

JYU DISSERTATIONS 121

Sebastiano De Bona

Dispersal, Habitat Use, and the Invasion Dynamics of Introduced Populations

A Case Study on the Guppy (*Poecilia reticulata*)



UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS
AND SCIENCE

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ABSTRACT

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Diss.

Invasive populations are a major driver of biodiversity loss. Most invasions are discovered after the population is established, spreading, and often adapting to the new ecological conditions, hampering effective eradication. Understanding the spatial dynamics of introduced populations, and how these change throughout the invasion, is crucial to predicting their spread and restricting their harm. In this thesis, I studied density-dependent dispersal, habitat use, and changes in population spread after the introduction of guppies (*Poecilia reticulata*) in montane streams. This was done by combining the analyses of long-term individual-based data with short-term manipulations in the field, and with the mathematical modelling of spread. Introduced populations were shown to grow rapidly after translocation, and attain densities beyond those of natural populations if the habitat is disturbed. The study highlighted that the effect of density on habitat use is scale-dependent: at the landscape scale, guppies occupy habitat patches according to the ideal free distribution; at the local scale, size-dependent responses to density suggest that large individuals displace smaller ones from good quality microhabitats, implying an ideal despotic distribution. Moreover, density at both the local (within habitat patch) and landscape (whole stream) scales was shown to affect dispersal. Finally, guppies were found to be successful invaders upon introduction, but to rapidly lose their invasive potential as they adapt to limiting resources in the environment. In the later phases of the invasion, individual dispersal distance negatively affects the speed of spread of the population. This counterintuitive result can be explained when considering how population growth and individual dispersal interact in determining population spread. I conclude that 1) disturbance can favour invasions; 2) studies of spatial dynamics should be explicit about the scale examined and; 3) integrative approaches are crucial to understanding the spread of introduced populations.

Keywords: Density-dependent dispersal; experimental introduction; habitat use; invasive populations; spatial dynamics; speed of spread.

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TIIVISTELMÄ

De Bona, Sebastiano

Vieraslajien levittäytyminen, elinympäristön käyttö ja invasiodynamiikka: tapaustutkimus miljoonakalalla (*Poecilia reticulata*)

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Vieraslajit ovat merkittävä uhkatekijä luonnon monimuotoisuudelle. Useimmat invaasiot havaitaan vasta, kun vieraslajien kannat ovat jo vakiintuneet ja sopeutuneet uusiin ympäristöoloihin, mikä hankaloittaa niiden tehokasta torjuntaa. Vieraslajien tilankäytön ja tilankäytön muutosten ymmärtäminen on elintärkeää leviämisen ennustamiseksi ja haitan rajoittamiseksi. Väitöskirjassani tutkin miljoonakalojen elinympäristön käyttöä ja populaation leviämiseen vaikuttavia tekijöitä, erityisesti tiheydestä riippuvaa dispersaalia. Tutkimusta varten yhdistettiin pitkän aikavälin tiedot yksilöiden käyttäytymisestä, maastossa tehdyt kokeet sekä matemaattinen mallinnus. Miljoonakalapopulaatioiden havaittiin kasvavan nopeasti uudelle alueelle siirtämisen jälkeen. Häiriityissä ympäristöissä ne saavuttavat jopa suuremman populaatiotiheyden kuin alkuperäisissä elinympäristöissä. Kun tarkastellaan miljoonakalojen elinympäristön käyttöä laajassa mittakaavassa, ne hakeutuvat habitaattilaikuille vapaasti (*ideal free distribution*). Tarkempi tarkastelu kuitenkin paljastaa, että suuremmat yksilöt syrjäyttävät pienempiä yksilöitä laikkujen sisällä (*ideal despotic distribution*). Tutkimuksissa osoitettiin lisäksi, että populaatiotiheys sekä pienessä että suuressa mittakaavassa vaikuttaa dispersaaliin. Invaasion alussa miljoonakalat ovat tehokkaita levittäytyjiä, mutta ne menettävät nopeasti levittäytymiskykynsä sopeuduttuaan resursseiltaan rajoittuneempaan ympäristöön. Invaasion myöhemmissä vaiheissa yksilön dispersaalietäisyys korreloi negatiivisesti populaation leviämisenopeuteen. Tulos on ymmärrettävissä, kun tarkastellaan populaation kasvun ja yksilön dispersaalityyppien vuorovaikutusta populaation leviämistä säätelevinä tekijöinä. Yhteenvedonä totean, että 1) ympäristön häiriöt voivat lisätä invaasioiden onnistumista, 2) spatiaalidynamiikan tutkimuksissa pitäisi ottaa huomioon tutkitun alueen laajuus ja 3) vieraslajien tutkimuksessa integroitu lähestymistapa on välttämätön, jotta ymmärtäisimme vieraslajien leviämistä.

Avainsanat: Elinympäristön käyttö; levittäytymisen nopeus; levittäytyvä populaatio; spatiaalinen dynamiikka; tiheydestä riippuva dispersaali.

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Alla mia mamma e al mio papà.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original manuscripts and published paper. In the thesis introduction I will refer to the studies using the Roman numerals I-IV, as follows:

- I. Reznick D.N., De Bona S., López-Sepulcre A., Torres-Mejía M., Bassar R.D., Bentzen P. & Travis J., 2019. Experimental study of species invasion in a natural community - early population dynamics and role of disturbance in invasion success. Submitted manuscript.
- II. De Bona S., Bruneaux M., Lee A.E.G., Reznick D.N., Bentzen P., López-Sepulcre A., 2019. Spatio-temporal dynamics of density-dependent dispersal during a population colonisation. *Ecology Letters* 22: 634-644.
- III. De Bona S., Sidhu K.K., Enroth H.M., López-Sepulcre A., 2019. Density-dependent dispersal and habitat use in size-structured populations: an experiment in wild Trinidadian guppies. Manuscript.
- IV. De Bona S., López-Sepulcre A., 2019. Rapid changes in dispersal and vital rates alter the invasiveness of introduced guppies. Manuscript.

Table of author contributions to the original publications.

Study	I	II	III	IV
Original idea	DNR, JT, ALS	SDB, ALS	SDB	SDB, ALS
Study design	DNR, JT, ALS, MTM	SDB, ALS, AEGL, MB	SDB, ALS, KKS, HME	SDB, ALS
Data analysis	SDB, ALS, JT, MTM, PB, RDB	SDB, MB, PB, DNR	SDB	SDB
Writing	DNR, SDB, ALS, MTM, JT	SDB, ALS, MB	SDB, ALS	SDB, ALS

AEGL = Alex E.G. Lee, ALS = Andrés López-Sepulcre, DNR = David N. Reznick, HME = Hanna M. Enroth, JT = Joe Travis, KKS = Karendeep K. Sidhu, MB = Matthieu Bruneaux, MTM = Mauricio Torres-Mejía, PB = Paul Bentzen, RDB = Ronald D Bassar, SDB = Sebastiano De Bona.

1 INTRODUCTION

1.1 The challenge ahead

In a report published in May 2019, the UN Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) stated that one million species are at risk of extinction, highlighting the need for a “transformative change” to reverse the dreadful trend (IPBES 2019). The current human-induced loss of biodiversity proceeds at a higher rate than background extinction (Pimm *et al.* 1995, Barnosky *et al.* 2011). Conservative estimates warn us that a sixth extinction event, comparable to the Big Five mass extinctions of the past (Ordovician, Devonian, Permian, Triassic and Cretaceous - the last of which wiped out most Dinosaurs) is already on its way (Kolbert 2014, Pievani 2014, Ceballos *et al.* 2015, 2017). Today more than ever, we need to understand the drivers of this unprecedented biodiversity loss, to take radical actions that mitigate it.

1.2 Invasive species

1.2.1 The impact of invasive populations

Invasive alien species are among the major direct drivers of biodiversity loss (IPBES 2019), and represent the second most common threat in recent extinction events (Bellard *et al.* 2016). Many invasive alien populations inflict severe harm on native biodiversity (Vitousek *et al.* 1997, Mcneely 2001, Clavero and García-Berthou 2005, Molnar *et al.* 2008, Doherty *et al.* 2016). Some of the direct effects are predation and competition for resources with native populations (Mooney and Cleland 2001, Doherty *et al.* 2016), while the indirect effects often represent whole ecosystem impacts (Gordon 1998, Zavaleta *et al.* 2001, Levine *et al.* 2003, Brooks *et al.* 2004, Gallardo *et al.* 2016) and may occur on large timescales (Strayer *et al.* 2006). An emblematic example is that of the invasive Argentine

Ant (*Linepithema humile*), which in North Carolina caused the decline of their direct competitors, the native ant species, and triggered a decrease in the abundance of other invertebrates and a remodelling of the trophic structure (Human and Gordon 1997). Similarly, many invasive bivalve species alter the ecosystem structure and functioning, acting as true “ecosystem engineers” (Sousa *et al.* 2009). The effect of invasive species can differ among levels of ecological complexity. Invasive plant species, for instance, can alter the ecosystem by increasing community production while reducing native plant and animal abundance and diversity (Vilà *et al.* 2011).

Despite many non-indigenous species being originally introduced for their economic value, invasive species represent a costly burden to national economies (Lovell *et al.* 2006, Olson 2006). Management actions, eradication efforts, and damaged agriculture and ecosystem services add up to an estimated cost of €10-12 billion EUR/year in the European Union (Kettunen *et al.* 2008, Hulme 2009, Scalera 2010), \$13.6 billion AUD/year in Australia (Hoffmann and Broadhurst 2016) and \$120 billion USD/year in the United States (Pimentel *et al.* 2005).

1.2.2 Stages of an invasion

The process by which a non-native population becomes invasive can be divided into four stages: transport, introduction, establishment and spread (Blackburn *et al.* 2011). The stages are separated for ease of explanation, but in reality can overlap. During transport, a group of individuals is moved to an area outside its native range. Transport can be intentional, fuelled by commercial or aesthetic interests in exotic species, or accidental, favoured by globalisation (Meyerson and Mooney 2007) and by long distance transport of people and goods (Hulme 2009). Introduction occurs when individuals are released from captivity or cultivation, either accidentally or intentionally, as when non-native populations are used to control pests (Howarth 1991, Simberloff and Stiling 1996), or are “liberated” from fur farms (Bonesi and Palazon 2007). Introduction can happen concurrently with transport, such as in the release of aquatic organisms with ballast water (Bax *et al.* 2003) or the introduction of invertebrates and grasses with wood or soil transport (Capowiez *et al.* 2000, Kiritani and Yamamura 2003, Suarez *et al.* 2005, Lehan *et al.* 2013). The introduced individuals can then become established, surviving until reproduction and generating a self-sustaining population. When the population spreads in space, occupying a larger area than the original site of introduction, the non-native population becomes invasive (Blackburn *et al.* 2011).

Transport and introduction are hard to witness during natural invasions, given how often they are accidental. Prevention of these two stages can be the most effective strategy to counter the threat of invasive species (Leung *et al.* 2002, Finnoff *et al.* 2007). A practical example of this is the success of the strict biosecurity policies put into place by Australia and New Zealand to limit introductions of non-native species (see Fig. 1 in Simberloff *et al.* 2013). Prevention is not always possible, however, and can only reduce the probability

that an introduction will occur. Most non-native populations are in fact detected after introduction, while established and spreading, a risk that can be amplified when lags in the invasion process exist (Crooks and Soulé 1999). If a non-native population is already established, eradication can be effective if practiced early (Rejmánek and Pitcairn 2002), making detection a priority over prevention in some scenarios (Mehta *et al.* 2007). For well established non-native populations, control might be more cost-effective (and realistic) than eradication (Davis *et al.* 2011, Simberloff *et al.* 2013). A better understanding of the establishment and spread will aid the effective planning of control actions, and it is the focus of this thesis.

1.2.3 A word on words

In this thesis, I use the term *invasive population* to mean an “introduced population that spreads and maintains itself without human assistance” (Richardson 2011, Simberloff *et al.* 2013), in a narrow sense, regardless of its impact (Davis 2009). This definition is not perfect but suits the four-stage framework described above (Blackburn *et al.* 2011), which I adopted in an effort to be taxon-unbiased. The terminology used in invasion biology is vast, often redundant, and sometimes misleading (Colautti *et al.* 2004). The field of invasion biology could benefit if a shared terminology across different disciplines (such as research, management and outreach) were implemented. Nonetheless, a deep dive into the terminology used in invasion biology, and the numerous attempts to unify and simplify it, is far beyond the scope of this introduction. I quote Mark A. Davis to clarify my approach: “I believe, at this point, our time is better spent on other things” (Davis 2009, page 3). One clarification and a pinch of caution are required, though, when discussing *invasive* and *non-native* species. The narrative should never be oversimplified into the dichotomy “*native-good, non-native-bad*”. Some *non-native* populations are shown to help maintain biodiversity: for example introduced saltcedar (*Tamarix* spp.), in the western United States, have become the preferred nesting site of the endangered southwestern willow flycatcher (*Empidonax trailii extimus*). Judgement on a population (or a species) should not be based on its origin, but on its impact (Davis *et al.* 2011).

1.3 Dispersal and spread

When dealing with an invasive population, the answer to the question “where will it be next and when?” is crucial to plan effective control. Spread is the product of population growth and dispersal in space (Fisher 1937). It is important to highlight that spread is a population-level feature that defines the portion of space occupied by a group of individuals. Spread emerges from traits at the individual level, such as dispersal, survival, and reproduction.

Individual dispersal is probably the most intuitive determinant of population spread (Bowler and Benton 2005, Kokko and López-Sepulcre 2006). Dispersal is defined as the movement of individuals or propagules that can lead to the movement of genes (Ronce 2007), and can be divided into three phases: emigration, transfer, and settlement (Clobert *et al.* 2009). In animals with distinct life-stages we can recognize natal dispersal, i.e. a movement from the place of birth to the location where first reproduction occurs, and adult dispersal, corresponding to the movement between successive reproductive events (Matthysen 2005). This complex behaviour results from the evaluation of the fitness costs and benefits of leaving the current habitat patch for another (Clobert *et al.* 2009, Matthysen 2012, Bonte *et al.* 2012). Understanding what drives individuals to disperse enables us to predict the spread of a population based on the ecological conditions.

Often, in theoretical studies, individual dispersal is summarised at the population level by *dispersal kernels*. Dispersal kernels are density functions describing the probability of individuals of a population moving a given distance away from the position in space they occupy (Nathan *et al.* 2012). Classic theoretical work uses reaction-diffusion models— where the dispersal kernel is a Gaussian curve— deriving a constant rate of spread for a hypothetical population, based on individual vital rates (Fisher 1937, Skellam 1951). A Gaussian distribution is an extreme simplification of movement, even though it is very effective in some scenarios (Hastings 1996a, b). More realistic fat-tailed dispersal kernels that account for rare long-distance movements produce accelerating waves of spread (Kot *et al.* 1996). These long-distance dispersal events, even if rare, contribute disproportionately to the speed of spread (Kot *et al.* 1996, Shigesada and Kawasaki 2002, Caswell *et al.* 2003). Selecting a realistic representation of dispersal behaviour will improve the prediction of population spread.

Large fluctuations in population density are an inherent feature of invasions (Sakai *et al.* 2001), increasing the likelihood of introduced individuals experiencing a wide range of densities. This is relevant since density has a complex relationship with the traits that determine spread (i.e. vital rates and dispersal). Population density emerges as the product of survival, reproduction, emigration, and immigration. At the same time, these individual traits are often affected by density, creating a feedback structure. When resources are limiting, high population density is expected to reduce individuals' vital rates, such as survival, fecundity, and individual growth, regulating population growth (Nicholson 1933). Dispersal is often affected by density, although the direction of the effect is not easy to generalise (Matthysen 2012). High local density might cause higher competition over resources and increase the propensity of individuals to emigrate from a habitat patch (Waser 1985, Léna *et al.* 1998, Bitume *et al.* 2013). Alternatively, individuals might be attracted to high conspecific density, either because it is interpreted as a cue for habitat quality (Stamps 1988) or for the benefits of living in a group (Dehn 1990, Kramer *et al.* 2009). Through its effect on vital rates and dispersal, population density

indirectly influences the spread of populations. Because of this, it is important to examine the influence of density fluctuations on individual traits, and ultimately invasion spread.

When non-native populations have been introduced in the past, the potential for their rapid evolutionary change in response to the new environment has often been neglected. As an example, mosquitofish (*Gambusia* spp.) were introduced in Australia in 1925 to act as mosquito control. Unfortunately, feeding on undefended native invertebrates over mosquito larvae proved to grant a fitness advantage, prompting an adaptive change in diet. The result: an explosion of mosquitofish populations, the loss of endemic invertebrates, and little impact on mosquitoes (Lloyd *et al.* 1986). Adaptation can also concern traits that are involved in determining spread. The evolution of dispersal and vital rates can be rapid in experimental range expansions, and lead to faster spreading populations (Fronhofer and Altermatt 2015, Williams *et al.* 2016, Fronhofer *et al.* 2017, Szűcs *et al.* 2017, Weiss-Lehman *et al.* 2017). In the wild, one of the best studied examples of the effects of evolution on invasive spread is that of the cane toad (*Rhinella marina*) in Australia. Cane toads were introduced in Queensland in 1935 as a way to control insects in cane plantations. Today, their invasion is seen as an ecological disaster: toads cover an area of 1.2 million km² in Australia (Urban *et al.* 2007), and negatively impact native wildlife in several ways (Shine 2010, Jolly *et al.* 2015). The key to their invasive success is the rapid evolution of dispersal and growth rate (Phillips *et al.* 2010a). Toads at the front of the invasion have faster growth (Phillips 2009) and longer legs, which allow them to travel faster and over longer distances (Phillips *et al.* 2006). The evolution of dispersal in cane toads has been explained through evolution by *spatial sorting* (Shine *et al.* 2011). Spatial sorting predicts that pioneers at the front of the invasion will likely be individuals with high dispersal abilities, which will mate assortatively and produce fast dispersing offspring (Phillips *et al.* 2010b). A simulation study by Perkins and colleagues (2013) best showcases the price of neglecting evolution. The predicted rate of spread of the cane toad in the absence of evolutionary change, over the course of 72 years (1935–2006), is 300 km. In 2006 the toad was found at Timber Creek, Northern Territories, almost 2000 km from the site of introduction.

1.4 Habitat use

While the spread of invasive populations determines where they will be next, the spatial dynamics within the area they already occupy define potential ecological interactions and niche overlap with native species. Understanding the way invasive populations occupy habitats in the landscape enables us to generate expectations on whether the habitat use of native species will be altered (Brenchley and Carlton 1983, Evans 2004, D'Amore *et al.* 2009).

Demographic processes during the establishment of introduced populations can shape habitat use, for instance as a result of population growth.

Pietrek and Gonzalez-Roglich (2015) show invasive beavers (*Castor canadensis*) in Patagonia move to less preferred habitats as density increases. Nummi and Saari (2003) studied population regulation in the introduced mute swan (*Cygnus olor*) in Finland, and explain the reduction in the number of fledged young at high density with an increasing use of suboptimal nesting sites. Moreover, the nature of the competitive interactions between individuals will determine how space is filled as population density increases. Two contrasting theories can explain how differences in competitive interactions between individuals can drive habitat use.

The *ideal free distribution* theory assumes individuals have equal competitive abilities and are free to choose the habitat they settle in (Fretwell and Lucas 1970). The decision will be based on the inherent quality of the habitat (food resources, predation pressure, shelter etc.), and on the number of individuals with whom the patch is to be shared. A consequence of the ideal free distribution is that the average fitness across habitats will be equalised (Fretwell and Lucas 1970, Haugen *et al.* 2006). Conversely, when competitive abilities differ between individuals, an *ideal despotic distribution* (Fretwell 1972) is expected. Good quality habitat will be occupied by dominant individuals, who will displace subordinate ones to lower quality habitats (e.g. Davey *et al.* 2005). The ideal despotic distribution predicts that suboptimal habitats will be occupied disproportionately when density increases (Bult *et al.* 1999, Purchase and Hutchings 2008). Exploring competitive interactions within a species and how they affect habitat use can help us foresee repercussions on other species, such as native ones. Duckworth and Badyaev (2007), for instance, find a correlation between aggressiveness and dispersal propensity in male western bluebirds (*Sialia mexicana*). When these dispersing males come into contact with the less aggressive mountain bluebird (*Sialia currucoides*), the latter is displaced.

1.5 The Trinidadian guppy as a study system

1.5.1 Guppies in a nutshell

The Trinidadian guppy (*Poecilia reticulata*) is a small freshwater fish native to northeast South America and the Caribbean islands (Venezuela, Northern Brazil, the Guyanans, Barbados, Surinam and, of course, Trinidad and Tobago; Welcomme 1988; Magurran 2005) (Fig. 1). Guppies are livebearers, reproduce year round (Alkins-Koo 2000), and have a fast reproductive cycle (25–30 days; Houde 1997). Guppies are sexually dimorphic, with males showing an extraordinary degree of polymorphism in body colouration, which is both under natural and sexual selection (Endler 1980, Kodric-Brown 1985). Colouration can evolve rapidly (Gordon *et al.* 2015) and can be selected with relative ease in both males and females (Houde 1994, Khoo *et al.* 2007), contributing to the plethora of breeds available to fish hobbyists. These traits, combined with the ease of maintaining populations in the laboratory, contribute

to making guppies a widespread pet and an extremely versatile model organism. Guppies are used as a model system to study behavioural ecology, sexual selection, genetics, and evolution (Houde 1997, Magurran 2005, Breden 2006).

1.5.2 Guppies as an invasive species

Poeciliid fish, the family to which guppies belong, represent 10% of all freshwater fish species listed in the Global Invasive Species Database, despite amounting to only 0.1% of all described freshwater fish species (Deacon and Magurran 2016). Guppies are introduced in every continent except Antarctica (Deacon *et al.* 2011) as a result of intentional introductions as mosquito control or accidental release of pets. Their broad tolerance of environmental conditions (from montane streams to brackish waters, from pristine habitats to ponds over tar lakes; Magurran 2005; Schelkle *et al.* 2012), generalist diet (Dussault and Kramer 1981), rapid population growth, and an ability to switch from fast to slow life histories within ecologically relevant timescales (Reznick *et al.* 1990, 2001) are characteristics commonly found among invasive fish species (Moyle 1987, Sakai *et al.* 2001). Female guppies can store the sperm of various males for long periods of time (Lopez-Sepulcre *et al.* 2013), creating the potential for successful introductions from the release of a single individual (Sakai *et al.* 2001, Deacon *et al.* 2011).



FIGURE 1 A montane stream (the Caigual) in the Northern Range of Trinidad (*top left*). Wild guppies (*top right*). Guppies are released in the field after processing in the laboratory. Individuals are transported from the stream to the laboratory, and back, in small groups inside HDPE bottles (*bottom right*). *Anablepsoides hartii* is the only other fish species, in addition to guppies, in low-predation communities (*bottom left*). Photos by Sebastiano De Bona.

Where introduced, guppies have harmful effects on native ecosystems; guppies compete with native fish species (Courtenay and Meffe 1989), harass heterospecific females (Valero *et al.* 2008) and predate on larval invertebrates (Englund 1999). Guppies have also been shown to preferentially prey on other native invertebrates rather than larval mosquitoes (Manna *et al.* 2008), challenging their effectiveness as mosquito control agents (El-Sabaawi *et al.* 2016). In Hawaiian streams, introduced Poeciliid fish have effects at the whole-ecosystem level, changing nutrient cycles, altering macroinvertebrate composition, and reducing population density of native fish species (Holitzki *et al.* 2013).

1.5.3 Guppies in their native range

Besides the obvious interest in introduced guppy populations, the natural history of this species in its native range makes it an extraordinary system for evolutionary ecology, and a great model to study biological invasions. The southern slope of the Northern Range mountains of Trinidad is characterised by several parallel streams flowing into two main drainages (Caroni and Oropuche) (Fig. 2, *left*). The streams feature a gradient in fish communities: downstream are high-predation (HP) communities, where guppies coexist with large predators (e.g. *Crenicichla alta*, *Hoplias malabaricus*); close to the headwaters, low-predation communities include only the generalist Hart's killifish (*Anablepsoides hartii*, syn. *Rivulus hartii*) besides guppies (Endler 1980, 1995) (Fig. 1, *bottom left*). Barrier waterfalls prevent the upstream movement of large predators— but not of guppies and killifish— into low-predation communities (Reznick and Endler 1982). The natural history of guppies in Trinidad is characterised by repeated and independent colonisations of upstream, low-predation tributaries from the high-predation communities in the main stem (Alexander *et al.* 2006). Moreover, these natural colonisations can be experimentally replicated by translocating guppies from HP to guppy-free, LP sites (Haskins *et al.* 1961, Endler 1980, Reznick and Bryga 1987, Reznick *et al.* 1990, Gordon *et al.* 2009), creating a “natural laboratory” (Haskins *et al.* 1961).

Guppies adapted to high predation pressure are smaller, have high reproductive allocation, produce many small offspring, and have faster growth rate compared to guppies found in low-predation sites (Reznick and Endler 1982, Reznick *et al.* 1996). In short, HP and LP guppies sit on opposite ends of the fast-slow life-history continuum. When HP guppies are introduced into LP sites, their high reproductive allocation, combined with the release from predation, results in rapid population growth. In fact, population biomass in natural LP sites can be up to 6 times that of HP ones (Reznick and Bryant 2007). This triggers resource limitation which selects for the slow life histories typical of LP guppies, which are better able to cope with a scarcity of resources (Bassar *et al.* 2013, Travis *et al.* 2014).

The translocation of guppies into a predator-free environment reproduces some of the key aspects of invasion dynamics. The reduced predation risk mirrors the release from enemies often experienced by successful

invaders (*enemy release hypothesis*, Keane and Crawley 2002). Moreover, guppies have a dramatic impact on low predation sites, after introduction. They reduce the density of killifish populations by preying on young individuals (Walsh *et al.* 2011) and cause evolutionary change in the killifish through direct and indirect effects (Walsh and Reznick 2010a, b). Introduced guppies affect the entire ecosystem, altering nutrient cycling, food webs, and ecosystem processes (Bassar *et al.* 2010, El-Sabaawi *et al.* 2015a, b, Collins *et al.* 2016, Simon *et al.* 2017). Experimental translocations allow us to observe the very onset of the invasion process, which is hard to capture during natural invasions. Crucially, by happening within the native range of guppies, these natural experiments come at no risk of disrupting natural environments elsewhere.

1.5.4 Guppy habitat

The typical structure of the montane streams where guppies are found can be thought of as the alternation of two different habitat types: pools and riffles. Most guppies are found in pools, where slow-flowing water allows for the deposition of organic matter. Pools are separated by fast-flowing, shallow riffles. While riffles are relatively homogeneous, pools can be further subdivided into different microhabitats. I define 5 microhabitat types, which can be present in various proportions within a pool: an inflow characterised by fast-running water; a relatively deep, slow-flowing core area; a marginal sandy shore; still embayments rich in benthic deposits of organic matter; and a shallow yet fast-flowing run leading to the pool's outflow. Due to this structure, guppies' space use and movement can be observed at two different scales: landscape (between pools) and microhabitat (within pool).

1.6 Aim of the thesis

Invasive species represent a looming threat to native biodiversity. One cost-effective way to reduce the impact of introduced populations is to control their spread. Thus, the components that determine spread— such as demographic and spatial dynamics— need to be studied. The aim of this thesis is to improve our understanding of the establishment, habitat use, and dispersal of introduced populations in order to better predict their spread. To do so, I use the guppy (*Poecilia reticulata*) as a system to study three main research questions.

First, what are the population dynamics after the introduction of guppies, and how does habitat disturbance affect establishment? I address this question by analysing individual-based data collected from four guppy populations that were translocated into montane streams with either intact or thinned canopy (study I). The latter is a common form of disturbance in tropical streams.

Second, are dispersal and habitat use affected by fluctuations in population density, which are typical during the establishment of invasive

populations? I study this by a) observing patterns of density-dependent dispersal and habitat use in the four introduced populations (study II) and b) performing short-term manipulations of density in natural guppy populations to trigger spatial responses in the form of dispersal and habitat use (study III). I observe the effects of density both at the landscape scale (whole stream density) and at the local scale (within a habitat patch).

Third, do changes in dispersal and vital rates after introduction affect the invasive potential of guppy populations? To test this, I parameterise a spatially-explicit model of population dynamics using individual traits collected from one of the translocated populations (study IV). Using this model, I simulate population spread at three separate phases throughout the invasion process to infer changes in invasiveness.

2 METHODS

2.1 Overview

In this thesis, I use three main approaches: a) statistical analyses of long-term, individual-based data collected from four introduced guppy populations; b) statistical analyses of a short-term experiment on natural guppy populations and; c) mathematical modelling of population dynamics using integral projection models.

The main features of the long-term study, the short-term experiment, and the mathematical modelling are explained below. Further details on the methods can be found in the individual studies.

2.2 Long-term monitoring of guppies introductions (I, II, IV)

In 2008 and 2009, four translocations of guppies from a high-predation river to four low-predation streams were performed (Travis *et al.* 2014) (Fig. 2, right). The original ecological features were similar among introduction sites, although in two out of the four streams the surrounding canopy was thinned, reproducing a common form of habitat disturbance. The thinned canopy has been maintained since by periodically removing riparian vegetation. The founder individuals and all new recruits were uniquely marked and followed through monthly mark-recapture for 10 years. At each capture, the position of each individual in the stream was recorded, allowing for the analysis of movement between capture events. Wet weight and standard length were also measured at each capture. DNA sampling allowed for the reconstruction of pedigrees, for one of the four populations.

2.3 Short-term experiment (III)

I performed density manipulation experiments on natural guppy populations in three separate stream sections in the Northern Range of Trinidad. In each section I captured individuals of all sizes, recording their sex, size, weight, location in the stream, and the microhabitat they were found in. Before release, fish were given a unique mark. Within each section, I altered the number of released guppies in three adjacent pools to produce three density treatments: a control treatment, a decreased density treatment, and an increased density treatment. I recaptured individuals 3 to 5 weeks after release to evaluate how the perturbation of population density affected life-history traits, dispersal, and microhabitat use.

2.4 Modelling of population dynamics (IV)

I built integral projection models (IPMs, Easterling *et al.* 2000; Ellner *et al.* 2016) to simulate the spread of a population through space given density-dependent vital rates (survival, reproduction, natal and adult dispersal). In the models, an individual's vital rates are determined by its position in a one-dimensional space and are affected by population density at that position. I parameterised three versions of the model using data collected at three phases (early, mid and late) throughout a population invasion. This resulted in three IPMs that I used to obtain phase-specific estimates of population spread. By comparing these estimates, I studied how changes in individual vital rates throughout the invasion produced changes in the predicted spread. Finally, I ran perturbation analyses on each IPM to evaluate the relative contribution of individual vital rates in determining the population spread.



FIGURE 2 Map of the Northern part of Trinidad (*left*), with the two main drainages (Caroni and Oropuche) highlighted in different shades of blue. The red dot indicates the approximate location of the introduction sites, magnified on the right. Redrawn from Kohler *et al.* 2012 (*left*) and from study I (*right*).

3 RESULTS: A SYNTHESIS

3.1 Population dynamics during establishment (I)

A fast life history characterises many invasive species (Sakai *et al.* 2001, Van Kleunen *et al.* 2010, Capellini *et al.* 2015, Allen *et al.* 2017), as well as the guppies introduced into our four study streams to observe the progress of their invasion from its onset (Torres Dowdall *et al.* 2012). A consequence of a fast life history in the absence of external regulation (e.g. predators) is a rapid and explosive population growth that can cause density to overshoot beyond natural population densities observed in the wild. I find guppy populations introduced into streams with intact canopy to grow rapidly, but without significantly exceeding the typical range of population density observed in natural streams (I). The density of introduced populations decreases during and immediately after the wet season (September – March), and increases during the dry season (April – August). The seasonal fluctuation matches that observed in natural populations (I). The population dynamics after introduction in streams characterised by canopy thinning— a common form of disturbance— are somewhat different. There, guppy populations rapidly attain densities above those observed in natural streams and maintain them throughout the observation time (I). The difference in population density between streams with intact and thinned canopy is due to a higher recruitment rate, rather than to differences in mortality rate (I). In both stream types, recruitment is negatively affected by density, but the slope of the decrease in *per capita* recruitment is much steeper in the intact canopy streams compared to the thinned canopy ones (I). Moreover, both female growth rate and male size at maturity are increased in thinned canopy streams (I).

The difference in population dynamics between the closed and thinned canopy streams is likely due to the higher productivity that results from the increased light penetrating through the canopy (Kohler *et al.* 2012). El-Sabaawi *et al.* (2015a) conducted a factorial experiment in mesocosms to study the effects of light conditions on the fitness and life history of guppies adapted to high and low predation pressure (HP and LP). The light conditions tested were set to

recreate the typical light environment of a closed-canopy, upstream tributary (low light) and a wide river with less overhanging vegetation (high light). The light difference between the two was approximately four-fold. Light condition had a stronger effect on fitness and life history than the guppies' own phenotype. High light conditions resulted in a population growth rate 1.5 times higher compared to that in low light (El-Sabaawi *et al.* 2015a). I show a similar impact of light conditions in wild populations.

The findings of this study suggest that even mild yet common forms of disturbance could radically change the demography of a population invasion. The notion that habitat disturbance could facilitate invasions was formalised early on (Elton 1958), and has some experimental support (Lake and Leishman 2004; Altman and Whitlatch 2007; reviewed in Lozon and MacIsaac 1997). Davies *et al.* (2000) suggested an increase in resource availability, such as that caused by higher light penetration in my study, might be a key factor that establishes the invasibility of an environment. Casatti *et al.* (2009) compared the fish assemblages in Brazilian streams to find that the removal of riparian vegetation produced communities dominated by the invasive guppy. They linked heavy logging to the takeover by grassy vegetation, which causes a simplified habitat ideal for guppies.

3.2 Density and spatial ecology

3.2.1 Population regulation (I-III)

In a population at equilibrium, density is expected to negatively affect life-history traits (survival, growth, reproduction) in a way that regulates the population back to its equilibrium (Nicholson 1933). In this thesis I find higher local population density to reduce both lifetime reproductive success in females and lifetime mating success in males (I). Moreover, in a density manipulation on wild guppy populations, I show that increasing density reduces recruitment, individual growth, and female and juvenile survival (III). These results are expected since wild guppy populations in low-predation communities are density regulated (Bassar *et al.* 2013) and previous density manipulation experiments show life-history traits to change quickly after density is altered (Reznick *et al.* 2012, Bassar *et al.* 2013). In response to the fitness consequences of the reduced availability of resources at high density, one might expect “spatial responses” – in the form of positive density-dependent dispersal (Bowler and Benton 2005, Matthysen 2005) and/or density-dependent habitat use (Kie and Bowyer 1999, Davey *et al.* 2005) – to evolve.

3.2.2 Density-dependent dispersal (II-III)

The study of dispersal during a population invasion provides an opportunity to observe this behaviour through a wide variety of population densities (I).

Moreover, the new environmental conditions in the site of introduction could promote dispersal evolution. In this thesis, I find different drivers for natal and adult dispersal, which I analysed separately (II). Natal dispersal is affected by population density at both the local scale (within a habitat patch) and the landscape scale (at the whole stream level). Local population density increases the probability of juvenile guppies to disperse, but only when density at the landscape scale is low, suggesting alternative patches at lower density are available for dispersers. As the landscape becomes saturated and landscape density increases, the strength of the effect of local density on natal dispersal lessens until local density ceases to be a driver of dispersal (II). Positive density-dependent dispersal is well documented (reviewed in Lambin *et al.* 2001; Matthysen 2005), although the simultaneous effect of multiple spatial scales is seldom considered, with a few notable exceptions. Wojan *et al.* (2015) studied how the difference in density between the patch of origin and the patch of settlement affects dispersal in the brush mouse (*Peromyscus boylii*). They found mice to disperse towards patches at higher density compared to that of origin, possibly as a result of conspecific attraction. When they adjusted for the landscape population density around the two patches (origin and settlement) the results were unchanged. Erm *et al.* (2019) directly manipulated resources instead of density, and found *Daphnia carinata* to base dispersal decisions only on the level of resources present in their current patch, ignoring information at the landscape level. Here I show population density at the landscape scale has a role in determining dispersal, but the mechanisms by which landscape information is collected are unknown.

In adult guppies, I show dispersal to be affected by population density at the local scale only (II). Interestingly, the direction of the effect changed throughout the invasion process. In the early phases, guppies showed conspecific attraction (resulting in negative density-dependent dispersal), which turned into conspecific avoidance (positive density-dependent dispersal) as the population became established (II). The initial conspecific attraction can be explained by two non-mutually-exclusive observations. First, the founder individuals were collected from a portion of the river characterised by high predation pressure (HP, Travis *et al.* 2014), where groups of guppies use schooling behaviour as an anti-predation strategy (Magurran 1990, Magurran *et al.* 1993). Guppies might have retained this tendency, which has a genetic basis (Magurran and Seghers 1991), before losing it in a site where no major predators are present. Second, guppies might be unfamiliar to the new environment and use conspecific density as a cue to recognise good quality habitats (Fletcher 2006). The subsequent conspecific avoidance, emerging after overall density increased, could be a symptom of density becoming a cue for resource limitation.

The density manipulation experiment on wild guppy populations (III) does not exactly replicate the results of the long-term observational study: dispersal is not significantly affected by increasing or decreasing local population density. Ours is not the first experimental study unable to detect

density-dependent dispersal where expected (Clutton-Brock *et al.* 1985, Massot *et al.* 1992). The incongruence of the results can be due to the small sample size and large stochastic effects that characterise a short-term experiment lasting a few weeks compared to a long-term observation spanning several years. There are other similarities among the results, however: in both studies I find dispersal to vary between sexes, with males being more likely to disperse than females (II, III). This corroborates previous evidence (Croft *et al.* 2003a). Moreover, I show dispersal to be costly, in the form of reduced body condition of all individuals and growth of the smaller size classes (III). Dispersal is energetically demanding (Bonte *et al.* 2012), and can impact individuals differently based on their phenotype.

3.2.3 Density-dependent habitat use (I-III)

In natural streams, the density of guppies is much higher in pools than it is in riffles (I). This suggests pools are a preferred habitat type. The same difference is found in the introduced populations (I), although the occupancy of the two habitats changes with time since introduction. Initially, a very small proportion of guppies is found in riffles (2–10%). With time, and as local density in pools increases, the average use of riffles increases significantly (I). Lifetime reproductive success for females and lifetime mating success for males does not depend on the proportion of lifespan spent in riffles. This finding suggests that guppies are distributed between pools and riffles following an *ideal free distribution* (Fretwell and Lucas 1970). According to this theory, individuals should distribute freely between different habitats based on resource availability and local density, in order to equalise average fitness among the different habitats.

Through the density manipulation (III) I am able to study individual spatial responses at a smaller scale, within a habitat patch. Guppies occupy the different microhabitats within a pool differently based on size and stage. Large females are mostly found in the deep, fast-running inflow of the pool and in the deep yet slow-flowing core. Small individuals are predominant in peripheral microhabitats, such as the sandy shores of the pool and the still embayments rich in detritus (III). Spatial segregation based on size was previously observed in guppies in high predation communities: large individuals were more likely to be found further away from the bank, in deeper waters, while small individuals were close to shore (Croft *et al.* 2003b). Croft *et al.* (2004) later investigated whether the difference in size between males and females lead to the spatial segregation of sexes. They found that larger females prefer areas further away from the bank compared to the smaller males, but only in high predation sites, while in low predation sexes were not segregated (Croft *et al.* 2004). I find large females to prefer microhabitats with deeper water, regardless of their distance from the shore. In fact, the inflow habitat where most large females are found is very close to the bank, despite the deep water.

When analysing changes in microhabitat use in response to density perturbations, I find microhabitat shift to be affected by density, and the

response to be size-specific (III). When density is increased, large individuals become more likely to remain in the same microhabitat, whereas small individuals are likely to shift to a different microhabitat type. The opposite is true at decreased density. Moreover, microhabitat shift affects size-specific growth, and the effect varies among the density treatments. Microhabitat shift is costly for all individuals at increased density, suggesting the increased movement of small individuals might force them to use suboptimal microhabitats. Large individuals, more likely to stay, might be monopolising the limiting resources and forcing small individuals away. In guppies, large individuals are more likely to show aggression towards conspecifics (Gorlick 1976) and monopolise resources (Magurran and Seghers 1991). The competitive interactions between females are shown to be costly for both parties, but especially for the smaller subordinate individuals, whose growth is lowered more (Borg *et al.* 2012). In my density manipulation experiment, when density is decreased, a “win – win” situation emerges (III). Large individuals are more likely to shift microhabitat and benefit from it in terms of growth; small individuals become more likely to remain, which improves their growth, probably as a result of the freed ecological space (III).

The dominance interactions at the microhabitat level emerging from the results of the density manipulation experiment suggest this small scale conforms to the *ideal despotic distribution* (Fretwell 1972). The theory acknowledges competitive abilities can differ between individuals as a result of phenotypic traits or acquired status. In this case, individuals are not free to choose a habitat where their fitness is maximised, but might settle for suboptimal habitat types. The fitness would not be equalised among habitats, as expected by the *ideal free distribution* (Fretwell and Lucas 1970). In this thesis, I show the pattern with which the habitat is filled varies among scales. Habitat use at the landscape level (between habitat patches) suggests guppy distribute between riffles and pools following the ideal free distribution. At the local scale (within habitat patch), on the other hand, individuals follow an ideal despotic distribution. Different scales are seldom accounted for in studies of habitat use (but see Bult *et al.* 1999), but it could be important to do so since the processes at play might be scale-dependent.

3.3 Changes in population spread and invasiveness (IV)

Using integral projection models (IPMs) parameterised with the individual-based data collected after the introduction of guppies, I am able to simulate how their invasive spread changes with time (IV). In the early phase, high individual survival and reproduction drive rapid population growth, and the simulated invasion proceeds at a fast, accelerating pace. By month 12 of the simulation, guppies are proceeding at a speed of spread of 10 m/month, in the one-dimensional space. Simulations parameterised with data pertaining to later phases show a different invasive story. Guppy populations become stable

shortly after introduction, and as a result their invasive potential decreases dramatically and the predicted speed of spread in the late phase decreases throughout the simulation. Overall, I find guppies to be extremely successful invaders upon introduction, but to quickly become poor invaders as a result of changes in demographic parameters. This result could help illuminate an anecdotal observation in the field. In Trinidad, guppies have colonised upstream tributaries from lower-altitude rivers, sometimes crossing barrier waterfalls of impressive height. Nonetheless, walking upstream along these tributaries, guppies often disappear closer to the headwaters. The natural barriers that separate colonised areas from guppy-free reaches do not appear insurmountable. It is a suggestive idea that the decreased invasive potential I show here might be at the root of this observation.

Perturbation analyses allow me to evaluate the relative contribution of the different vital rates to the speed of spread (IV). I find parameters defining survival and reproduction to disproportionately affect spread, compared to parameters describing dispersal. Previous studies have shown demographic parameters to be important. Jongejans *et al.* (2011) model the invasive spread of thistles (*Carduus nutans*), adopting a spatial IPM, and show the effect of survival, reproduction, and dispersal on the speed of spread to have similar magnitude. Veit and Lewis (1996) simulate the invasive spread of the house finch (*Carpodacus mexicanus*) after introduction in the Eastern United States. As I do here, they start from first principles and project an invasion dynamic that starts as a slow wave but rapidly accelerates. Their simulations match rather well the observed invasion and are similar to what I obtain in the early-phase projection. Finally, Veit and Lewis (1996) point out a strong correlation between population growth rate and population spread, which I also find to be true of the simulated guppy invasions.

Perhaps the most relevant yet surprising result of this study is the negative effect of adult dispersal distance on the speed of spread, emerging in the later phases of the invasion (IV). The perturbation analysis suggests that increasing the parameter defining the mean distance dispersed by 1% would cause the predicted speed of spread to decrease by 10%. This contradicts previous predictions of a positive effect of long-distance dispersal on the spread of invasions. For example, Kot *et al.* (1996) show fat-tailed dispersal kernels that allow for rare long-distance dispersal produce an accelerating wave of spread. The negative effect of dispersal, though, can be explained if the population growth rate and the demographic traits are considered. In the mid and late phase, the population is stable, and this causes individuals to disperse without being replaced at the range core by new recruits. Survival is positively density-dependent, causing the individuals to be more likely to perish in the low-density populations at the range margin, which become non-viable. Reduced dispersal distance would concentrate individuals at higher local densities near the range core, granting higher survival and buffering the retreat of the front.

4 WHERE DO WE GO FROM HERE?

Understanding what drives the spread of invasive populations is the first step towards taking actions to reduce their impact. The involvement of the public in control initiatives can be a resource (e.g. Malpica-Cruz *et al.* 2016), and new technology can reduce the labour requirement of control measures (see the “SuperSucker” developed to remove invasive algae from coral reefs in Hawaii; Neilson *et al.* 2018). Management plans, however, are likely to be effective only when supported by scientific evidence (Lodge *et al.* 2006). In this thesis, I study the dynamics and spatial ecology of introduced guppy populations to better understand how individual traits contribute to determining the spread of populations. I believe the *take-home message* of the studies I present here can be articulated in three points.

I show that disturbance can favour introduced populations and increase their population density (I). This is not a new concept (Elton 1958, Davis *et al.* 2000), yet it reiterates that invasive species should not be considered in isolation but in the context of a changing world shaped by anthropogenic impact.

When considering multiple spatial scales simultaneously, two patterns emerge. First, properties at different scales can interact in determining an individual’s behaviour: dispersal is determined by the interaction between density at both local and landscape scales (II). Second, the same process can differ when it manifests at different scales: density-dependent habitat use is governed by an ideal free distribution (Fretwell and Lucas 1970) at the landscape scale, but follows an ideal despotic distribution (Fretwell 1972) locally, between microhabitat types within a patch (III). The spatial scale of a study should always be made explicit, given how it affects the patterns described (Levin 1992).

Finally, as the introduced population adapts, I find guppies’ invasive potential to decrease (IV). Moreover, I find higher dispersal distance— a key component shown to produce accelerating waves of spread in theoretical studies (Kot *et al.* 1996, Neubert and Caswell 2000, Nehrbass *et al.* 2007)— to *negatively* affect the speed of spread (IV). I explain this result in connection with the low population growth rate and the positive density-dependent survival.

This study suggests that an integrative approach that accounts for life history, dispersal, and their evolution can aid in understanding the complex interactions that drive the spread of populations, even when the outcome is seemingly counterintuitive.

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RIASSUNTO (RÉSUMÉ IN ITALIAN)

Dispersione, utilizzo dell'habitat, e dinamiche durante la diffusione di popolazioni introdotte: caso-studio sul guppy (*Poecilia reticulata*)

Secondo un rapporto delle Nazioni Unite pubblicato nel maggio 2019, un milione di specie è a rischio d'estinzione. Le attività umane stanno cambiando il pianeta e causando una perdita di biodiversità¹ che procede ad una velocità senza precedenti. Per invertire questa tendenza sono necessarie azioni radicali, guidate da solide basi scientifiche.

L'introduzione di specie "aliene" è uno dei principali fattori che contribuiscono a ridurre la biodiversità. Una specie è ritenuta aliena quando è introdotta – accidentalmente o volontariamente – al di fuori del suo areale naturale. Benché molte popolazioni introdotte non siano in grado di sopravvivere nel nuovo ambiente, alcune prosperano tanto da diventare nocive, espandendo il territorio occupato e arrecando danni all'ambiente e all'economia locale. La completa rimozione delle popolazioni introdotte è spesso impraticabile o eccessivamente costosa, ma un'efficace alternativa è il controllo della loro espansione, al fine di ridurre l'area in cui sono presenti. Questa tesi nasce dalla necessità di approfondire la conoscenza di cause e meccanismi che regolano la diffusione² delle popolazioni introdotte, per poterne combattere l'espansione.

La velocità con cui una popolazione introdotta si diffonde nel territorio è il prodotto di due componenti: la crescita di popolazione e la dispersione³ degli individui che ne fanno parte. Per comprendere processo di diffusione è quindi necessario studiare i fattori che regolano i tassi di mortalità e natalità (tassi che determinano la crescita di popolazione) e quelli che influenzano il fenomeno di dispersione. Un fattore d'interesse è la densità di popolazione, definita come il numero di individui che occupano una certa area. La densità di popolazione emerge dai tassi demografici (mortalità, natalità e dispersione determinano il numero di individui presenti), ma allo stesso tempo influisce su questi tassi, creando un'interazione reciproca. Una densità elevata, ad esempio, comporta una riduzione delle risorse (cibo, rifugi ecc.) disponibili per ciascun individuo, e può causare una riduzione delle nascite, un aumento della mortalità, e/o spingere alcuni individui ad emigrare in cerca di un habitat più favorevole.

Un secondo fattore chiave che influisce sulla velocità di diffusione riguarda i cambiamenti evolutivi. Dopo essere introdotta in un nuovo ambiente,

¹ La *biodiversità* (o diversità biologica) rappresenta l'insieme degli organismi, in tutte le loro forme e varietà, e degli ecosistemi in cui essi vivono.

² Con *diffusione* s'intende il processo biologico con cui una popolazione di organismi cambia l'area di territorio da essa occupato.

³ In biologia, il termine *dispersione* indica lo spostamento di un individuo dal luogo d'origine ad un nuovo territorio, in seguito ad un movimento attivo o al trasporto passivo. Al contrario di *diffusione*, che si riferisce ad un processo inerente ad una popolazione, *dispersione* è un comportamento individuale.

una popolazione aliena incontra pressioni selettive diverse da quelle a cui si è adattata nell'ambiente naturale da cui proviene. Qualora l'adattamento alle nuove condizioni riguardasse i tratti che determinano la diffusione della popolazione, la velocità con cui la popolazione si espande sul territorio potrebbe essere diversa da quella osservata nel luogo d'origine. Un esempio è la rapida diffusione del rospo delle canne (*Rhinella marina*) in Australia. Introdotto per ridurre il numero di insetti nelle piantagioni di canna da zucchero, in pochi decenni il rospo si è diffuso in tutta l'Australia del nord, espandendo il suo areale a una velocità molto più elevata di quanto previsto. Questo è stato attribuito principalmente all'evoluzione di tratti che garantiscono una dispersione più efficace: i rospi in Australia hanno sviluppato zampe più lunghe e robuste, che garantiscono spostamenti più rapidi e una maggiore resistenza.

In natura è difficile osservare il corso di un'espansione da parte di una popolazione aliena, poiché spesso l'introduzione è accidentale e la popolazione è scoperta solo dopo essersi stabilita. In alternativa, è possibile studiare popolazioni introdotte intenzionalmente allo scopo di monitorarle sin dal principio, per comprendere le fasi iniziali del processo di stabilimento e diffusione.

Questa tesi descrive lo studio approfondito su diverse popolazioni di guppy (*Poecilia reticulata*), un piccolo pesce d'acqua dolce. Originario del Sud America e dei Caraibi, il guppy è stato introdotto in ogni continente eccetto l'Antartide, come controllo biologico per combattere le zanzare oppure a seguito di liberazioni involontarie di animali tenuti in acquario, con conseguenze negative sulle specie locali. Nella mia tesi, prendo in considerazione sia popolazioni naturali, sia popolazioni introdotte in quattro torrenti in cui i guppy erano storicamente assenti. Per studiare queste popolazioni ho utilizzato sia tecniche di analisi statistica dei dati raccolti, su base mensile per dieci anni, sulle quattro popolazioni introdotte, sia esperimenti sul campo a breve termine svolti sulle popolazioni naturali. Inoltre, ho sviluppato modelli matematici (*integral projection models, IPM*) per ricostruire la dinamica di diffusione delle popolazioni partendo dai fattori che la determinano (come i tassi demografici e i comportamenti individuali). Con questi modelli è possibile determinare come la velocità di diffusione cambia in base ai fattori chiave e ai cambiamenti evolutivi osservati nelle popolazioni introdotte. Nei successivi paragrafi sono descritti brevemente i risultati principali della ricerca.

Le quattro popolazioni di guppy crescono rapidamente dopo essere state introdotte, e la crescita dipende dalle condizioni ambientali. In due dei quattro torrenti, la vegetazione sovrastante è stata sfoltita prima dell'introduzione e così mantenuta per la durata dell'esperimento, riproducendo una forma comune di disturbo ambientale (la deforestazione); la densità di popolazione raggiunta in questi casi eccede di molto quella osservata nelle popolazioni naturali. Questo risultato suggerisce che le attività umane di disturbo (come la deforestazione) possano promuovere il successo di una popolazione aliena introdotta.

Uno studio approfondito in uno dei quattro siti d'introduzione rivela che la densità di popolazione influenza la probabilità di dispersione degli individui. Densità elevate a livello locale, all'interno di un habitat, promuovono l'emigrazione di individui giovani, ma questo avviene solo quando la densità di popolazione complessiva, a livello dell'intero torrente, è relativamente bassa. La bassa densità complessiva suggerisce che habitat poco affollati sono presenti altrove, rendendo benefica l'emigrazione da habitat ad alta densità locale. A differenza di quanto avviene per gli individui giovani, il comportamento degli individui adulti cambia nel tempo, indicando possibili cambiamenti evolutivi. Immediatamente dopo l'introduzione nel torrente, la correlazione fra densità di popolazione e probabilità di dispersione è negativa; gli individui preferiscono rimanere in gruppo piuttosto che abbandonare habitat a densità elevata. Col passare del tempo gli individui sviluppano la tendenza opposta: dopo circa 15-20 generazioni, la correlazione diventa positiva, e gli individui adulti preferiscono evitare l'affollamento, emigrando quando la densità in un habitat è elevata.

Allo scopo di studiare come la diffusione delle popolazioni introdotte cambia nel tempo, ho costruito tre modelli matematici distinti (IPM), utilizzando dati provenienti da tre fasi del processo: la fase di colonizzazione (iniziale), di assestamento (centrale), e di adattamento (finale). Comparando le previsioni generate dagli IPM riguardanti le tre fasi, è possibile non solo riconoscere cambiamenti nella velocità di diffusione, ma anche osservare se si modificano le componenti chiave che controllano il processo. Le previsioni generate evidenziano, col passare del tempo, un calo nella velocità di diffusione, al contrario di quanto dimostrano studi precedenti (vedi l'esempio del rospo delle canne). Appena introdotti, i guppy si diffondono velocemente, occupando un'area sempre più vasta. Già dalla fase di assestamento, la diffusione è molto più lenta, a fronte soprattutto di una ridotta crescita della popolazione. In tutte le fasi, le componenti chiave nel determinare la velocità di diffusione sono i tassi di mortalità e natalità, mentre i tratti legati alla dispersione degli individui hanno un effetto solo marginale.

Un risultato controintuitivo particolarmente interessante è che, nella fase finale di adattamento, se gli individui si disperdono su lunghe distanze, la velocità di dispersione cala ulteriormente. Questo, ancora una volta, è in controtendenza con quanto dimostrato, ad esempio, dagli studi sull'espansione del rospo delle canne, dai quali si evince che distanze di dispersione più alte aumentano di molto la velocità di diffusione. Il risultato del mio studio è dovuto alla crescita molto lenta della popolazione di guppy, nella fase finale: la dispersione lontano dal centro della popolazione crea piccoli gruppi isolati, non in grado di persistere e creare nuove popolazioni stabili.

Questa tesi dimostra come la scomposizione di un processo complesso nelle sue minime parti può aiutare a comprenderlo in misura maggiore. Ricostruire la dinamica di diffusione di una popolazione partendo dai comportamenti degli individui che la compongono aiuta a gettare luce sui meccanismi che determinano il processo. Una conoscenza approfondita di tali

meccanismi offre una solida base scientifica alle azioni volte a limitare l'avanzata delle popolazioni aliene, e a rallentare la perdita di biodiversità.

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