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Habitat and Climate Constraints on the Southern Distribution of *Salamandra infraimmaculata*

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Abstract

The fire salamander (*Salamandra infraimmaculata*) is a prominent urodele amphibian inhabiting the Mediterranean region of northern Israel. Like other salamandrids, this species requires two distinct habitat types to complete its life cycle: aquatic habitats for larval development and terrestrial habitats for juvenile and adult stages. While the availability of aquatic breeding sites has traditionally been considered a major factor influencing salamander distribution, the northern Israeli landscape presents a unique opportunity to test this assumption. Across northern Israel—from Mount Hermon and the Golan Heights through Upper and Central Galilee to the Carmel range—*S. infraimmaculata* occupies a wide array of aquatic breeding habitats, including perennial streams, seasonal winter ponds, and artificial stone-lined water pits. However, the species' distribution terminates sharply south of the Carmel region, despite the continued presence of similar aquatic habitats further south. This review synthesizes published ecological, climatic, and biogeographical studies to evaluate the factors limiting the southern distribution of *S. infraimmaculata*. We conclude that terrestrial climatic conditions—particularly reduced precipitation, increased aridity, and prolonged dry seasons—constitute the primary limiting factor, rather than the availability or type of aquatic breeding sites.

Keywords

Salamandra infraimmaculata, Aquatic and Terrestrial Habitats, Distribution

1. Introduction

Amphibians are widely recognized as sensitive indicators of environmental conditions due to their biphasic life cycles, permeable skin, and dependence on both aquatic and terrestrial habitats [1] [2]. Salamanders of the genus *Salamandra* are particularly dependent on stable terrestrial microhabitats with high humidity, moderate temperatures, and sufficient shelter, in addition to suitable aquatic sites for larval development.

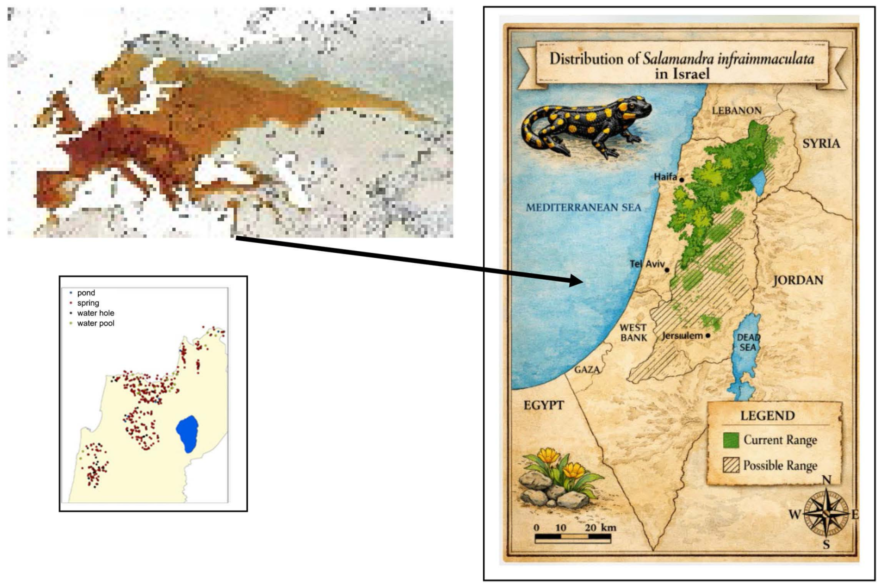


Figure 1. Map showing aquatic habitats that may serve as breeding sites for *Salamandra infraimmaculata*, based on official maps issued by the Government of Israel between 1941 and 2018, covering the known distribution range of the species in Israel. Winter reservoirs are indicated in blue, springs and streams in red, water holes in black, and winter pools in yellow. The dataset of water bodies used to identify potential breeding sites was obtained from the Tel-Hai Map Archive [3].

In Israel, *Salamandra infraimmaculata* represents the southernmost distribution of the genus globally [4]-[6]. Its distribution spans a pronounced climatic gradient, from humid Mediterranean and montane environments in the north to semi-arid regions toward the south (**Figure 1**).

Distribution of the fire salamander (*Salamandra infraimmaculata*) in Israel. The species is restricted to the Mediterranean climatic zone of northern Israel, occurring from Mount Hermon and the Golan Heights, through the Upper and Central Galilee, and reaching its southern distribution limit in the Carmel Mountains. Despite the presence of suitable aquatic breeding habitats (perennial streams, seasonal winter ponds, and artificial stone-lined water pits) further south, *S. infraimmaculata* is absent from regions beyond the Carmel, indicating that terrestrial climatic conditions, rather than aquatic habitat availability, constrain its southward distribution [6]. Key Geographic Units shown in Israel are: Mount Hermon, northernmost and highest-elevation populations, Golan Heights, montane Mediterranean habitats, Upper Galilee, core distribution area, Central Galilee, fragmented but stable populations, Carmel Mountains, southern range boundary [6].

2. Life Cycle Requirements: Dual Habitat Dependency

Below is a clear, detailed, stage-by-stage life-cycle diagram description of *Salamandra infraimmaculata* in Israel, adapted exactly to Israeli conditions (Mediterranean climate, winter breeding, ovoviviparity).

I present it as if it were a scientific figure legend + schematic explanation, so you can directly use it for a paper, proposal, or illustration brief (**Figure 2**).

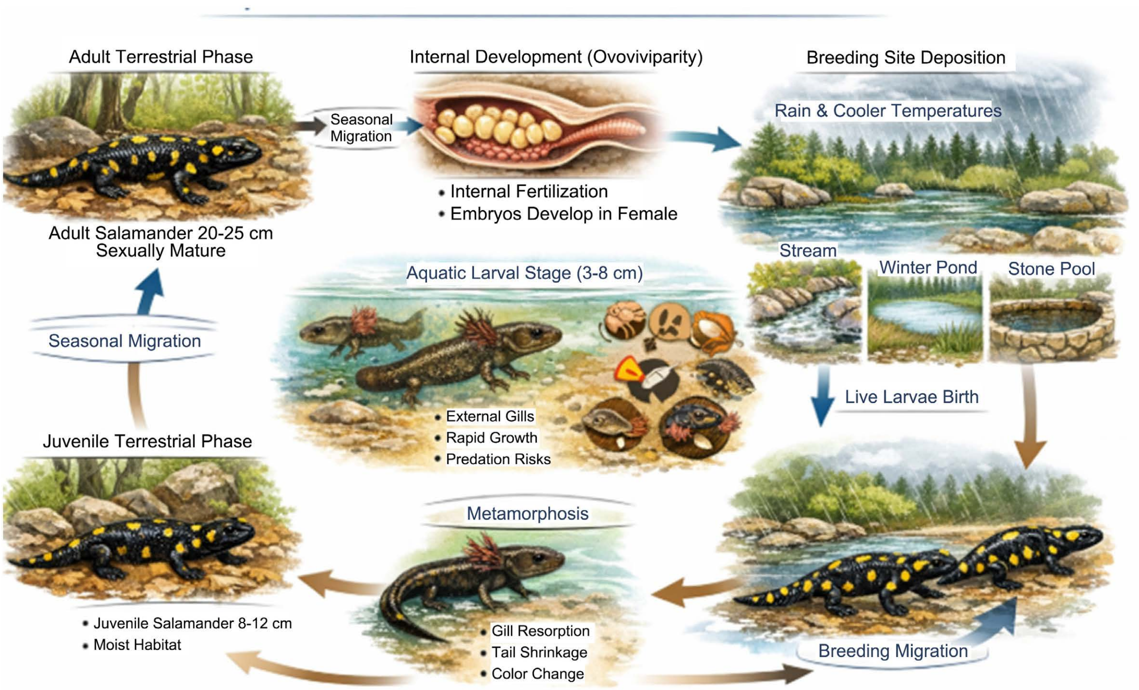


Figure 2. Life cycle in Mediterranean habitats in Israel [6]-[8].

Life cycle of *Salamandra infraimmaculata* in Mediterranean habitats of Israel [7] (**Figure 2**). Adult salamanders inhabit terrestrial Mediterranean woodlands and exhibit strong site fidelity. During late autumn and winter, adults migrate to aquatic breeding sites in response to rainfall, decreasing temperatures, and high humidity. Reproduction is ovoviviparous: fertilization is internal, embryos develop within the female oviducts, and eggs hatch internally. Females deposit live, fully developed aquatic larvae (3 - 8 cm total length) [8] into a range of water bodies, including permanent streams, seasonal winter ponds, and stone-structured or man-made pits [6]. Larvae are immediately active swimmers, possessing external gills, a laterally compressed tail, and well-developed limbs [6]. The aquatic larval phase lasts several weeks to months, depending on hydroperiod stability, and is characterized by rapid somatic growth and active predation on aquatic invertebrates, but also by high mortality risks due to pond desiccation, predation, and cannibalism. Juveniles (8 - 12 cm) leave the water and adopt a terrestrial, nocturnal, and moisture-dependent lifestyle. Growth to sexual maturity (20 - 25 cm) occurs over several years, after which adults re-enter the seasonal breeding migration, completing the life cycle (**Table 1**). Warburg described the larval developmental processes of *Salamandra infraimmaculata* in the Carmel region of Israel and reported on the breeding dynamics of edge populations [9]. In Israel, information on the lifespan and longevity of *Salamandra infraimmaculata* under natural conditions is limited. One of the most comprehensive studies was conducted by Prof. M. R. Warburg on Mount Carmel. In this long-term study, a population of *S. infraimmaculata* was monitored over 25 consecutive breeding seasons. Many individual salamanders were recaptured repeatedly at the same breeding site—near or within the ponds where metamorphosis occurs. Some males were recaptured up to 40 times over the years. Several individuals returned to the breeding site for many consecutive years, with maximum recorded durations of 17 years for females and 19 years for males. Because *S. infraimmaculata* visits breeding ponds only after reaching sexual maturity, which occurs at approximately 3 - 4 years of age, the minimum age of individuals could be reliably estimated. Based on these observations, the estimated longevity under natural conditions was approximately 22 - 23 years in males and 20 - 21 years in females. The study also discusses the different methods used to estimate longevity in amphibians and provides a partial overview of lifespan records in urodele species [10].

Table 1. Approximate duration of the different life-cycle phases of the fire salamander (*Salamandra infraimmaculata*) across different aquatic and terrestrial habitats in northern Israel, based on published studies [6] [7].

0 - 1 year post-metamorphosis	8 - 10 cm (young juveniles; highest mortality; strict moisture dependence).
1 - 2 years	10 - 13 cm (juveniles; nocturnal terrestrial feeding).
2 - 3 years	13 - 16 cm (late juveniles/subadults; increasing site fidelity).
3 - 4 years	16 - 19 cm (subadults; gonadal development begins).
4 - 6 years	20 - 25 cm (sexually mature adults; participate in breeding migrations).

The life cycle of *S. infraimmaculata* is obligatorily biphasic. Adult and juvenile salamanders after metamorphosis are predominantly terrestrial, inhabiting moist forested environments, dense shrublands, and rocky karst landscapes. Reproduction, however, depends on aquatic habitats in which females deposit fully developed larvae rather than eggs. In northern Israel, although various aquatic habitats used by fire salamander larvae have been extensively described, these breeding environments can generally be grouped into three main categories: winter ponds, rock pools, and permanent flowing streams, as illustrated in **Figure 2**.

2.1. Aquatic Habitat Requirements

Larvae develop in a wide range of water bodies, including perennial streams (e.g., the Dan Stream), seasonal winter ponds (e.g., Kibbutz Sasa), and artificial stone-lined water pits and reservoirs. Larval development can occur successfully in both permanent and temporary waters, provided that the hydroperiod is sufficiently long to allow metamorphosis.

All aquatic habitat types described in **Figure 2**—including water holes (stone pits), seasonal winter ponds, reservoirs, and permanent flowing streams—were recorded throughout the entire distribution range of *Salamandra infraimmaculata* in northern Israel [6] [7]. These habitat types occur consistently across all regions where the species is present (**Figure 3**).

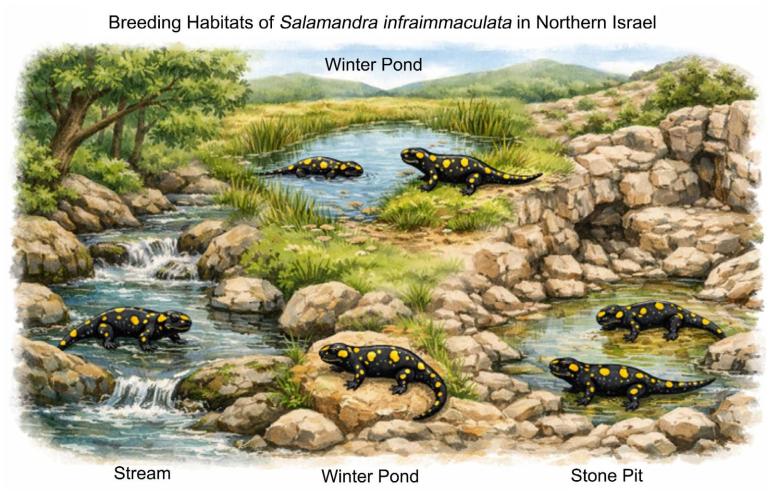
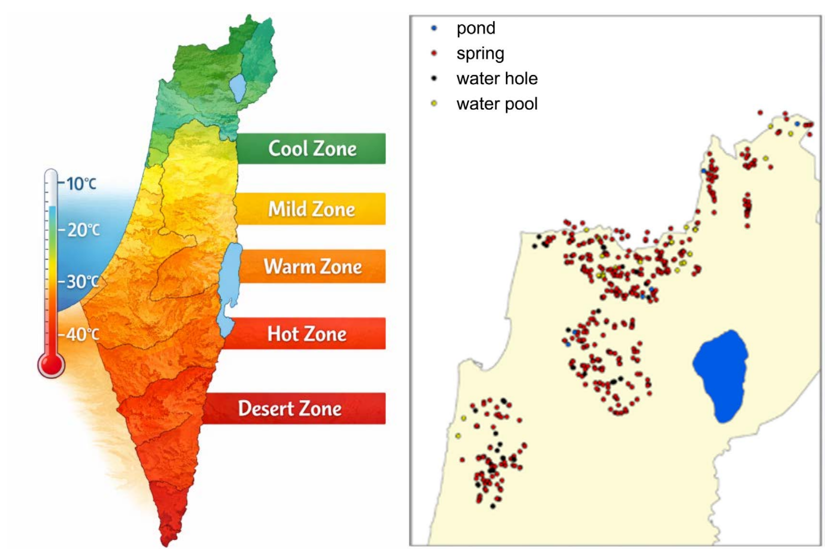


Figure 3. Based on numerous studies examining the breeding habitats of the fire salamander, we propose that larval development of *Salamandra infraimmaculata* in northern Israel occurs predominantly in three principal types of aquatic environments. These include 1) temporary winter ponds, 2) small rock pools and water-filled depressions, and 3) permanent flowing streams. This classification synthesizes extensive field observations and published ecological studies and provides a unifying framework for understanding variation in larval growth, survival, and life-history strategies across the species' Mediterranean range in northern Israel. [2] [3] [6] [7] [9] [11]-[36].



(a) (b)

Figure 4. Illustrates the north-to-south temperature gradient across Israel, highlighting distinct climatic zones that broadly correspond to latitude, topography, and aridity.

Therefore, it can be concluded that the type of aquatic water body does not constitute a limiting factor for the geographic distribution of *Salamandra infraimmaculata*. Importantly, the same categories of aquatic habitats are also widespread outside the known distribution range of the species, indicating that additional ecological or climatic factors, rather than the availability or type of aquatic breeding sites, are likely responsible for constraining its southern distribution limits (**Figure 4**).

Figure 4(a) From north to south, the zones are:

1) Cool Zone (green)

Located in the Upper Galilee, Mount Hermon, and northern Golan Heights, this zone is characterized by relatively low temperatures, higher elevation, and increased precipitation.

2) Mild Zone (yellow-green)

Covers parts of the central Galilee and northern coastal plain, showing moderate temperatures with seasonal variation.

3) Warm Zone (yellow-orange)

Extends across the central coastal plain and inland lowlands, where temperatures are higher, especially during summer.

4) Hot Zone (orange-red)

Includes the southern coastal plain, Jordan Valley, and northern Negev, characterized by high summer temperatures and reduced rainfall.

5) Desert Zone (dark red)

Encompasses the Negev Desert and Arava Valley, representing extreme heat, very low precipitation, and arid to hyper-arid conditions.

A temperature scale on the left indicates increasing thermal intensity from approximately 10˚C in the north to over 40˚C in the south, emphasizing Israel's sharp climatic gradient over a relatively short geographic distance.

Figure 4(b) shows the breeding sites of *Salamandra infraimmaculata* [6] [23].

2.2. Water Quality and Thermal Conditions Supporting Larval Growth and Metamorphosis of *Salamandra infraimmaculata* in Northern Israel

Larval development and successful completion of metamorphosis in *Salamandra infraimmaculata* in northern Israel take place in a variety of freshwater habitats, including permanent streams, seasonal winter ponds, and stone-structured or man-made pits, all of which show strong seasonal variability in physicochemical conditions [2] [6].

Water temperature

Water temperature in breeding sites inhabited by *S. infraimmaculata* larvae typically ranges from approximately 5˚C - 10˚C during mid-winter to 20˚C - 30˚C in late spring, reflecting seasonal climatic warming and declining water levels toward the end of the hydroperiod.

Larval growth and development are optimal at cool to moderate temperatures (approximately 10˚C - 20˚C), whereas prolonged exposure to temperatures below ~6˚C or above ~23˚C - 25˚C may impair growth, development, and survival [37].

Duration of the larval period

In northern Israel, the aquatic larval stage of *Salamandra infraimmaculata* generally lasts about 3 - 4 months in temporary winter ponds, whereas in permanent streams and springs it may extend up to 8 months or more, including in stone pits or caves. After completing metamorphosis, juveniles migrate to terrestrial habitats; however, the timing of metamorphosis varies depending on water permanence and the local temperature regime [14].

Dissolved oxygen

Dissolved oxygen concentrations differ markedly among habitat types. Permanent streams usually maintain high and relatively stable oxygen levels, whereas winter ponds and stone pits frequently experience large temporal fluctuations and periodic hypoxia, especially toward the end of the hydroperiod [31].

Larvae of *S. infraimmaculata* exhibit pronounced phenotypic plasticity in gill size and morphology in response to oxygen availability, allowing development under reduced oxygen conditions typical of stagnant or shrinking water bodies [38].

pH and conductivity

Breeding sites occupied by *S. infraimmaculata* larvae in northern Israel typically show a pH range of approximately 6.5 - 10, reflecting variation in geological substrate, soil composition, and evaporation intensity.

Electrical conductivity in these freshwater habitats usually ranges from ~150 to 800 $\mu S \cdot cm^{-1}$, with values often increasing toward late spring as water volume decreases and solute concentrations rise [14].

Nitrogenous compounds

Measurements from winter ponds and other breeding sites in northern Israel indicate that concentrations of ammonium ($\mathbf{NH_4^+}$) and nitrite ($\mathbf{NO_2^-}$) are generally low during larval development (typically $\mathbf{NH_4^+} < 1\ mg \cdot L^{-1}$ and $\mathbf{NO_2^-} < 0.25\ mg \cdot L^{-1}$), conditions compatible with normal larval growth and successful metamorphosis [14].

Ecological interpretation

Overall, these findings indicate that *S. infraimmaculata* larvae in northern Israel are adapted to cool, freshwater systems with moderate to high oxygen availability and low levels of nitrogenous pollution, and that successful metamorphosis is most likely under spring water temperatures of approximately 10˚C - 20˚C combined with sufficient dissolved oxygen [38]. Rapid warming and declining oxygen levels toward the end of the hydroperiod represent major ecological constraints, particularly in shallow winter ponds and stone-structured pits [14].

3. Description of the Terrestrial Habitat of the Post-Metamorphosed Salamander

After metamorphosis, both juvenile and adult *Salamandra infraimmaculata* inhabit terrestrial environments characterized by diverse Mediterranean vegetation or exposed rocky areas that provide numerous shelters. These habitats offer essential refuges that enable the species in northern Israel to survive the hot and dry summer months, as well as the winter season, which may occasionally be cold and even covered with snow at higher elevations.

This terrestrial habitat occurs within a Mediterranean climate, where summers are dry and rainfall is absent, although relative humidity may remain locally high, particularly at night. Seasonal patterns of activity in these habitats have been described extensively, with salamander activity occurring mainly during periods of high humidity and following rainfall events.

The Mediterranean forest habitat illustrated in **Figure 5** is characterized by a closed canopy with dense vegetation, providing high levels of shade and relatively stable humidity. Such conditions protect salamanders from desiccation and temperature extremes and constitute the primary terrestrial habitat for most of the year. Activity in this habitat is predominantly nocturnal, especially after rainfall [6].

Figure 5 illustrates the characteristic Mediterranean forest habitats occupied by juvenile and adult *Salamandra infraimmaculata* after metamorphosis. The images show a mosaic of forest structures ranging from dense, closed-canopy woodland to more open stands depict more open Mediterranean woodland and rocky habitats, where trees are spaced farther apart and sunlight reaches the ground. Despite lower canopy cover, these with scattered trees, rocky substrates, and shallow soils typical of northern Israel.

In the upper images, the forest is dominated by a closed canopy formed mainly by evergreen and semi-deciduous Mediterranean trees (e.g., oaks and pines). This canopy creates deep shade, reduces temperature fluctuations, and maintains relatively stable humidity near the forest floor. The ground layer consists of leaf litter, stones, fallen branches, and crevices, providing abundant shelters that protect salamanders from desiccation during the hot, dry summer months and from low temperatures during winter, which at higher elevations may include frost or occasional snow cover [6].

The lower images also show habitats that still offer suitable refuges in the form of rock piles, soil cracks, and vegetation cover. Such microhabitats allow salamanders to retreat during daytime and unfavorable conditions, while enabling nocturnal surface activity when humidity is high.

Across all habitats shown in **Figure 5**, the Mediterranean climate is characterized by dry summers without rainfall and mild to cool, wet winters. Salamander activity in these terrestrial environments is mainly nocturnal and strongly associated with periods of high humidity and rainfall. Together, the habitats depicted emphasize the importance of structural complexity, shade, and shelter availability in sustaining *S. infraimmaculata* populations throughout most of the year in northern Israel [6].

Mediterranean Forest

- Closed canopy forest with high shade and stable humidity;
- Provides protection from desiccation and temperature extremes;
- Main terrestrial habitat during most of the year;
- Activity mainly nocturnal, especially after rainfall.

Figure 5. Habitat diversity of *Salamandra infraimmaculata* in northern Israel. Mediterranean forest habitats are characterized by dense vegetation, high canopy cover, stable humidity, and abundant shelters.

Geographic coordinates (WGS84) of freshwater streams, winter pools, rock pools, and reservoirs in southern Israel that may potentially maintain water temperatures below 20˚C for at least three consecutive winter months.

Figure 6. Freshwater Water Bodies, Southern Israel.

(*sites with potential* <20˚C *for* ≥3 *consecutive winter months*)

1) Nahal Yatir

- **Latitude:** 31.356˚N
- **Longitude:** 35.015˚E

2) Nahal Anim

- **Latitude:** 31.347˚N
- **Longitude:** 35.075˚E

3) Upper Nahal Dimona

- **Latitude:** 31.060˚N
- **Longitude:** 35.030˚E

4) Yatir Winter Pools

- **Latitude:** 31.335˚N
- **Longitude:** 35.040˚E

5) Lehavim East Winter Pools

- **Latitude:** 31.360˚N
- **Longitude:** 34.805˚E

6) Gabei Yatir

- **Latitude:** 31.330˚N
- **Longitude:** 35.060˚E

7) Gabei Nahal Amsha

- **Latitude:** 31.220˚N
- **Longitude:** 35.095˚E

8) Yatir Reservoir

- **Latitude:** 31.315˚N
- **Longitude:** 35.010˚E

9) South Hebron Hills Reservoir

- **Latitude:** 31.190˚N
- **Longitude:** 35.030˚E

Based on an extensive review of the scientific literature, numerous freshwater habitats in central and northern Israel have been identified in which the environmental conditions are suitable for the successful completion of larval development and metamorphosis of *Salamandra infraimmaculata*. These habitats include permanent streams, seasonal winter ponds, rock pools, and artificial water bodies that provide adequate hydroperiod length, appropriate water temperatures, sufficient dissolved oxygen, and suitable substrate and shelter. Under these conditions, salamander larvae are able to complete their aquatic developmental phase, undergo metamorphosis, and emerge as fully transformed juveniles that subsequently disperse into surrounding terrestrial habitats, where they continue growth and maturation [6].

4. Discussion

The analysis of numerous records on the distribution of salamander larvae in freshwater habitats across central and northern Israel reveals a clear and consistent pattern. A wide variety of aquatic water bodies—including permanent streams, seasonal winter ponds, rock pools, and artificial reservoirs—exhibit physical and chemical conditions suitable for larval growth and the successful completion of metamorphosis, such as adequate hydroperiod length, appropriate winter water temperatures, and sufficient dissolved oxygen (**Figure 6**).

Despite the availability of these favorable aquatic conditions, many of the surveyed water bodies do not support salamander larvae. This discrepancy between habitat suitability and actual larval presence indicates that the availability of suitable aquatic breeding sites alone cannot fully explain the current distribution of *Salamandra infraimmaculata* in Israel (**Figure 6**).

These findings strongly support the hypothesis that the terrestrial phase of the fire salamander is subject to more severe environmental constraints than the aquatic larval phase and that these terrestrial constraints exert a stronger influence on species distribution. Adult salamanders and post-metamorphic juveniles depend on humid, shaded terrestrial habitats that provide protection from desiccation and temperature extremes—conditions that are spatially restricted in Mediterranean and semi-arid environments.

Previous studies have demonstrated that adult salamanders exhibit strong site fidelity and limited dispersal, with seasonal activity and survival closely linked to moisture availability and microclimatic stability rather than solely to the presence of suitable aquatic habitats. Consequently, even when aquatic larval habitats are suitable, the absence of high-quality terrestrial habitats in their vicinity may prevent colonization, persistence, or recolonization of breeding sites.

Similar patterns have been reported in other Mediterranean and marginal populations of salamanders, where terrestrial habitat degradation, fragmentation, and increasing aridity have been identified as key factors shaping population structure and range limits.

5. Conclusions

The present synthesis demonstrates that numerous freshwater habitats in central and northern Israel provide suitable conditions for the growth of salamander larvae and the completion of metamorphosis. However, the absence of larvae from many of these suitable aquatic habitats indicates that aquatic environmental conditions are not the primary limiting factor for the distribution of *Salamandra infraimmaculata*. Instead, environmental pressures acting on the terrestrial phase—particularly moisture limitation, habitat fragmentation, and microclimatic instability—play a dominant role in shaping population distribution. These conclusions are consistent with earlier ecological, physiological, and biogeographical studies of salamanders occurring at the southern margins of their distribution range (**Figure 7**).

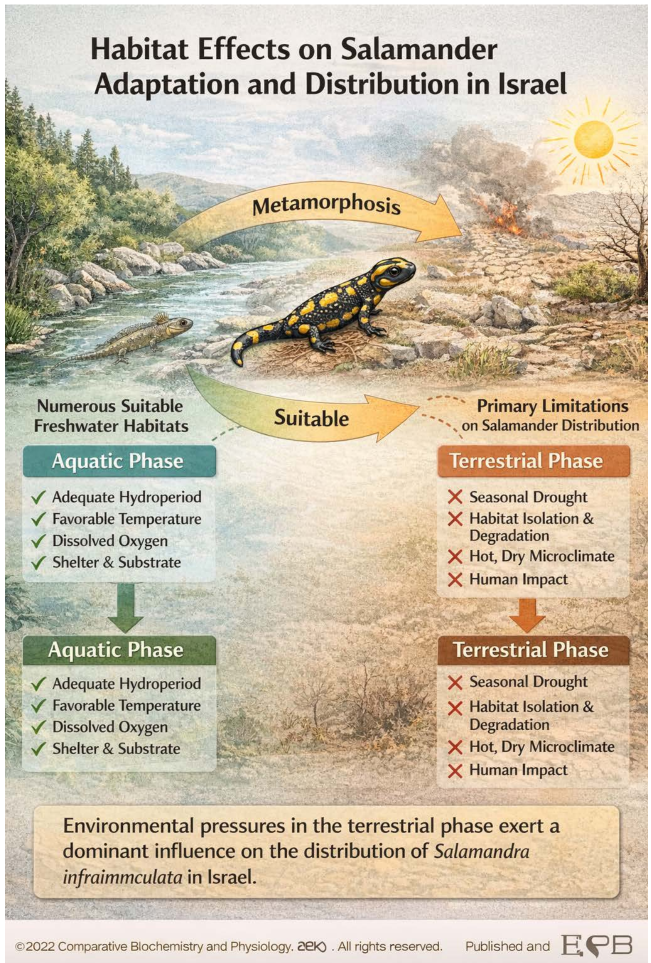


Figure 7. A conceptual model illustrating the adaptation of the Near Eastern fire salamander (*Salamandra infraimmaculata*) to Mediterranean environments in Israel. The model integrates both aquatic and terrestrial habitat components required to complete the species' life cycle. Although suitable aquatic habitats (e.g., streams, winter ponds, rock pools, and artificial water bodies) are widespread and frequently provide appropriate conditions for larval development and successful metamorphosis, the species' geographic distribution is primarily constrained by limitations acting on the terrestrial phase. In particular, reduced moisture availability, habitat fragmentation, and unstable microclimatic conditions in terrestrial habitats restrict adult survival, dispersal, and population persistence. These terrestrial constraints likely prevent the southward expansion of the species beyond northern Israel and the Carmel slopes, despite the apparent availability of suitable aquatic breeding sites.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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