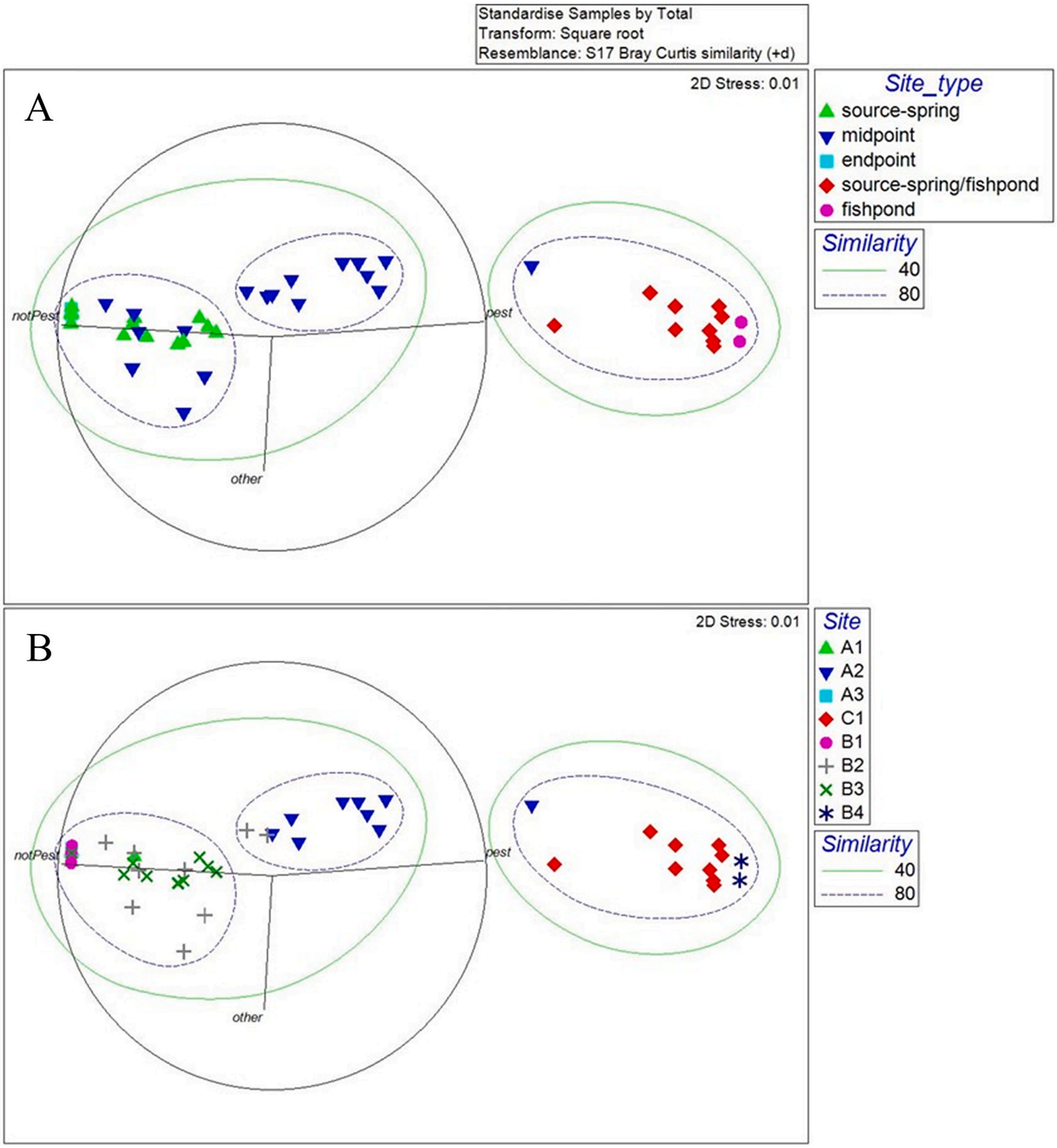

Fig. 4. Non-metric multi-dimensional scaling (nMDS) ordination based on a Bray-Curtis dissimilarity matrix illustrating the changes in the snail community composition along the source-spring-to-fishpond gradient (A, upper panel) and between the different sites (B, bottom panel). Pearson correlation vectors are presented for all snail species (threshold> 0.5). Circles represent resemblance levels of 40% and 80%. Note that site type "endpoint" is site A3, which is an endpoint that is not a fishpond.

sites C1 and E1. Site C1, which is also a fishpond, had the greatest absolute snail abundance among the source springs, which averaged nearly 3500 snails per 0.25 m^2, and a composition of nearly 97% pest snails. Site E1 contained nearly 69% pest snails on average.

In all fishpond endpoints or in tracks ending with a fishpond, the snail community comprised nearly 100% pest species. In addition, the average absolute abundance of the snails in the fishponds was between 2- and 100-fold greater than that in the source springs when comparing each source spring to its corresponding fishpond.

4. Discussion

Most agricultural lands are integrated into and interact with natural areas, which can cause agriculture-related problems to spill over into the adjacent natural environments; such problems may include the presence of invaders and parasites alongside deteriorating land and water quality (Bellamy and Ioris, 2017; Frankic and Hershner, 2003; Ong and Liao, 2020). This scenario is also true for unsustainable aquaculture (Cao et al., 2007; Frankic and Hershner, 2003), as evident in the case of our study area. Research on spatially heterogenous agroecological systems can shed light on mechanisms that can be leveraged for the protection of local biodiversity in natural patches and for designing preventative and managerial measures to contain and counter these adverse effects (Genovesi, 2007; Saunders et al., 1991) as well as potentially increase agricultural yields (Garbach et al., 2017). Application of agroecological approaches in aquaculture [adapted from (Dumont et al., 2013)] has similarly been discussed (Cao et al., 2007; Diana, 2009; Dumont et al., 2013; HLPE, 2014; Pant et al., 2004). Against this background, the present study focuses on the impact of disease-vector and drainage-clogging snails in the spatially structured agroecological

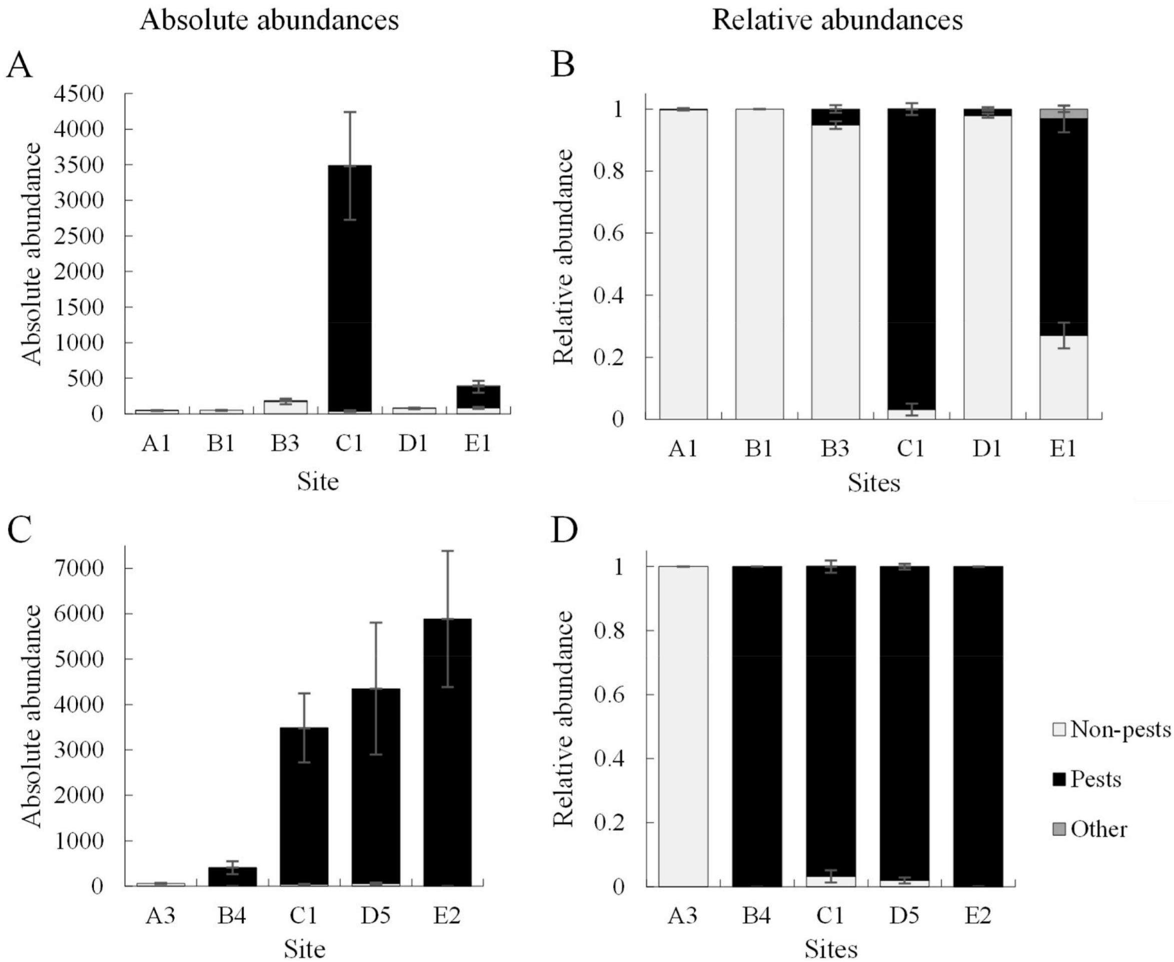

Fig. 5. Absolute (A) and relative (B) abundances (mean±1SE) of snails for all the sources (top subfigures) of the five tracks and for all the endpoints/fishponds of the five tracks (C, D, respectively, bottom subfigures).

system of Emek HaMa'ayanot. The approach taken here is in concert with that of Saunders et al. (1991), who suggested that large landscapes – such as Emek HaMa'ayanot – should be managed according to the internal dynamics of the local species, i.e., in our case, the composition and interactions of the snail species in the area. According to this approach, understanding the snail dynamics in the local water systems such as Emek HaMa'ayanot and elsewhere in the world would be the first milestone in delineating an environmental managerial agroecological approach to managing the inland freshwater fishponds while considering both the farmed fish industry and local biodiversity.

Many variables can impact the species composition of snails, such as water turbidity and flow rate, sediment type, water quality, predator abundance, etc. Following the complaints of the farmers and previous work in the area (see *Introduction*, section 1.1) that the snails are a problem in the fish farms, we assumed that if the farmed fish were good predators of snails, then perhaps the problem of snails and snail-borne diseases would not have been as prominent – thus we did not factor predation in the fishponds. Turning to natural areas, there are low densities, if any, of small fish (personal observations), such as loaches and small carps (*Acanthobrama*); however, their main diet is zooplankton, insect larvae, and Amphipoda. Thus, we assumed that predation in the natural areas can be abstracted. In this study, our scope focused on water quality and biological burden indicators, NO_2^- and NH_4^+, as a correlator for snail abundance, as snails are highly affected by water quality (Elder and Collins, 1991) and serve as water quality bioindicators (generalized from Baroudi et al., 2020).

Other than some seasonal variation in the snail composition between the sites, the main factors significantly affecting snail community composition along all the waterways monitored in this study were the particular characteristics of the site. The results were reproducible for all the fishpond-related tracks, suggesting a possibly universal trend in the aquacultural-agroecological systems: pest snails dominate the fishponds and some upstream sites. In contrast, where there is no aquaculture industry activity, non-pest snails remain dominant throughout the entire waterway. These results validate our hypotheses and agree with similar studies of land-use matrices showing the negative influences of species spillovers from anthropogenically influenced and agricultural areas into natural areas, as discussed in previous work (Blitzer et al., 2012; Rand et al., 2006; Rotem et al., 2014).

Both nitrite and ammonium varied along the waterways, being higher at the endpoints than at the source springs. In tracks B, C, and E, the endpoints had higher NO_2^- and NH_4^+ levels, associated with lower water quality and greater toxicity – as expected in aquacultural areas and their effluents in other parts of the world (Devi et al., 2017; Schenone et al., 2011). In contrast, in tracks A and D there were relatively low levels of NO_2^- and NH_4^+ all along the tracks, from the source to the endpoint. Since track D ends at a pumping station, it is possible that the similarity in values between the endpoint and intermediate sites of the track could stem from the distance to the closest fishpond (several kilometers downstream from the pumping station). In the sources water quality was better, showing lower NO_2^- and NH_4^+ levels than further downstream, indicating that the water quality was generally good with a low biological burden.

In terms of snail abundance and composition, sources exhibited similar characteristics for both. All sources (except for the source that is also a fishpond, site C1, and the man-made source in the nature reserve, site E1, which will be discussed in greater detail below) were similarly dominated by relatively low abundances of non-pest snails.

Contrary to the sources, the endpoints and the fishponds (except for the reference track endpoint, for which there was no fishpond interference) were dominated by pest species, mainly Thiaridae snails. This finding is no surprise and agrees with other studies of Thiaridae species associated with anthropogenically disturbed areas and for water bodies with a high biological burden, e.g., in irrigation and drainage canals or aquacultural areas in the Middle East (Al-Akel and Suliman, 2012; Simon and Ben-Ami, 2014), in anthropogenically or agriculturally disturbed areas in Australia and Africa (Glaubrecht et al., 2009; Makherana et al., 2022), and in Caribbean and African areas with decreasing water quality (Facon and David, 2006; Oloyede et al., 2017). Overall, all the endpoints of the fishpond-related tracks were composed of nearly 100% pest snails, and snail abundances were much higher than those in their upstream sites. It is clear that the fishponds are dominated by invasive species that could be a threat to local biodiversity and the integrity of the local food web if they are transported or moved out of the fish farms.

The most striking result of this study was the complete absence of pest species at the end of the reference track (site A3), supporting our hypothesis that the composition of the snail population is dictated by the presence of a fish farm, since there was a full recovery of the local, non-pest species at the end of the reference track even though pest snails were found at the track's midpoint (Supplemental results section 3).

Turning to intermediate sites, generally, the snail abundances increased between the sources and the downstream sites, consistent with other findings in other locations in the world of high abundances of freshwater snails along waterways (Facon and David, 2006). The relatively high abundances of invasive snails at intermediate sites along the tracks, together with consistent differences in snail composition between the sources and intermediate sites as well as between the intermediate sites and endpoints, support our central hypothesis. At the intermediate sites, the combinations of non-pest and pest species, as well as the increasing abundance, indicate a possible upstream invasion of species from the fishponds towards the sources. Such upstream invasion possibility agrees with previous studies describing the upstream invasion of pest snail species (Facon and David, 2006; Pointier et al., 1998; Quintana et al., 2001) and indicates that this invasion is ongoing.

There were differences in snail species compositions at the different intermediate sites, with one (B2) being more similar to the composition at the source, while others (D2 and D4) were more similar to the composition at the endpoint. The dissimilarity in snail species composition between B2 and that of the endpoint indicates that the effect of the fishpond had not yet reached that intermediate point, probably due to the underground pumping that is assumed to make upstream movement more difficult (see section 2.1, *Waterways*). Unlike B2, the location of the intermediate points D2 and D3 at the entrance and exit of a reservoir that is sometimes populated with fish further strengthens the conclusion that the fishpond characteristics impact the snail species composition, even though the location was not considered a fishpond in this study. The high abundance of invasive species at sites close to regularly populated fish farms further strengthens this conclusion.

One of the most convincing results supporting our hypothesis is that for the midpoint of the reference track without a fishpond, showing that even with the presence of pest snails in high proportion and abundance at the midpoint, the snail composition at the endpoint was similar to that at the source — and to that at other sources. A possible explanation to the disturbance phenomena in the reference track midpoint is that the site is likely a highly disrupted spot since it is located between two popular tourist locations (see section 2 *Materials and methods* and table S1.1). It is probably a site where there are accidental introductions of invasive species from sandals and water sports equipment due to "recreational trench swimming" (Fig. 6) of people who 'hop' between the trenches in the Valley. This difference between the snail composition in the endpoint of the reference track, even with the intermediate site disturbance, compared to the other endpoints, further emphasizes the upstream effect of fishpond presence or absence on the local snail species and strengthens our hypothesis.

Returning to the two odd sites, C1 and E1, the site for which the source had fishpond characteristics both biotically and abiotically (C1) showed a consistently higher resemblance to endpoints rather than sources. Under the working assumption that undisturbed springs would have similar snail communities, we can assume that prior to the stocking of this site, the snail community was similar to that in other sources and springs in the region (generalized from Amundsen et al., 2013). Unfortunately, there is no information about the snail community of site C1 prior to its being stocked with fish. We thus assume that the current community followed the change in water quality caused by the fish stocking, which also created an opportunity for the accidental introductions of invasive species, comprising the now evident snail community in the source spring used as a fishpond. These findings imply a strong effect of the fish stocking – as an anthropogenic agricultural disturbance – on the endpoints and their surroundings, which is in accord with literature describing the negative impacts of anthropogenic disturbances, i.e., high detritus, low water quality, and disturbed local ecosystems, as discussed in (Cao et al., 2007; Facon and David, 2006; Jones et al., 2017; Tolley-Jordan and Chadwick, 2019), as well as in the literature describing higher abundances of pest species in aquacultural environments (Leventer, 1981; Simon and Ben-Ami, 2014). The results support our hypothesis that fish stocking has a stronger effect on the snail composition than the characteristics of the sources.

The second odd site, located in the man-made nature reserve (E1) shows further evidence of the effect of the fish farms on the snail composition. E1 has higher proportions of invasive pest snails, despite the good water quality. The abundances of invasive pest species in the man-made source are higher than those in the other sources. This finding implies that the invasive pest species is already establishing itself in the man-made nature reserve, as has happened in other disturbed sites in northern Israel (Heller et al., 2014). The site was most probably disturbed when it was initially dug, and it can be assumed that the site was contaminated either by an accidental introduction of pest snails during its construction via contaminated equipment or footwear (Cianfanelli et al., 2007) or by upstream invasion from the connected fish farm (Leibowitz et al., 2019; Quintana et al., 2001). The site downstream from the man-made nature reserve, the fish-farm trench E2, has high abundances of pest snails, which implies that there was no recovery in the track and that the local non-pest species were unable to reclaim the upstream area. This contrasted with the reference track, which showed recovery of the local non-pest community downstream from the disturbed site.

Altogether, these findings further strengthen the conclusion that the fish industry has an upstream effect on the snail community

Fig. 6. Local residents playing in the trenches of sites A3 (left) and D5 (right).

composition. It is, therefore, likely that further anthropogenic activities will disturb and skew the composition of the local snail community [(Genovesi, 2007), *conservation challenges* in (Lysne et al., 2008)] in the direction of higher abundances of invasive or pest species.

According to the results of this natural experiment, if a disturbance occurs upstream from another pest-dominated site, such as a site upstream from a contaminated fishpond, the site is not expected to recover its local non-pest species after the disturbance. Indeed, these finding from Emek Hama'ayanot, a unique study area, might be generalized to the wide-spread use of freshwater systems for aquaculture around the world, such as in Africa (Makherana et al., 2022; Oloyede et al., 2017; Sokolow et al., 2015), and could be expanded to a universal pattern.

The results of the present study also have ecological implications regarding the possible dynamics between the snail species (Supplemental information section 3). Furthermore, suppose the invasive and pest snails reach the springs. In that case, their abundances are predicted to grow, as derived from previous studies that monitored these species' colonization abilities in the Caribbean and North America (Facon and David, 2006; Tolley-Jordan and Owen, 2008). Preventative measures against the continued invasion of pest snails in the Valley and other areas, alongside eradication and biocontrol, are essential for 1) maintaining local biodiversity, 2) preventing the exclusion of local non-pest snails, and 3) the integrity and sustainability of local food webs in the springs, as suggested in the literature (Genovesi, 2007; Keesing et al., 2010; Lysne et al., 2008) and, particularly, in the literature discussing spillover from agricultural to natural areas (Rand et al., 2006). It can be concluded that fish farming in the study area generally has ecological implications for the sites closer to the sources, and that its effects are not limited solely to the farmed area. Support for these ideas may be derived from other studies of the negative ecological impacts of agriculture and tourism, which fragment the natural area (de Silva, 2012; Kareiva et al., 2007; Saunders et al., 1991), support the spread of invasive species and diseases, and alter local ecosystems (Cianfanelli et al., 2007; Genovesi, 2007; Nobile et al., 2020; Simon and Ben-Ami, 2014). Our natural experiment thus indicates that management of sources, or natural springs, that are connected to fish farms is critical and that protection of natural areas should be implemented not only in the vicinity of the source [which has already been invaded, see track E and (Cohen et al., 2020)], but also further downstream not just in the Valley, but possibly also in similarly structured freshwater regions worldwide.

Future studies should focus on studying the resilience of local non-pest snail species to anthropogenic disturbances and to small-scale snail invasions. There is also a need to study appropriate biocontrol agents and the application of biocontrol in the waterways leading from sources to fishponds to eradicate invasive pest species and to better control outbreak overabundant species before they invade springs and nature conservation sites as part of environmental managerial decisions. In addition, a broader regional approach is recommended in which connective waterways within and between active aquaculture industry areas should be studied to examine the effectiveness of snail biocontrol on a larger scale, and in a global perspective regarding snail and snail-borne human disease-struck areas.

5. Conclusions

The aquaculture industry impacts the snail community composition upstream from the fishponds, and the effect of the fish stocking is not limited solely to the farmed area. There is a crucial need for environmental management in the form of snail biocontrol to make the aquaculture industry more sustainable and reduce the upstream effect of aquaculture. Moreover, snail biocontrol is a win-win strategy for the fish farming industry because snails are the primary disease vector of farmed fish. To date, biocontrol efforts and solutions have been successful in the lab and within individual fishponds (Ben-Ami and Heller, 2001; Savaya et al., 2020; Sokolow et al., 2015), but our results imply that snail control in the fishponds alone might not be enough to eradicate the entire pest snail community, owing to the implied upstream invasion that could feed back into the fishponds. Hence, regional biocontrol efforts may be necessary for the waterways leading to the fishponds, where adult snails can remain and reproduce after their initial population has stabilized and from where the juveniles could be dispersed to the fish farms. This pattern could be significant for other aquacultural regions around the world, such as in Africa (Makherana et al., 2022; Oloyede et al., 2017; Sokolow et al., 2015).

The study could also have managerial implications for treating other similarly integrated aquacultural areas, including areas suffering from snail-borne fish diseases (Leibowitz et al., 2019; Pinto and Melo, 2012; Pinto et al., 2014; Tolley-Jordan and Chadwick, 2019) or human diseases, such as schistosomiasis, in which snails are an intermediate host for the disease-causing helminth (Ciddio et al., 2017; Garchitorena et al., 2017; Ozretich et al., 2022; Prichard et al., 2012; Sokolow et al., 2015; Stothard et al., 2017). Future studies of the snail community and metapopulation dynamics in the connective trenches within fish farms are required to investigate systematically whether biocontrol treatment of the individual pond is sufficient or whether trenches and waterways should be treated as well.

CRediT

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Data availability

Our data is available in the following link, published in Medeley Data.

Freshwater snail community composition in representative waterways in Emek HaMa'ayanot, Israel, summer 2020 (Original data) (Mendeley Data)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.119653.

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