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Niche Occupation and Rapid Adaptation Mechanisms of Invasive Guppies in Polluted Water Bodies

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Abstract. Freshwater ecosystems are facing a global biodiversity crisis and biological invasion crisis at the same time. The guppy (Poecilia reticulata) is one of the most invasive fish species worldwide. It can successfully live in polluted water, providing a good model for studying eco-evolutionary processes of rapid adaptation and ecological niche occupation. This paper reviews the progress of ecological niche occupation and rapid adaptation mechanisms of invasive guppies in polluted waters. Existing research shows that the guppy can have its native range from South America to almost 70 countries in the world, and it often affects native species, such as resource competition, reproductive interference and changes in ecological functions. A polluted environment is conducive to rapid adaptation of guppy with multi-level, including life-history characteristics (transformation to an r-selection strategy), sexually selected characteristics (change and microevolution of sexually selected characteristics such as ornamental colors), the molecular-level variation or response (for example, CYP1A gene selection, transcriptome changes).On the other hand, the rapid adaptation of guppies, in turn, favours their niche occupation, giving rise to a positive feedback loop of "pollution→adaptation→invasion persistence". Currently, this field still has deficiencies in the balance of geographic coverage and the degree of contributions from phenotypic plasticity and genetic adaptation. This paper suggests that future studies should strengthen the cross-regional comparison and utilize genomic methods to integrate with field ecological observations to provide a scientific basis for the governance of invasion of polluted waters.

Keywords: Invasion ecology, guppy (Poecilia reticulata), niche occupation, pollution adaptation, eco-evolutionary dynamics

1. Introduction

Global freshwater biodiversity is currently undergoing unprecedented losses, with biological invasions one of the major drivers of community change (along with chemical pollution, habitat fragmentation and overexploitation) in communities around the world [1, 2]. Unlike many alien species limited by strict environmental requirements, the guppy (Poecilia reticulata), originally introduced globally for ornamental trade and larval mosquito suppression, has founded stable reproducing populations across tropical and subtropical zones, with established records spanning more than 70 countries and regions [3]. The invasion success of this small live-bearing fish has

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attracted substantial research attention, because introduced guppy populations encounter heterogeneous selective pressures including variable predation intensity, resource availability and toxic contamination, which can reshape phenotypic traits over remarkably short timescales [1]. Water pollution represents a particularly powerful selective filter within urban and peri-urban watersheds. Contaminants modify biotic and abiotic conditions simultaneously, reducing the fitness of native species and creating vacant niche space that tolerant invaders exploit. In recent years, an accumulating body of empirical work has used guppies as study organisms to unpack how pollution shapes evolutionary trajectories when biological invasion occurs. Meanwhile, the guppy populations themselves can also drive cascading top-down effects on invaded systems: grazing pressures change algal standing stocks, predation reduces local populations of macroinvertebrates, and reproductive interference may suppress recruitment of sympatric native and alien livebearers. Yet, despite a stockpile of observations and experiments, many open questions remain about how adaptive evolution and plasticity of traits jointly lead to niche expansion under pollution stress. Existing reviews tend to treat invasion ecology and contaminant toxicology separately, and rarely entail reciprocal feedbacks between adaptation driven by pollution and niche occupation.

To combine information on global invasion records, life-history and sexual trait responses, molecular adaptive signals, and eco-evolutionary feedbacks. This paper first sets out the global invasion distribution and the life-history and sexual trait niche competitive effects of guppy. Then, it discusses adaptation at the phenotypic and genetic levels along environmental pollution gradients. It next goes on to discuss the bidirectional interaction effects between a contaminant selection and invasion persistence bidirectional interaction effects. Finally, this paper summarizes the main research limitations and calls for integrated empirical approaches to research in the future.

2. Global invasion patterns and ecological niche occupation of the guppy

2.1. Current status of guppy invasion

Human-mediated biological introductions have proliferated along with global trade and urbanization, making a significant part of contemporary global environmental change, and the guppy, a member of Poeciliidae, is a model for the study of invasions [2]. Native to northern South America and Central America, guppies have been widely distributed in tropical waters as a consequence of their popularity as ornamental fishes and perceived effectiveness at mosquito control. In continental Africa, the occurrence of guppies has been reported in 41% of sovereign countries and populations can occur not only in tropical warm freshwater habitats but also in inland water bodies in the temperate zones where thermal regimes are favourable and even in coastal waters of low salinities [3, 4]. Their relatively high tolerance to varying environmental conditions has made them one of the most geographically widely distributed tropical freshwater fishes on Earth. Human release events are often accidental or intentional, but ornamental aquarium discard is often the main introduction pathway for human outpouring into urban watersheds. Once they arrive, their live-bearing reproductive strategy, short generation times and wide diet have meant that guppy populations can readily expand in both pristine and degraded aquatic habitats. Exclusion of native species and occupation of ecological niches by the guppy.

2.2. Competitive exclusion of native species and ecological niche occupation by the guppy

When guppies colonize recipient aquatic communities, exploitative resource competition ensues because of their dietary overlap with native taxa. By monopolizing competing food and by

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occupying vacant niches, invasive guppies exert continuous negative impacts on native diversity and ecosystem function [4]. There are multiple ecological channels for these negative impacts. Guppy grazing can increase algal biomass by grazing away herbivorous invertebrates. When co-occurring with closely related livebearing fishes, heterospecific reproductive interference can ensue and lower fertilization and population recruitment success of the native taxa [5]. In addition, guppies can transmit novel parasites to a recipient community and they feed on local macroinvertebrates and larvae of local fishes, also disrupting native food webs [3]. In heavily urbanized catchments, organic pollution has the effect of increasing biomass of chironomids and other benthic invertebrates, and this increased biomass of prey resource sustains substantially larger population densities of guppies than in a nearby undisturbed reference site [6]. Collectively, pollution remodels basal resource availability, a different niche space facilitating the invasion of invasive guppy populations over less invasive, tolerant local aquatic organisms. Pollution-driven rapid adaptation: from phenotype to gene. Adaptive differentiation of life-history strategies.

3. Pollution-driven rapid adaptation: from phenotype to gene

3.1. Adaptive differentiation of life-history strategies

Organisms are inevitably faced with energy-allocation trade-offs between somatic maintenance and reproduction. Theory predicts that benign environments allow for high investment in reproduction, while stressful, contaminated environments require more energetic investment in detoxification and resistance to stress, reducing investment in reproduction [7]. Classical work on guppy life-history shows examples of trait divergence selected for by predation pressure: populations under high predation evolve larger caudal peduncles (a measure of body robustness) and have more offspring (fewer offspring of larger size). In polluted water, populations of guppies exhibit characteristic life-history shifts: the proportion of reproducing animals decreases, the male body mass becomes smaller, female fecundity increases, body size of individual offspring decreases. This battery of trait shifts represents a move towards an r-strategist life-history tactic, allowing the population to sustain recruitment under increasing mortality induced by chemical contaminant stress. Such contaminant-induced life-history divergences are not unique to guppies and have been found for several different freshwater fish taxa [8].

3.2. Pollution responses of sexually selected traits: phenotypic plasticity and microevolution of ornamentation

Other than life-history traits, sexual selection dynamics of guppies are very strongly affected by water quality. Male guppy colour ornaments are important visual courtship signals that dictate male mating success. Along pollution gradients, males develop a higher coverage and abundance of purple body ornaments with increasing levels of contaminants [9]. This pattern may result from a combination of several interacting processes. Polluted environments often contain a relaxed predation pressure because visually oriented predators are rare in turbid or contaminated waters; predation is likely to penalize conspicuous colouration, and reduced predation relaxes sexual selection for bright ornaments. Turbidity and altered colours of water in polluted environments also alter signal transmission properties of visual mating signals. Separately, EDCs can alter guppy pigment phenotypes directly. For example, environmental androgens darken female guppy body colouration, which can, in turn, change male mate evaluation and reproductive decisions [10]. These observations have illustrated that sexual ornamentation responses are a mixture of short-term

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phenotypic plasticity and cumulative microevolutionary responses in populations chronically exposed to pollution. Molecular evidence of adaptation and a genomic perspective.

3.3. Molecular evidence of adaptation and a genomic perspective

Guppy responses to polluted environments can occur at the molecular and genetic levels, and contaminants affect multiple interlinked metabolic pathways. AHR belongs to the bHLH/PAS transcription factor superfamily and is involved in cellular defence against oxidative stress. Exposure to domestic wastewater can dramatically change the hepatic transcript expression of Ahr and PXR; their activation can also modulate downstream phase I and phase II detoxification enzyme networks. With CYP1A, a well-established aquatic pollution biomarker, catalysing the oxidative biotransformation of some organic pollutants and being induced transcriptionally by sewage and crude oil pollution, in guppies living in crude-oil-polluted rivers, a 192-bp microsatellite allele of the CYP1A locus gets an extremely high frequency, whilst this specific allele is not detected in guppies of conspecifics from unpolluted upstream rivers. This striking allelic difference indicates that CYP1A is under directional selection in the polluted habitat [8]. Contaminant exposure also increases reactive oxygen species and leads to the up-regulation of antioxidant enzymes including SOD and GPX to attenuate oxidative cellular damage [11]. Experiments with other closely related poeciliid fishes have shown that copper contamination depresses muscle mRNA expression of ghr2, igf1 and igf2, leading to a slowdown of somatic growth; these regulatory pathways may be candidate mechanisms for the growth reduction that can exist across livebearers. Molecular studies have indeed identified that guppies have sizeable heritable potential to adapt to toxic waters; much less is known about costs for the associated evolutionary adaptation and cascading ecological impacts. Integrating genomic, epigenomic, evolutionary theory, and field ecology research will be needed to unpack the genetic mechanisms underlying invasion success under contaminant exposure.

4. Eco-evolutionary dynamics: interactions among invasion, pollution and adaptation

4.1. How pollution alters selective pressures and the fitness landscape

As outlined above, toxic environments force organisms to make extra investments in their detoxification and somatic maintenance and reduce population reproductive output overall, but sometimes buffer predation pressure. Many fish species switch towards an r-selected life-history strategy under environmental stress, a life-history profile favoured by contaminated waters where death is likely. A shift in water optical properties can alter visual mate signals used for mate searching by species that sense via vision, and can increase reproductive output of guppies with suitably modified mating ornamentation. In heavily polluted urban rivers, biomass of invertebrate prey, such as chironomids and other invertebrates, increases and sustains guppy population sizes several times larger than those in the undisturbed reference habitat [6]. Water pollution is one of the strongest contemporary forces reshaping fitness landscapes of aquatic species. It creates novel selective pressures such as toxin tolerance and reshapes existing selective regimes such as predation and mate choice, shifting fitness peaks and enhancing establishment and spread of highly tolerant alien taxa.

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4.2. Can evolutionary adaptation promote invasion persistence and niche expansion of the invasive guppy

Two processes are contained in the idea of 'niche expansion'—that is, species exploit novel resources, colonise new habitats or tolerate new and formerly unsuitable environmental conditions —and this process defines successful biological invasion. Under intensive predation pressure, guppies adapt by producing more, smaller offspring, along with profound effects on colour, morphology and behaviour compared with populations under low predation pressure. But when predation pressure declines, guppy populations can evolve morphological adaptations that enhance feeding efficiency [12, 13]. Field surveys also show a higher density of guppies in contaminated sites than in surrounding unpolluted reference waters [9]. The pattern is caused by plastic metabolic adjustment and evolved life-history changes associated with contaminant exposure. Taxa with higher contaminant tolerance are more common in polluted freshwater habitats. When tolerance is a heritable trait, pollution-induced selection for tolerant individuals promotes rapid spread of the invasive populations [14]. Guppies therefore occupy the niche of polluted freshwater environments by generating novel phenotypes and accumulating genetic differentiation under persistent contaminant selection.

5. Research deficiencies and prospects

Guppies have flexible phenotypic plasticity both in response to predation, interspecific competition, climate change and chemical contamination. At the same time, important uncertainties remain about how (phenotypic) plasticity and contamination jointly contribute to an invasion [15]. Habitat pollution strongly affects the ecological damage inflicted by an invasive alien species. Contamination reduces native community biodiversity and opens up space for a small number of fully tolerant taxa, among which are invasive fishes [14]. This has practical management implications: the environmental pollution status of a habitat must be carefully considered when assessing proposals to release guppies or any other exotic poeciliid species for mosquito biocontrol because polluted habitats with reduced biodiversity may accentuate an invasion risk.

6. Conclusion

The paper focuses on niche occupation and rapid adaptive responses of invasive guppy populations within polluted freshwater ecosystems. Invasive guppies utilise polluted freshwater niches through coupled phenotypic and genetic adaptation to produce a reinforcing eco-evolutionary feedback loop that facilitates persistence of their populations in the polluted freshwater habitat. First, helped by high fertility and wide tolerance, guppies originating from northern South America and Central America have colonized more than 70 countries and regions all over the world. Invading guppies compete with and hamper the indigenous aquatic taxa on account of coexistence and hybridization, and also perturb whole ecosystem functions by modifying primary productivity and nutrient cycling; water pollution conditions further facilitate the establishment of guppies by lowering the competitive ability of native species and thereby rendering resources and ecological niches available for guppies. Second, polluted habitats impose multi-directional pressures on the guppies, causing rapid guppy responses at phenotypic and molecular levels.

At the life-history level, guppies exhibit r-selected strategies (invest more in reproduction at the cost of offspring size). For sexual selection, male ornamental trait responses to pollution involve phenotypic plasticity and microevolution in combined traits. At the molecular level, allelic shifts in

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CYP1A and changes in the transcriptome of genes on oxidative stress and the immune system reflect the genetic basis of contaminant adaptation. Third, these evolved and plastic adaptive traits are improving guppy persistence and consolidating occupation of contaminated-water niches, thus creating positive eco-evolutionary feedback. Current efforts still have shortcomings. Most studies are presently unevenly spread geographically; quantification of the extent of the contribution of phenotypic plasticity and of heritable genetic adaptation remains problematic. Fitness costs for pollution tolerance, as well as those arising from multiple co-occurring environmental stressors, are poorly understood. Future work should focus on coordinated cross-regional comparative sampling, integrated with genomic analysis and repeated ecological field surveys. Such an integrated framework will produce experimental evidence to inform invasive species control and ecological restoration of polluted freshwater catchments.

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