Evolution in a Complicated World

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SUMMARY

The principle of natural selection is fundamentally a simple one, but the circumstances under which it operates can be very complicated. Selection pressures derive from a dynamic environment and the interactions with conspecifics and other organisms. Phenotypic variation is shaped by genetic and developmental mechanisms that cannot be solely understood from an evolutionary perspective. A good theoretical understanding of evolution is therefore a task of considerable difficulty. The frameworks that currently inform our understanding of evolution have a limited capacity to account for such complications as by necessity they focus on simple scenarios that may be unrepresentative of nature at large. In contrast, evolutionary individual-based models can give detailed accounts of the interactions between individuals as well as between individuals and the environment and may therefore more comprehensively represent the settings in which natural selection occurs. Using this approach, I here investigate the evolution of movement and competition strategies in populations of individuals acting as predators, kleptoparasites and foragers competing for resource items and shares. An excursion into life history theory and two commentaries on published works complement these chapters and complete the thesis.

Chapter 2 presents an individual-based model of predator-prey coevolution, where predators and prey move and interact in a spatially explicit setting via their inherited movement strategies. In contrast to coarse-grained models that often focus on population-level processes, important ecological and evolutionary features such as changes in local densities or differences in survival and reproduction emerge in this model naturally from the interactions between individuals. Predators and prey are engaged in a behavioural response race, which may entail considerable strategic complexity, as predators need to predict the movements of prey, which in turn need to be unpredictable to predators while covering their resource requirements. The spatial distributions of predators and prey are thus determined by the movement strategies and the local ecological and evolutionary responses of predators and prey, which often manifest in patterns such as dynamic spiral waves or static spotted patterns. It turns out that evolutionary transitions between movement strategies occur rapidly and are accompanied by shifts between these ecological patterns. Evolution regularly leads to the emergence of alternative movement strategies that coexist in the same population. I

argue that rapid evolution, coexistent movement types, and phase shifts between different ecological regimes are not a peculiarity of our model but a result of more realistic assumptions on eco-evolutionary feedbacks and the enhanced number of evolutionary degrees of freedom.

In **chapter 3**, I take a closer look at the within-population interactions of competitors. Birds such as Oystercatchers often steal food items directly from conspecifics, a foraging strategy known as kleptoparasitism that causes a conflict of interest with potentially wide-ranging consequences. I investigated scenarios of resource competition where 1) individuals only forage, 2) individuals either forage or steal, and 3) individuals can flexibly switch between foraging and stealing. While foragers in scenario 1 utilise each other's presence as an indication of resource abundance, conspecifics are generally avoided as soon as stealing occurs. Resource consumption is much lower in populations with obligatory kleptoparasites, but less so when individuals can choose strategies flexibly. If resources become very abundant, obligate kleptoparasites go extinct, but stealing remains a common occurrence in facultative kleptoparasites. The study emphasises the advantages of a mechanistic approach when studying competition in a spatial context, and suggests how evolutionary modelling could be integrated with current work in animal movement ecology.

Competing conspecifics may differ considerably in their competitive ability, which may also impact their distribution in space. One of the classical models used to understand the distribution of unequal competitors is the ideal free distribution, which predicts that, at equilibrium, the competitive intensity at each location should be proportional to the resource richness of that location. How different types are distributed across different resource levels is however not determined; in principle, weak competitors can freely co-occur with strong competitors. By means of simulations and analytical arguments, I show in **chapter 4** that unequal competitors nevertheless have a tendency to segregate, such that strong competitors predominate on resource-rich patches, whereas weak competitors become increasingly restricted to patches of a lower resource level. If competitive abilities are then allowed to evolve over successive generations, I observe that this spatial assortment can lead to a diversification into different competitive types. The difference in habitat preference between strong and weak competitors is therefore not only ecologically important but also can give rise to the coexistence of unequal competitors in the first place.

Chapter 5 presents a change in topic from evolutionary ecology to life-history theory, and also a change in method from individual-based simulations to the mathematical analysis of a class-structured model. Evolutionary theories of ageing explain the universal occurrence of senescence by arguing that selection for survival early in life is much stronger than selection for survival late in life. This argument is quantified by showing that the ‘force of selection’, a measure for the intensity of natural selection, decreases with age after the onset of reproduction. Before the onset of reproduction, the force of selection is supposed to be constant. This latter finding however rests on the assumption that offspring become independent immediately after birth. In contrast, I show in this chapter that if offspring depend on their parents, either during gestation or in periods of obligate parental care, the force of selection increases up until the age at which offspring become independent from their parents. The fact that the force of selection is weaker at early life stages presents a possible evolutionary mechanism for the commonly observed elevated mortality rates during early stages of ontogeny.

Individual-based models have significant advantages over analytical approaches, but they can also be difficult to interpret and are prone to implementation errors, and a critical engagement with the published literature is therefore important. Part of this thesis are two commentaries, the first of which treats an article that considered how personality variation influences the speed at which foragers reach an ideal free distribution on a resource landscape. A brief inspection indicated significant conceptual and technical weaknesses. Without much effort, we could demonstrate that some of the more surprising ’findings’, such as that a higher proportion of active individuals or a larger population size retards the approach to the ideal free distribution, reflect questionable model assumptions or technical errors. If we want to rely on the conclusions drawn from individual-based models, attention must be given to such detail.

The second commentary concerns a paper that studies how adaptive response modes such as adaptive tracking or developmental plasticity evolve under different environmental regimes. The authors observed that different response modes evolve in distinctive regions of the parameter space, and that regime shifts are often accompanied by extinction if populations are forced to cross the border between response mode regions. When I reimplemented this model, I achieved the same overall results but in the process arrived at a somewhat different interpretation. The authors argue that the borders between response mode regions correspond to evolutionary tipping points that entail an elevated extinction risk. In contrast, I find there to be no reason why response mode borders should incur any extinction risk, since it is primarily the suitability of each response mode by itself that determines extinction risk, not the contrast between response modes. Only when a population presently is at risk of extinction, a comparison of evolutionary rescue potential within and between adaptive response modes may give cause to speak of ‘tipping points in evolutionary rescue potential’. These however not necessarily correspond to response mode borders. If nothing else, this commentary shows the difficulty of interpreting the results of individual-based models, even if the technical implementation is noncontroversial.

Evolutionary individual-based models are incredibly versatile and provide an important complement to analytical approaches that rely heavily on certain standardised simplifications. Individual-based models have the downside that the conclusions drawn are often very context-dependent and difficult to interpret. These models may thus not give us novel general insights but rather teach us that the general insights we hold dear may not be as general and firm as is commonly suggested. In the beginning, I highlighted the importance of the mechanisms underlying phenotypic variation, but the models I presented do not give explicit consideration to said mechanisms. Going forward, I believe it is of the essence for evolutionary biology to jointly consider what is selected for (and how strongly) and what kinds of variation can emerge (and how much variation is introduced). Only through the combination of both perspectives can a balanced view of evolution be achieved. Simulation models may also here play an important and useful role.

NEDERLANDSE SAMENVATTING

Het principe van natuurlijke selectie is in wezen eenvoudig, maar de omstandigheden waaronder natuurlijke selectie werkt, kunnen zeer ingewikkeld zijn: selectiedrukken komen voort uit een dynamische omgeving en de interacties met soortgenoten en andere organismen, en fenotypische variatie is het resultaat van ontwikkelingsmechanismen die niet uitsluitend vanuit een evolutionair perspectief kunnen worden begrepen. Een diepgaand begrip van evolutie is dan ook een zeer moeilijke taak. De theoretische kaders die momenteel ons begrip van evolutie onderbouwen, zijn maar beperkt in staat om dergelijke complicaties mee te nemen en zijn daarom wellicht niet representatief voor de natuur als geheel. Daarentegen kunnen “individu-gebaseerde” modellen een gedetailleerde beschrijving geven van de interacties tussen individuen onderling en tussen individuen en de omgeving, en daardoor een vollediger beeld geven van de omstandigheden waarin natuurlijke selectie plaatsvindt. Met behulp van deze modellen onderzoek ik in drie hoofdstukken van mijn proefschrift de evolutie van bewegings- en competitiestrategieën in populaties waar de individuen concurreren om voedsel en andere resources. Een uitstap naar life-history theorie en twee commentaren op artikelen van vakgenoten vullen deze hoofdstukken aan.

Hoofdstuk 2 presenteert een individu-gebaseerd model van co-evolutie tussen een roofdier- en een prooipopulatie, waarbij roofdieren en prooien, gestuurd door erfelijke bewegingsstrategieën, bewegen in de ruimte. In tegenstelling tot de standaard modellen voor predator-prooi co-evolutie ontstaan in mijn model de belangrijkste ecologische en evolutionaire processen, zoals de verandering in lokale dichtheden of verschillen in overleving en reproductie, op natuurlijke wijze uit de interacties tussen individuen. Roofdieren en prooien zijn verwikkeld in een ingewikkelde evolutionaire wedstrijd om hun gedrag aan te passen aan het gedrag van soortgenoten en het gedrag van de tegenpartij. Dit brengt een aanzienlijke strategische complexiteit met zich mee, aangezien roofdieren de bewegingen van prooien moeten voorspellen, terwijl prooien op hun beurt onvoorspelbaar moeten zijn voor roofdieren en tegelijkertijd op een efficiënte manier naar voedsel moeten zoeken. De evoluerende bewegingsstrategieën leiden tot ruimtelijke verdelingen van roofdieren en prooien die sterk af kunnen wijken van de voorspellingen van reeds bestaande modellen. Zo kunnen dynamische “spiraalgolven” op basis van de co-evolutie van bewegingsstrategieën snel afwisselen met statische “vlekkenpatronen”. Bovendien leidt evolutie vaak tot aanzienlijke variatie in beide populaties: in roofdieren en prooien ontstaan alternatieve bewegingsstrategieën die voor vele generaties naast elkaar blijven bestaan. Ik ben ervan overtuigd dat snelle evolutie, naast elkaar bestaande bewegingstypen en faseverschuivingen tussen verschillende ecologische regimes geen eigenaardigheden zijn van dit specifieke model, maar een gevolg van meer realistische aannames over eco-evolutionaire terugkoppelingen en het grotere aantal evolutionaire vrijheidsgraden.

In **hoofdstuk 3** ga ik dieper in op de interacties van concurrenten binnen een populatie. Vogels zoals Scholeksters stelen vaak voedsel van soortgenoten, een foerageerstrategie die bekend staat als kleptoparasitisme, en het is bekend dat dit gedrag verstrekkende ecologische gevolgen heeft. Ik onderzocht de evolutie van bewegingsstrategieën in drie scenario’s van voedselconcurrentie waarbij 1) individuen alleen foerageren, 2) individuen ofwel foerageren ofwel stelen, en 3) individuen flexibel kunnen wisselen tussen foerageren en stelen. De individugebaseerde simulaties laten zien dat in de drie scenario’s zeer verschillende bewegingspatronen ontstaan. Terwijl foerageerders in scenario 1 elkaars aanwezigheid gebruiken als indicatie van voedseldichtheid, worden soortgenoten in het algemeen gemeden zodra stelen plaatsvindt. In populaties met verplichte kleptoparasieten (scenario 2) is de consumptie van resources veel lager, maar dit is niet het geval als individuen flexibel hun strategie kunnen kiezen (scenario 3). Als de voedseldichtheid heel hoog wordt, sterven obligate kleptoparasieten uit, maar bij facultatieve kleptoparasieten blijft stelen veel voorkomend. Deze studie toont de voordelen van een mechanistische, individu-georiënteerde benadering en laat zien hoe evolutionaire modellering kan worden geïntegreerd in de “movement ecology” (bewegingsecologie) van dieren.

Concurrerende soortgenoten kunnen aanzienlijk verschillen in hun concurrentievermogen, wat ook hun verspreiding in de ruimte kan beïnvloeden. Een van de klassieke modellen hiervoor is de “ideale vrije verdeling”, die voorspelt dat de verdeling van ongelijke concurrenten pas dan in evenwicht is als de competitie intensiteit op elke plaats evenredig is met de voedseldichtheid op die plek. Hoe de verschillende types concurrenten verdeeld zijn over verschillende voedselniveaus blijft echter onduidelijk: in principe kunnen zich zwakke concurrenten richten op voedselrijke plaatsen, terwijl sterke concurrenten op arme plekken accumuleren. Door middel van simulaties en analytische argumenten toon ik in **hoofdstuk 4** aan dat dit, bij nader inzicht, toch onmogelijk is. Ik laat zien dat ongelijke concurrenten de neiging hebben om te segregeren, zodat sterke concurrenten overheersen op voedselrijke plekken, terwijl zwakke concurrenten accumuleren op plekken met minder voedsel. Deze segregatie heeft interessante evolutionaire consequenties. Als ik namelijk begin met een populatie van individuen die niet verschillen in concurrentievermogen en vervolgens het concurrentievermogen laat evolueren, dan ontstaat, onder bepaalde omstandigheden, een diversificatie in verschillende concurrentietypen. Het verschil in habitatvoorkeur tussen sterke en zwakke concurrenten is dus niet alleen ecologisch belangrijk, maar kan ook de aanleiding zijn van het naast elkaar bestaan van ongelijke concurrenten.

In **hoofdstuk 5** verandert het onderwerp van evolutionaire ecologie naar life-history theorie, en ook de methode verandert van individu-gebaseerde simulaties naar de wiskundige analyse van een leeftijds-gestructureerd model. Evolutionaire theorieën over veroudering verklaren het universele optreden van veroudering door aan te voeren dat selectie voor overleving op jonge leeftijd veel sterker is dan selectie voor overleving op latere leeftijd. Dit argument wordt gekwantificeerd door aan te tonen dat de "force of selection" (selectiekracht), een maat voor de intensiteit van natuurlijke selectie, (a) constant is tot de leeftijd van eerste reproductie en (b) vanaf dat moment continu afneemt met de leeftijd. Ik laat echter zien dat onderdeel (a) van dit argument op de veronderstelling berust dat nakomelingen onmiddellijk na de geboorte onafhankelijk van hun ouders worden. Als nakomelingen wel afhankelijk zijn van hun ouders, hetzij tijdens de dracht, hetzij in perioden van ouderlijke zorg, neemt de selectiekracht toe tot de leeftijd waarop nakomelingen onafhankelijk worden. Het feit dat de selectiekracht zwakker is in de vroegste levensstadia geeft een mogelijke evolutionaire verklaring voor de waarneming dat in veel organismen het sterftecijfer aan het begin van hun leven bijzonder hoog is.

Individu-gebaseerde modellen hebben belangrijke voordelen boven analytische benaderingen, maar ze zijn gevoelig voor implementatiefouten en kunnen ook moeilijk te interpreteren zijn. Daarom is een kritische houding naar gepubliceerde literatuur belangrijk. Onderdeel van dit proefschrift zijn twee commentaren, waarvan het eerste een artikel behandelt waarin wordt nagegaan hoe variatie in “animal personalities” (persoonlijkheid van dieren) van invloed is op de snelheid waarmee foerageerders een ideale vrije verdeling bereiken. Een korte inspectie van het artikel wees op belangrijke conceptuele en technische tekortkomingen. Zonder veel moeite konden we aantonen dat sommige van de meer verrassende “bevindingen”, zoals dat een groter aandeel actieve individuen of een grotere populatiegrootte de weg naar de ideale vrije verdeling vertraagt, het gevolg zijn van twijfelachtige modelaannames of technische fouten. Als we willen vertrouwen op de conclusies van individu-gebaseerde modellen, moet aan dergelijke details aandacht worden besteed.

Het tweede commentaar betreft een artikel waarin de auteurs eerst laten zien dat afhankelijk van het “omgevingsregime” (de snelheid en voorspelbaarheid van omgevingsverandering) verschillende types responsstrategieën evolueren (zoals fenotypische plasticiteit of “bet-hedging”). Vervolgens bestuderen zij de consequenties van een verandering in het omgevingsregime (bijvoorbeeld door klimaatverandering) op het aanpassingsvermogen van de geëvolueerde populaties. Hierbij komen zij tot de opmerkelijke conclusie dat omgevingsveranderingen die een omschakeling naar een ander type responsstrategie noodzakelijk maken “tipping points” (kantelpunten) zijn voor de levensvatbaarheid van de populatie: als zo’n punt bereikt wordt is, volgens de auteurs, de kans op extinctie zeer groot. Toen ik dit model opnieuw implementeerde, verkreeg ik dezelfde algemene resultaten, maar kwam daarbij tot een enigszins andere interpretatie. Ik laat zien dat het uitsterfrisico van de populatie in eerste instantie door andere factoren wordt bepaald. Alleen wanneer een populatie al op basis van deze factoren met uitsterven wordt bedreigd, worden de in het artikel beschreven kantelpunten relevant, want op zo’n punt kan de kans op “evolutionary rescue” (evolutionaire redding) sterk afnemen. Uit dit commentaar blijkt hoe moeilijk het kan zijn om de resultaten van individu-gebaseerde modellen te interpreteren, zelfs als de technische uitvoering niet controversieel is.

Evolutionaire individu-gebaseerde modellen zijn ongelooflijk veelzijdig en vormen een belangrijke aanvulling op analytische benaderingen die sterk steunen op bepaalde gestandaardiseerde vereenvoudigingen. Individu-gebaseerde modellen hebben echter als nadeel dat de getrokken conclusies vaak zeer contextafhankelijk en moeilijk te interpreteren zijn. Deze modellen geven ons dus misschien geen nieuwe algemene inzichten, maar leren ons eerder dat de “algemene” inzichten die ons dierbaar zijn misschien minder algemeen en robuust zijn dan gewoonlijk wordt gesuggereerd. Aan het begin van mijn proefschrift benadruk ik dat, naast een individu-georiënteerde benadering, ook rekening zou moeten worden gehouden met andere factoren. Hierbij noem ik vooral de mechanismen die ten grondslag liggen aan fenotypische variatie. Aan het einde van mijn proefschrift moet ik concluderen dat de modellen die ik presenteerde hier geen expliciete aandacht aan besteden. Ik geloof dat het voor de evolutiebiologie van essentieel belang is om zowel na te gaan waarop wordt geselecteerd (en hoe sterk), als welke soorten variatie kunnen ontstaan (en hoeveel variatie wordt geïntroduceerd). Alleen door de combinatie van beide perspectieven kan een evenwichtige kijk op evolutie worden bereikt. Ook hier kunnen simulatiemodellen een belangrijke en nuttige rol spelen.

1

INTRODUCTION

The fundamental premise of the present work is that there exists a gross disparity between the complicated world in which evolution takes place, and the situations that can be considered through existing model frameworks. This is not to reject these frameworks and their accomplishments, but to emancipate our view of evolution from the simplifying assumptions that they entail.

The task of accurately capturing reality in theoretical models is particularly challenging in evolutionary biology. As we move from atoms and simple molecules to higher levels of organization, from proteins and genes to organisms and species, the things we consider as units become less clearly delineated. What precisely a species is can be discussed endlessly without ever arriving at a definite answer, and even the border between organisms and their environment proves elusive upon close examination. The boundaries we draw to conceptualise nature are absent from reality, and attempts at rigorous, universal definitions must be doomed to fail at such higher levels of organization. The amount of pattern captured in our concepts however allows us to develop theories that portray the essence of certain natural phenomena. Our models are therefore always somewhat provisional because we never know exactly when critical failure strikes. In this thesis, I present a number of different models, that start off where our simple theoretical frameworks stop. The aim is to investigate whether adding more complexity leads to new conclusions and insights. My method of choice is an individual-based simulation approach, but in several places, mathematical models are also studied, particularly in the later chapters. Individual-based models are great tools for exploration, as they come with very little conceptual baggage and allow the modeller to pretty much do as he or she pleases. Particularly, the mechanisms behind complicated strategic behaviour, genotype-phenotype mappings or the interactions between individuals, can be considered.

Before I start to describe and motivate my approach, I first discuss the principles underlying Darwin's theory of natural selection (Darwin, 1859). In a nutshell, Darwin recognized that the apparent presence of design and function in organisms can be explained through the differential reproductive success of organisms with different phenotypes, a measure for which he introduced the term 'fitness'. More explicitly, the necessary conditions for natural selection to occur are 1) the presence of phenotypic variation, 2) the inheritance of phenotypes from parents to offspring, and 3) a systematic effect of the phenotype on survival and reproduction (Lewontin, 1970). Together, these three conditions are sufficient to produce natural selection.

From the very start, Darwin's theory was only loosely based on biological mechanisms. To this day, gaping holes remain in our understanding of the three conditions that natural selection requires. Mutations, the source of variation, are often assumed to occur randomly and in an unbiased fashion, but at the same time can be observed to be distributed unevenly over the genome (Ellegren et al., 2003). Indeed, it is far from settled what determines mutation rates, potential factors including position in the genome, physiological or environmental conditions such as free radicals and radiation, as well as transcription and replication frequency. Likewise, how mutations impact phenotypes, and analogously how the genome gives rise to phenotypes, is virtually unknown except in a small number of cases, and so far emerging general principles are scarce. The elemental principles of inheritance only became known after Darwin's theory of natural selection had already risen to prominence: Gregor Mendel's results (1866) only passed into the communal scientific consciousness in the early 1900s (Correns, 1900; Bateson, 1902), August Weismann's theory of the separation between germline and soma was published in 1893, and the role of DNA as the medium of inheritance was only discovered in the 1950s (Hershey and Chase, 1952). Instead of neatly filling the gaps in our conceptual framework, new research often shows that dearly-held convictions need to be revised. For example, while inheritance is commonly thought to be limited to DNA sequences and the germline, research of the last 30 years has shown that DNA methylation patterns transmitted from parents and even grandparents to offspring can influence the phenotypes of offspring, providing the basis for a new kind of epigenetic inheritance (Jablonka and Raz, 2009). As another case in point, the gestational environment can have profound influences on developmental processes, another mechanism of extra-genomic inheritance that also highlights the importance of developmental processes. Experiments in two mice strains that differ in the number of lumbar vertebrae (five and six, respectively), showed that hybrid embryos generally developed into the maternal phenotype, irrespective of the embryo's genotype (McLaren and Michie, 1958). Even more intriguingly, if embryos from a 5' mother were transplanted into the other strain, embryos developed six lumbar vertebrae (McLaren and Michie, 1958; Newman, 2002). The womb of a mother with six lumbar vertebrae thus impressed its phenotype onto the developing offspring, independently of the underlying genotype or cellular characteristics. Weismann would have been astonished.

If the mechanisms behind inheritance and phenotypic variation play a contentious role in evolutionary theory, the role of the environment in selecting different phenotypes takes the central stage. It is clear that the reproduction and survival of organisms can be affected by a tremendously large number of factors in their environment, and determining the selection pressures acting on populations and traits may be *the* key challenge of evolutionary ecology. Selection pressures can arise from abiotic factors such as temperature and pH as well as the interactions between individuals of the same or different species. In the latter case, evolution may directly alter the environment from which selection arises, and as we are to see, such feedbacks are pervasive and produce many of the complications for which sophisticated models need to be employed. If in contrast the selective environment is constant, we can imagine that a certain phenotype achieves maximal survival and reproduction and that ultimately evolution will arrive at this point regardless of the exact details of genetic variation or inheritance.

This is the rationale behind the optimality approach, arguably the simplest way to model evolution by natural selection. To start, a 'proxy for fitness' is identified, that is, a measure that is closely associated with survival and reproduction and therefore assumed to be optimized by natural selection. The optimal bone structure can for example be calculated based on expected load and tissue expense, the optimal diameter of insect ommatidia in relation to resolution and diffraction (limiting the minimum size of ommatidia), and the pore size of eggshells by the trade-off between oxygen conduit and water evaporation (Alexander, 1996). There is no guarantee that an appropriate target of optimization can be found or that biological constraints are correctly identified. The optimality approach has found wide application in the field of optimal foraging theory: The marginal value theorem predicts when foragers should leave a patch (Charnov, 1976), and the ideal free distribution determines the optimal distribution of foragers on a resource landscape (Fretwell and Lucas, 1969), in both cases using (net) energy consumption as a proxy for fitness.

Evolution will produce optimal phenotypes only under certain restrictive conditions. There is no guarantee that natural selection dominates over drift or that sufficient variation is indeed present. Further, individuals and their conspecifics form and influence the very environment they inhabit. The selection pressures that emanate from sexual reproduction, cooperation or resource competition depend crucially on the phenotypes of conspecifics. Natural selection that arises from interspecific competition or predator-prey interactions depends on the dynamically evolving phenotypic characteristics of two (or more) species. The process of evolution itself then alters the selective environment in which it occurs, and the product is evolutionary dynamics that may be significantly more involved than a simple optimization process taking place under static environmental conditions. Different analytical frameworks have been developed over time, the three most prominent of which are population genetics (Fisher, 1930; Crow and Kimura, 1970; Hartl et al., 1997), quantitative genetics (Lande, 1976; Roff, 2012; Walsh and Lynch, 2018) and adaptive dynamics (Metz et al., 1995; Dieckmann and Law, 1996; Geritz et al., 1998; Diekmann et al., 2002). Here I give only a brief account of the underlying philosophy and basic assumptions that have shaped the development in these three fields.

Population genetics arose directly out of the union of Mendelian Inheritance with Darwin's evolutionary theory at the beginning of the 20^{th} century. The basic unit of consideration is the genetic variation at a gene locus and the measure of interest are the allele frequencies in a population. Models then differ in the number of alleles per locus and the number of loci, and in the case of multilocus models how recombination is included. Fitness is generally assigned to genotypes in an *ad hoc* manner, but in some extensions can also include the genotype-phenotype mapping and interactions between phenotypes and the environment. However, the basic assumptions of population genetics may predispose its practitioners to a 'gene's eye view' on evolution (Ågren, 2021). In his bean-bag debate, Ernst Mayr (1959) criticized this view, as it encourages a reductionist account of the way genes determine the phenotype. Indeed, it is easy to forget that alleles never determine phenotypes alone but always in a dynamic developmental process in which many different genes and the environment are always involved. Simple population genetics models are therefore only suitable if the genetic environment of the focal allele(s) is constant or neutral. Multi-locus models can already produce very complicated dynamics, and while models in principle can incorporate epistasis (the interactions between different gene loci, Wolf et al. 2000; Carter et al. 2005), a detailed empirical account of such interactions is usually still not available (Walsh and Lynch, 2018).

Quantitative genetics in contrast emerged from the discipline of biometricians and animal breeders. Contrary to its name, quantitative genetics does not necessarily require extensive genetic information. Instead, evolution is modelled based on the observed heritable variation in phenotypes. Generally, the theory considers phenotypic traits such as body size, fur length or speed of growth that show measurable, quantitative variation, and which are considered to be encoded by a large number of genes. The laws governing the inheritance of phenotypic traits are captured by the G-matrix, which collects the additive genetic variances and co-variances between traits. The change of trait means across generations is then given by the product of the G-matrix with the so-called selection gradient. If the G-matrix would remain constant over generations, this would allow long-term evolutionary predictions. The stability of the G-matrix is however controversial, because selection itself affects the additive genetic variance and covariance in a population, and hence the G-matrix. For example, if phenotypic traits are driven to extreme values, it seems plausible that additive genetic (co-)variation vanishes in the face of developmental constraints. Likewise, very strong selection should at least temporarily deplete variation. Understanding the evolution of the G-matrix itself is therefore a challenge of particular importance (Revell, 2007; Arnold et al., 2008), albeit one that may need to require extensive biological detail in each and every case.

Evolutionary game theory and adaptive dynamics have a common root in game theory and search for evolutionary equilibria that cannot be invaded by newly occurring variants. The focus of interest is on the strategic interactions between individuals, whereas genetics, inheritance and the reproductive system are in comparison less prioritized. Models develop a rigorous mathematical formulation of fitness based on the nature of interactions that occur between or within populations. Phenotypes may include involved strategies such as the Tit-for-Tat strategy of the Prisoner's Dilemma, or simple quantitative traits. In the case of the latter, approaches differ with regard to how phenotypic variation is considered. The evolutionarily stable strategy (ESS) approach assumes that mutations can produce phenotypes that differ a lot from current residents, which can potentially invade the population (Maynard Smith and Price, 1973; Maynard Smith, 1974). Adaptive dynamics on the other hand considers monomorphic populations, into which mutations of infinitesimal effect are introduced (Dieckmann and Law, 1996). If the new phenotype, at first at a vanishingly small frequency, has a fitness advantage over the resident phenotype, it can invade the population. A product of these assumptions are the pairwise-invasibility plots of adaptive dynamics, which show that four different types of evolutionary equilibria can exist that differ in evolutionary and convergence stability. Next to the evolutionary and convergent stable 'standard' equilibrium, the branching point equilibrium is of particular interest. Here, a population converges on a fitness minimum, at which point the population may diverge into two different morphs.

Each of the three frameworks entails a whole range of approaches that may differ strongly among themselves, and sometimes a border is difficult to draw. Population genetics and quantitative genetics converge on each other in the limit of a large number of additively interacting loci (Walsh and Lynch, 2018). Likewise, adaptive dynamics and quantitative genetics share the characteristic that the mean values of a trait within a homogeneous population change in relation to the fitness gradient (Abrams, 2001), and both approaches often make predictions that are in agreement with each other.

ECO-EVOLUTIONARY DYNAMICS

The interaction between phenotype and environment produces on the one hand selection on phenotypes, but on the other hand may also change the state of the environment. The ecological and evolutionary dynamics can thus be coupled. Traditionally, eco-evolutionary models assume that ecological dynamics and evolutionary dynamics occur at different timescales, allowing to apply the ‘separation of timescales’ technique that considerably simplifies the mathematical analysis. The rationale is that ecological dynamics assume an equilibrium so quickly that relevant evolutionary changes occur only under ecological equilibrium conditions. The interaction between evolution and the environment is therefore explicit, but transient ecological dynamics are considered negligible. This assumption is particularly plausible if evolution is mutation-limited, as in adaptive dynamics.

Recent experimental results have shown, however, that evolution may sometimes proceed so rapidly that transient ecological and evolutionary dynamics affect each other (Yoshida et al., 2003; Hairston Jr et al., 2005; Ellner, 2013). The key experiment showed that combined ecological and evolutionary dynamics in a predator-prey system can produce countercyclical population dynamics between predators and prey, something considered to be impossible in purely ecological models. Interestingly, many experiments in this field consider asexually reproducing populations, which contain a number of distinctive strains, the change in frequencies of which is then considered to be evolution (Yoshida et al., 2003; Turcotte et al., 2011; Hart et al., 2019). Such an experimental setup drives at a conceptual difficulty at the boundary between evolution and ecology just as much as it highlights the importance of rapid evolution: If we consider two prey strains as part of the same population, we indeed observe evolution as a change in gene frequencies at the loci at which the two strains diverge, and this evolutionary change very much occurs at ecological timescales. However, if we consider the two strains as separate populations, we observe purely ecological dynamics driven by apparent competition (Holt, 1977). It is therefore somewhat unclear whether these results constitute an important novelty or merely a change in perspective. Other studies however were able to show that rapid evolution also occurs in sexually reproducing populations (Pimentel et al., 1963; Pimentel, 1968; Tuda and Iwasa, 1998; Grant and Grant, 2006) and even asexual populations containing only a single strain, where evolution is mutation-limited (Bohannan and Lenski, 2000). The recognition that evolutionary dynamics can influence ecological dynamics in real-time is therefore in any case an important one.

Interestingly, the field of eco-evolutionary dynamics has focused primarily on abundances as the relevant ecological variable, and not so much on the spatial distribution of populations (but see the pioneering work of Pimentel et al. 1963, as well as Hanski and Mononen 2011). Spatial considerations can fundamentally change our conclusions obtained from non-spatial ecological and evolutionary models, e.g. with regards to the evolution of altruism (Nowak and

May, 1992; Le Galliard et al., 2003) or the stability of host-parasite populations in the Nicholson-Bailey model (Hassell et al., 1991, 1994). Including space in models however comes with significant analytical complications, and sometimes necessitates the shift to a simulation-based approach (Gilpin, 1987).

And again, we find that evolutionary and ecological processes are entangled. Most animals do not move randomly but have very specific habitat preferences and movement patterns, which in turn drive spatial distributions and local interactions. Particularly since the advent of animal tracking and movement ecology (Nathan et al., 2008), questions of how movement behaviour might evolve receive increasing attention (de Jager et al., 2011; Gupte, 2022). Again, such questions can be approached from an optimality paradigm, and this has been done in optimal foraging theory since the 1970s (Fretwell and Lucas, 1969; Charnov, 1976). Particularly in questions of foraging behaviour, however, resource dynamics and competitive interactions with conspecifics could play a significant role, such that the optimal behaviour might be strategically complex and a moving target. The proximate mechanisms that control behaviour, and which are subject to evolution should then be taken into account as best we can with our current state of knowledge. The spatial distribution of animals, their interactions in space and the evolution of the strategies that guide their movements will be a core theme of this thesis. In the next section, I will lay out the preferred methodology for this purpose.

SIMULATIONS AND INDIVIDUAL-BASED MODELS

Any model needs to wrangle with the complicated interactions of the natural world, and how to negotiate this landscape is often less clear in biology than in physics or chemistry. On the one hand, models should be as simple as possible. On the other hand, it seems clear that most ecological and evolutionary dynamics underlie complex mechanisms, reaching from gene-regulatory networks to cognition and environmental feedbacks. Mathematical models, or analytical techniques used on models, impose severe limitations on the processes that can be considered. First, if ecological and evolutionary timescales significantly overlap, and transient dynamics are important, the separation of timescales as classically adopted in adaptive dynamics may fail to give an accurate account of reality. Secondly, phenotypic variation is often left unaccounted for or considered through a mean-field approach. Third, the dynamical process of development, by which genetic information is translated into phenotypes, is barely considered in models of evolution, on the one hand due to a lack of insight into developmental processes, but on the other because only very simple genotype-phenotype mappings are permissible to analysis (phenotypic gambit, Grafen 1984). Last, spatial heterogeneity and population distributions are difficult to accurately portray, the method of choice usually introducing a substructure of patches, within which populations are again considered well-mixed. The consistency, with which these assumptions are made has the potential to distort our theoretical understanding of evolutionary processes.

Simulation models in general and individual-based models in particular do not obey the same constraints as analytical models and are capable to portray any process that can be run on a computer, the sole limitations are the programmer's abilities and runtime constraints. Individual-based models simulate the behaviour and interactions of individual organisms or agents, and therefore consider populations at the level at which phenotypic variation and ecological interactions naturally occur (Wolf et al., 2007). While most individual-based models are purely ecological, the fact that natural selection fundamentally acts as a birth-death process at the level of individuals makes individual-based models also a compelling approach for evolutionary theory (Doebeli et al., 2017). Further, the consideration of individual-level processes naturally gives rise to a mechanistic approach. Thus, models that are labelled 'mechanistic' often try to replace commonly made assumptions, which may gloss over many of the underlying details, with a more detailed portrayal of the processes (Duarte et al., 2012; van Gestel and Weissing, 2016; Van den Berg and Weissing, 2015). However, not all simulation models are mechanistic, and some analytical models can have mechanistic interpretations. Often the latter models are particularly valuable. A brief example follows (Case, 2000).

MECHANISMS IN MODELS

Picture a predator placed in a spatial environment, which is populated by a certain number of prey (fig. 1.1A). The predator detects any prey in a radius $d/2$ around its current position. If the predator now moves at a speed S, the area it searches for prey is simply $a = dS$, and the number of prey encountered per unit of time is $f_1(N) = aN$. This function is known as a functional response of type I (Holling, 1959) and has a clear mechanistic interpretation. The per-capita prey consumption of a predator under the functional response type I increases in proportion to the density of prey, and this may be perceived as a conceptual weakness. If predators need a certain amount of time to overcome and process each individual prey, there should be a natural maximum rate, at which predators can process prey. Indeed, we may now want to extend our verbal model such that whenever predators encounter a prey individual, the predator needs to stand

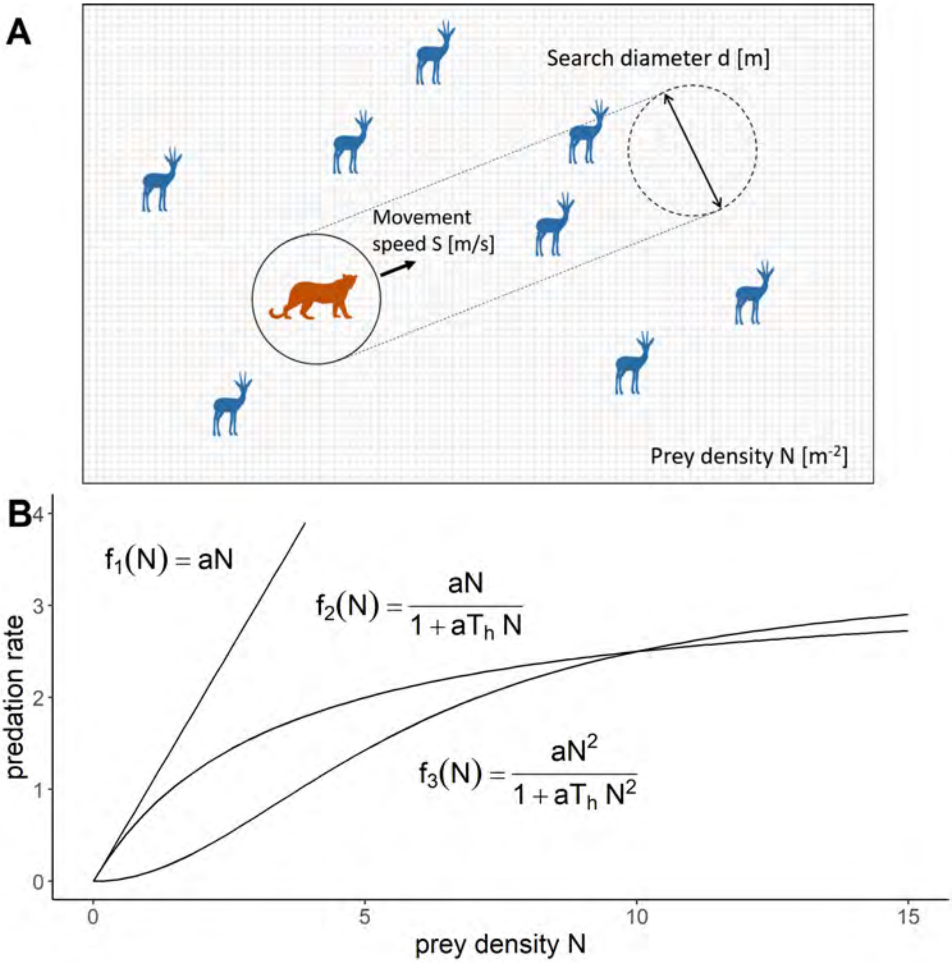

Figure 1.1 | The functional response of predators. **(A)** A predator set in a landscape inhabited by prey may be assumed to detect prey in a certain range d and move at a speed *S*. Depending on further assumptions in relation to handling time and encounter rate, predators catch prey in relation to prey density as determined by a functional response type I, II or III. **(B)** The functional responses type I, II and III, with parameters $a = 1$ for f_1 and f_2, $a = 0.1$ for f_3, $T_h = 0.3$.

still and handle the caught prey for a time period T_h. This yields the functional response type II, which indeed saturates:

$$f_2(N) = \frac{aN}{1 + aT_hN} \tag{1.1}$$

This equation still has a clear mechanistic interpretation, and is widely used in various modelling studies. Further scrutinizing this function, we may conclude that the predation rate should not increase linearly with prey density when prey is very rare. After all, many predators habituate to their prey and develop a search image, such that the rate of prey detection increases with prey abundance. Assuming for example that prey detection increases linearly with prey abundance, we replace a with aN and obtain the following functional response function, which is known as Holling's functional response of type III:

$$f_3(N) = \frac{aN^2}{1 + aT_hN^2} \tag{1.2}$$

This function no longer has a mechanistic interpretation, even though it may intuitively make sense and even be very useful. This is because our plausible assumption that prey detection should increase linearly with prey density is not grounded in any particular underlying mechanism, and may therefore be described as phenomenological. Through substantial further assumptions about predator cognition, a mechanistically motivated functional response of type III might be derived, but we would probably need to make a large number of additional assumptions, each of which with substantial associated uncertainty. It is therefore doubtful whether such an attempt would be useful. After all, also the functional responses I and II are based on assumptions that may be deemed unrealistic as well, such as the assumption that predators *do not* develop search images for example, or the absence of antipredator responses or escape movements in prey. One might say that mechanistic models simplify by omission, and thus have a very clear interpretation, whereas phenomenological models include that which cannot be known in detail, carrying along a lot of ambiguity. Often however the distinction is a relative one, where a mechanistic model tries to go beyond commonly made phenomenological assumptions by including some hypothetical underlying mechanisms.

THIS THESIS

Natural selection in its fundamental logic is a very simple mechanism, but how variation is generated and inherited, and the reasons why some individuals survive better than others, can be very intricate. The frameworks that inform our theoretical understanding have a limited capacity to account for such complications and often focus on simple scenarios that may be rather unrepresentative of nature at large. In particular, feedbacks between evolution and ecology are now known to be pervasive, and the phenotypes and interactions with the environment can be substantially more complicated than often assumed. There is no simple solution to these issues, and a wide array of theoretical approaches should be explored to provide further insights. This thesis presents my efforts in this direction.

The feedback between population dynamics and evolution was first experimentally demonstrated in predator-prey systems. Both ecological and evolutionary dynamics of predators and prey can also have an important spatial component, however, and in addition predators and prey are also engaged in a behavioural response race for space. This may entail considerable strategic complexity, as predators need to predict the movements of prey, which in turn need to be unpredictable while covering their resource requirements. The spatial distributions of predators and prey are thus determined both by the evolved movement strategies and the local ecological and evolutionary responses of predators and prey. This feedback loop is not ordinarily considered in eco-evolutionary dynamics. In **chapter 2**, I therefore present an individual-based model of coevolution, where predators and prey move and interact in a spatially explicit setting via their evolved movement strategies. The coevolution between predators and prey leads to rapid and repeated transitions in movement strategies. The movement strategies of predators and prey in turn produce ecological patterns such as dynamic spiral waves or static spots, and evolutionary transitions are often accompanied by changes in ecological patterns. While previous work has shown that spatial distributions are important for population stability and evolutionary dynamics, this study is novel in its consideration of the local interactions between predator and prey individuals as a function of their evolved strategies.

Chapter 2 looked at the evolution of movement strategies in predators and prey. Often, however, alternative foraging strategies coexist within a single population, and movement and foraging strategies evolve together. Birds such as the Oystercatcher sometimes steal food items directly from conspecifics, a foraging strategy which is called kleptoparasitism. This creates a conflict of interest, with wide-ranging consequences for movement and foraging behaviour, the spatial distribution of individuals as well as the overall food intake of the population. In **chapter 3**, we investigate scenarios of resource competition where 1) only foraging is permitted, 2) individuals either forage or steal, and 3) individuals can flexibly choose between foraging and stealing. While foragers in scenario 1 utilize each other's presence as an indication of resource abundance, conspecifics are generally avoided as soon as stealing is introduced. The resource consumption levels are lower in a population with kleptoparasites, but less so when foragers can choose flexibly. If resources become very abundant, obligate kleptoparasites go extinct, but stealing remains a common occurrence in facultative kleptoparasites. The study emphasises the advantages of a mechanistic approach when studying competition in a spatial context, and suggests how evolutionary modelling could be integrated with current work in animal movement ecology.

The ideal free distribution is the approach through which to understand the spatial distribution of foragers. In chapter 3 we found substantial deviations from ideal free predictions, which is not too surprising as the foragers make their small-step movement dependent on local information and are therefore neither 'ideal' (fully informed about the global state of the system) nor 'free' (able to move wherever they want at no costs). In **chapter 4**, we consider an individual-based model that gives unequal competitors ideal knowledge and the ability to move around freely. This model still yields some unexpected results. How unequal competitors should distribute over different patches has been extensively studied in the ideal-free-distribution literature, and the equilibrium condition predicts a broad range of neutral equilibria, where the ratio between resource abundance and competition intensity is homogenized over patches, but where different competitive types may freely co-occur with each other. By means of simulations and analytical arguments, I show instead that unequal competitors actually have a tendency to segregate, such that strong competitors predominate on resource-rich patches, whereas weak competitors become increasingly restricted to patches of a lower resource level. Up to this point, I followed the literature in assuming that there is a stable mixture of competitive abilities in the population. But shouldn't one expect that a single optimal competitive strategy should outcompete all other strategies? To investigate this question, I allowed competitive abilities to evolve over successive generations of the simulation. When the resource landscape was static, indeed only a single competitive type evolved. A very different outcome was obtained in case of a fluctuating resource landscape. Now, the spatial assortment of unequal competitors caused the diversification into a large number of different competitive morphs. The difference in habitat preference between strong and weak competitors is therefore not only ecologically important but also can give rise to the coexistence of unequal competitors in the first place.

While the preceding chapters investigated the ecology and evolution of animal movement by making the models in certain respects just a bit more realistic, **chapter 5** considers a complication in a quite different area, namely the effect of parent-offspring dependencies in life history evolution. Phenotypic variation in survival rates affects population growth differently depending on the stage of life, at which it occurs. This is tied to the strength, with which natural selection acts on such variation, a concept known as the force of selection (Hamilton, 1966). It can be shown that after the onset of reproduction, the force of selection must decrease as age cohorts grow thinner and reproductive values do not increase apace. Before the onset of reproduction, however, the force of selection is expected to be constant. The classic life-history models on which this finding is based implicitly consider offspring to become independent right after birth. In contrast, I show that if offspring depend on their parents, either during gestation or periods of obligate parental care, the force of selection must increase up until the age at which offspring become independent from their parents. This chapter thus presents a possible evolutionary mechanism for decreasing mortality rates during early life stages, as they are widely observed in nature.

These main chapters are followed by two **commentaries** (here listed as chapter 6 and 7). The first is on an article by DiNuzzo and Griffen (2020) that considered how personality variation influences the speed at which foragers reach an ideal free distribution on a resource landscape. The authors made several surprising observations, such as that higher proportions of active vs. inactive individuals can prolong the time it takes, until the ideal free distribution is achieved, or that a larger population size generally increases this waiting time. A brief look at their code warranted further attention. We reimplemented their model and showed, that the time required to attain the ideal free distribution always decreases with the proportion of active individuals. Further, larger population sizes in fact accelerate the time, in which an ideal free distribution is achieved, and the functional responses I and II lead to identical results with respect to the ideal free distribution.

The second commentary concerns a paper by Botero et al. (2015), that inspired some of the work of my colleagues and me. The two key conclusions of the original paper are that adaptive response strategies evolve in distinctive regions of the parameter space and that when populations are shifted to novel parameter regimes, extinction can be caused by the crossing of response mode borders. A model reimplementation here confirmed the simulation results but caused me to arrive at a different interpretation of the latter conclusion: While response mode borders and extinction thresholds may occasionally coincide with each other, they are not causally connected, at least not within the model framework considered.

Thus extinction risk cannot be predicted from adaptive response mode borders.

In the final **chapter 8**, I discuss the presented research, models of various types of complexity and simple mechanisms that can give rise to complex phenomena, in the broader context of current evolutionary biology. I argue that we should content ourselves with leaky concepts, and rather focus on employing a wide variety of approaches to identify regularity in nature. I conclude with some thoughts and ideas about the current research environment in academia and how the effects of intensified competition could be channelled into more constructive ways.

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2

COMPLEX ECO-EVOLUTIONARY DYNAMICS INDUCED BY THE COEVOLUTION OF PREDATOR–PREY MOVEMENT STRATEGIES

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ABSTRACT

The coevolution of predators and prey has been the subject of much empirical and theoretical research that produced intriguing insights into the interplay of ecology and evolution. To allow for mathematical analysis, models of predator–prey coevolution are often coarse-grained, focussing on population-level processes and largely neglecting individual-level behaviour. As selection is acting on individual-level properties, we here present a more mechanistic approach: an individual-based simulation model for the coevolution of predators and prey on a fine-grained resource landscape, where features relevant for ecology (like changes in local densities) and evolution (like differences in survival and reproduction) emerge naturally from interactions between individuals. Our focus is on predator–prey movement behaviour, and we present a new method for implementing evolving movement strategies in an efficient and intuitively appealing manner. Throughout their lifetime, predators and prey make repeated movement decisions on the basis of their movement strategies. Over the generations, the movement strategies evolve, as individuals that successfully survive and reproduce leave their strategy to more descendants. We show that the movement strategies in our model evolve rapidly, thereby inducing characteristic spatial patterns like spiral waves and static spots. Transitions between these patterns occur frequently, induced by antagonistic coevolution rather than by external events. Regularly, evolution leads to the emergence and stable coexistence of qualitatively different movement strategies within the same population. Although the strategy space of our model is continuous, we often observe the evolution of discrete movement types. We argue that rapid evolution, coexistent movement types, and phase shifts between different ecological regimes are not a peculiarity of our model but a result of more realistic assumptions on eco-evolutionary feedbacks and the number of evolutionary degrees of freedom.

2.1. INTRODUCTION

Predator-prey coevolution has fascinated biologists for decades (Cott, 1940; Pimentel, 1961; Levin and Udovic, 1977; Dawkins and Krebs, 1979). In the ecological arena, predator-prey interactions can lead to complex non-equilibrium dynamics (Turchin, 2003). On top of these ecological predator-prey interactions, an evolutionary arms race may occur, where adaptive changes in the prey population impose new selective pressures on the predator population, and vice versa. Experimental findings suggest that the ecological and the evolutionary dynamics can be intertwined in an intricate manner (Yoshida et al., 2003, 2007; Becks et al., 2010). In natural systems, it is a major challenge to unravel this complexity (Hendry, 2019). It is therefore no surprise that theoretical models have played a crucial role for the understanding of the ecology and evolution of predator-prey interactions (Fussmann et al., 2007; Govaert et al., 2019).

Predator-prey coevolution models have traditionally been based on the frameworks of population genetics (Nuismer et al., 2005; Kopp and Gavrilets, 2006; Cortez and Weitz, 2014; Yamamichi and Ellner, 2016), quantitative genetics (Gavrilets, 1997; Mougi and Iwasa, 2010; Cortez, 2018), and adaptive dynamics (Dieckmann and Law, 1996; Marrow et al., 1996; Flaxman and Lou, 2009), where each approach encompasses a wide range of models. The approaches differ in their assumptions on the nature of genetic variation (discrete vs continuous), the occurrence and distribution of mutations, and the interaction of alleles within and across loci, but they have in common that they strive for analytical tractability. To achieve this, highly simplifying assumptions need to be made on the traits that are the target of selection. For example, predators are often characterized by a one-dimensional attack strategy, prey by a one-dimensional avoidance strategy, and prey capture rates are assumed to be maximal when the predator attack strategy matches the prey avoidance strategy (Van Der Laan and Hogeweg 1995; Dieckmann and Law 1996; Marrow et al. 1996; Gavrilets 1997; Nuismer et al. 2005; Kopp and Gavrilets 2006; Yamamichi and Ellner 2016, see Abrams 2000 for a general overview). Such simplification allows for an elegant and seemingly general characterisation of coevolutionary outcomes, but the question arises whether it captures the essence of predator-prey interactions, which in natural systems are mediated by complex behavioural action and reaction patterns. More recent studies have explored a multidimensional trait space (Gilman et al., 2012; Débarre et al., 2014), demonstrating that an increasing number of traits may have a destabilizing effect, as there are more possibilities for instability. However, these models also assume that the predation rate is determined by the match between unspecified traits of the two species.

Behavioural traits play an important role in predator-prey interactions. Experiments have demonstrated that predators and prey show strong behavioural responses to each other (Gilliam and Fraser, 1987; Savino and Stein, 1989; Ehlinger, 1990; Hammond et al., 2007; Simon et al., 2019). These responses differ across species and spatial scales, and they are likely the product of strategies that incorporate various information sources from the environment. In the literature, behavioural interactions between predators and prey are often discussed in game-theoretical terms as 'behavioural response races' (Sih, 1984, 2005) or 'predator-prey shell games' (Mitchell and Lima, 2002). These games usually play out in space, where resources, prey and predators are heterogeneously distributed among different patches. Prey have to balance foraging for a resource with predator avoidance, while predators are faced with the task of predicting prey behaviour. A full dynamical analysis of such interactions is a forbidding task (Flaxman and Lou, 2009). Therefore, analytical approaches have to use short-cuts, such as the assumption that at all times individual predators or prey behave in such a way that they maximize their fitness under their given local circumstances (Iwasa, 1982; Gilliam and Fraser, 1987; Abrams, 2007). It is often doubtful whether such short-cuts are realistic. For example, it is unlikely that evolution will fine-tune behaviour to such an extent that it is locally optimal under all circumstances and when conditions rapidly change (McNamara and Houston, 2009; McNamara and Weissing, 2010). It is therefore important to complement analytical theory with simulation-based approaches that can make more realistic assumptions on the ecological setting and the (evolving) traits governing the behaviour or predator and prey.

Several such simulation models have been developed (Huse et al., 1999; Kimbrell and Holt, 2004; Flaxman et al., 2011; Patin et al., 2020). All these models are individual-based, meaning that both the ecology and the evolution of predator-prey interactions reflect the fate of individual agents. Such an approach is natural because selection acts on individual characteristics, while population-level phenomena are aggregates and/or emerging features of these characteristics. Additionally, individual-based models enable the implementation of mechanisms, both at the level of individual behaviour and with regard to the environmental setting. The existing individual-based models have shown that they can validate findings of analytical models (Huse et al. 1999, cf. Iwasa 1982) and theoretical expectations such as the ideal free distribution (Flaxman et al., 2011). As illustrated by the recent study of Patin et al. (2020), such models can unravel the importance of random movement, memory use, and other factors that are difficult to study within the scope of analytical models.

Virtually all individual-based models consider individual interactions at a coarse-grained spatial scale (for an exception see Kimbrell and Holt 2004). The environment is assumed to be structured in discrete patches and individuals have the task of choosing a patch that provides an optimal balance between resource abundance and safety. Within patches, predator-prey interactions are governed by patch-level population dynamics and not based on single individuals moving and behaving in space. Accordingly, these models do not capture interactions that take place at the individual level.

Here, we consider a model where individuals move and interact in more fine-grained space, where only few individuals co-occur at the same location. Predators and prey evolve situation-dependent movement strategies that determine the likelihood of finding food resources and avoiding predation. The implementation of movement strategies is a crucial ingredient of our model. Instead of assuming that movement is directly guided by fitness expectations (as, for example, in Iwasa 1982; Abrams 2007), the strategies in our model are different realisations of an inherited proximate mechanism that uses environmental inputs to evaluate the 'suitability' of environmental situations. We assume that predator and prey individuals continually scan their environment and judge the suitability of each movement direction on basis of the local densities of resources, prey and predators in these directions; subsequently, they move in the direction with the highest suitability score. The movements made by individuals determine their survival and foraging success in case of prey, and their prey capture rate in case of predators. These in turn affect the number of offspring produced. On an evolutionary timescale, successful individuals transmit their evaluation strategy to many offspring, subject to some mutation. Over the generations, successful strategies will spread, thus selecting evaluation mechanisms, that use proximate environmental cues to make adaptive decisions under the local circumstances. The evolution of the resulting movement strategies in turn has the potential to change the spatial pattern of resource densities and abundances and, hence, the nature of the trophic interactions. We would like to stress that our model is not intended to mimic any particular biological system. Instead, our goal is to obtain conceptual insights into the coevolution of predators and prey, when movement decisions are the target of selection and commonly made simplifications on the environment and trait interactions are relaxed. For this purpose, we have kept the other aspects of our model, including our assumptions on the evolving movement strategies, as simple as possible. With this conceptual model, we want to gain insight into the following questions: What kinds of movement strategies do evolve and which information sources are used by predators and prey? How do predator-prey interactions reflect and shape the resource landscape? Are the evolved populations monomorphic, or do different movement strategies coexist in the same population? How fast is evolutionary change in relation to ecological change; does the interplay of ecology and evolution lead to novel eco-evolutionary patterns and dynamics?

2.2. THE MODEL

2.2.1. ECOLOGICAL INTERACTIONS

To aid intuition, consider the prey to be herbivores feeding on a resource, henceforth called grass, and predators feeding on herbivores. All individuals live in an environment consisting of a grid of 512^2 cells with wrap-around boundaries, such that individuals leaving the grid on one side reappear on the diametrically opposed side. A cell can host one or several herbivores and predators, but larger concentrations are unlikely as the number of grid cells is an order of magnitude larger than the typical number of individuals. Ecological interactions occur in discrete time steps. A time step (we think of a day) contains a grass growth phase, a movement phase and a foraging phase with predator–prey interactions. Grass grows at a constant rate of 0.01 per time step up to a maximum density of 1. Next, herbivores and predators move between cells based on their inherited movement strategy as described below. Herbivores visiting a cell deplete the grass and gain the corresponding amount of energy. Multiple herbivores occupying the same cell share the amount of grass on that cell. If a predator encounters a herbivore on the same cell, the predator succeeds to capture the herbivore with probability 0.5, in which case the herbivore is killed and the predator gains one unit of energy. If several predators co-occur with several herbivores (which only rarely ever happens), the successful predators kill and consume all the herbivores present in the cell. The killed herbivores are equally distributed between successful predators.

2.2.2. MOVEMENT STRATEGIES

Movement strategies are based on the evaluation of nearby cells (see fig. 2.1). For each evaluated grid cell, a ‘suitability score’ S is calculated. S is the weighted sum $S = w_g G + w_h H + w_p P$, where G, H and P are the grass density, herbivore density, and predator density in the cell, respectively. The weighing factors w_g, w_h, and w_p are individual properties; they are genetically encoded and transmitted from parent to offspring.

Grass density represents the total amount of grass in a given cell, while for herbivore and predator densities we convoluted the otherwise discrete presence-absence values of agents via a Gaussian filter in a neighbourhood distance of one (Lindeberg, 1994). This yields continuous values of herbivore and predator densities that are diffused around the actual positions of the agents, much like we

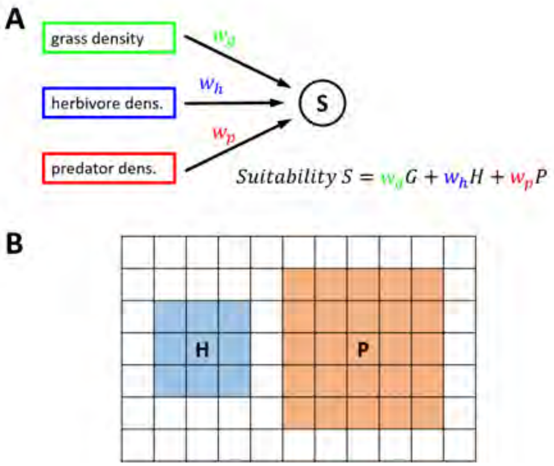

Figure 2.1 | Movement and decision-making. **(A)** Individuals evaluate all cells in their movement range as to their 'suitability' and move to the cell of highest suitability. The suitability S of each cell is the weighted sum of the local grass density G, the local herbivore density H, and the predator density P, where the weighing factors w_g, w_h, and w_p are genetically determined and hence evolvable. **(B)** Herbivores and predators move on the same rectangular grid, but their movement range per time step can be different. The plot illustrates the movement range of herbivores (blue, radius = 1) and predators (red, radius = 2) for our standard configuration.

would expect from olfactory cues or similar. An individual can thus sense the presence of other individuals even when they are outside, but close to, the individual's movement range. The density furthermore indicates cells where individuals could move to in the next timestep. Individuals evaluate all cells in their movement range, and move to the cell with the highest suitability. We apply a certain amount of noise to the calculated suitability scores. This adds the possibility for stochastic movements, particularly if weights are small. When the weights are large, this noise becomes trivial to the comparison between cells. In the simulations shown, the movement range has a radius of one for the herbivores (9 cells, fig. 2.1B), and a radius of two for the predators (25 cells). If predators have the same movement radius as their prey, herbivores can reliably escape predation by moving away from high predator densities. Only when predators can move further than herbivores do both parties need to predict the behaviour of the other party, and interactions become more intricate.

2.2.3. EVOLUTION OF THE EVALUATION MECHANISM

We consider haploid parthenogenetic populations with discrete, non-overlapping generations. Population sizes vary throughout the simulation, as herbivore numbers are diminished by predation and herbivores and predators produce offspring in relation to consumed resources. Herbivores produce on average 0.1 offspring per unit of resource consumed. The predators are supposed to be generalists; their expected number of offspring is a baseline value of 0.6, with 0.6 offspring added per prey caught. The realized number of offspring of an individual is drawn from a Poisson distribution based on the calculated expected value. At the start of a new generation, offspring are placed at random in the 'dispersal range' around the position of their parent. In the simulations shown below we used a dispersal radius of 1 for both species (9 cells, fig. 2.1B). The above values for the food-to-offspring conversion rates and the dispersal range are used in our default scenario, but other parameter settings will be discussed as well. Each individual has three gene loci with alleles w_g, w_h, and w_p that correspond to the weights encoding the evaluation of environmental suitability (fig. 2.1A) and, hence, determine the individual movement strategy. The movement strategy determines the types of habitat most likely visited and therefore the individual's intake rate and, in the case of the herbivore, the individual's probability of escaping predation. At the end of a generation (after 100 time steps), surviving individuals produce offspring depending on their total food intake. Each offspring inherits the genetic parameters of its parent, subject to rare mutations. A mutation occurs with probability $\mu = 0.001$ per locus, in which case the original value is changed by an amount drawn from a Cauchy distribution with location 0 and scale parameter 0.001. At the beginning of the simulation, the weights of predators and prey were initialised with a draw from this distribution, implying that most weights started close to zero.

2.3. RESULTS

We conducted many hundreds of long-term simulations that shared the characteristic features that we will demonstrate for one exemplary simulation run. Over a wide range of parameter combinations (see below), extinction of the predator or prey population is virtually assured. We therefore chose parameters that allow for extended coexistence between predators and prey, still permitting for extinction to occur as a result of the ecological and evolutionary dynamics. A video of such a simulation can be accessed under `https://youtu.be/cLUCEx6Mlnk`, and the program can be easily run locally by download from our digital resources or the github repository.

2.3.1. OVERVIEW: TRANSITIONS, PATTERN FORMATION, AND POLYMORPHISM

Figure 2.2 shows a typical simulation run of our model. Over a period of 25,000 generations, the interacting movement strategies of predators and prey induce characteristic population dynamics (fig. 2.2A) that appears regular for a while but then switches to a new dynamical state. The snapshots in fig. 2.2B illustrate that spatial patterns underlie these states, which in turn reflect the dominant movement strategies in the predator and prey populations (fig. 2.2C). It is apparent that the phase shifts in the population dynamics and spatial patterns reflect evolutionary changes in the movement strategies. Sometimes, these shifts occur within a few generations. Evolution is stochastic, highly dynamic and continually produces new strategies and ecological patterns.

Between generation 35,000 and 38,000, the herbivore and predator populations show fairly regular oscillations (fig. 2.3A). On the landscape level (fig. 2.2B.1), this manifests as the repeated expansion and depletion of herbivores and predators across the landscape. Figure 2.2C.1 illustrates the underlying movement strategies of predators and prey in generation 37,000. For ease of comparison, the weights of the three inputs were normalized by dividing each weight by the sum of the absolute values of all three weights. The purple and the cyan dots indicate that two movement strategies coexist in the prey population: both give a very low weight to grass density and a (different) negative weight to prey density. Hence, herbivores care surprisingly little about resource availability and move primarily to avoid conspecifics. The two morphs differ in the way predator density is considered. As indicated by the colours of the dots, prey morph 1 weighs predator density negatively (with a relative weight of 0.25), while prey morph 2 weighs predator density slightly positively (0.03). In other words, morph 1 avoids areas with high predator density, while morph 2 is, surprisingly, attracted to such areas. We will elaborate on this counterintuitive finding and the dynamics between the morphs in the next section. Also the predator population is dimorphic: morph *a* (red dot) mainly considers (and strongly avoids) conspecifics (with a relative weight of 0.99), while morph *b* (black dots) primarily moves according to large prey densities, while being split on its preference for grass, otherwise having a slight positive preference for conspecifics (0.15).

After generation 38,000, the polymorphism in the herbivore population is lost, and a new predator morph emerges that has a strong preference for high grass densities (fig. 2.2C, generation 45,000). These predators aggregate on high grass patches and exclude herbivores from such areas. As a consequence, stable spatial patterns form in the distributions of predators, herbivores and the resource, and

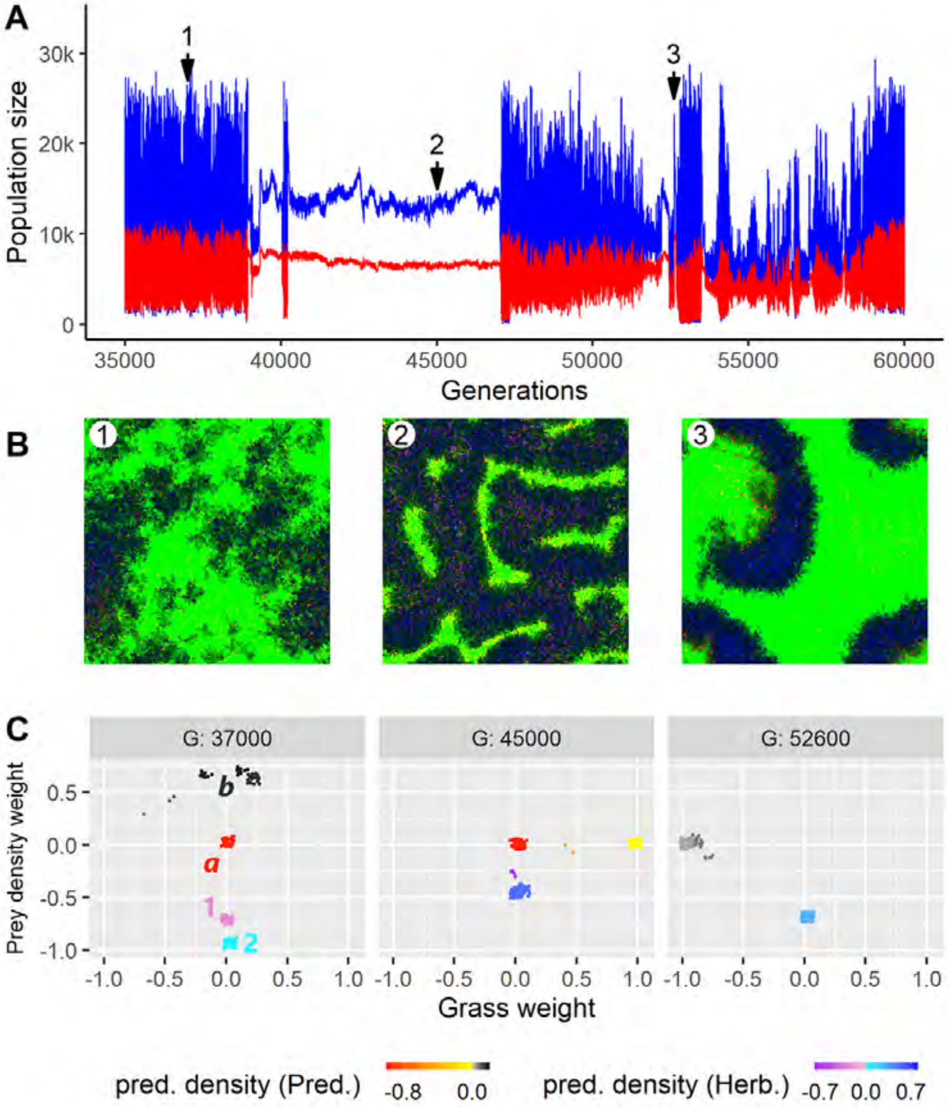

Figure 2.2 | Eco-evolutionary pattern formation (A) Population size of predators (red) and herbivores (blue). **(B)** Landscape snapshots at three time points of the simulation (indicated by arrows in panel A). Grass density is shown in green, herbivore density in blue and predator density in red. Other colours emerge from additive colour mixing, yellow for example signifies areas of high grass and predator density, purple that herbivores and predators occupy the same area. Black areas correspond to empty cells with low resources. **(C)** Movement strategies of herbivores (purple-cyan-blue) and predators (red-yellow-black) at each of the three snapshots, measured by the relative magnitude of each the three weights (absolute values sum to one). Shown is a subsample of 100 individuals per population, with jitter noise added around the true position (0.08 in x and y).

Figure 2.2 | The relative magnitude of the weight for predator density is colour-coded for herbivores from -0.7 (=purple) to 0.0 (pink/cyan) and 0.7 (=blue), and for predators from -1.0 (=red) to 0.0 (=yellow/grey) and 0.2 (=black). In the panel of generation 37,000, the herbivore population consists of a predator-averse (-0.25, morph 1), and a predator-prone morph (+0.03, morph 2). Also the predator population consists a predator-averse (-0.99, morph *a*), and a predator-prone morph (+0.15, morph *b*).

the population dynamics are stabilized (fig. 2.2B.2). The other predator morph strongly avoids conspecifics and roams also within the herbivore aggregations.

After generation 47,000, the spatial organisation is lost and population cycles emerge again. The population cycles are repeatedly interrupted by brief periods of stability (generation 52,300; 52,650; 53,500), and cycles differ in amplitude as a function of the involved movement types. In generation 52,600, we observe spiral wave patterns. Both populations are monomorphic at this point. Predators track low grass densities, allowing them to follow the herbivores, as these leave tracks of depleted grass in their way. The herbivores primarily avoid conspecifics, but also have a preference for predator densities and a small positive preference for grass. The reaction norms of these morphs are depicted in figure S3.

In summary, population dynamics and spatial patterns both reflect the evolved movement strategies of herbivores and predators. For example, dynamic spatial patterns such as spirals (fig. 2.2B.3) are produced by predators chasing after herbivores, as these expand across the landscape. In contrast, spatial aggregations as in figure 2.2B.2 reflect a ‘sit-and-wait’ strategy of the predator, where individual predators prefer high grass densities and tend to remain there; the predators can thus monopolize high grass patches and consume those herbivores that are eventually lured in by the high grass density. The population dynamics of the entire simulation as well as the evolution of weights is shown in figures 2.A1 and 2.A2 of the appendix. For a more dynamical depiction of the spatial dynamics, we refer the reader to the animation videos and executable of our model in the digital supplement.

2.3.2. POLYMORPHISMS AND TRAIT CYCLES

We now take a closer look at the oscillations that dominate the simulation between generations 35,000 and 38,000, and the polymorphisms that occur during this phase. The densities of both populations are subject to oscillations with a period length of ca. 8 generations and a quarter phase lag between herbivores and predators (fig. 2.3A). As we have seen in figure 2.2C.1, both populations are polymorphic at this point: some herbivores are ‘predator-averse’ in that they avoid high predator densities (morph 1), while other herbivores are ‘predator-prone’ in that they have a slight positive preference for high predator densities (morph 2). Figure 3B shows how the relative frequencies of the two morphs fluctuate over a period of 500 generations (pink: predator-averse morph 1; cyan: predator-prone morph 2). Likewise, figure 2.3C shows the fluctuations in the two predator morphs: the predator-averse morph *a* that strongly avoids locations with high predator densities and the predator-prone morph *b* that has a weak positive preference for high predator densities (and, in addition, is strongly attracted by high prey densities).

The four morphs exhibit stochastic but regular oscillations in relative frequency, with a period of ca. 50 generations. Each of the two morphs in the two populations is adapted to a morph in the other population, and increases when this morph is common: When the predator-averse herbivore morph 1 is common, the predator-averse predator morph *b* increases, followed by the increase of the predator-prone herbivore morph 2, which when common induces the increase of the predator-prone predator morph *a*. The predator-averse herbivore morph 1, which avoids high predator densities, is adapted to escape predation from predators with a positive preference for predator densities (morph *b*), but suffers from predation by the predator-averse predator morph *a*. In turn, morph *a* does not efficiently capture predator-prone herbivores, because it moves away from the patches with high predator density that are attractive for the herbivore morph 2. Thus, even though the behaviour of the predator-prone herbivore morph 2 seems counter-intuitive, it is an effective adaptation against predators within the framework of our model, where individuals need to predict each other’s location in the next timestep.

In addition to the large-scale oscillations, the morph frequencies show epicycles influenced by the oscillating population dynamics. These do not show a consistent pattern and emerge from the repeated expansions and contractions of both populations across the landscape, as well as stochastic effects in the spatial distributions of individuals.

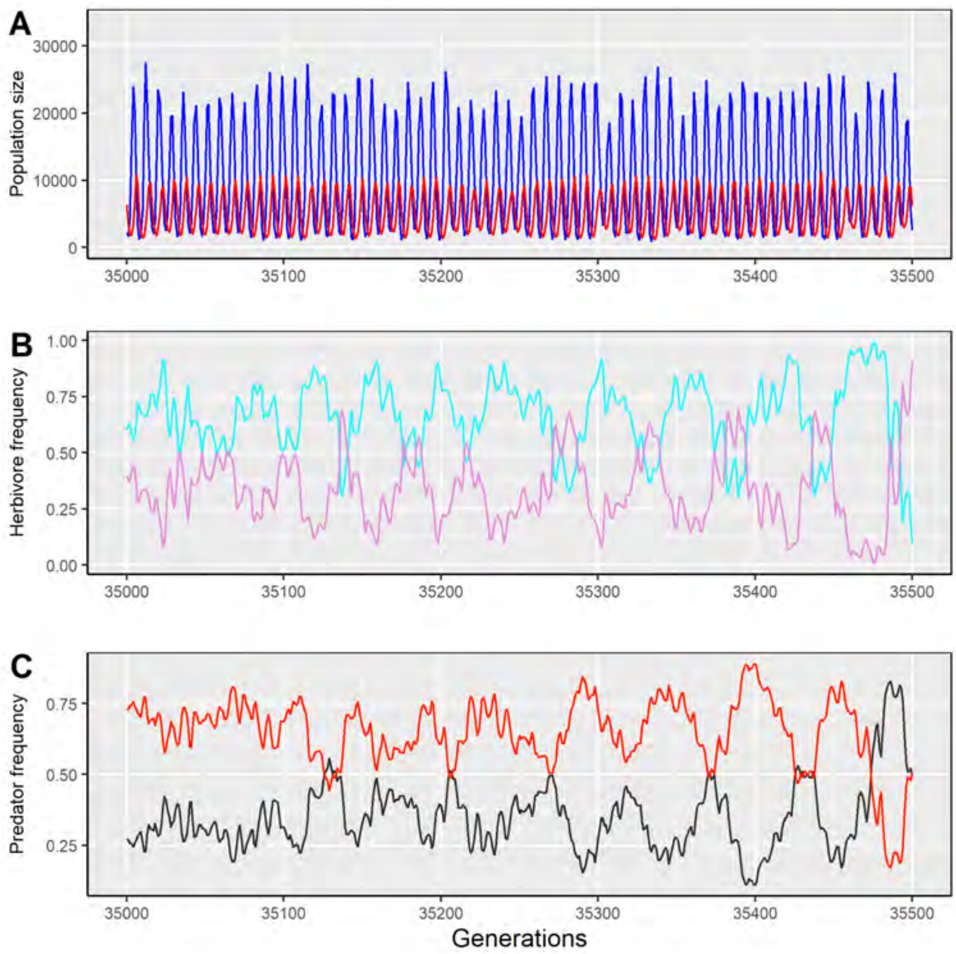

Figure 2.3 | Polymorphism and trait cycles. **(A)** Population size of predators (red) and herbivores (blue) between generations 35,000 and 35,500. The shown dynamic continues until generation 38,000. **(B)** Relative frequency of the predator-avoiding morph 1 (pink) and the predator-prone morph 2 (cyan) in the herbivore population. **(C)** Relative frequency of the predator-avoiding (red) and the predator-prone (black) morph in the predator population.

2.3.3. EVOLUTIONARY TRANSITIONS AND THEIR EFFECT ON ECOLOGICAL PATTERNS

We now take a closer look at one of the evolutionary transitions from one kind of pattern to another one. For this purpose, we will focus on a 400-generation segment between generation 52,400 and 52,800 (which includes snapshot 3 of fig. 2.2). In this period, the simulation undergoes three shifts. At first, predator and prey population sizes are stable, and the landscape configuration is stable as well, with herbivores forming loose aggregations (fig. 2.4A.1). Around generation 52,450, the situation changes, the spatial structure is lost and predator and prey populations begin to oscillate. After generation 52,600, a rapid shift occurs that stabilizes the population dynamics again, only to fall back into oscillations after generation 52,700, with a now higher amplitude than before. Indeed, both the predator and prey populations come close to extinction during this phase.

The phase transitions can be traced back to mutations of movement strategies in the predator and prey population. The rapid shift in generation 52,610 for example is caused by a mutation in the herbivore population, changing predator preference from positive to strongly negative. The other two shifts are induced by mutational changes in the predator population. Figure 2.4 shows the distribution of all three weights in the predator population during this time. The first shift (in generation 52,445) occurs when two new predator mutations appear that both have a negative grass weight (i.e., an aversion of high grass densities). During the following oscillations, the previous two grass-prone morphs disappear. In addition, the other two weights of the movement strategy of the predator shift to values close to zero, implying that in this time period the predators are only guided by their aversion for high grass densities. The predator population then remains largely static for 100 generations, after which the above-mentioned adaptation in the prey population occurs, which leads to counter-adaptations in the predator population: First, the predator density weight mutates back to be negative, then the grass weight mutates to be near-neutral, and finally the herbivore density weight mutates to a more positive value, thereby producing again population oscillations and spatial dynamics (fig. 2.4.2). Thus, from generation 52,610 to generation 52,700, three mutations occur in the predator population that ultimately lead to the phase shift.

Several things should be noted here: First, evolutionary changes occur on a similar time scale as ecological changes, and the occurrence and spread of new movement strategies shapes the ecological dynamics, which in turn determine the success of the different strategies. Ecological and evolutionary processes are thus strongly intertwined. Second, the predator population displays a high

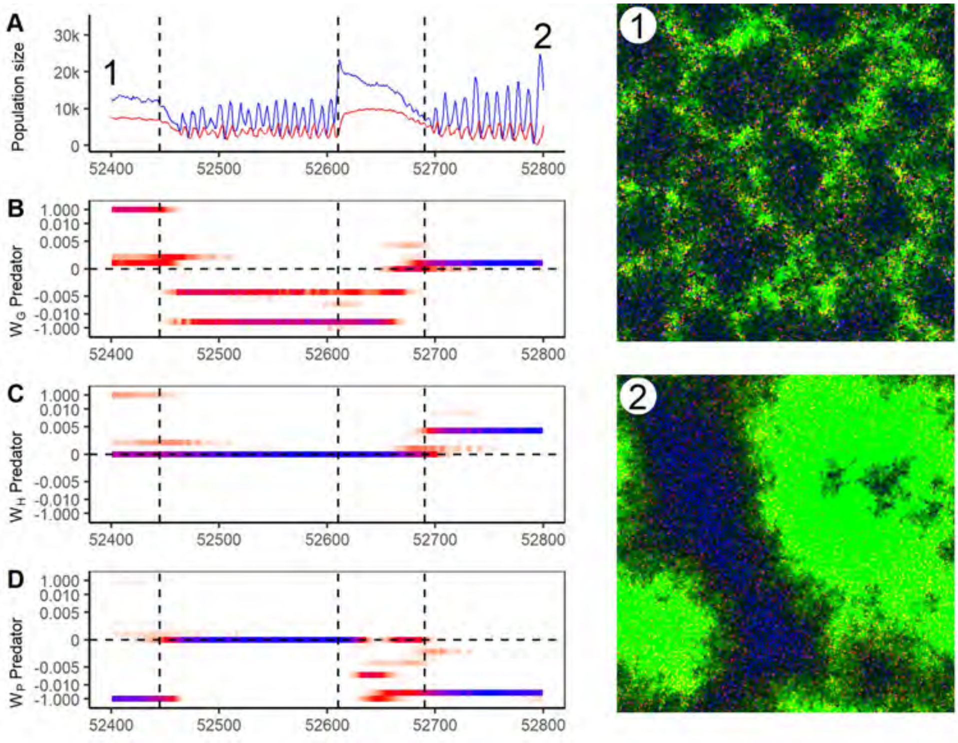

Figure 2.4 | Effect of mutations on evolutionary transitions.. **(A)** Population size of predators (red) and herbivores (blue) between generations 52,400 and 52,800. **(B, C, D)** Evolution of the three weighing factors determining the movement strategy in the predator population: **(B)** weighing factor w_g (= the weight given to grass density); **(C)** weighing factor w_h (= the weight given to herbivore density); **(D)** weighing factor w_p (= the weight given to predator density). In most of the generations shown, the predator population is polymorphic for one or more weighing factors. The relative frequencies of the coexisting trait values within each generation are encoded by a colour gradient from 0.0 (=white) to 0.3 (=red) and 1.0 (=blue). Weight values are shown on a tanh-transformed scale. (1) and (2) show snapshots of the landscape snapshots at generation 52400 and 52800.

level of polymorphism during this period. The existence of these polymorphisms allows for subsequent adaptive change. Third, phase shifts can require several antecedent mutations, that can then lead to an abrupt change of the ecological dynamics. And finally, evolution can both be stabilizing and destabilizing, and adaptations in the predator population not necessarily lead to an improvement of population-level fitness.

2.3.4. MODEL SENSITIVITY AND PARAMETER SETTINGS

We have deliberately focussed on a single simulation run in order to explore the dynamics in great detail. In the presented simulation, dispersal occurs locally in a range of one around the parental individual. Herbivores produce offspring at a conversion rate of 0.1. Predators produce offspring at a conversion rate of 0.6, and have a baseline food intake of 0.6. For the same parameter settings, replicate simulations can strongly differ from each other (fig. 2.A7 in the appendix). However, the basal elements discussed above (periods of stasis followed by periods of oscillations, and vice versa; abrupt transitions; polymorphism) were observed in all simulation runs based on our default parameter values. The duration of the various phases can be very different, with some replicates maintaining oscillations or remaining static for long periods of time. Extinction occurs frequently in our simulations, with four simulations out of ten running beyond generation 100,000, and one going extinct around generation 10,000 (fig. S7).

Different parameter settings have a predictable effect on the eco-evolutionary patterns generated by our simulations. For example, offspring dispersal has a strong influence on the simulations. By default, we considered local offspring dispersal (dispersal radius = 1). When offspring are dispersed more widely (dispersal radius = 10), phase shifts still occur and spatial patterns emerge, but extinction occurs more regularly than before (fig. 2.A8 in the appendix). When offspring are distributed randomly across the landscape, extinction occurs within few generations. The spatial structure emerging from local reproduction thus promotes stability.

The conversion rates of herbivores and predators influence the stability and overall level of the population dynamics. If the conversion rate of herbivores is increased from 0.1 to 0.2, their average population size increases, but extinction becomes much more frequent, with few replicates reaching generation 10,000 (fig. 2.A9 in the appendix). If the conversion rate or the baseline food intake of the predator is reduced, the overall abundance of predators decreases and the ratio of prey to predators becomes larger, oscillations dampen, and spatial patterns like spiral waves or rapid expansions vanish. As a consequence, the feedback between landscape structure and movement strategy evolution is diminished and the simulations tend to produce stable ecological and evolutionary dynamics, although polymorphism remains common (fig. 2.A10 in the appendix). In the digital supplement, we provide an executable of our model that allows the interested reader to explore other parameter settings such as lower conversion rates, random movement or more complex movement strategies controlled by recursive networks.

2.4. DISCUSSION

We introduced a new method to model evolvable movement strategies and applied this method to the antagonistic coevolution of movement decisions in predators and prey. The movement strategies are characterized by heritable parameters that determine how an individual evaluates the environmental cues that determine its movement decisions. Movement is thus not guided directly by fitness expectations (as in Iwasa 1982; Abrams 2007), but by an inherited mechanism that evaluates the 'suitability' of the available options on the basis of proximate environmental information and then bases the next move on the comparison of suitabilities. Suitability judgements are not necessarily aligned with fitness expectations (which may not be well-defined in a highly dynamic setting), but they are 'adaptive' in the sense that they are shaped by natural selection. As movement affects foraging success and predator-prey encounter rates, the evaluation mechanism is an important determinant of lifetime reproductive success and hence subject to natural selection.

In our model of antagonistic coevolution, selection pressures vary strongly in space and time, leading to rapid evolution and rich spatial dynamics. Although our model is still very simple, we observe a range of phenomena that do not occur in models with coarser spatial scales and with fewer evolutionary degrees of freedom. The populations in our model do not evolve stable movement patterns but instead exhibit intricate ecological and evolutionary dynamics, including regular frequency cycles between movement strategies and the spontaneous advent of novel strategies and counter-strategies. Regularly, qualitatively different movement strategies coexist as polymorphisms for extended periods of time. For example, we observed the evolutionary emergence of sit-and-wait predators, while other predators were chasing their prey (fig. 2.2C.2). The movement strategies in herbivores and predators determine the spatial pattern of resource depletion and predator-prey encounters. Over the generations, these patterns are fluent, as they change with the evolution of the underlying movement strategies. Rapid transitions between patterns (e.g. between static spots and spiral waves) can occur; these reflect coevolutionary changes rather than changes in external conditions. We will now discuss some of these findings in more detail and in the context of other models of predator-prey coevolution.

Previous work on the coevolution of predator-prey movement has produced interesting spatial dynamics, such as evolutionarily optimal strategies leading to ‘predator-prey chases’ across habitats (Abrams, 2007) and the coupling of ecological dynamics across habitats via evolving conditional strategies (Flaxman et al., 2011). However, in these studies ‘movement’ corresponds to a choice between a small number of densely populated habitats. Within habitat patches, the interactions of predators and their prey is not modelled at the individual level but by patch-level dynamic equations (but see Patin et al. 2020). In contrast to these habitat choice models, we consider movement in a fine-grained spatial environment. From ecological models, it is known that in such fine-grained environments the interplay of diffusion and predator-prey interactions can induce a diversity of spatial patterns, including rotating spirals and static stripes or spots, depending on the parameters of the ecological interaction (Hassell et al., 1991; Comins and Hassell, 1996; Alonso et al., 2002; Banerjee, 2015). Hence, patterns may shift abruptly when ecological parameters change, either externally as in the publications above, or intrinsically through evolutionary processes as in our model. Repeated switches between patterns can thus occur even though the extrinsic parameters have not changed. Further, evolution of movement strategies can produce qualitatively novel patterns unknown from ecological models that assume random dispersal. These eco-evolutionary patterns are a product of the feedback between the movement-generated distribution of individuals in space and the evolution of movement strategies based on the local conditions that individuals experience.

Behavioural polymorphisms commonly occur in our simulations and can either be persistent (fig. 2.3) or fleeting (fig. 2.4); either fluctuate or remain stable over time. Polymorphisms are also predicted by analytical models of coevolution (Senthilnathan and Gavrilets, 2021), but they occur much more frequently in mechanistic individual-based models (Botero et al., 2010; Long and Weissing, 2020). The behavioural dimorphisms emerging in the herbivore and predator population (fig. 2.3) show that systematic behavioural variation can emerge in two species due to coevolution. The existence of behavioural polymorphism can have important ecological and evolutionary implications (Sih et al., 2012; Wolf and Weissing, 2010). In predator-prey systems, intraspecific variation can, for example, be crucial for the sustained persistence of both species (Senthilnathan and Gavrilets, 2021).

Evolution in our model is either dominated by the advent of novel mutations, or by frequency-dependent oscillations between different morphs present in the population. The latter produce trait cycles reminiscent of population genetics models (Nuismer et al., 2005; Kopp and Gavrilets, 2006; Cortez and Weitz, 2014), where oscillations occur between the frequencies of different alleles present in the population. This is exactly the pattern we see in figure 3, where two morphs of predators and prey oscillate in frequency, with each morph being adapted to one specific morph of the other species. We thus recover the matching alleles assumption of population genetics models, but without assuming this interaction *a priori.* Instead it naturally emerges from the ecological interactions of our model. Mutation-limited evolution is much more erratic, as it depends on the stochastic occurrence of one or several sequential mutations (fig. 2.4). The newly arising morphs frequently induce phase shifts that transform the ecological dynamics. We did not observe trait cycles as described in quantitative genetics (Gavrilets, 1997; Mougi and Iwasa, 2010; Cortez, 2018) or adaptive dynamics approaches (Dieckmann et al., 1995; Dieckmann and Law, 1996; Marrow et al., 1996), where oscillations occur due to systematic shifts in a continuous trait that either corresponds to the mean value of a normal distribution (quantitative genetics) or to the trait value of a monomorphic resident population (adaptive dynamics). In line with these modelling frameworks, we also assume that mutational step sizes are typically small. However, the Cauchy distribution of mutational step sizes allows for rare mutations of large effect, which may explain why continuous variation plays a less prominent role in the evolutionary processes observed here (see Wolf et al. 2008).

We kept our model as simple as possible, in order to demonstrate that not much structure is required for obtaining the ecological and evolutionary patterns described above. It would be interesting to study the implications of features such as sexual reproduction and different modes of inheritance, or a spatially heterogeneous resource distribution, but this is beyond the scope of our study. Here we only discuss the implementation of movement strategies by three weighing factors (w_g, w_h and w_p) in our model. This way, there are three 'evolutionary degrees of freedom' in our model, giving larger scope to nonequilibrium dynamics than traditional single-trait models (Leimar, 2009; McNamara and Weissing, 2010; Débarre et al., 2014). While previous work on coevolution in multidimensional phenotype space is still framed in terms of simple phenotype matching rules (Gilman et al., 2012; Débarre et al., 2014), the interactions in our model are mediated by movement strategies. How these strategies interact is, however, an emergent property of the model. The nature of this interaction not only depends on the evolved strategies in conspecifics and antagonists, but also on the local environmental conditions, in which individuals encounter each other. Trade-offs for herbivores between resource acquisition and predation avoidance come about naturally in this case and do not need to be assumed *ad hoc.* The emergent interactions between individuals allows for much more rapid and unpredictable evolution due to the emergence of 'surprising' (and sometimes counterintuitive) strategies and counter-strategies, the advent of novel forms of behaviour, and by allowing for behaviour that is (at least partly) stochastic and unpredictable. We anticipate that, quite generally, models with more evolutionary degrees have much richer eco-evolutionary dynamics than most conventional models.

Having said this, we are fully aware that our behavioural model is still unrealistically simple and well-behaved. Our model could be extended quite naturally by exploring different modes of inheritance, and by basing the calculation of environmental suitability on a more complex algorithm, such as an evolving artificial neural network (ANN) (Huse et al., 1999; Enquist and Ghirlanda, 2005; Morales et al., 2005). Evolving regulatory networks (including ANNs) have a number of important features (Wagner, 2005; van den Berg and Weissing, 2015; van Gestel and Weissing, 2016), such as the emergence of cryptic variation (since the same phenotypic strategy can be encoded by very different networks), which allows for much faster evolution in the face of environmental change. Perhaps most importantly, network models tend to have an intricate genotype-phenotype map, implying that small mutations can have large and unexpected implications at the phenotypic level. It is therefore not surprising that ANN-based pilot simulations on predator-prey coevolution exhibit even richer eco-evolutionary dynamics than occurring in the present model.

DATA AND CODE AVAILABILITY

Simulation model code is available on Github: `https://github.com/christophnetz/Cinema_git`.

Digital resources: `https://doi.org/10.34894/UYTA7S`

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APPENDIX

In our manuscript, we present in great detail the features of a single simulation, in order to show the relation between population dynamics, spatial patterns and evolution. The selected segment runs from generation 35,000 to 60,000, the entire simulation lasted until briefly past generation 90,000, after which the herbivore population went extinct. The full course of the population dynamics during the simulation is shown in figure 2.A1, with the segment selected for the main manuscript highlighted. Even before the long period of stasis around generation 45,000, stasis occurs at three different points in time, the longest of which occurs around generation 17,500. As shown in the manuscript, these periods correspond to stable spatial configurations and static spot patterns. Also the amplitude of oscillations dampens and increases again during the simulated time. This is especially obvious after generation 75,000. After generation 90,000, oscillations rapidly increase, ultimately leading to the extinction of the herbivore and the end of the simulation.

The weight evolution during this time frame is shown in figure 2.A2. Herbivores have consistently a strong negative preference for conspecifics, as shown in figure 2.A2D. The weights for predator density, which signified the morphs considered in figure 2.3, consistently show a dimorphism where both populations fall into a negative and a positive-valued morph for this weight. Even when these morphs briefly disappear during certain stages of the simulation, they reoccur shortly after. The weighing factor for grass is consistently positive for both populations, although the predator population occasionally negative-valued morphs occur. The herbivore density weight of predators is consistently positive. The morphs of generations 37,000, 45,000 and 52,600, shown in figure 2.2C, have different reaction norms with regard to grass, prey density and predator density. Figure 2.A3 shows the reaction norms of these morphs over continuous values of grass density, and for three types of cells in relation to prey and predator absence: Empty cells, with no nearby individuals of predators and prey, cells occupied by a herbivore and cells occupied by a herbivore and a predator. As can be seen, all morphs generally have reaction norms with a positive slope for grass density, with the exception of the predator morphs in generation 52,600. Grass density tends to have less influence on suitability scores than the absence or presence of other individuals. The predator morphs in generation 52,600 and the second predator morph in generation 45,000 however predominately respond to grass densities, and several other morphs do not react to either prey or predator densities: Predator morph 2 in generation 37,000 and predator morph 1 in generation 47,000 show hardly any reaction to prey density, while the predator morph 1 and prey morph 1 in generation 37,000, react only very weakly to changing predator densities. The movement strategies realized by these reaction norms depend on the local environment of the individual: If grass density is homogeneous among several patches, a decision is based solely on the other two weighing factors, no matter the relative magnitude of the weight for grass.

The polymorphism in predator-density weights is closely inspected in figure 2.3 of the main text, that concentrates on generations 35,000 to 35,500, and figure 2.A4 complements this figure by showing the evolution of all three weight values in both populations. The dimorphism in the predator density weight is clearly visible in the last row of the figure, as are the oscillations in frequency signified by the change in color from blue to red. The two predator morphs not only differ with respect to this one weight, but also with regards to the weights for grass and herbivores, where the same pattern of oscillations reoccurs. The differences in magnitude are small however, and therefore might not represent fundamentally different movement strategies but rather neutral variation.

In our results section, we show how the morphs of predators and herbivores fluctuate in response to each other, and it is to be expected that this occurs through the predation pressure of one predator morph exerted on one herbivore morph. This is shown in figure 2.A5: Next to the frequencies of the predator-prone herbivore and predator morphs (cyan and black, A) are shown the expected reproductive values of the predator-prone morph as compared to the predator-avoiding morph. This should be the growth rate of the morph frequency curve in panel A. While difficult to see through the strong fluctuations, the rolling average with a window of 20 shows that this matches indeed quite well. Herbivore reproductive values are determined both by their survival of predation and the number of resources consumed, and this is shown in panel C and D. The curve of panel C, showing the difference in survival of the two herbivore morphs, closely resembles the curve in panel B. The food consumed among surviving individuals on the other hand is inversely related to these two curves. Thus survival seems to be the dominant factor determining the reproductive values of individuals here. The inverse relation in panel D to reproductive values is explained by the competition for resources among kin: If fewer individuals survive predation, more resources are consumed by the survivors, and since reproduction is local, this concerns primarily related individuals. This effect is however not strong enough to outweigh predation pressure.

In figure 2.4, the abrupt phase transitions are closely inspected at the example of mutations arising in the predator population during generations 52,400 to 52,800. Figure 2.A6 shows the evolution of all six weights, including the evolution of the weights in the herbivore population. We here see an abrupt transition in the herbivore population briefly after generation 52,600, where the weight for predator density shifts from negative to positive. The evolution of movement strategies along this period is also visualized in figure 2.A7: In timesteps of 50, the movement strategies of predators and herbivores are plotted. The predator morph changes very dynamically during this time interval and hosts several morphs. At the beginning in generation 52,400, the predator has a strongly self-avoiding morph, that is otherwise neutral to the other cues. A second yellow morph is weakly self-avoiding, and otherwise orients itself primarily to high grass densities. 50 generations later, several new morphs occur: A morph that has a positive self-preference, otherwise identical to the former yellow morph, and two grey morphs, one of which strongly avoids high grass densities, the other following herbivore densities. The former has taken over the population 50 generations later and has caused population oscillations and a destabilization of spatial structure in doing so. Briefly after generation 52,600, the large mutation occurs in the herbivore population, that now switches from a positive to a negative preference for predator densities, but otherwise remains identical and monomorphic. Quickly after, the predator population is taken over by two new morphs, both with a negative preference for grass and predator densities, and different only in the weighing of the two. In generation 52,700, these morphs are replaced by a red morph that strongly avoids other predators much like at the beginning of the timeframe, and an orange morph avoiding predators and following herbivore densities, which becomes the only predator morph 50 timesteps later and until the end of generation 52,800.

As described in the last section of our results, simulation replicates can be quite different, but all show alternating elements of stasis, oscillations and polymorphisms. In figure 2.A8, we show ten simulation replicates that give an overview of the simulation behavior under default parameters. The first simulation goes extinct briefly after generation 10,000, four simulations run until the end of the simulated timeframe. The simulation presented in the main manuscript is replicate 3. Some simulations undergo frequent shifts (replicates 3, 6, 9), while others settle in one pattern for long periods of time (replicates 5, 10).

We continue to inspect the influence of some key parameters of our model, namely the radius for offspring dispersal and the grass-herbivore and prey-predator conversion rates. If the offspring dispersal radius is increased from 1 (default) to 10, the population dynamics (fig. 2.A9) and spatial dynamics (not shown) still show the characteristics of shifts between phases of static spatial configurations and dynamic oscillations. The spatial patterns are therefore maintained, even if the offspring are randomly dispersed over an area that comprises 441 cells. The population dynamics have a greater tendency to lead to extinction, however:

Extinction occurs before generation 10,000 in three out of six simulations, and only one simulation reaches the end of the simulated timeframe. When offspring are distributed globally across the landscape, population dynamics are further destabilized, and extinction occurs within 10 generations (not shown).

The conversion rates control the amount of offspring produced based on the food intake by individuals. By default, herbivores produced 0.1 offspring per unit of grass consumed. Predators produced 0.6 offspring per consumed prey, with a baseline food intake of 0.6. We tried different values for these rates, and here want to briefly depict the overall influence of these parameters. If the conversion rate of herbivores is increased from the value of 0.1 to 0.2, the amplitude of oscillations is increased, leading ultimately to the extinction of the herbivore (fig. 2.A10). Thus, akin to the paradox of enrichment, an increase in the growth rate of the herbivores leads to the destabilization of their population dynamics. An increase of the growth rates of predators has the same effect.

If the conversion rate or the baseline food intake of the predator is reduced (e.g. by setting the baseline food intake to 0.0, fig. 2.A11), the ratio of prey to predators increases. The sharp phase transitions observed under the other parameter settings vanish, and instead stable oscillations occur. These oscillations dampen out with decreasing growth rates of the predator population. The diminished growth rate of the predator population in figure 2.A11 causes population expansions to be less rapid and spatial patterns to be less dynamic. As there are overall few predators, the effect of predators on the spatial distribution of herbivores is weaker, and instead of spiral patterns or static spots predators are distributed among the herbivores and occupy small patches of high grass densities (landscape plots, fig. 2.A11). The predator and herbivore populations exhibit the same dimorphism documented under default parameters in figure 2.3 of the main text.

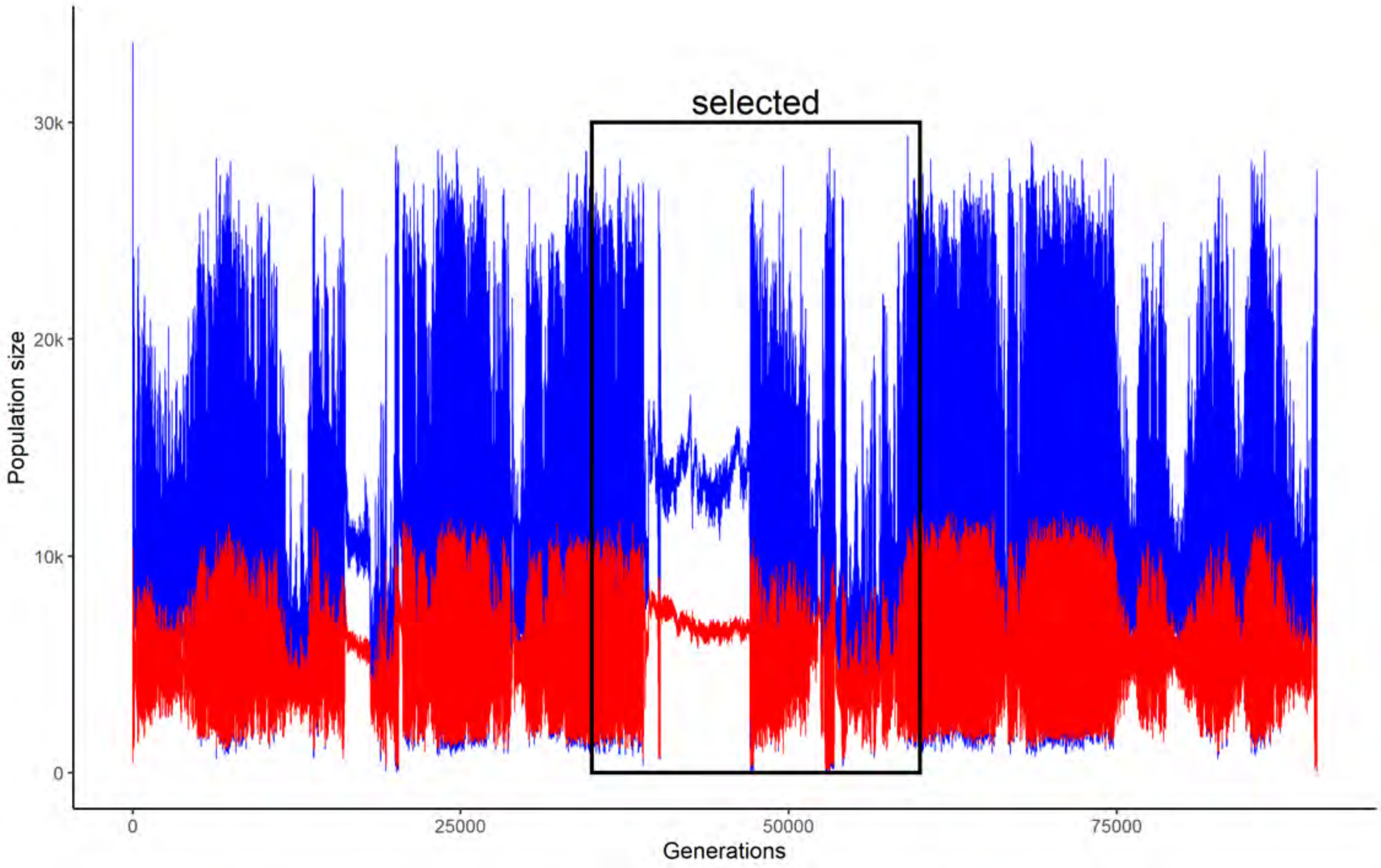

Figure 2.A1 | Population dynamics of predators (red) and herbivores (blue) until the extinction of the herbivore population briefly after generation 90,000. The black box highlights the simulation segment considered in our main article.

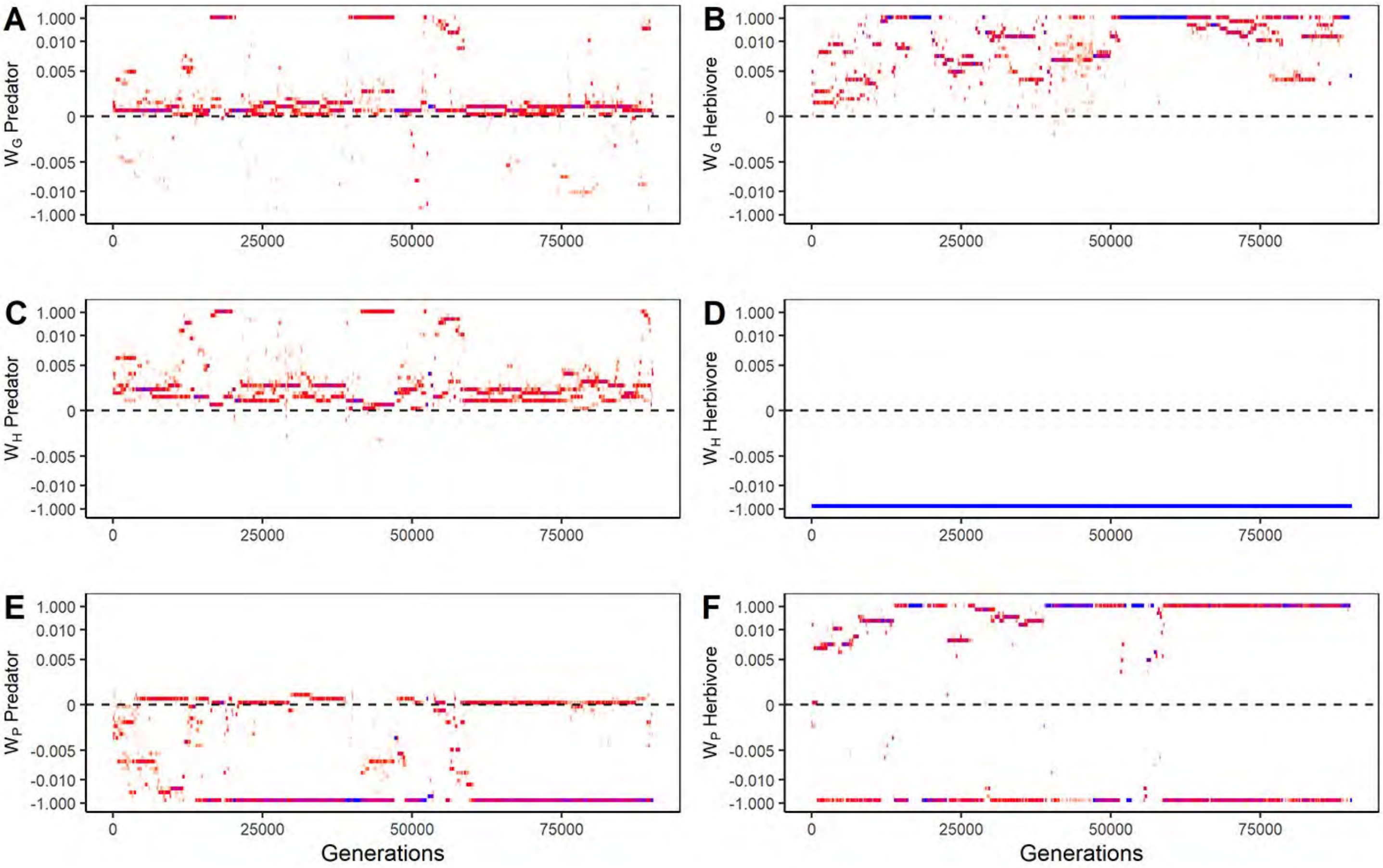

Figure 2.A2 | Weight evolution of herbivores and predators over the entire simulation. The y-axis denotes the weight values, and frequencies of different trait values within each generation are coded by a colour gradient from 0.0 (=white) to 0.3 (=red) and 1 (=blue). Weight values are shown on a tanh-transformed scale.

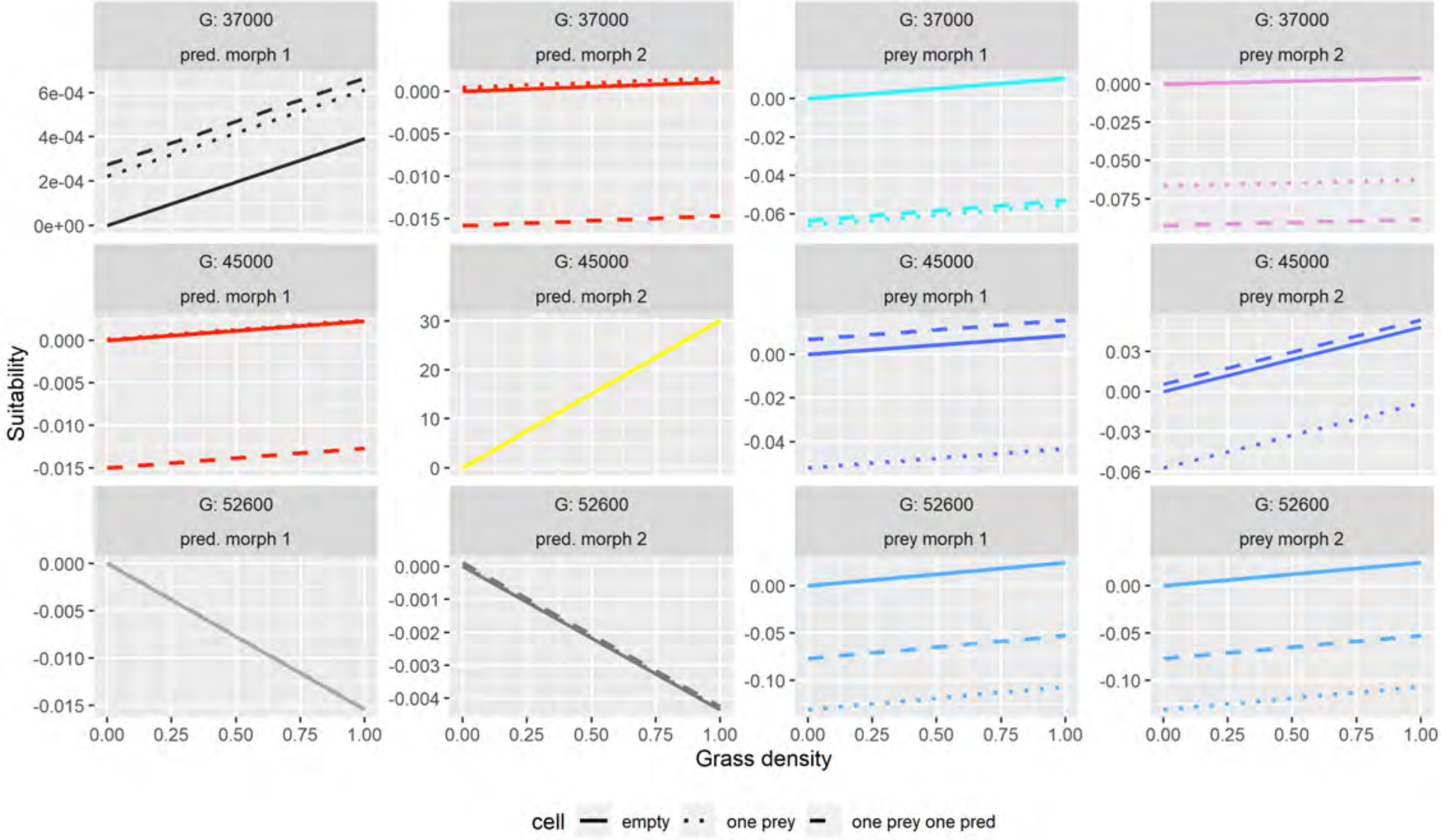

Figure 2.A3 | Reaction norms of the two most common predator and prey morphs for the three generation snapshots shown in figure 2.2. Colour code as in figure 2.2C. Shown is the suitability score in relation to grass density (0 to 1, x axis) for three different constellations of prey and predator densities: Suitability scores in the absence of prey and predators (solid lines), with a single prey individual present (dotted) and with a prey and a predator individual present (dashed).

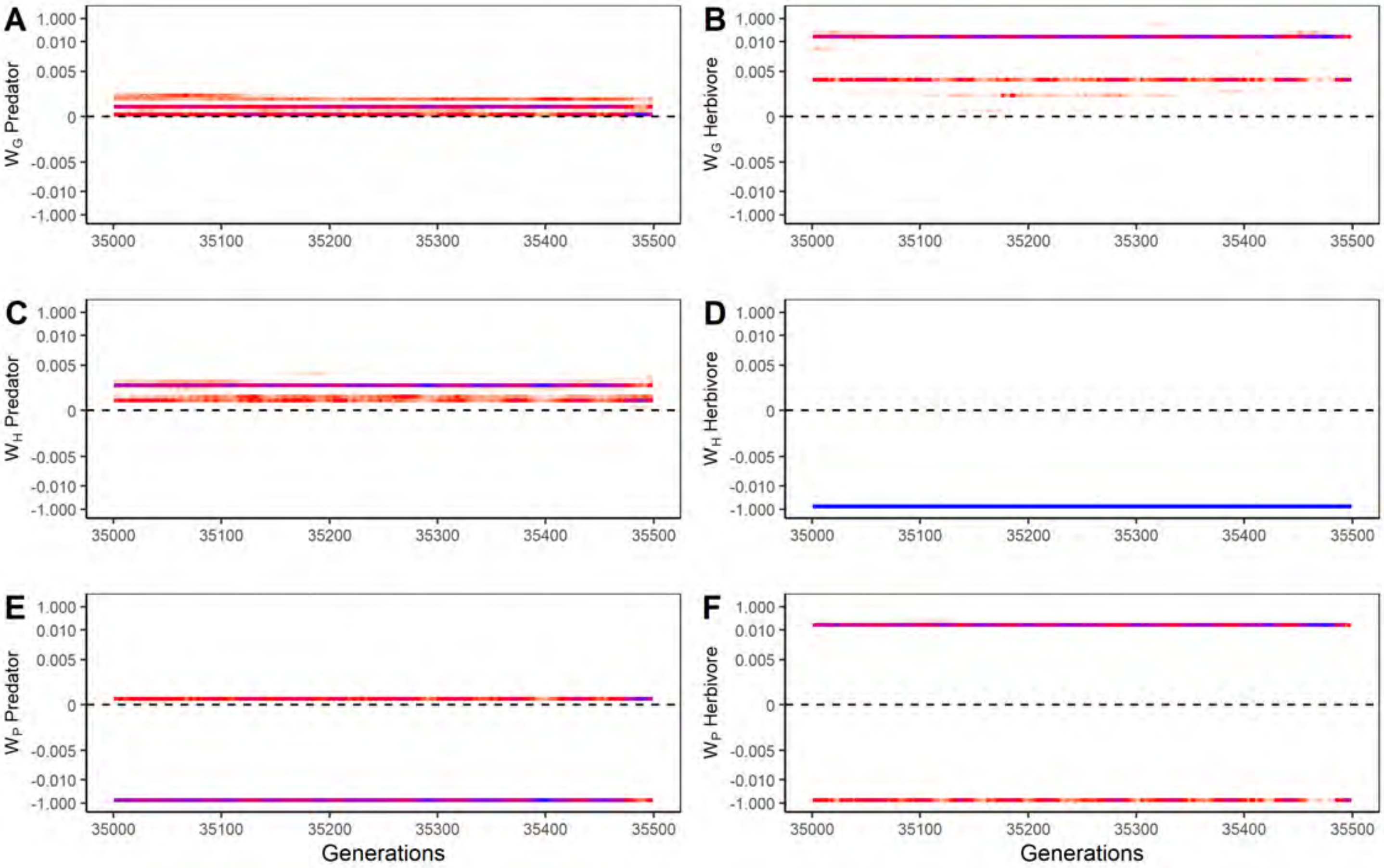

Figure 2.A4 | Weight evolution of herbivores and predators between generation 35,000 and 35,500, compare figure 2.3. The y-axis denotes the weight values, and frequencies of different trait values within each generation are coded by a colour gradient from 0.0 (=white) to 0.3 (=red) and 1 (=blue). Weight values are shown on a tanh-transformed scale.

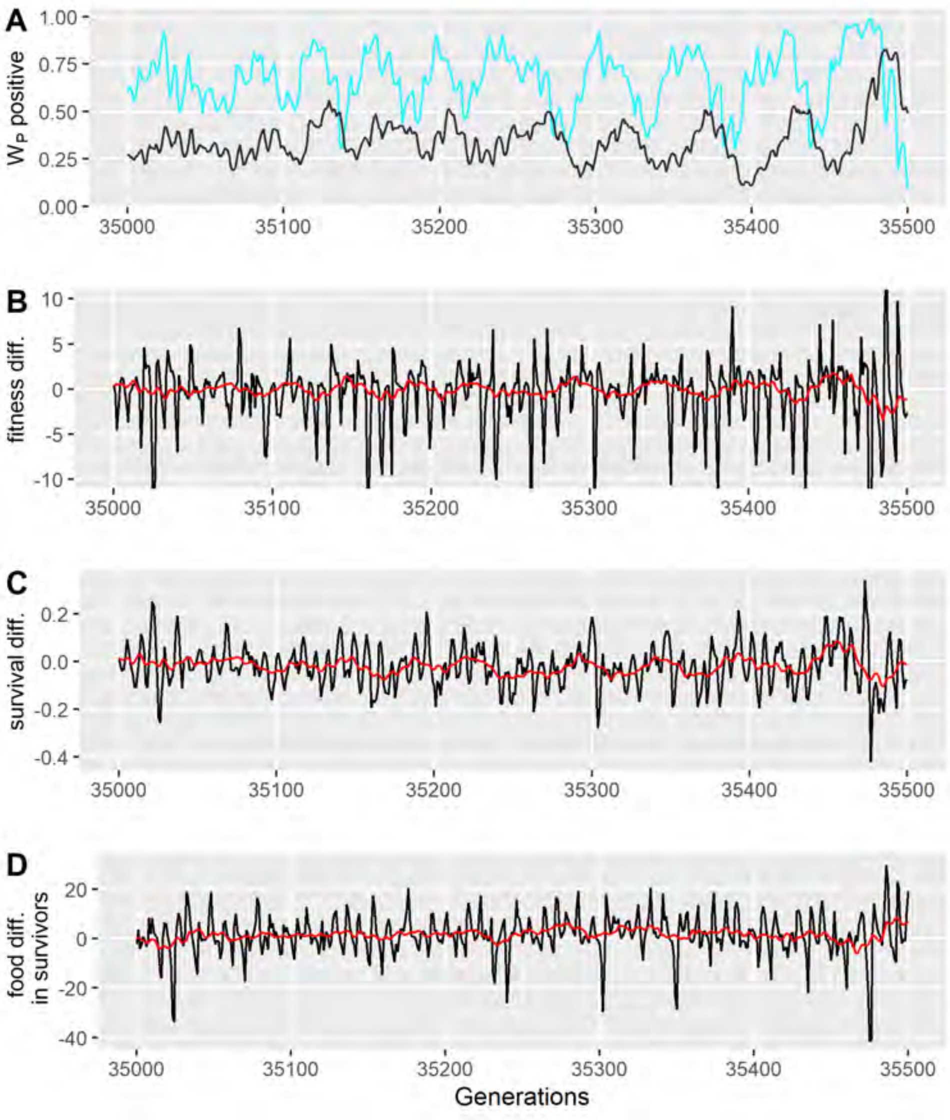

Figure 2.A5 | The effect of morph frequencies on survival and resource consumption. **(A)** The frequency of morphs with a positive predator density weight in the herbivore (cyan) and the predator population (black). **(B)** Difference in expected offspring number between the positive morph (cyan) and the negative morph (pink, not shown) of the herbivore population (black), and the rolling mean with a window of 20 generations (red). Note that peaks are associated with minima in the frequency of the W_p positive predator morph. **(C)** Same as in B, except for survival probability instead of expected offspring number. **(D)** Same as in B, except for food collected by surviving individuals. C and D are thus the constituents of B.

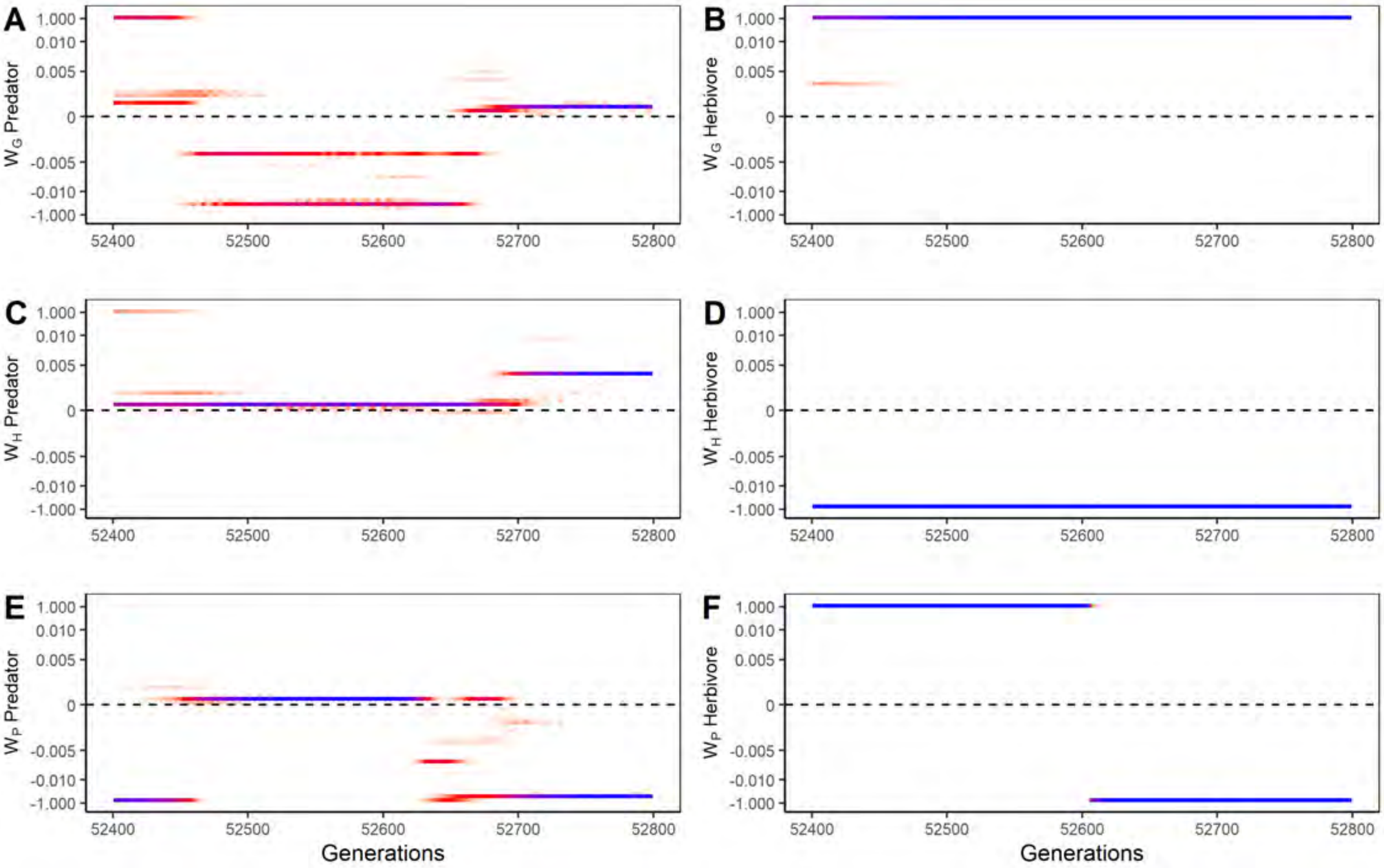

Figure 2.A6 | Weight evolution of herbivores and predators between generation 52,400 and 52,800, compare figure 2.4. The y-axis denotes the weight values, and frequencies of different trait values within each generation are coded by a colour gradient from 0.0 (=white) to 0.3 (=red) and 1 (=blue). Weight values are shown on a tanh-transformed scale.

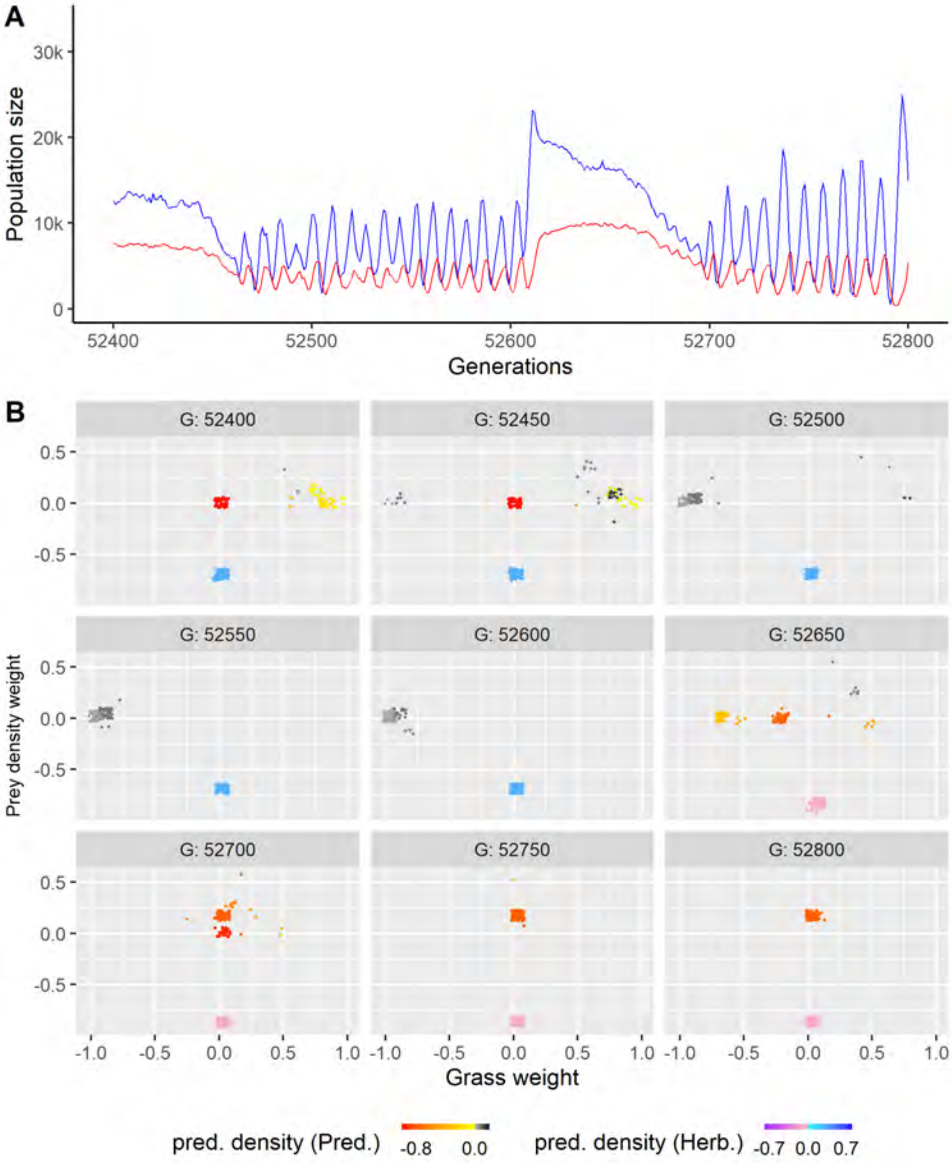

Figure 2.A7 | Population dynamics and evolution of movement strategies between generations 52,400 and 52,800. **(A)** Population dynamics of predators (red) and herbivores (blue). **(B)** Movement strategies of herbivores (violet-blue) and predators (red-black) at each of the three snapshots, measured by the relative magnitude of each the three weights (absolute values sum to one). The relative magnitude of the weight for predator density is color-coded for herbivores from -0.7 (=purple) to 0.0 (pink/cyan) and 0.7 (=blue), and for predators from -1.0 (=red) to 0.0 (=yellow/grey) and 0.2 (=black).

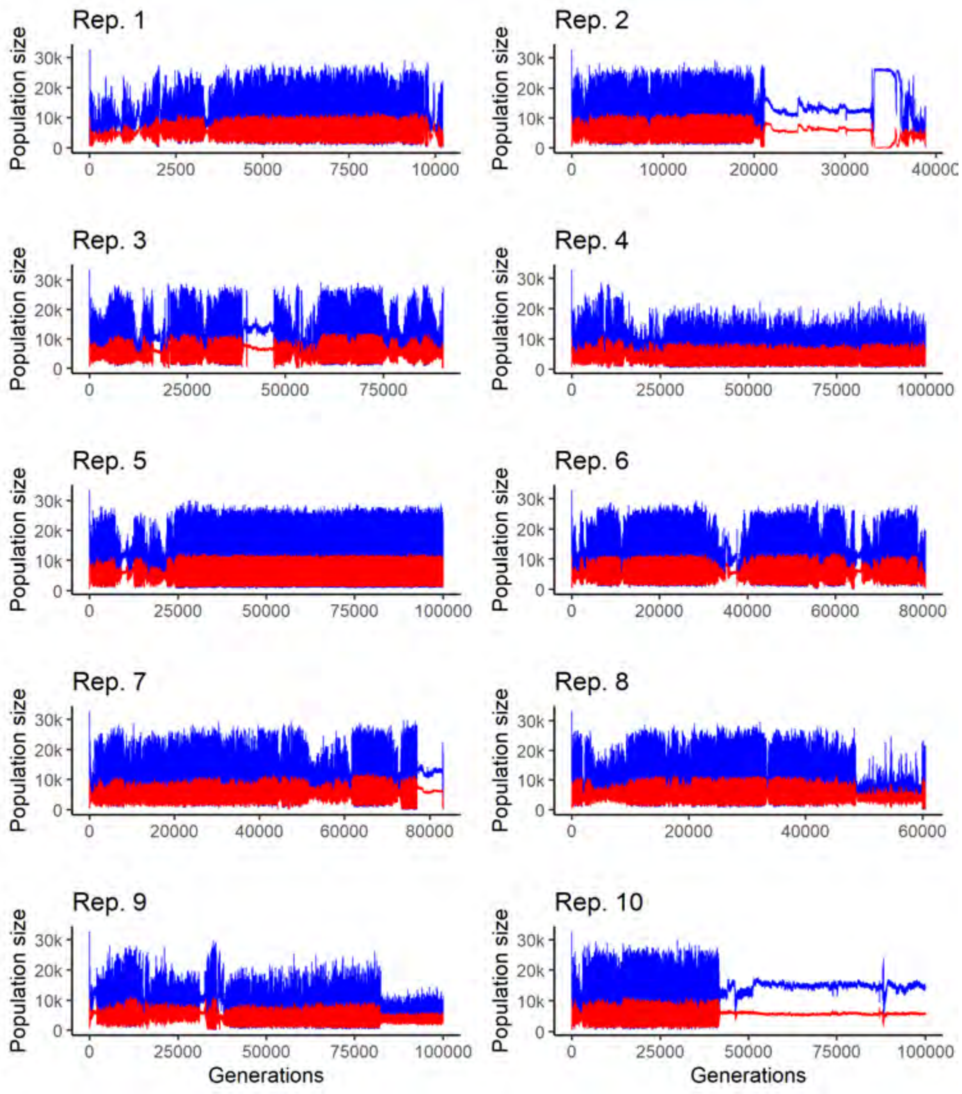

Figure 2.A8 | Population dynamics across 10 simulation replicates under default parameters (dispersal radius 1, grass-herbivore conversion rate 0.1, prey-predator conversion rate 0.6, baseline food intake of predators 0.6). Simulations ended at extinction of one of the populations or ran until generation 100,000. Note the different x axis across replicates.

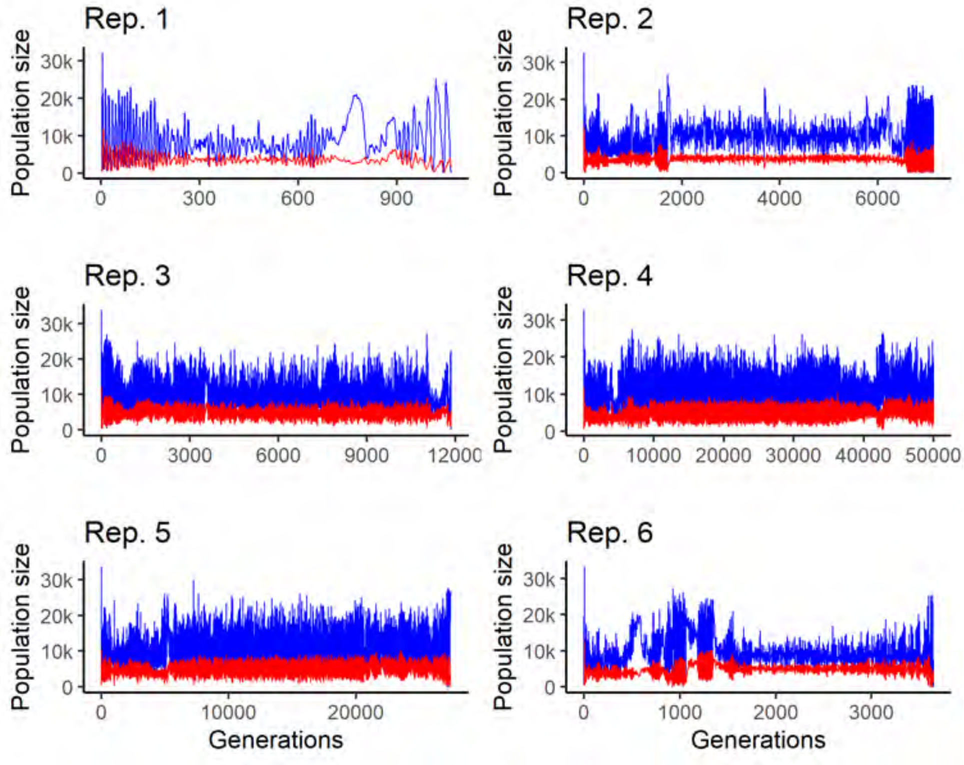

Figure 2.A9 | Population dynamics across 6 simulation replicates with a wider offspring dispersal range (dispersal radius 10, other parameters grass-herbivore conversion rate 0.1, prey-predator conversion rate 0.6, baseline food intake of predators 0.6). Simulations ended at extinction of one of the populations or ran until generation 50,000. Note the different x axis across replicates.

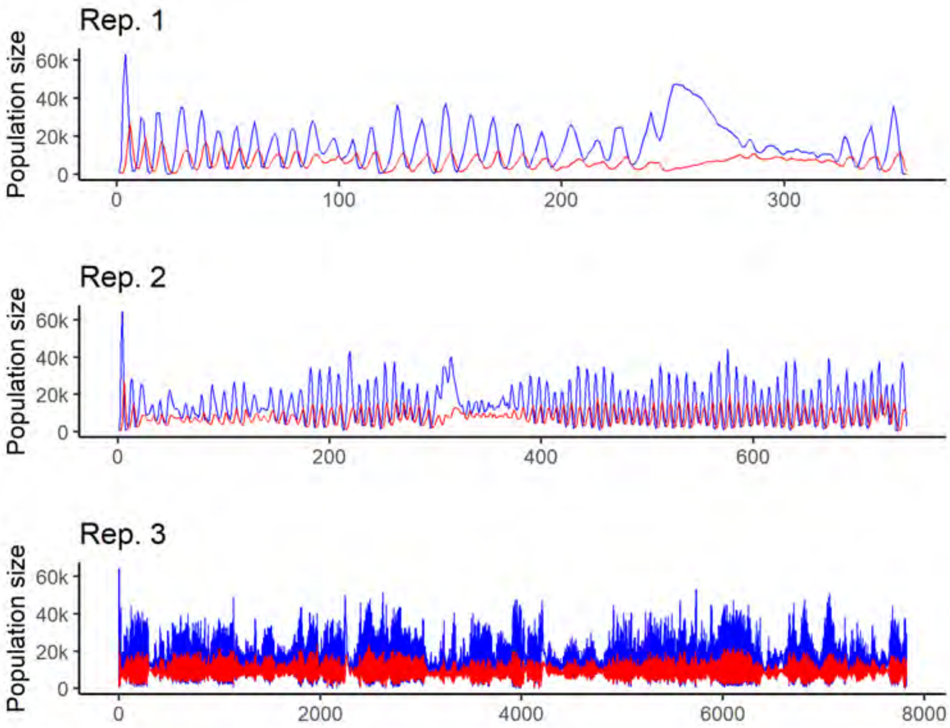

Figure 2.A10 | Population dynamics in three simulation replicates, where herbivores have a twice as large resource-to-offspring conversion rate (grass-herbivore conversion rate 0.2, other parameters dispersal radius 1, grass-herbivore conversion rate 0.1, prey-predator conversion rate 0.6, baseline food intake of predators 0.6). Simulations ended at extinction of one of the two populations. Note the different x axis across replicates.

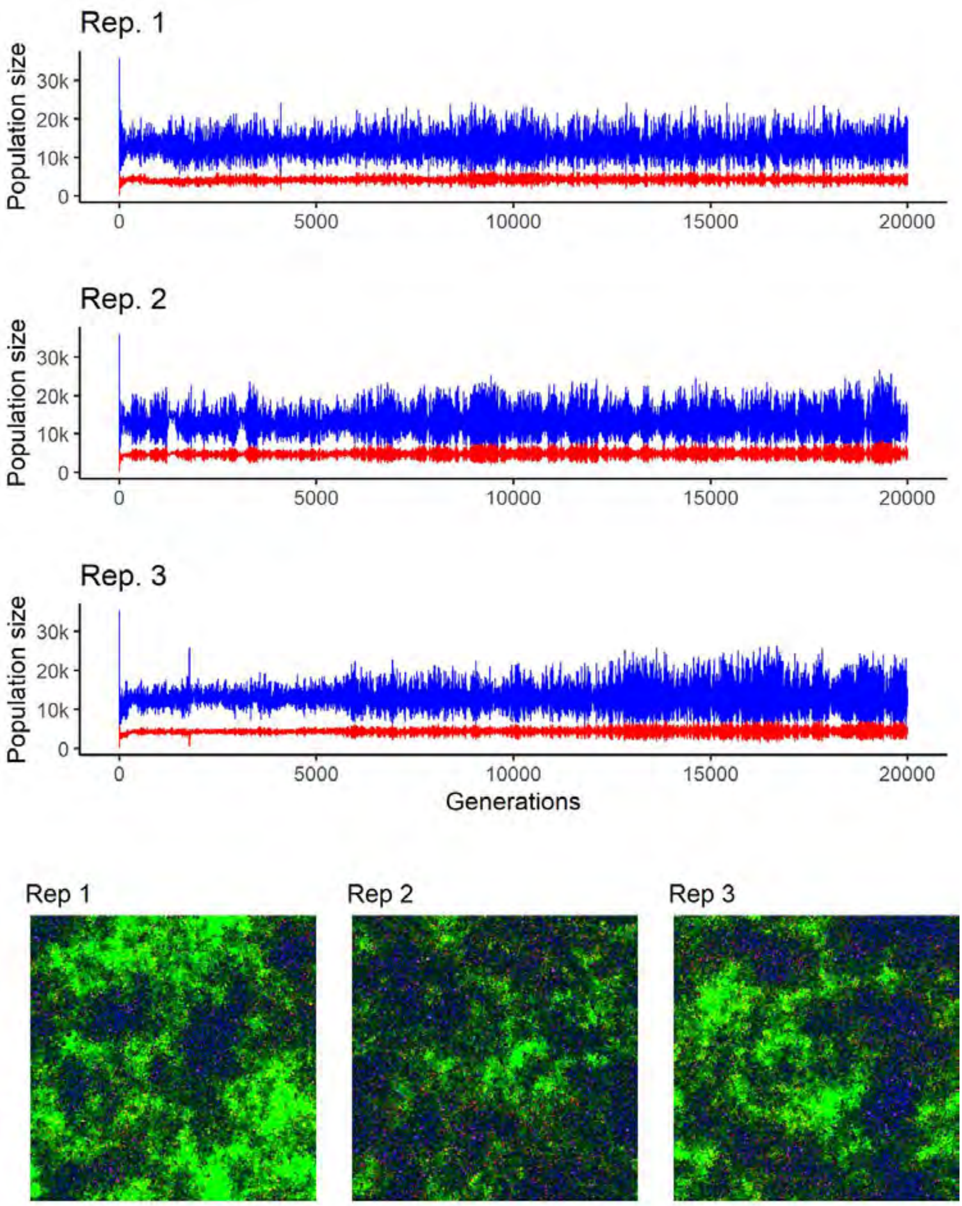

Figure 2.A11 | Population dynamics and landscape structure in three replicates, where predator baseline food intake was reduced to 0.0 (other parameters dispersal radius 1, grass-herbivore conversion rate 0.1, prey-predator conversion rate 0.6). Simulations ended at extinction of one of the two populations or ran until generation 100,000. Note the different x axis across replicates.

3

THE JOINT EVOLUTION OF ANIMAL MOVEMENT AND COMPETITION STRATEGIES

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ABSTRACT

Competition typically takes place in a spatial context, but eco-evolutionary models rarely address the joint evolution of movement and competition strategies. Here we investigate a spatially explicit forager-kleptoparasite model where consumers can either forage on a heterogeneous resource landscape or steal resource items from conspecifics (kleptoparasitism). We consider three scenarios: (1) foragers without kleptoparasites; (2) consumers specializing as foragers or as kleptoparasites; and (3) consumers that can switch between foraging and kleptoparasitism depending on local conditions. We model movement strategies as individual-specific combinations of preferences for environmental cues, similar to step-selection coefficients. Using mechanistic, individual-based simulations, we study the joint evolution of movement and competition strategies, and we investigate the implications for the distribution of consumers over this landscape. Movement and competition strategies evolve rapidly and consistently across scenarios, with marked differences among scenarios, leading to differences in resource exploitation patterns. In scenario 1, foragers evolve considerable individual variation in movement strategies, while in scenario 2, movement strategies show a swift divergence between foragers and kleptoparasites. In scenario 3, where individuals' competition strategy is conditional on local cues, movement strategies facilitate kleptoparasitism, and individual consistency in competition strategy also emerges. Even in the absence of kleptoparasitism (scenario 1), the distribution of consumers deviates considerably from 'ideal free' predictions, arising from the intrinsic difficulty of moving effectively on a depleted resource landscape with few reliable cues. Our study emphasises the advantages of a mechanistic approach when studying competition in a spatial context, and suggests how evolutionary modelling can be integrated with current work in animal movement ecology.

3.1. INTRODUCTION

Intraspecific competition is an important driver of population dynamics and the spatial distribution of organisms (Krebs and Davies, 1978), and has two main types, 'exploitation' and 'interference'. In exploitation competition, individuals compete indirectly by depleting a common resource, while in interference competition, individuals compete directly by interacting with each other (Birch, 1957; Case and Gilpin, 1974; Keddy, 2001). A special case of interference competition which is widespread among animal taxa is 'kleptoparasitism', in which an individual steals a resource from its owner (Iyengar, 2008). Since competition has an obvious spatial context, animals should account for the locations of competitors when deciding where to move (Nathan et al., 2008). This is expected to have downstream effects on animal distributions across spatial scales (from resource patches: Fretwell and Lucas, 1969, to species distributions: Duckworth and Badyaev 2007; Schlägel et al. 2020). Animal movement strategies are thus likely to be adaptive responses to landscapes of competition, with competitive strategies themselves being evolved responses to animal distributions. Empirical studies of this joint evolution are nearly impossible at large spatiotemporal scales. This makes models linking individual movement and competition strategies with population distributions necessary.

Contemporary individual-to-population models of animal space use (reviewed in DeAngelis and Diaz, 2019) and competition, however, are only sufficient to represent very simple movement and prey-choice decisions. For example, models including the ideal free distribution (IFD; Fretwell and Lucas, 1969), information-sharing models (Giraldeau and Beauchamp, 1999; Folmer et al., 2012), and producer scrounger models (Barnard and Sibly, 1981; Vickery et al., 1991; Beauchamp, 2008), often treat foraging competition in highly simplified ways. Most IFD models consider resource depletion unimportant or negligible (continuous input models, see Tregenza, 1995; van der Meer and Ens, 1997), make simplifying assumptions about interference competition, or even model an *ad hoc* benefit of grouping (e.g. Amano et al., 2006). Meanwhile, producer-scrounger models primarily examine the benefits of choosing either a producer or scrounger strategy given local conditions, such as conspecific density (Vickery et al., 1991), or the order of arrival on a patch (Beauchamp, 2008). Overall, these models simplify the mechanisms by which competition decisions are made and downplay spatial structure (see also Holmgren, 1995; Garay et al., 2020; Spencer and Broom, 2018).

In contrast, spatial structure is key to foraging decisions (Beauchamp, 2008). How animals are assumed to integrate the costs (and potential benefits) of competition into their movement decisions has important consequences for theoretical expectations of population distributions (van der Meer and Ens, 1997; Hamilton, 2002; Beauchamp, 2008). In addition to short-term, ecological effects, competition also likely has evolutionary consequences for individual *movement strategies*, setting up feedback loops between ecology and evolution. Modelling competition and movement decisions jointly is thus a major challenge. Some models take an entirely ecological view, assuming that individuals move or compete ideally, or according to fixed strategies (Vickery et al., 1991; Holmgren, 1995; Tregenza, 1995; Amano et al., 2006, but see Hamilton 2002). Models that include evolutionary dynamics in movement (de Jager et al., 2011, 2020) and foraging competition strategies (Beauchamp, 2008; Tania et al., 2012) are more plausible, but they too make arbitrary assumptions about the functional importance of environmental cues to individual decisions.

Mechanistic, individual-based models are well suited to capturing the complexities of spatial structure, animal decision-making, and evolutionary dynamics (Guttal and Couzin, 2010; Kuijper et al., 2012; Getz et al., 2015, 2016; White et al., 2018; Long and Weissing, 2020; Netz et al., 2022; Gupte et al., 2022, for conceptual underpinnings see: Huston et al. 1988; Mueller et al. 2011; DeAngelis and Diaz 2019). Individual-based models can incorporate the often significant variation in movement and competition preferences found in populations, allowing individuals to make different decisions given similar cues (Laskowski and Bell, 2013; Bierbach et al., 2017). Individual-based models also force researchers to be explicit about their modelling assumptions, such as how exactly competition affects fitness. Similarly, rather than taking a purely ecological approach and assuming individual differences (e.g. in movement rules: White et al., 2018), allowing movement strategies to evolve in a competitive landscape can reveal whether individual variation emerges in plausible ecological scenarios (as in Getz et al., 2015). This allows the functional importance of environmental cues for movement (see e.g. Scherer et al., 2020) and competition decisions in evolutionary models to be joint outcomes of selection, and lets different competition strategies be associated with different movement strategies (Getz et al., 2015).

Here, we present a spatially-explicit, mechanistic, individual-based model of intraspecific foraging competition, where movement and competition strategies jointly evolve on a resource landscape with discrete, depletable food items that need to be processed ('handled') before consumption. In our model, foragers make movement decisions using inherited, evolvable preferences for local ecological cues, such as resource and competitor densities; the combination of preferences for each cue forms individuals' movement strategy (similar to relative step-selection: Fortin et al., 2005; Avgar et al., 2016). We consider three scenarios: in the first scenario, we examine only exploitation competition. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual's life. In the third scenario, we model kleptoparasitism as a behavioural strategy conditioned on local environmental and social cues; the mechanism underlying this foraging choice is also inherited.

Our model allows us to examine the evolution of individual movement strategies, population level resource intake, and the spatial structure of the resource landscape. The model enables us to take ecological snapshots of consumer-resource dynamics (animal distributions, resource depletion, and competition) proceeding at evolutionary time scales. We investigate *(1)* which movement strategies evolve in our three competition scenarios, *(2)* whether movement strategies differ within and between competition strategies in our scenarios, and *(3)* how resource densities and the association between forager and resource densities differ between scenarios.

3.2. THE MODEL

Individual-based models have to explicitly specify numerous assumptions (e.g. spatial structure, individual interactions, event timescales), but this helps expose assumptions that are often hidden below the surface in analytical models. We kept our model assumptions as simple and generic as possible, striving for general, conceptual insights. To be concrete, the model reflects the foraging behaviour of shorebirds such as oystercatchers (*Haematopus* spp.), which are extensively studied in the context of foraging competition, both empirically (e.g. Vahl et al., 2005a,b, 2007; Rutten et al., 2010a,b), and using individual-based models (reviewed in Stillman and Goss-Custard, 2010). Our environment is a fine grid of cells, and each grid cell can hold multiple individuals. Resources are discrete, as is our conception of time within and between generations. Our population, with a fixed number of individuals (N = 10,000), moves on a landscape of 512^2 grid cells (approx. 1 individual per 26 cells), with wrapped boundaries (i.e., a torus); individuals passing beyond the bounds at one end re-appear on the opposite side. The model has two time scales, first, an ecological time scale of T timesteps comprising one generation (default $T = 400$), during which individuals move, make foraging decisions, and handle prey items they find or steal. Individuals are immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard, 1979; Ruxton et al., 1992). At the end of each generation, individuals reproduce, transmitting their movement and foraging strategies to their offspring, whose number is proportional to individual intake at the ecological time scale. Our model has 1,000 generations, and this comprises the evolutionary timescale.

3.2.1. RESOURCE LANDSCAPE

Prey Abundance We considered our discrete resources, called ‘prey items’ to represent mussels, a common prey of many shorebirds, whose abundances are largely driven by external gradients. We assigned each cell a constant probability of generating a new prey item per timestep, which we refer to as the cell-specific growth rate r. We modelled clustering in landscape productivity by having the distribution of r across the grid take the form of 1,024 resource peaks, placed at regular distances of 16 grid cells from the peaks around them. The distance between peaks corresponds to the average lifetime diffusion distance of a randomly-moving individual, thus individuals shift between resource peaks regularly and can experience the whole range of environmental variation throughout their lifetime. The growth rate r declines from the centre of each peak (called r_{max}) to its periphery (see fig. 3.1A)); the central cell generates prey items five times more frequently than a peripheral cell: at $r_{max} = 0.01$, central cells generate one item per 100 timesteps (four items/generation), while the peripheral cells generate one item only every 500 timesteps (< one item/generation). All landscape cells have a uniform carrying capacity K of 5 prey items. While a cell is at carrying capacity its r is 0. Cells are initialized with prey items proportional to their r (see fig. 3.1A).

Prey Acquisition by Foragers Foragers perceive a cue indicating the number of prey items P in a cell, but fail to detect each item with a probability q, and are thus successful in finding a prey item with probability $1 - q^P$. Individuals on a cell forage in a randomised sequence and the probability of finding a prey item is updated if other individuals find prey, reducing P. Foragers that find a prey item must handle it for a fixed handling time T_H (default = 5 timesteps), before consuming it (Ruxton et al., 1992). Natural examples include the time required for an oystercatcher to break through a mussel shell, or a raptor to subdue prey; overall, the handling action is obvious, and the prey is not fully under the control of the finder (Brockmann and Barnard, 1979). Foragers that do not find a prey item are considered idle in that timestep and are counted as ‘non-handlers’. Similarly, handlers that finish processing their prey in timestep t can only forage again in timestep $t + 1$, i.e., they are idle in the timestep t.

3.2.2. MOVEMENT STRATEGIES

All individuals move simultaneously at the end of each timestep, and then implement their foraging or kleptoparasitic behaviour to acquire prey. Handlers do not make any movements until they have fully handled and consumed their prey. We model movement as comprised of small, discrete steps between adjacent cells. Across scenarios, individuals make movement decisions using evolved cue preferences. Individuals select a destination cell, after assessing potential destinations based on available cues, similar to approaches used previously (Getz et al., 2015, 2016; White et al., 2018; Scherer et al., 2020; Netz et al., 2022).

To move, individuals scan the nine cells of their Moore neighbourhood for three environmental cues, *(1)* an indication of the number P of discrete prey items, *(2)* the number H of individuals handling prey ('handlers'), and *(3)* the number N of individuals not handling prey ('nonhandlers'). Individuals rank the potential destinations (including their current cell) by their suitability $S = s_P P + s_H H + s_N N$ and move to the most suitable cell in timestep $t+1$. The individual weighing factors for each cue, s_P, s_H, and s_N, (numeric values that can be positive or negative), are evolvable traits that are submitted from parents to their offspring, subject to rare mutations. Since individuals are constrained to perceiving and moving short distances, they may not always sense their best long-term move.

It is the combination of cue preferences, and especially their value relative to each other, that determines individual movement decisions (similar to relative selection coefficients, Fortin et al., 2005; Avgar et al., 2016; White et al., 2018). For example, an extreme value of s_P relative to the other weighing factors would mean that an individual's movement decisions are guided primarily by differences in the local density of prey items. We call an individual's combination of inherited weighing factors its *movement strategy* (see e.g. fig. 3.1E).

3.2.3. COMPETITION STRATEGIES

Scenario 1: Exploitative Competition In scenario 1, we simulate only exploitative competition; individuals (henceforth called 'foragers') move about on the landscape and probabilistically find, handle, and consume prey-items. Foragers can be either in a 'searching' or a 'handling' state (Holmgren, 1995).

Scenario 2: Foraging or Kleptoparasitism as Fixed Strategies In scenario 2, the competition strategy is genetically determined and transmitted from parents to offspring: exploitative competition (by foragers), or kleptoparasitic interference (by kleptoparasites). Kleptoparasites thus cannot extract prey items directly from the landscape, and only steal from handlers (see Holmgren, 1995). With probability K, kleptoparasites are successful in stealing from handlers. Throughout, we chose $K = 1$, as successful surprise attacks are commonly observed among birds (Brockmann and Barnard, 1979). For smaller values of K, the prevalence of kleptoparasitism decreases up to the point where it becomes unviable, but the effect of K was gradual, rather than leading to qualitatively different outcomes. When multiple kleptoparasites target the same handler, only one (randomly selected) is considered successful — thus kleptoparasites compete exploitatively among themselves. Kleptoparasites displace the handler that they robbed of prey up to 5 cells away from their location. Having acquired prey, kleptoparasites become handlers, but need only handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by its previous owner. Once a kleptoparasite becomes a handler, it can also be targeted by other kleptoparasites. Unsuccessful kleptoparasites are considered idle, and are counted as non-handlers. Movement strategies evolve independently of the competition strategy, as in scenario 1; however, the optimal movement strategy for foragers need not be the same as that for kleptoparasites.

Scenario 3: Conditional Interference Competition In scenario 3, each individual can either act as a forager, or as a kleptoparasite, depending on its assessment of local conditions. Similar to how movement decisions are made based on local cues, individuals process cell-specific environmental cues in timestep t to determine their competition strategy in the next timestep as

$$\text{strategy} = \begin{cases} \text{forager}, & \text{if } w_P P + w_H H + w_N N \geq w_0 \\ \text{kleptoparasite}, & \text{otherwise} \end{cases} \tag{3.1}$$

where the weighing factors w_P, w_H and w_N, of the cues and the threshold value w_0 are evolvable parameters that are transmitted from parents to their offspring (subject to rare mutations). The combination of the four weighing factors forms each individual's competition strategy. Individuals' competition strategies may lead to specialisation as foragers or kleptoparasites (as in scenario 2), or to plastic behaviour conditioned on local cues. The competition dynamics are the same as in scenario 2.

3.2.4. REPRODUCTION AND INHERITANCE

Our model considers a population of fixed size (10,000 individuals) with discrete, non-overlapping generations. For simplicity, we assume that individuals are haploid and reproduction is asexual. In scenarios 1 and 2, individuals only inherit and transmit the weighing factors (s_P, s_H, s_N) determining their movement decisions. In scenario 3, individuals also inherit and transmit the weighing factors (w_P, w_H, w_N, w_0) determining their competition decisions. Each individual's expected number of offspring is proportional to the individual's total lifetime intake of resources; hence, resource intake is used as a proxy for fitness. A weighted lottery (with weights proportional to lifetime resource intake) selects a parent for each offspring in the subsequent generation (see e.g. Tania et al., 2012; Netz et al., 2022).

Each offspring is placed at a random location on the landscape, leading individuals to experience conditions potentially different from those of their parent. Across scenarios, the weighing factors for movement and competition are subject to rare, independent mutations that occur with probability $\mu = 0.001$ per weighing factor. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with scale parameter 0.01 that is centred on zero, allowing for the rare occurrence of large mutations, while most mutations are small. In scenario 2, foragers may infrequently mutate into a kleptoparasite or *vice versa*; both events happen with probability $\mu = 0.001$.

3.2.5. SIMULATION OUTPUT AND ANALYSIS

We ran all three scenarios at a default r_{max} of 0.01, which we present in the RESULTS, and also across a range of r_{max} values between 0.001 and 0.05 (see fig. 3.6 and Appendix figs. 3.A7 – 3.A9). We initialized all weighing factors with values drawn independently from a Cauchy distribution with scale parameter 0.01 centred on zero. Although the initial amount of variation in weighing factors was very small (see e.g. fig. 3.1E), the simulations started with a considerable range of movement strategies. Starting with high-variation conditions is not unrealistic (Wolf and Weissing, 2012) and it speeds up evolutionary simulations, as evolution is less mutation-limited in the early phases. To confirm that our results do not merely reflect initialisation conditions, we also ran simulations starting in a monomorphic state (see Supplementary Materials Section 7). We found that the initialisation does not significantly affect the evolutionary outcome and so only present the default implementation here. Below, we visualize the movement strategies by dividing the weighing factors s_i by the sum $s_I = s_I/(|s_P| + |s_H| + |s_N|)$ of their absolute values. After this normalization (which does not affect the movement behaviour), the individual movement strategies are represented by points in a three-dimensional trait space of relative preferences that is bounded by -1.0 (*strongly avoid*) and +1.0: (*strongly prefer*). This visualisation indicated that the evolutionary outcome of replicate simulations is remarkably consistent. We therefore only show three replicates here. More data can be generated and analysed using the code linked below.

Population Activities and Intake Across scenarios, in each generation, we counted the number of times foragers were searching for prey, kleptoparasites were searching for handlers, and the number of timesteps that individuals of either strategy were handling a prey item. We refer to the ratio of these values as the population's 'activity budget'. We examined how the population activity budget developed over evolutionary time, and whether a stable equilibrium was reached. Furthermore, we counted the population's mean per-capita intake per generation as a measure of population productivity.

Spatial distribution of individuals A basic prediction of the IFD and the related input matching rule is that the number of individuals on occupied patches should be proportional to patch productivity (Fretwell and Lucas, 1969; Parker, 1978; Houston, 2008). Patch productivity is challenging to measure in real world systems, but is among our model's building blocks. We examined the correlation between the number of individuals and the cell-specific productivity r to see whether, and to what extent, the spatial distribution of individuals aligned with productivity.

3.3. RESULTS

3.3.1. SCENARIO 1: NO KLEPTOPARASITISM

In scenario 1, foragers deplete prey-items faster than they are replenished, drastically reducing the overall number of prey within 50 generations (fig. 3.1A). The population activity budget is split between searching and handling (fig. 3.1B); while handling and the mean per-capita intake are both initially low, they peak within ten generations (fig. 3.1C), as individuals easily acquire prey-items from the fully stocked landscape in the first few generations. With dwindling prey-items, fewer searching foragers find prey, and handling as a share of the activity budget declines to a stable ~ 45% within 50 generations, and mean per-capita intake also stabilises (fig. 3.1C). Across generations, the correlation between the number of foragers and cell productivity is only moderately positive (fig. 3.1D). This is in contrast with 'ideal free' theory that predicts a perfect correspondence between local forager density and local productivity (Parker, 1978; Houston, 2008). Obviously, a perfect correlation between the number of foragers and cell productivity is not to be expected in a stochastic model like ours, but one might expect a stronger correlation between forager density and productivity than in case of random movement. However, as shown in figure 3.A1 of the Appendix, this is not the case. We think that the relatively low correlation between forager density and productivity is related to the fact that foragers cannot directly sense the local cell productivity r; instead they can only use the (small) number of prey items available in a cell as a cue for local productivity. Evolved movement strategies overall exhibit a preference for handlers and prey, and avoid non-handlers ($s_P > 0, s_H > 0, s_N < 0$, fig. 3.1E). Given these conditions, a wide range of movement strategies co-exist; some individuals focus mainly on prey density ($s_P \approx 1, s_H \approx 0, s_N \approx 0$), others move primarily towards successful foragers (handlers), while still others primarily move away from unsuccessful foragers ($s_N \approx -1$) which are potential competitors.

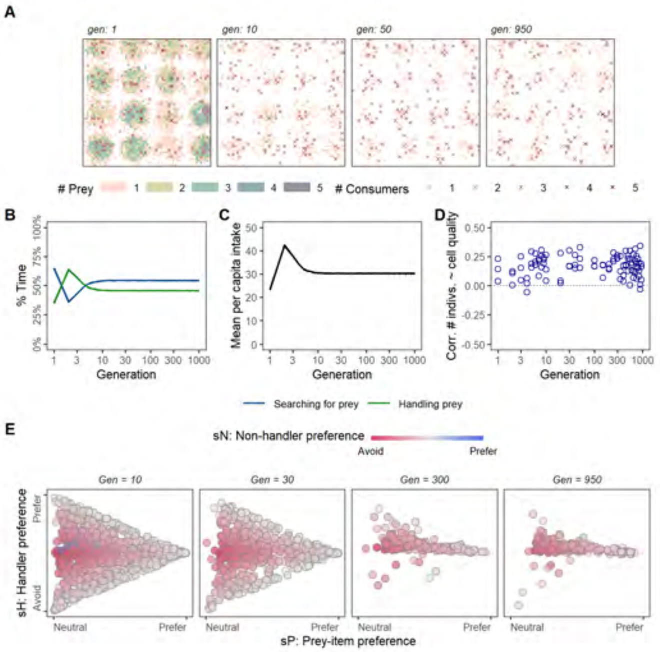

Figure 3.1 | Eco-evolutionary implications of pure exploitation competition in scenario 1. (A) A population comprised solely of foragers seeking prey on a resource landscape swiftly depletes initially abundant prey-items within 10 generations (of 1,000 simulated). Foragers maintain this prey item scarcity throughout the remaining generations of the simulation, despite regular resource regeneration (see G = 950). **(B)** Within 20 generations of evolution, the population reaches an equilibrium in the relative proportion of time spent on searching for prey and handling prey, and in **(C)** mean per-capita intake. **(D)** The number of foragers per cell is only weakly correlated with cell productivity r, contrary to the input matching rule of Ideal Free Distribution theory. **(E)** Individuals evolve preferences for handlers and prey and avoid non-handlers. Given the signs of the preferences, a wide range of movement strategies co-exist over hundreds of generations. Individuals may focus on moving up gradients of prey-items ($s_P \approx 1.0$: *prefer*), moving towards successful foragers (handlers), or moving away from unsuccessful foragers which are potential competitors ($s_N \approx$ red). Panels **A, E** show a single replicate, panels **B, C** and **D** show three replicate simulations with log-scaled X-axes (lines overlap almost perfectly); all panels are for $r_{max} = 0.01$; panel **E** shows 2,500 individuals.

3.3.2. SCENARIO 2: COEXISTENCE OF FORAGERS AND KLEPTOPARASITES

In scenario 2, with fixed foraging and kleptoparasitism allowed, the spatial distribution of prey-items at equilibrium is very different from scenario 1. Initially, consumers graze down resource peaks until few prey-items remain on the landscape; however, within 50 generations the resource landscape recovers, with prey abundances higher than in the earliest generations (fig. 3.2A). This is because of the emergence of kleptoparasites (fig. 3.2B): in early generations, kleptoparasites are rare, and the activity budget, the mean per-capita intake, and the distribution of consumers over the landscape are similar to scenario 1. As resources are depleted and kleptoparasite-handler encounters become more common than forager-prey encounters, kleptoparasitism becomes the majority strategy (a stable ~70% of the population; see fig. 3.2B), and searching for handlers to rob becomes the commonest activity. However, the high frequency of this activity and the low frequency of handling, indicate that few kleptoparasites are successful at robbing handlers.

With few foragers, few prey-items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (fig. 3.2A). As fewer prey-items are extracted overall, mean per-capita intake also declines from an initial peak (fig. 3.2C). The re-emergence of strong spatial structure of the resource landscape within 50 generations should easily allow individuals to move to areas with more resources, and thus match the productivity of the landscape, but this does not happen. Instead, the correlation between individuals and cell productivity — initially weak — actually becomes negative once kleptoparasites become prevalent ($G \approx 30$; fig. 3.2D). This may be explained by the prevalence of kleptoparasitism near resource peaks: Since handlers flee from a site after being stolen from and kleptoparasitism occurs more frequently on resource peaks, individuals overall get displaced away from resource peaks. As shown in figure 3.3, the movement strategies of foragers and kleptoparasites rapidly diverge (see also Appendix fig. 3.A3, 3.A5). While both foragers and kleptoparasites evolve a near-neutral but positive preference for prey and avoidance of non-handlers, their response to handlers is very different. Kleptoparasites very rapidly evolve a strong preference for moving towards handlers, which are their primary resource (fig. 3.3). In the absence of kleptoparasites, foragers would also evolve a similar preference (fig. 3.1E), but, with kleptoparasites common in the population, foragers converge upon a handler-avoiding strategy (fig. 3.3). This completes the explanation for why consumers do not match landscape productivity: foragers evolve strategies to avoid high productivity areas (which are more likely to have many handlers), while kleptoparasites evolve strategies to find handlers (which need not be on high productivity cells).

3.3.3. SCENARIO 3: CONDITION-DEPENDENT KLEPTOPARASITISM

When individuals are allowed to choose their competition strategy (foraging or kleptoparasitism) based on local environmental cues, the distribution of prey items is substantially different from the two previous scenarios (fig. 3.4A). Initially, individuals deplete the resource landscape of prey-items within ten generations.

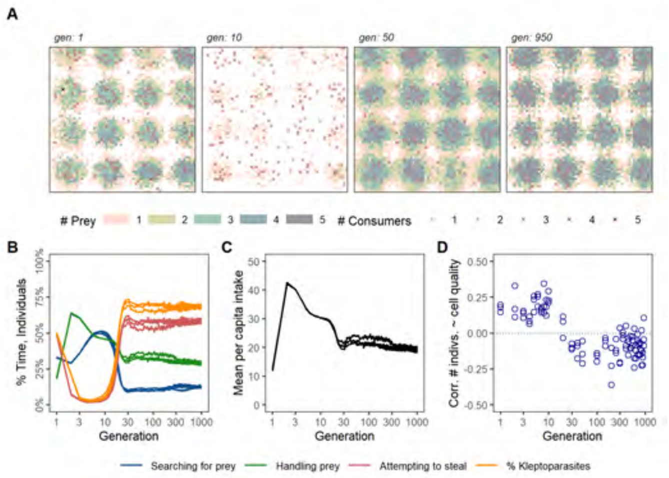

Figure 3.2 | Eco-evolutionary implications of the coexistence of foragers and kleptoparasites following fixed competition strategies in scenario 2. **(A)** Populations with both foragers and kleptoparasites drastically deplete the initially well-stocked resource landscape by generation 10; however, prey densities recover strongly by generation 50, even beyond the densities in generation 1. **(B)** A surprisingly stable equilibrium between the forager and kleptoparasite strategies is reached within 30 generations, with the relative frequency of kleptoparasites (orange line) first dropping to very low levels but later recovering to reach a high level (~ 70%) in all three replicates. Consequently, at equilibrium, only about 10% of individuals are foragers searching for prey, 50% are kleptoparasites attempting to steal from handlers, and 40% are handlers processing prey-items (either foragers or kleptoparasites). **(C)** When kleptoparasites are rare, the population intake rate exhibits the same pattern as in scenario 1, dropping to a lower level with the emergence of kleptoparasites. Naturally, there is an increase in the proportion of time spent on stealing attempts (red line – **B**), and a corresponding decrease in prey seeking (by searching foragers; blue line – **B**), and handling (green line – **C**). **(D)** The correlation of consumers with cell productivity is initially only weakly positive, but after kleptoparasites become more prevalent (G = 30), the correlation of consumer abundance with cell productivity r is actually moderately negative. Panel **A** shows a single replicate, while **B, C** and **D** show three replicates with log-scaled X-axes; all panels are for $r_{max} = 0.01$.

By generation 50, the resource landscape recovers some of the spatial structure of early generations, but prey item abundances do not match the recovery seen in scenario 2. This is because unlike scenario 2, individuals search for prey more often and steal less (at or below 25%; compare figs. 3.4B and 3.2B), preventing a full recovery of the resource landscape. Consequently, mean per-capita intake stabilises (after an initial spike, as in scenarios 1 and 2) within ten generations to a level similar to scenario 1 (fig. 3.4C). The correlation between consumer abundance and cell productivity is perhaps a bit more positive than in scenario 1 (fig. 3.1D), but not larger than in the case of random movement (Appendix fig. 3.A1).

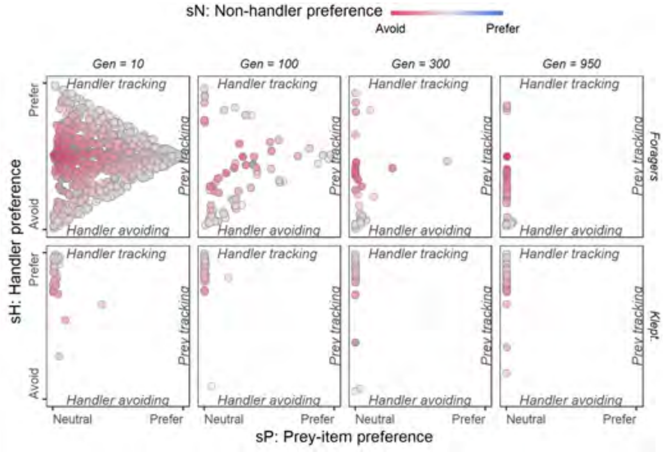

Figure 3.3 | Rapid divergence of movement strategies between foragers and kleptoparasites in scenario 2. In scenario 2, kleptoparasites rapidly diverge (within 10 generations) from foragers in their movement strategy, clustering around $s_H = 1.0$: a handler-tracking strategy. This strategy is stably maintained throughout the simulation (G = 100, 300, 950). Foragers retain substantial diversity in movement strategies for many generations (see G = 100), but unlike scenario 1, tend to be repelled (relative $s_H < 0$) by handlers. Over time, foragers adopt a strategy that helps them avoid all other individuals (G = 300, 950). A few individuals sporadically adopt a movement strategy associated with the opposite competition strategy (e.g. foragers with relative $s_H > 0$); this is most likely due to mutations in the competition strategy, rather than a new movement morph within either foragers or kleptoparasites. At the evolutionary equilibrium then, social information (either s_H or s_N) is the strongest component of all movement strategies. All panels show 2,500 individuals (25% of total) from the same simulation replicate ($r_{max} = 0.01$), and earlier generations are ancestors of later generations.

Using conditional foraging strategies, individuals are able to switch between resource types (prey and handlers) depending on which is more profitable (Emlen, 1966) ('opportunistic kleptoparasitism'; fig. 3.4F; see Appendix fig. 3.A6). All individuals would choose to steal when handlers are present, even when prey items are more common. Indeed, about 40% of individuals would choose to steal even when prey are abundant and there are no handlers at all. Whether individuals choose to forage or steal in the absence of both handlers and prey determines the variation observed between replicates (see activity budgets in fig. 3.4B), but does not impact the population level intake rates. Over longer evolutionary timescales the replicates' activity budgets converge. About 70% of individuals have an intrinsic bias towards kleptoparasitism, i.e., they would by default attempt to steal when there are no cues to inform their decision (fig. 3.4F: $P = 0$, $H = 0$).

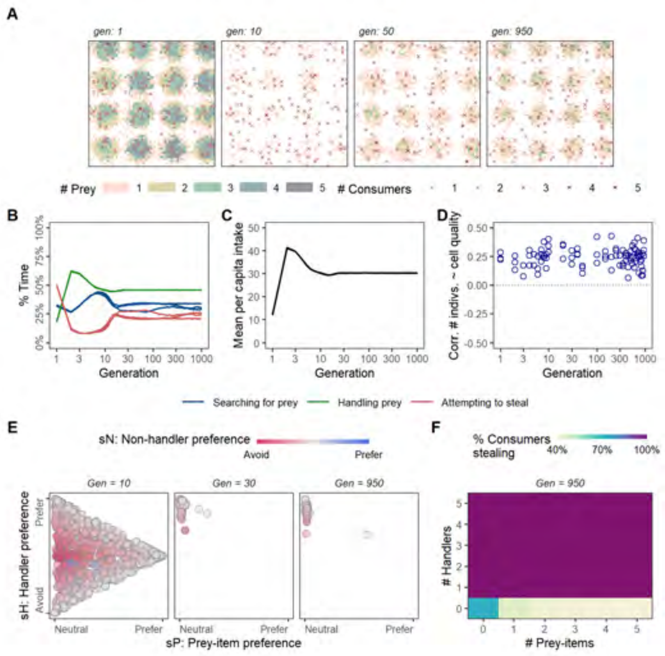

Figure 3.4 | Eco-evolutionary implications of conditional foraging strategies in scenario 3. (A) The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations, prey abundances recover on many cells, though not to the extent of scenario 2. The local density of individuals on occupied cells is shown as coloured crosses. **(B)** By generation 30, the proportion of time spent searching (blue line), handling (green line), and stealing prey (red line) reach an equilibrium that differs somewhat across replicates, but **(C)** the total intake of the population reaches the same equilibrium value in all three replicates. **(D)** The correlation between the local density of individuals on a cell, and its productivity r is stronger than in scenario 2. **(E)** From an initially high diversity of movement strategies, there is a rapid convergence (within 30 generations) of all individuals to strongly prefer moving towards successful foragers, or handlers, nearly to the exclusion of all other movement cues. This handler-tracking strategy once established is maintained (Gen = 300, 950). **(F)** Population competition strategies are more varied. While most individuals will choose to forage as prey density increases, about 40% of individuals attempt to steal even when prey is abundant and handlers are scarce. All individuals will steal when handlers are available. Panels **A, E** show a single replicate, while **B, C** and **D** show three replicates, **F** shows the mean across replicates; all panels are for $r_{max} = 0.01$.

3.3.4. MOVEMENT STRATEGIES ON DEPLETED LANDSCAPES

Orienting movement towards resources (Nathan et al., 2008, *where to move*) can be a challenge in a system with low densities of discrete prey-items. Resources are difficult to find, and landscape productivity is difficult to assess. In our model, prey-depletion leads parts of the resource landscape to become ‘clueless regions’

(Perkins, 1992), where foragers cannot make directed movements based on prey-item abundances, as all neighbouring item abundances are identical (see white areas in fig. 3.5A; A1: scenario 1, A2: scenario 2, A3: scenario 3). At the beginning of all three scenarios, about 75% of landscape cells have a different number of prey-items from the cells around them; these are primarily cells with an intermediate r, which have more prey than peripheral cells of resource peaks, but fewer prey than the central cells. This proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

The 'cluelessness' of the landscapes develops differently across scenarios on evolutionary timescales (fig. 3.5B). In scenario 1, the proportion of cells with a different number of items in the neighbourhood rapidly declines to ~25% within 10 generations, as foragers deplete most prey-items, making most of the landscape a clueless region. Interestingly, the evolved movement strategy itself (which includes an attraction to food items) may have contributed to rapid resource depletion and, hence, the cluelessness of the landscape. In the absence of prey cues, foragers evolve to move towards handlers, with > 75% of individuals showing a preference for handlers within 100 generations (fig. 3.5B1). Forager preference for handlers may be explained as the sensing of a long-term cue of local productivity. Since handlers are immobilised on the cell where they find a prey-item, handler density is an indirect indicator of cell r, and due to spatial autocorrelation, also of the r of bordering cells.

In early generations, scenario 2 landscapes develop similarly to scenario 1 landscapes (fig. 3.5A2). However, within 50 generations, most cells again contain items as extraction is reduced by the rise of kleptoparasitism, with differences among cells according to their r (see also fig. 3.2A). Thus > 75% of cells have a different number of items from neighbouring cells (fig. 3.5B2). Unlike scenario 1, the rapid increase in handler preference is driven by kleptoparasites becoming the majority strategy (see above). Scenario 3 is similar to scenario 2, except that only about half of all cells have a different number of prey-items from neighbouring cells (fig. 3.5A3, 3.5B3). Here, the rapid evolution of a handler preference in movement decisions cannot be assigned a clear cause, since handlers are both a potential direct resource as well as indirect cues to the location of productive cells.

3.3.5. EFFECT OF LANDSCAPE PRODUCTIVITY

The prey-item regrowth rate that characterises the peaks of the resource landscape (r_{max}) is a measure of the productivity of the resource landscape overall. Having thus far focused on scenarios with $r_{max} = 0.01$ (corresponding to a peak production of 4 food items per consumer lifetime), we find that, not unexpectedly, the

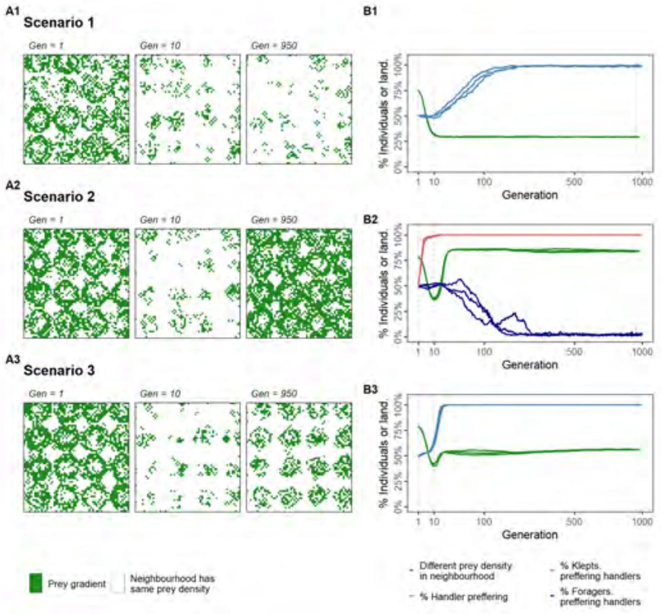

Figure 3.5 | Uninformative prey densities and the evolution of social information as an alternative movement cue. **(A1, A2, A3)** On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative cues for 'adaptive' movement in early generations, this is much less true once the resource landscape is depleted of prey-items (depending on the scenario). **(B1, B2, B3)** The proportion of cells where differences in local prey densities provide informative movement cues (green line), and the proportion of individuals preferring to move towards handlers (blue line), whose presence may be used as an alternative cue for movement towards higher-productivity areas of the landscape. In **(B2)** representing scenario 2, this proportion is shown separately for foragers (blue line) and kleptoparasites (red line). While panels in **(A)** show a single representative replicate for r_{max} = 0.01, panels in **(B)** show three replicates. All X-axes are scaled to show early generations more clearly.

value of r_{max} has a marked effect on evolved population activity budgets, mean per capita intake, and even evolved strategies. The frequency of foraging reduces with r_{max} in scenarios 1 and 3; this is caused by more frequent acquisition of prey-items (as regrowth keeps pace with depletion), which results in a greater frequency of handling rather than foraging.

In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max} (fig. 3.6A). The difference between scenarios 2 and 3 has to do with the change in the frequency of kleptoparasitism (fig. 3.6B). In scenario 2, kleptoparasitism forms > 75% of all activities at low r_{max}, and is much more common than in scenario 3 populations at the same regrowth rate. However, at relatively high

r_{max} (0.03), the fixed kleptoparasitic strategy goes extinct. This is because at high r_{max}, forager-prey encounters are more common than kleptoparasite-handler encounters, in both early (< 10) and later generations (> 50). Consequently, kleptoparasites have relatively much lower fitness than foragers, and do not proliferate. Thus at high r_{max}, a scenario 2 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen in later generations, these occur most likely due to ephemeral mutations in the forager strategy.

In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (fig. 3.6B); thus some foragers lose time in extracting items which are then stolen from them. Consequently, while populations in all three scenarios achieve very similar mean per-capita intakes at low r_{max}, at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic populations achieve a higher mean per-capita intake than populations using fixed strategies. Only at high r_{max}, when fixed strategy populations effectively convert to pure forager populations, do they achieve a higher intake than conditional strategy populations (fig. 3.6C).

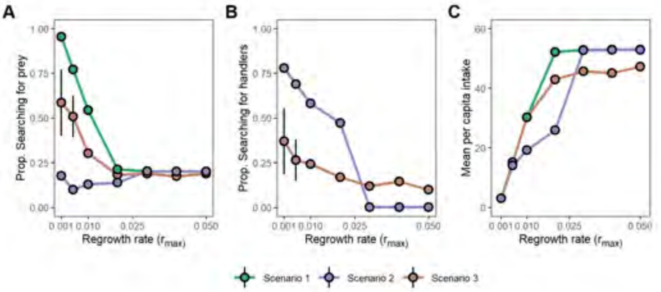

Figure 3.6 | Landscape productivity strongly affects scenario outcomes. **(A)** The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey densities. **(B)** The proportion of time spent searching for handlers (in order to steal prey from them) also decreases with increasing r_{max}. In scenario 2, kleptoparasites go extinct for r_{max} values above 0.025. **(C)** At low productivity, the average intake is similar in all three scenarios. For higher r_{max} values the average intake rate is lowest in scenario 2, until r_{max} is larger than 0.025 and kleptoparasites go extinct (leading to the same kind of population as in scenario 1). At high r_{max}, the average intake rate in populations with conditional kleptoparasites (scenario 3) is substantially lower than in populations without kleptoparasitism. All panels show conditions at G = 1,000; error ranges where present show standard deviation around values; some error ranges are too small to be visible.

3.4. DISCUSSION

Our spatially-explicit individual-based model implements the ecology and evolution of movement and foraging decisions, as well as resource dynamics, in biologically plausible ways, and offers a new perspective on the distribution of animals in relation to their resources under different scenarios of competition. First, individuals moving with a limited perception range and competing only by exploitation, evolve movement strategies for both direct and indirect resource cues (prey items and handlers, respectively). Regardless, on a resource landscape with discrete prey items, large areas may become devoid of any movement cues, leading to a mismatch between individual distribution, prey item distribution, and landscape productivity. Second, interference competition in the form of kleptoparasitism rapidly establishes itself on landscapes where stealing is more time-efficient than searching for prey, even when such interference is a fixed strategy and kleptoparasites cannot forage for prey. This rapid increase in kleptoparasitism as a strategy is accompanied by the divergent evolution of movement strategies that favour moving towards handlers, which are the primary resource of the kleptoparasites. In this sense, obligate kleptoparasites may be thought of as forming a higher trophic level, with handlers as their prey, and the ecological consequences of the rapidly evolving avoidance behavior of conspecifics are similar to those of the ’ecology of fear’ (Brown et al., 1999; Zanette and Clinchy, 2019), except that here the relevant interactions occur within the same species. Third, when the foraging strategy is allowed to be conditional on local cues, *(1)* the population’s mean per capita intake can be significantly higher than that of a population with fixed strategies, provided that kleptoparasitism occurs in both, and *(2)* unlike fixed-strategy populations, kleptoparasitism as a strategy does not go extinct on high-productivity landscapes.

3.4.1. COMPARISON WITH EXISTING MODELS

Existing models of competition and movement impose fixed movement rules on individuals to mimic either ideal or non-ideal individuals (Vickery et al., 1991; Cressman and Křivan, 2006; Amano et al., 2006; Beauchamp, 2008; Stillman and Goss-Custard, 2010; White et al., 2018). When individual competitive strategies are included in models, they represent differences in competitive ability (e.g. Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002; Netz et al., 2023), or a probabilistic switch between producing and scrounging (Beauchamp, 2008). In contrast, our model allows individuals’ movement (and competition) decisions to be adaptive responses to local environmental cues. Similar to Getz et al. (2015, 2016) and White et al. (2018), our individuals choose from among the available movement options after weighing the local environmental cues, similar to step selection functions (Fortin et al., 2005; Avgar et al., 2016; White et al., 2018). Local environmental cues are constantly changing, as we model discrete, depletable prey-items, contrasting with many IFD models (Tregenza, 1995; Amano et al., 2006). This allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected, and allows the cues sensed by individuals to strongly structure the distribution of competitors (see below).

Adaptive responses must have an explicit evolutionary context, and consider multiple generations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the cue preferences that decide movement, and variation therein, to be the outcomes of natural selection. However, instead of using ‘evolutionary algorithms’ (Beauchamp, 2008; Getz et al., 2015, 2016) to optimise individual movement rules through techniques such as ’simulated annealing’ (i.e., changing the mutation rates or mutation effect sizes as a local optimum is approached) or automatically discarding the lower 50% of the population, we tried to faithfully represent an evolutionary process as it occurs in natural populations.

3.4.2. EVOLUTION OF MOVEMENT STRATEGIES USING SOCIAL INFORMATION

In scenario 1, depletion of discrete prey can leave many areas empty of prey-items: in such areas, movement informed by a resource gradient is impossible, and individuals move more or less at random (Perkins, 1992). This lack of direct resource cues for locally optimal movement might be among the mechanisms by which unsuitable ‘matrix’ habitats modify animal movement on heterogeneous landscapes (Kuefler et al., 2010). When individuals do not sense resource gradients, the presence of more successful conspecifics may indicate a suitable foraging spot (local enhancement; Giraldeau and Beauchamp, 1999; Beauchamp, 2008; Cortés-Avizanda et al., 2014). The presence of unsuccessful individuals, meanwhile, may signal potential costs from exploitation or interference competition. This selects for movement strategies incorporating the presence and condition of competitors into individual movement decisions, or *social movement strategies* (see an example in Guttal and Couzin 2010; see Dall et al., 2005, for social information). Consequently, consumer aggregation — often explained by invoking external costs such as predation (Krause and Ruxton, 2002; Folmer et al., 2012) — could also be the outcome of movement strategies that have evolved to trade competition costs for valuable social information on the underlying spatial structure (here, r) of uninformative landscapes (Folmer et al., 2010; Cortés-Avizanda et al., 2014).

3.4.3. INDIVIDUAL VARIATION IN MOVEMENT STRATEGIES

Our movement strategies, comprising preferences for local ecological cues, may lead individuals to move in ways that are potentially unique to each individual. These strategies may not maximise their intake over short timescales (a few timesteps), but their coexistance implies equal intake rates over lifetime. This makes them consistent with prevalent ideas about consistent individual differences in behaviour, or 'animal personalities' (Wolf and Weissing, 2012; Laskowski and Bell, 2013; Bierbach et al., 2017; Spiegel et al., 2017; Shaw, 2020). In scenario 1, the persistence of multiple movement strategies across generations indicates that they have equivalent fitness (see Getz et al., 2015), and that there are multiple ways to navigate a heterogeneous environment (Wolf and Weissing, 2010; Shaw, 2020). Such differences may help reduce competition as individuals make subtly different movement decisions when presented with the same cues (Laskowski and Bell, 2013, see also Wolf and Weissing 2012). Interestingly, scenario 3 has the least individual variation in movement rules, presumably because plasticity in competition strategy reduces the need for such diversification (Pfennig et al., 2010; Botero et al., 2010).

Scenario 2 cautions that *(1)* Individual variation may only be evident when accounting for the main driver of movement decisions (s_H or s_N; see Appendix fig. 3.A8 for scenario 3 as well). *(2)* Spatial context determines whether individual differences in movement strategy lead to functional variation in movement outcomes. Subtle variation in relative prey density preferences (s_P) could be revealed if individuals were measured in isolation, and could lead to differences in movement paths (given a continuous gradient in prey cues). However, in natural settings with substantial collective behaviour, different social movement strategies (correlated with foraging competition strategy) would be the primary driver of movement. Overall, then, *(a)* measuring movement behaviour in settings that correspond to animals' evolutionary context, and *(b)* accounting for movement-competition strategy correlations, are both key when studying how individual differences translate to functional consequences.

3.4.4. COMPETITION STRATEGIES AND THE SPATIAL DISTRIBUTIONS OF FORAGERS

IFD models predict that individual movement should result in consumer distributions tracking the profitability of resource patches (Fretwell and Lucas, 1970; Parker, 1978). In scenario 1, where the situation is not complicated by the occurrence of kleptoparasitism, we observed a positive correlation between local productivity and local forager density. Nevertheless, it would be premature to interpret such a correlation as evidence that the model predictions are in line with ideal free theory. Instead, such a positive correlation is also predicted by random movement models (fig. 3.A1), where the correlation just reflects the fact that, because of prey handling, successful predators tend to stay a bit longer on productive sites. In scenarios 2 and 3, kleptoparasitic individuals unsurprisingly and rapidly evolve to track handlers (a direct resource), while avoiding non-handlers (potential competitors). These evolved rules however do not lead kleptoparasites to occupy the best cells as predicted by Parker and Sutherland, 1986, Holmgren, 1995, and Hamilton, 2002. In scenario 3, just as in scenario 1 and as observed under random movement, local population density is weakly positively correlated with cell productivity. Scenario 2 in contrast shows a negative correlation of population density with cell productivity. This is driven on the one hand by the handler-avoidance of other foragers, and on the other by the prevalence of kleptoparasitism on resource peaks. Handler presence may indicate a risk of kleptoparasitism, and is therefore avoided by foragers. Also, since foragers quickly turn into handlers when entering the resource peaks, they may then become victim of kleptoparasitism, whereupon they are displaced away from their original position. Thus foragers may spend a lot of time searching for prey items in resource-poor areas, but avoid resource peaks hosting handlers, and when entering the peaks, are quickly displaced. Which of the two mechanisms predominates we cannot say with certainty, but the correlation between cell quality and individuals turns out negative as a consequence. We would suggest that these results exemplify the pitfalls of simplistically linking current ecological conditions with population distributions without considering the presence of the competitive interactions that occur within a population.

3.4.5. CONSTRAINTS ON COMPETITION STRATEGIES

Foraging strategies involving specialisation on a resource type are expected to be constrained by the availability of that resource. Thus kleptoparasitism, seen as a prey-choice problem, should be constrained by the density of targets (Ens et al., 1990). In scenarios 2 and 3, more kleptoparasitism should be expected with increasing r_{max}, as prey and consequently, handlers, are expected to be more abundant. Instead, kleptoparasitism declines with increasing r_{max}, in line with Emlen (1966), who predicted that the commoner food type (prey) rather than the more efficiently exploited one (handlers) should be preferred. This prey choice problem, playing out at evolutionary scales, leads kleptoparasites in scenario 2 to go extinct when prey are very common at high r_{max}. At stable population densities, the persistence of fixed kleptoparasitism depends on their intake *relative to foragers*. Modelling discrete prey-items and individuals in a spatial context, then, leads to the finding that obligate kleptoparasitism is only a viable strategy when forager-prey encounters are less common than kleptoparasite-handler encounters. Reducing the relative profitability of kleptoparasitism in other ways — such as imposing a cost on kleptoparasitic attacks for the initiator, or reducing the probability of success (currently, 1.0) — would also lead to a reduced incidence of kleptoparasitism, and eventual extinction even on less productive landscapes. In scenario 3, about 40% of individuals choose to attempt to steal even when prey are available and handlers are not. This suggests a more realistic proportion of consistently kleptoparasitic individuals among populations with flexible foraging strategies. Many seabirds, which forage for prey when they are super-abundant, but also readily harass other birds for prey, are a good example (Brockmann and Barnard, 1979). Finally, comparing across regrowth rates shows why possibly cryptic behavioral complexity should be considered in predictions of the long-term effect of environmental change on populations. While in both scenario 1 and 2 populations appear identical at high r_{max}, even a small decrease in environmental productivity could lead to an abrupt drop in per-capita intake — and potentially, strongly reduced growth or survival — for fixed strategy populations due to unexpected, emergent kleptoparasitism.

3.4.6. MODEL LIMITATIONS

While we tried to make our model more 'life-like' in certain aspects, especially by allowing for individual variation, evolving movement strategies and a heterogeneous and dynamic resource landscape, in other places we have made simplifying assumptions, both for computational reasons and to ease the understanding of an already fairly complex model environment. Here, we briefly highlight two of these assumptions. First, we kept the population size constant throughout our simulations. Including population dynamics in the model is straightforward (e.g. Netz et al. 2022) and could have important implications. For example, our model predicts a strongly depleted resource landscape in scenario 1 (fig. 3.1A). If population sizes would decline due to resource depletion, resource levels might recover, potentially leading to a quite different eco-evolutionary outcome. Yet, in this first effort, we did not address population dynamics as the model results would presumably depend on additional parameters, such as the conversion efficiency of consumed items to offspring. More importantly, population sizes might fluctuate in response to the prevalence of kleptoparasitism, particularly in scenario 2 where distinctive types can be observed, and this could lead to rich eco-evolutionary dynamics involving different behavioral types (Netz et al., 2022). A lot more detail could be added to the assumptions underpinning how resource consumption influences mortality and reproduction, with potentially wide-reaching consequences for evolving movement strategies. If for example mortality of individuals occurred within generations, e.g. via starvation of unsuccessful foragers, the presence or absence of conspecifics could be a more reliable indicator of overall habitat quality.

Second, we assumed global offspring dispersal in all simulations presented in the main text (although local dispersal is implemented in our simulation programme). Considering primarily global dispersal, we produce a well-mixed system, in which local adaptation or spatial dynamics do not occur. The spatial scale of resource peaks was chosen such that individuals can easily move between peaks. The success or failure of different movement and foraging strategies over multiple generations is therefore determined by the environments encountered across the entire landscape and not of local conditions, where specific strategies might be concentrated. Under local dispersal, movement strategies can cluster locally, and local adaptation and kin-competition, as well as the spatial scale of resource peaks, may become important. However, in scenarios 1 and 3 simulations under local dispersal lead to the same activity budgets and evolved movement strategies as under global dispersal (Appendix fig. 3.A13 & 3.A14). Only the correlation between forager density and cell productivity is higher, a straightforward consequence of differential reproductive success in relation to cell productivity. In scenario 2, local dispersal produces strong oscillations and spatial dynamics, where kleptoparasites and foragers form the two required components of a reaction-diffusion system (Kondo and Miura 2010, Appendix fig. 3.A15).

3.4.7. INDIVIDUAL-BASED MODELS IN ANIMAL MOVEMENT ECOLOGY

Linking individual-based models with empirical data is difficult, and is still rarely done (see works tailored to management: Stillman and Goss-Custard, 2010; Diaz et al., 2021). Animal tracking technology is still on the cusp of allowing us to track entire populations (though small ones), and classifying their behaviour at the fine temporal scales of animal decision-making (Nathan et al., 2022, see e.g. Lieber et al. 2021; Sankey et al. 2021). Classifying dyadic and collective behaviour from animal tracking is especially challenging (Sankey et al., 2021; Vissat et al., 2021); this makes the detection of rapid competitive interactions in large populations unlikely. Instead, experimental approaches may reveal movement strategies that reduce competitive interactions (Vahl et al., 2005a,b; Rutten et al., 2010b; Bijleveld et al., 2012). However, consistent behaviour in cue-poor captive environments may not always translate to consistency in natural settings with abundant resource cues (Carter et al., 2013), making it necessary to corroborate experimental findings with field studies.

Animal movement ecology takes an explicitly individual-based approach, centred around individual decisions (Nathan et al., 2008). This makes individual-based models a good choice when seeking general insights into the evolutionary ecology of animal movement strategies (see e.g. Getz et al., 2015), whose ultimate causes are otherwise difficult to study empirically. Modelling mechanistic movement decisions has substantial consequences for ecological outcomes (e.g. Mueller et al., 2011; White et al., 2018; Scherer et al., 2020), yet few individual-based models in animal movement are mechanistic (see review in: DeAngelis and Diaz, 2019), and even fewer models include evolutionary dynamics (but see Getz et al., 2015, 2016; Netz et al., 2022; Gupte et al., 2022). Yet explicitly modelling both ecological interactions and evolutionary dynamics, as we do here, can reveal surprising outcomes ranging from innovative predator-prey strategies (Netz et al., 2022), to rapid disease-dominated eco-evolutionary cascades (Gupte et al., 2022), to sympatric speciation (Getz et al., 2016).

The use of resource- and step-selection functions in mechanistic modelling (see e.g. White et al., 2018) gives empirical movement ecologists a familiar starting point in individual-based modelling. Simulating an animal's potential space-use, conditional on environmental data (similar to our cues), and using selection coefficients estimated from tracking data (our cue preferences), is already accepted in movement ecology, and follows our grid-based approach (Avgar et al., 2016; Signer et al., 2019; Avgar et al., 2020; Fieberg et al., 2021). It is relatively easy to implement movement decisions in continuous space, by sampling cues at discrete locations and *(1)* choosing among them, or *(2)* translating these cues into a movement distance and turning angle. The second approach would require more complex functions with more coefficients (preferences), such as neural networks (Mueller et al., 2011), and this could make it difficult to interpret the evolved movement strategies. Models could implement survival and reproduction (the key ingredients of natural selection), as well as other demographic processes, and reproduction and inheritance can be incorporated in a more realistic manner.

DATA AND CODE AVAILABILITY

Simulation model code is on Github: `https://github.com/pratikunterwegs/Kleptomove` and Zenodo: `https://zenodo.org/record/5887618`. Simulation data are available from DataverseNL as a draft:

`https://dataverse.nl/privateurl.xhtml?token=1467641e-2c30-486b-a059-1e37be815b7c`

Data will be at this persistent link after publication: `doi.org/10.34894/JFSC41`.

Data analysis code is on Github: `https://github.com/pratikunterwegs/klepto-move-evol` and on Zenodo: `https://doi.org/10.5281/zenodo.6410868`

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APPENDIX

1. EVOLUTIONARY ECOLOGY OF RANDOM MOVEMENT

We ran our model on a fourth scenario: random movement. In this scenario, the landscape is set up as in our first three scenarios (see fig. 3.A1A). The prey-item handling dynamics are the same as well, and if individuals, which can choose their competition strategy depending on environmental conditions (as in scenario 3), ever encounter a handler and choose to steal from it, they can do so. Individuals have heritable, evolving preferences for environmental cues, as in all our previous scenarios. The major change in this scenario is that individuals cannot actually perceive any environmental cues, and are essentially then, moving to random locations in their neighbourhood. This scenario serves as a useful null model for what one should expect when directed movement is not possible, or has no bearing on fitness.

1. In contrast to scenario 1, the resource landscape regenerates much more strongly, suggesting that despite the paucity of movement cues in scenario 1, foragers are still capable of finding their way to isolated prey-items, and consuming them (panel A).

2. This scenario reveals that directed movement is, understandably, absolutely key to kleptoparasitism. When individuals cannot move towards handlers, the low density of foragers on the landscape, only some of which will be handling an item at any one time, means that encountering a handler is essentially impossible. As expected then, the number of stealing attempts drops to zero within only three generations, and all individuals thereon are foragers (panel B).

3. Despite being unable to move towards resources, the population's mean intake is comparable to scenarios 1 and 3, and actually higher than in scenario 2. This highlights the cost that fixed strategy kleptoparasitism imposes at a population wide level (panel C).

4. The near-zero correlation between consumer abundance and resource productivity is unsurprising (panel D). Nonetheless, it shows that regardless of whether individuals are moving with (relatively) sophisticated movement strategies, or at random, they are very far from following the ideal free distribution's input matching rule. This also confirms the true cost of

resource landscape depletion in scenario 1: The loss of prey-item gradients with which to orient movement leaves individuals navigating a clueless landscape, on which they simply cannot find the way to areas of high productivity.

5. Finally, the evolution of movement strategies, when they are not actually under selection, supports our findings of strong selection on movement in the first three scenarios (panel E).

2. EVOLUTION OF MOVEMENT STRATEGIES ACROSS REPLICATES

2.1 FREQUENCIES OF RELATIVE CUE PREFERENCES

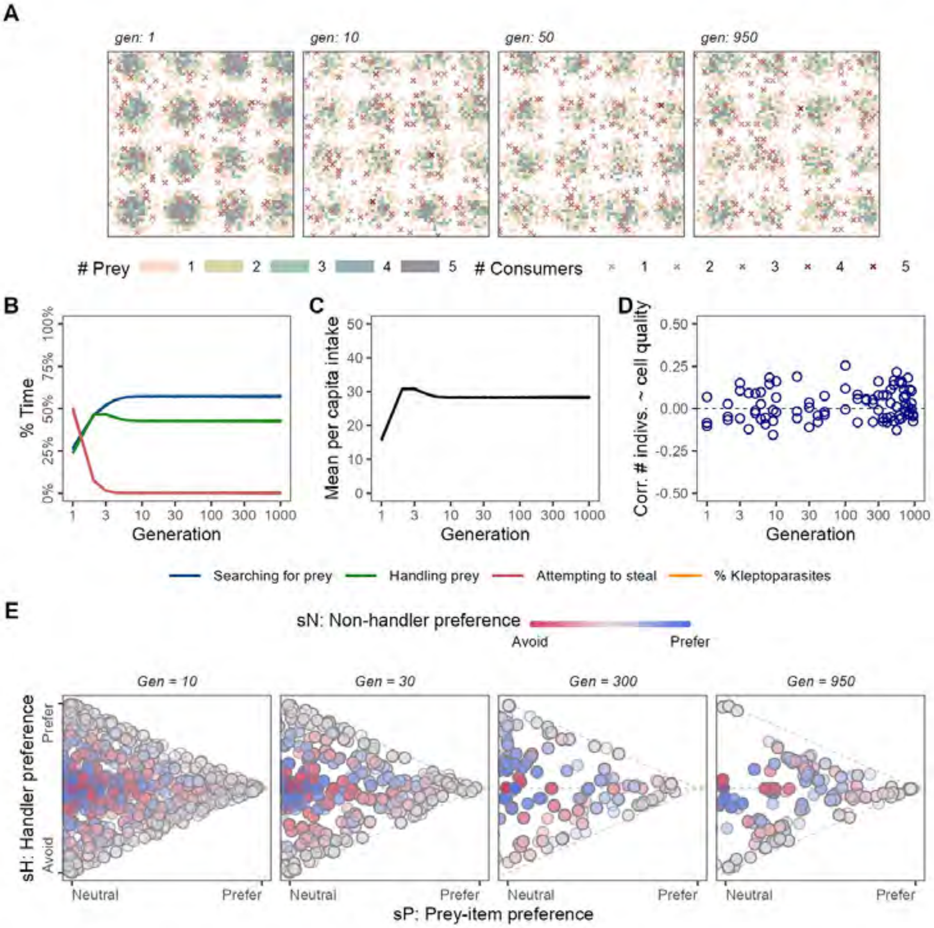

Figure 3.A1 | The evolutionary ecology of random movement serves as a useful baseline against which to compare other scenarios. **(A)** Individuals deplete the landscape ($r_{max} = 0.01$) at random, allowing it to regenerate more than scenario 1, yet less than scenario 2. **(B)** Kleptoparasitism as a strategy very rapidly goes extinct, as individuals cannot move towards handlers, and encountering a handler at random is very unlikely. **(C)** Surprisingly, moving at random yields a similar mean per-capita intake as in scenarios 1 and 3, and actually better than scenario 2. **(D)** Random movement leads, unsurprisingly, to no correlation with landscape productivity. **(E)** When movement strategies are not under selection, individuals occupy a large area of the potential strategy space, including negative values of s_P (which is not shown here).

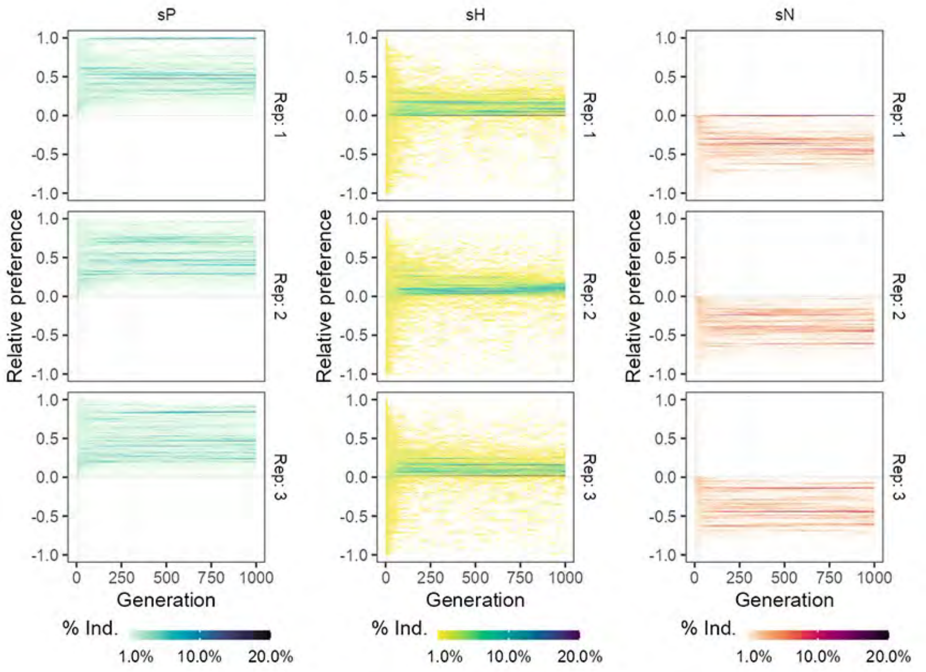

Figure 3.A2 | Evolution of relative cue preferences in scenario 1. Across simulation replicates (r_{max} = 0.01), populations of foragers consistently evolve a wide range of relative preferences, largely to move towards prey items (s_P), to largely move towards successful foragers (handlers; s_H), and to mostly avoid unsuccessful foragers (non-handlers; s_N).

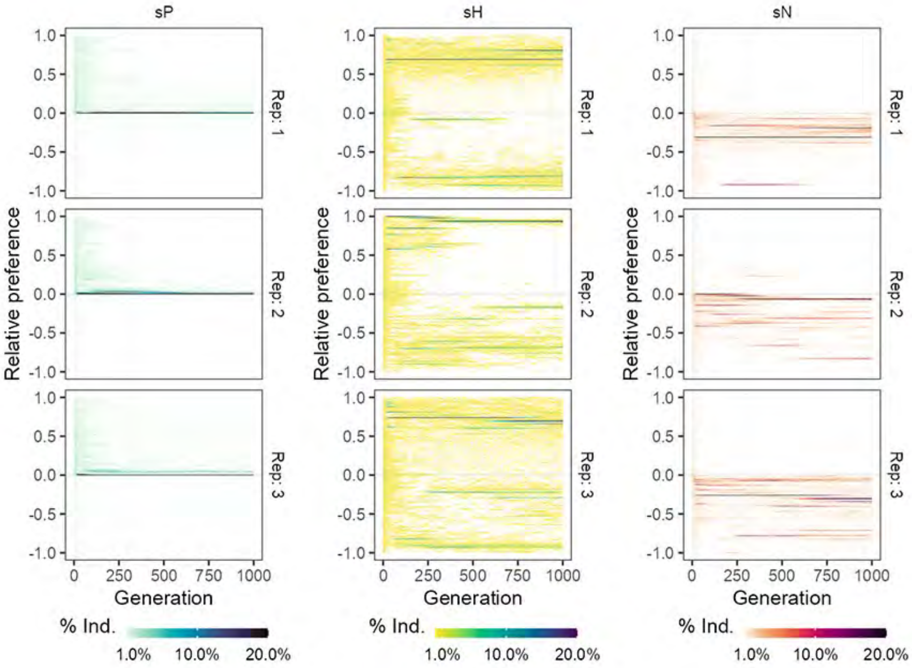

Figure 3.A3 | Evolution of relative cue preferences in scenario 2. Across simulation replicates (r_{max} = 0.01), in populations with fixed forager or kleptoparasite strategies, populations of foragers consistently evolve a very small relative preference to move towards prey items (s_P), and a range of preferences to move away from unsuccessful foragers (non-handlers; s_N). However, individuals show a strongly bimodal response to successful foragers, with both strong preferences and avoidances evolved. These preferences are correlated with individuals' competition strategies (see below; handlers; s_H).

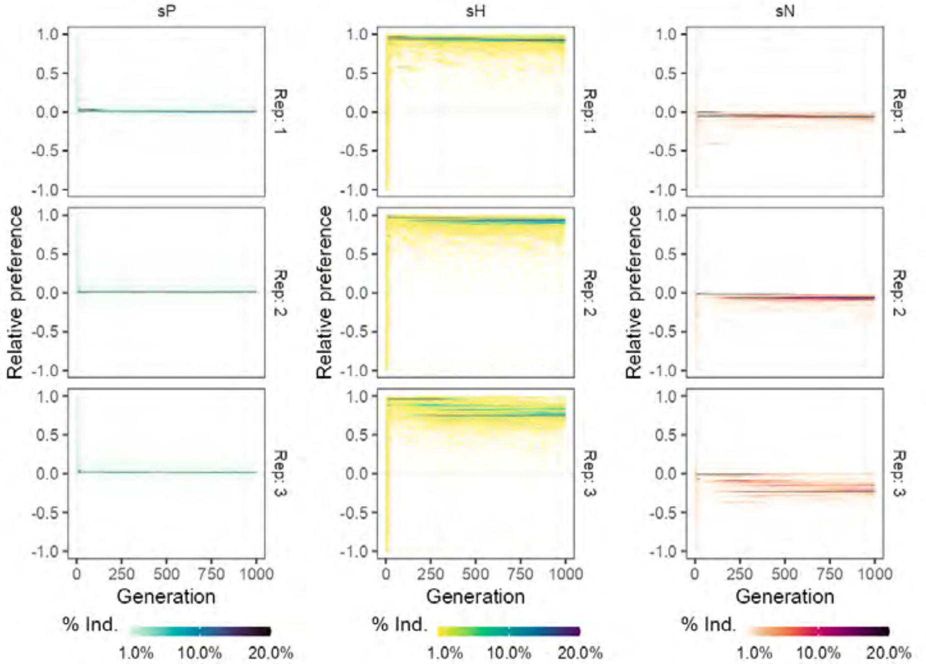

Figure 3.A4 | Evolution of movement strategies in scenario 3. Across simulation replicates (r_{max} = 0.01), populations of consumers that choose their competition strategy using inherited preferences, individual movement strategies are mostly driven by a preference for handlers (s_H), a moderate avoidance for non-handlers(s_N), and are mostly neutral to prey items (s_P).

2.2 CORRELATION OF RELATIVE PREFERENCES FORMS MOVEMENT STRATEGIES

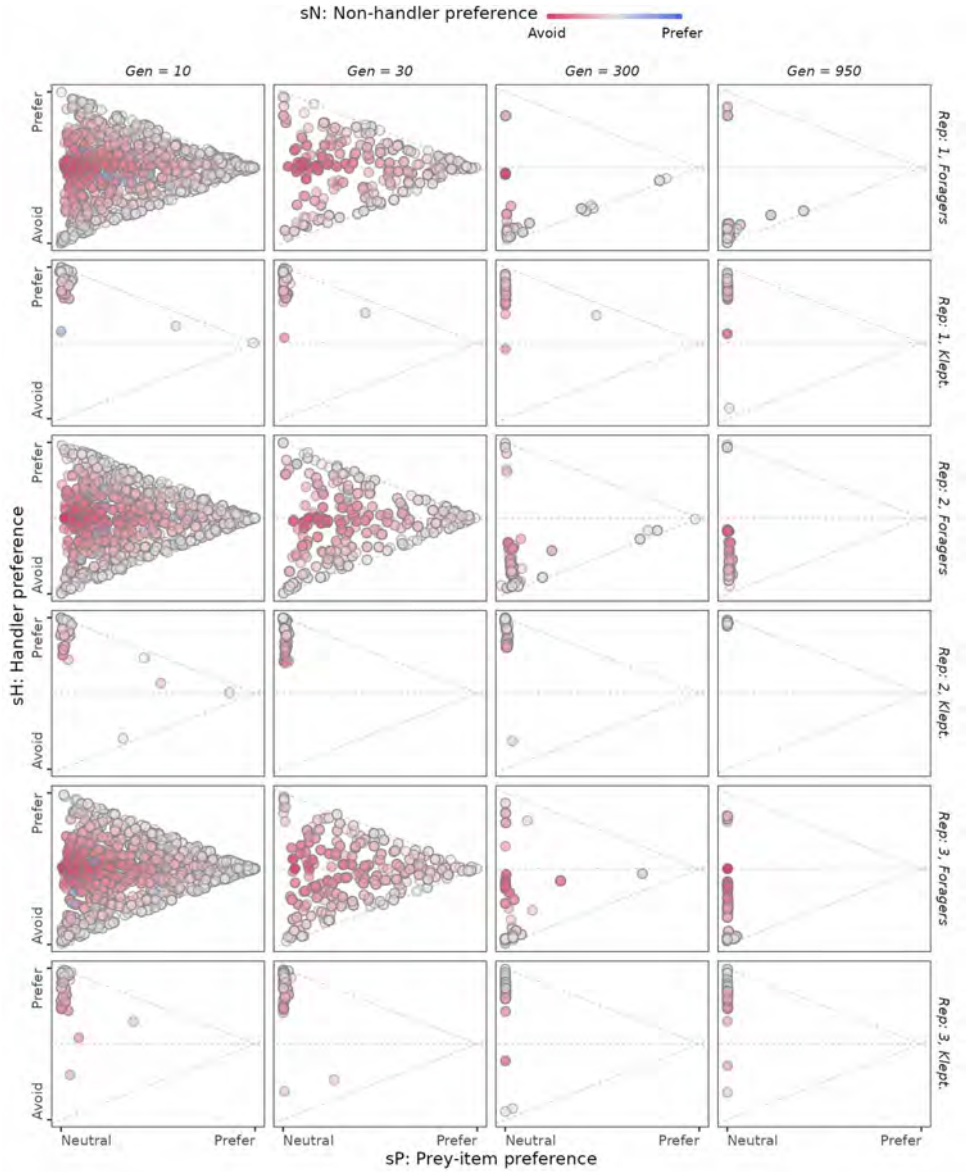

Figure 3.A5 | Evolution of movement strategies in scenario 2. Across simulation replicates (r_{max} = 0.01), in populations with fixed forager or kleptoparasite strategies, the two competition strategies consistently undergo rapid evolutionary divergence in movement strategies. Kleptoparasites evolve within 10 generations to primarily track handlers, and maintain this preference across hundreds of generations. Foragers are slower to converge upon a single movement strategy, but eventually (G = 300) mostly avoid handlers and non-handlers alike.

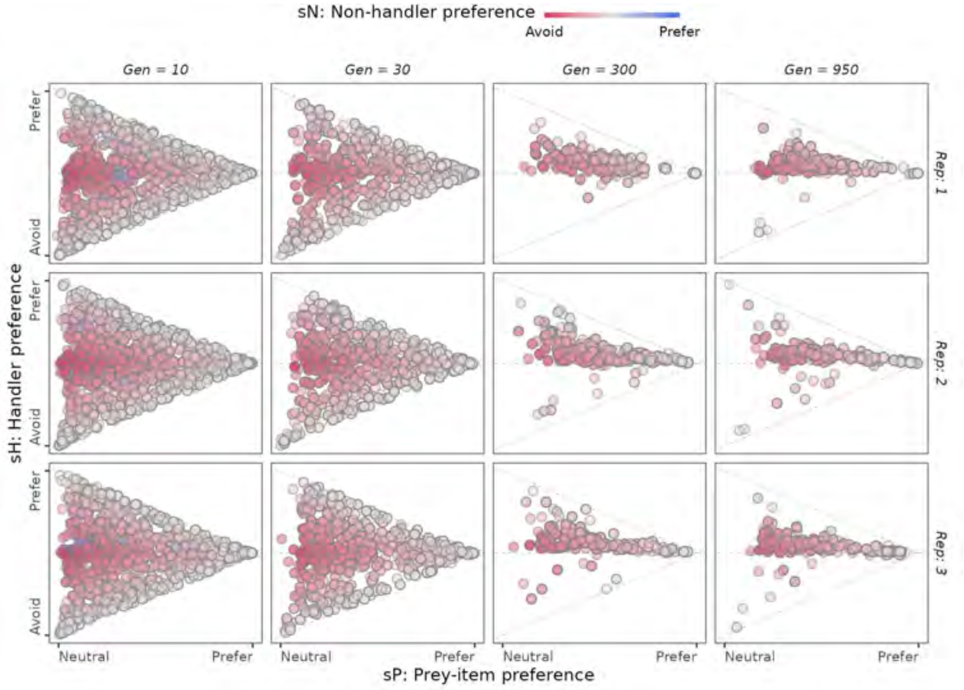

Figure 3.A6 | Evolution of movement strategies in scenario 1. Across simulation replicates (r_{max} = 0.01), populations of foragers consistently evolve a wide range of movement strategies to move towards prey items, largely move towards successful foragers (handlers), and avoid unsuccessful foragers (non-handlers).

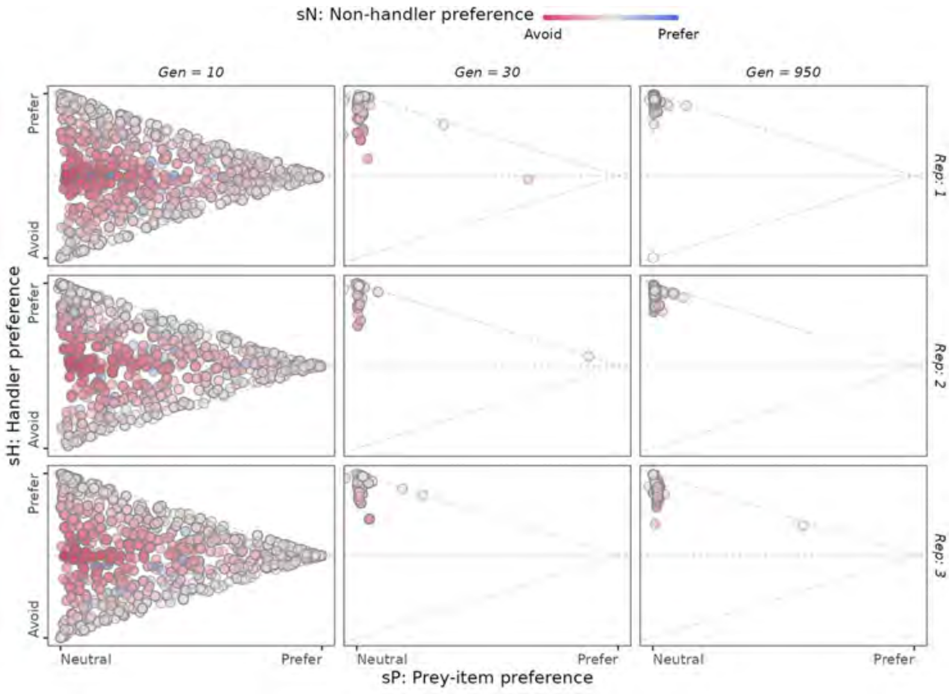

Figure 3.A7 | Evolution of movement strategies in scenario 3. Across simulation replicates ($r_{max} = 0.01$), populations of consumers that choose their competition strategy using inherited preferences, consistently evolve to move primarily towards handlers, a strategy that facilitates kleptoparasitism.

3. INDIVIDUAL DIFFERENCES IN MOVEMENT STRATEGIES IN SCENARIOS 2 AND 3

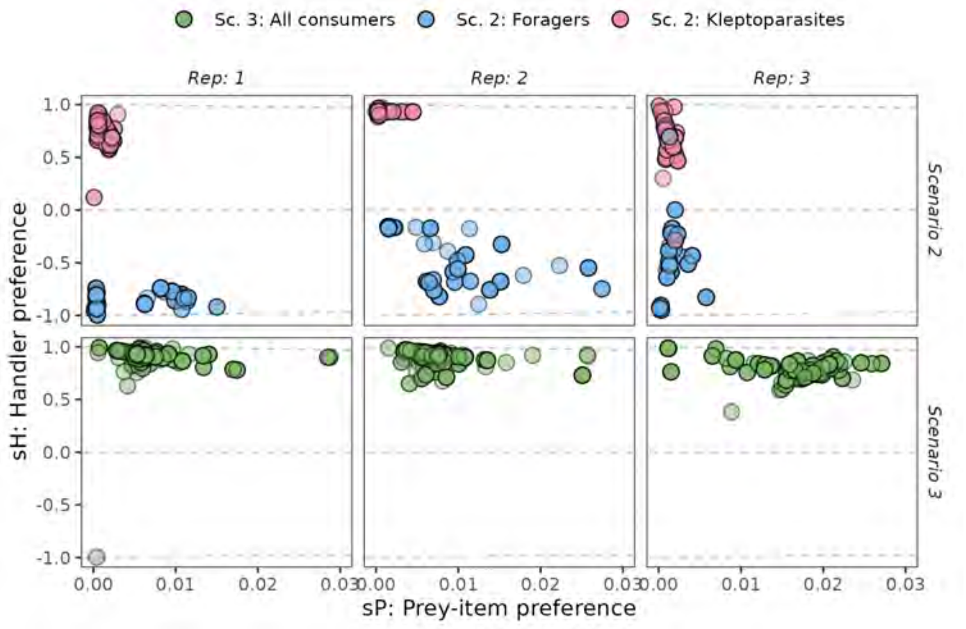

Figure 3.A8 | Small-scale individual variation may be hidden by primary drivers of behaviour. Across simulation replicates (r_{max} = 0.01), populations in scenarios 2 and 3 do show small-scale individual variation in preference for prey density cues (s_P). This variation is unlikely, in our model, to lead to functional differences in movement paths, but may cause very small emergent differences in model implementations of movement over a continuous space. It is key therefore to measure variation, and the relative contribution of such variation, along multiple axes of behaviour when studying the functional consequences of individual differences.

4. EVOLUTION OF COMPETITION STRATEGIES IN SCENARIO 3

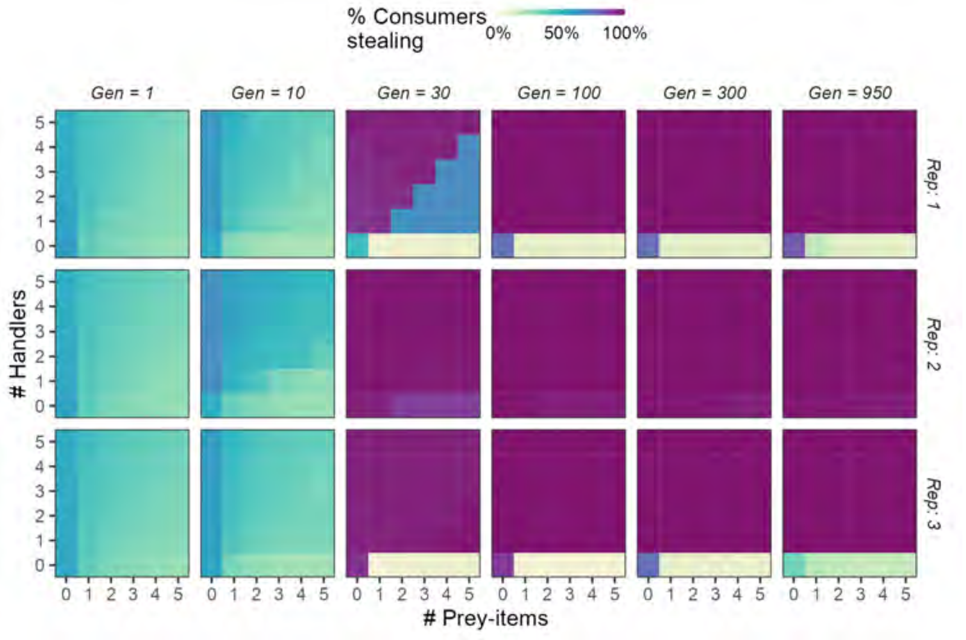

Figure 3.A9 | Evolution of conditional kleptoparasitic behaviour in scenario 3. Across replicates in scenario 3, individuals rapidly evolve conditional competition strategies that lead them to attempt to steal across a wide range of ecological conditions. Mainly, within 100 generations (and in some cases, only 30 generations), all individuals choose a kleptoparasitic strategy when handlers are available, even if there are multiple food items also available. Only when there are no handlers, do most individuals choose to forage for prey, with more individuals choosing to forage as prey density increases. Surprisingly, when there is no information, most individuals in later generations adopt a kleptoparasitic strategy by default. Replicate 2 shows why this is an incomplete assessment of individuals' competitive choices: all individuals appear to choose to steal regardless of ecological cues, with this strategy apparently persisting across many generations. This would lead to no intake at all, and no such drop is seen in mean per-capita intake. This points to the likely role of unsuccessful consumers, non-handlers, in determining competition strategy in this scenario.

5. Effect of Landscape Productivity on Resource Depletion

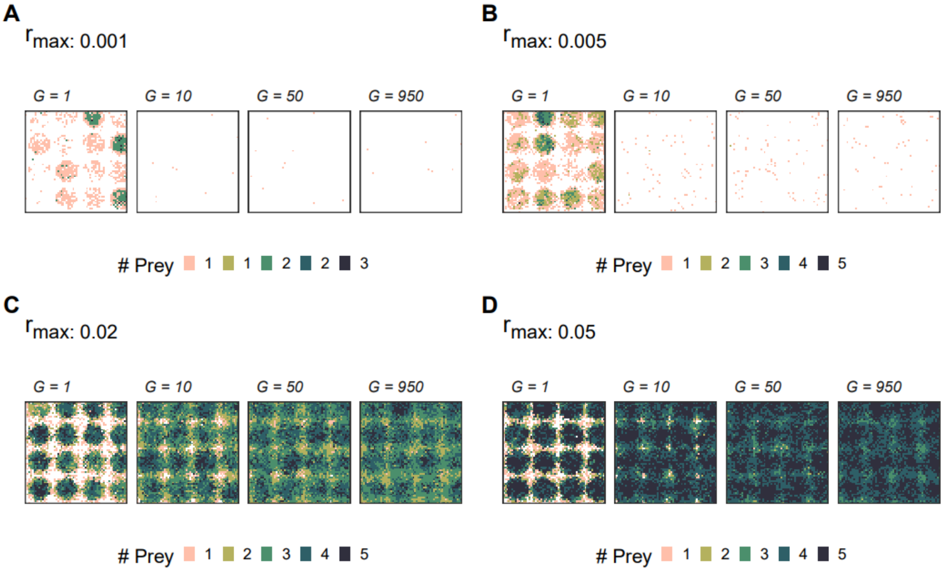

Figure 3.A10 | In scenario 1, foragers completely deplete the resource landscape within 10 generations at low r_{max} (A, B). However, at $r_{max} > 0.01$ (C, D), prey item regeneration exceeds depletion and the resource landscape is rapidly saturated until most cells carry 5 items, the maximum allowed in our model.

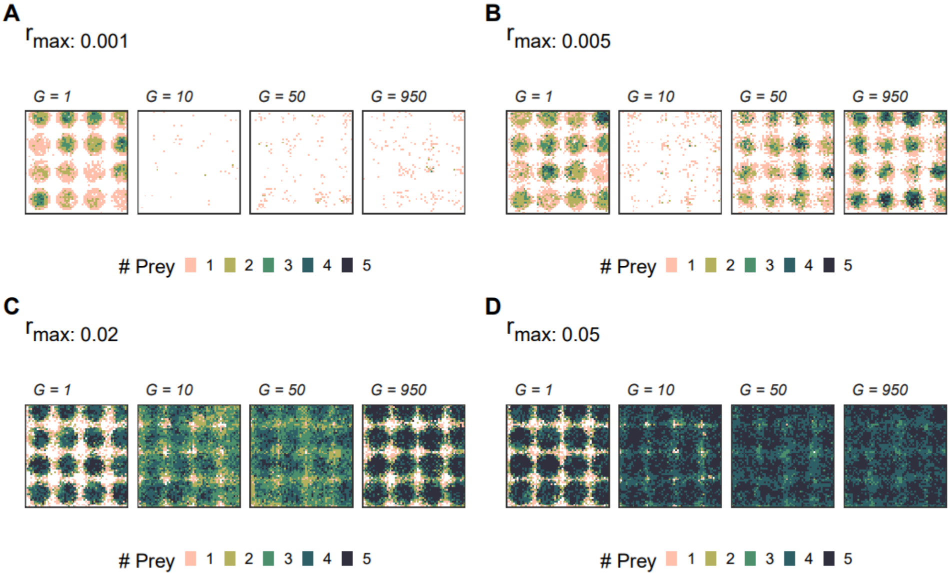

Figure 3.A11 | In scenario 2, foragers can only deplete the resource landscape at very low r_{max} (A): 1 prey item generated per 1,000 timesteps, or 2.5 generations. At all $r_{max} \leq 0.05$ (B, C, D), prey item regeneration matches or exceeds depletion and the resource landscape either shows strong spatial structure, or is entirely saturated with prey items.

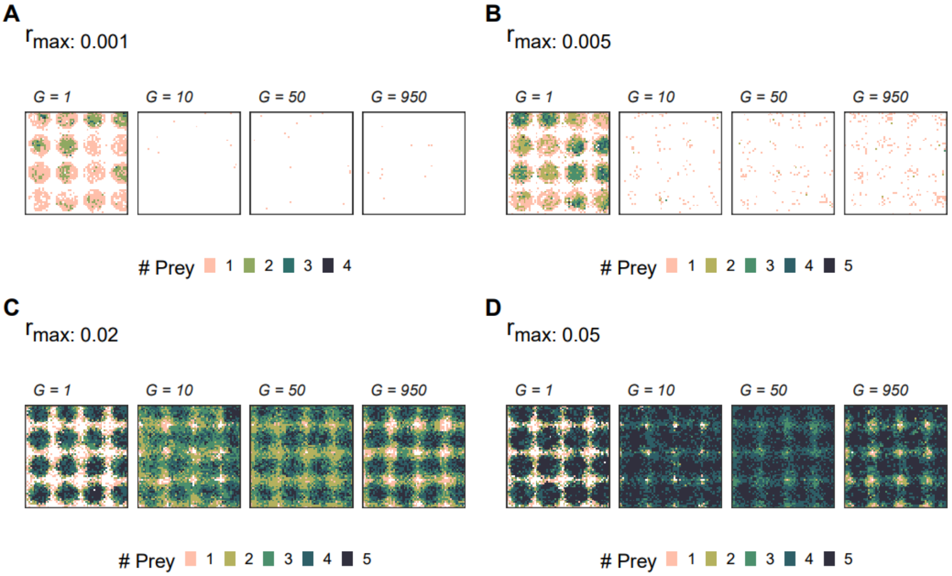

Figure 3.A12 | Scenario 3 is similar to scenario 1 at low r_{max} (A, B), where foragers completely deplete the resource landscape). Similarly, at $r_{max} > 0.01$ (C, D), prey item regeneration exceeds depletion and the resource landscape is rapidly saturated to a carrying capacity of 5 prey items per cell.

6. EFFECT OF LOCAL DISPERSAL

In order to focus on adaptive movement strategies, we chose to implement large dispersal distances in our default simulation setup, which we refer to as ‘global’ natal dispersal. Under global dispersal, offspring are homogeneously distributed over the entire landscape (dispersal radius = 512). Our results are not changed in any way when dispersal is much more strongly localised, which we refer to as simply ‘local’ natal dispersal. In this implementation, the natal dispersal distance is comparable in magnitude as the distance between resource peaks. If offspring dispersal is more local, the spatial population dynamics may become more intricate, and kin competition or local adaptation may become influential. We therefore ran the simulations presented in the main text also under local dispersal (dispersal radius = 2). In summary, scenarios 1 and 3 yield similar results under local as under global dispersal, while scenario 2 shows some interesting dynamics typical of reaction-diffusion systems. In scenario 1 (see fig. 3.A13), the resource landscape plots A, the activity budget and intake plots B and C, as well as the evolved movement strategies E exactly match the simulation results shown in figure 3.1 of the main text. Only the correlations between number of foragers and cell productivity are higher under local dispersal than under global dispersal (panel D). This is a straightforward consequence of local dispersal, where individuals occurring on more productive cells have a higher intake rate and therefore produce more offspring than individuals on less productive cells. Thus, under local dispersal many agents already start out on more productive cells. This does not seem to impact movement strategies. The same is true for scenario 3 (fig. 3.A14): After the initial depletion of the landscape, kleptoparasitic behavior spreads, and the landscape is somewhat replenished again. Also here, the landscape snapshots, the activity budget, as well as the intake plot and the evolved movement strategies match the global dispersal case. The difference in competition strategy (panel F) corresponds to the observed bistability (compare fig. 3.6). Again, the correlation between number of foragers and cell productivity is higher under local dispersal than under global dispersal, in the latter averaging in late generations around 0.1, and in the former around 0.2.

Scenario 2 is the only one where we observed a marked difference between local and global dispersal (see fig. 3.A15). As soon as kleptoparasites occur, they spread and become locally abundant, driving foragers to local extinction. The kleptoparasites themselves then wither away due to a lack of foragers to steal from, after which foragers may colonize the area once again. This spatial instability repeats itself over wide parts of the landscape, driven by the extinction, recolonization and diffusion of foragers and kleptoparasites. Kleptoparasites and foragers here effectively form a reaction-diffusion system, as observed in a number of studies, including our work on predator-prey interactions as well (Netz et al., 2022). Snapshots of this dynamic pattern can be seen in figure 3.A14A. As a consequence, the proportions of kleptoparasites and foragers, as well as the total per capita intake of the population fluctuate widely (panels B and C). The correlations between individual densities and cell quality lie around zero and are therefore not much different from the results observed under global dispersal (fig. 3.2D). An interesting contrast with global dispersal is to be found in the movement strategies. While kleptoparasites have similar preferences under global and local dispersal, foragers have much stronger item preferences under local dispersal. Due to the pattern of extinction and recolonization under local dispersal, there are parts of the landscape not only rich in food items, but also free from kleptoparasites, and thus a strong preference for items becomes beneficial.

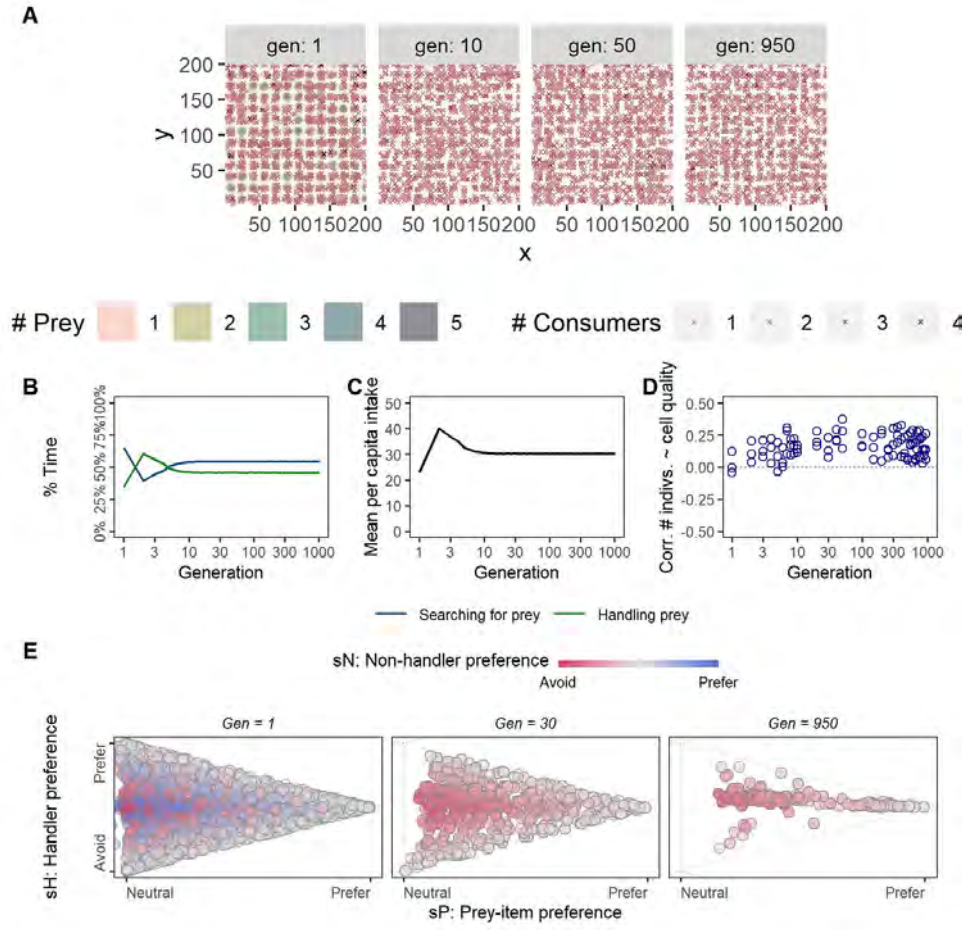

Figure 3.A13 | The effect of strongly localised dispersal in scenario 1. **(A)** Foragers swiftly deplete the resource landscape and maintain item scarcity throughout the rest of the simulation, just like under global dispersal. Items and agents are distributed in proportion to cell productivity, r. The population quickly reaches an equilibrium in its **(B)** activity budget and **(C)** mean per-capita intake, that is identical to global dispersal. **(D)** The number of foragers per cell is more positively correlated with cell productivity under strongly localised ('local') dispersal, compared with global dispersal. **(E)** The same wide range of movement strategies observed under global dispersal exists under local dispersal as well. Across simulation replicates ($r_{max} = 0.01$), populations of consumers that choose their competition strategy using inherited preferences, consistently evolve to move primarily towards handlers, a strategy that facilitates kleptoparasitism.

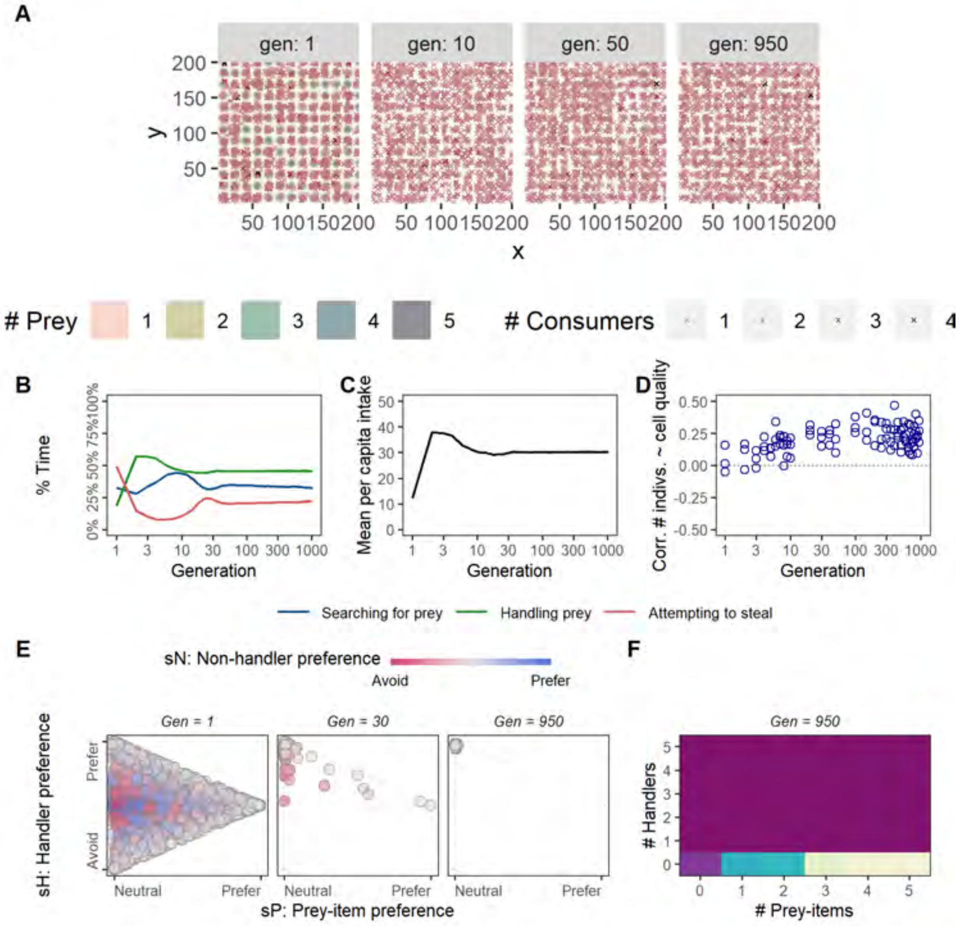

Figure 3.A14 | The effect of strongly localised dispersal in scenario 3. **(A)** Individuals swiftly deplete the resource landscape, but prey abundances recover with the rise of kleptoparasitism, as is observed under global dispersal. Items and agents are distributed in proportion to cell productivity, r. **(B)** By generation 30, the proportion of time spent searching (blue line), handling (green line), and stealing prey (red line) reach values in the range of the ones observed under global dispersal. **(C)** The mean per-capita intake drops after the initial peak, and then recovers slightly, identically to global dispersal. **(D)** The number of foragers per cell is more positively correlated with cell productivity under local than under global dispersal. **(E)** Movement strategies concentrate around a strong preference for handlers, and **(F)** individuals tend to steal even when there are no handlers and less than 3 prey items available. This falls into the range of variation observed between replicates under global dispersal.

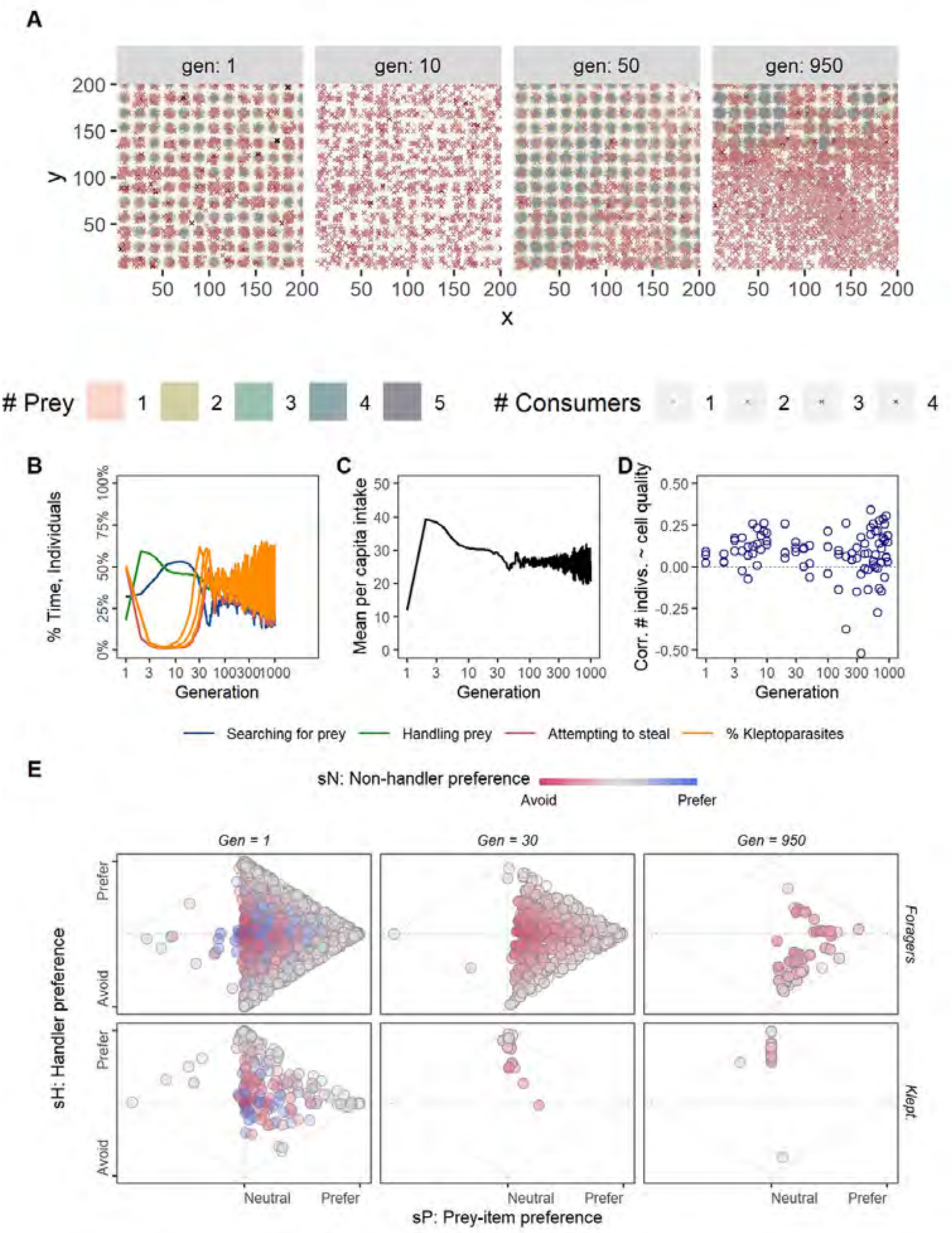

Figure 3.A15 | The effect of strongly localised dispersal in scenario 2. (A) Foragers initially deplete prey items, but with the rise of kleptoparasistism, the resource landscape becomes very heterogeneous, with some areas densely populated and scarce in prey items, and others without consumers and fully stocked with items. This pattern is produced by the local dynamics of kleptoparasites and foragers: Kleptoparasites become more common where foragers are common, until the latter go locally extinct. Thereupon also the kleptoparasites vanish, and prey items replenish until foragers are reintroduced via diffusion.

Figure 3.A15 | (B) Proportions of kleptoparasitses and foragers, as well as **(C)** mean per-capita intake fluctuate greatly.**(D)** Cell quality and number of individuals are uncorrelated as the spatial dynamics between kleptoparasites and foragers dominate over any interaction between cell quality and number of individuals. **(E)** Kleptoparasites evolve the same preferences under local dispersal as under global dispersal, but foragers have a much stronger preference for prey-items, caused by the abundance of deserted, fully-stocked parts of the landscape.

7. EFFECT OF INITIALIZATION OF CUE PREFERENCE

In our default implementation, the initial populations harbour a broad range of movement strategies. In other words, our simulations are not mutation-limited in the initial phase of evolution. In our default implementation, our model's population always begins with a broad range of movement strategies already present upon initialisation ($G = 1$). This speeds up adaptive evolution (and our simulations), but it is not self-evident that a monomorphic initialisation, where adaptive evolution requires the occurrence of 'suitable' new mutations, will lead to the same evolutionary outcome. This makes it unclear whether the movement strategies seen once ecological equilibrium is reached (at about $G = 50$) and beyond, have simply persisted since initialisation, or whether they would actually evolve from rather different strategies. Our model population could be suffering from a steady weathering away of standing variation, which leaves viable movement strategies, or whether the evolutionary process we model can actually generate variation, and specifically, the movement strategies we observe in our default implementation. Thus, it is not clear whether a similar degree of genetic polymorphism is achieved as in the default implementation of our model.

Here we demonstrate (1) that our model's ecological and evolutionary setup does generate variation, and (2) that this process leads to the same strategies we observed in the results presented in the main text. We focus on our most complex scenario, Scenario 3, in which individuals can choose both their next move, as well as their competition strategy at their destination, in each timestep. We initialized all individuals' cue preferences for movement decisions (s_P, s_H, s_N), and for competition decisions (w_0, w_P, w_H, w_N) at three identical values: 0.0, +0.001, and -0.001. This makes the population perfectly monomorphic for both movement and competition strategies. We ran the simulation as before, with 1,000 generations, 10,000 individuals on a landscape of 512^2 cells, with global natal dispersal, and implementing the same mutational process ($p_{mut} = 0.001$, mutational step size drawn from a Cauchy distribution with scale = 0.001).

In the figures that follow, we focus on the movement strategy trait space. We show that regardless of where in the movement and competition strategy trait space the population is initialized, within 30 generations, considerable functional variation is generated, and the population is no longer monomorphic in its movement strategy (figs. 3.A16 – 3.A18; panel $G = 30$). Furthermore, in each case, the population always evolves to occupy a small range of of the strategy space: (1) nearly neutral to food items (normalized $s_P \approx 0.0$), (2) strongly attracted to handlers (normalized $s_H > 0.75$), and (3) avoiding or neutral to non-handlers (normalized $s_N \leq 0.0$) (figs. 3.A16 – 3.A18; compare fig. 3.4E). We conclude that the results concerning movement strategies presented in the main text are robust to choices regarding initialisation of the cue preferences.

Since the evolved movement strategies converge upon our main results, it is not surprising that the main ecological outcomes of the activity budget — the time each generation spends on searching for prey, in handling prey, and in attempts to steal prey — also closely resemble findings from our default implementation (figs. 3.A19 – 3.A21; compare fig. 3.4B). A minor difference between monomorphic and 'diverse' initialisation is that monomorphic populations reach stable activity budget equilibria by about generation 100, while this is reached somewhat earlier in our default implementation, at about generation 30.

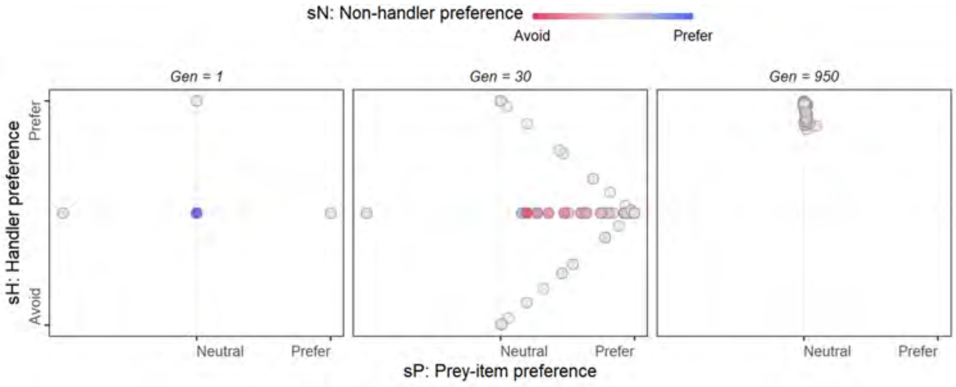

Figure 3.A16 | Evolution of movement strategies upon initializing all movement and competition preferences at 0.0. Each panel shows 2,500 individuals from a single replicate.

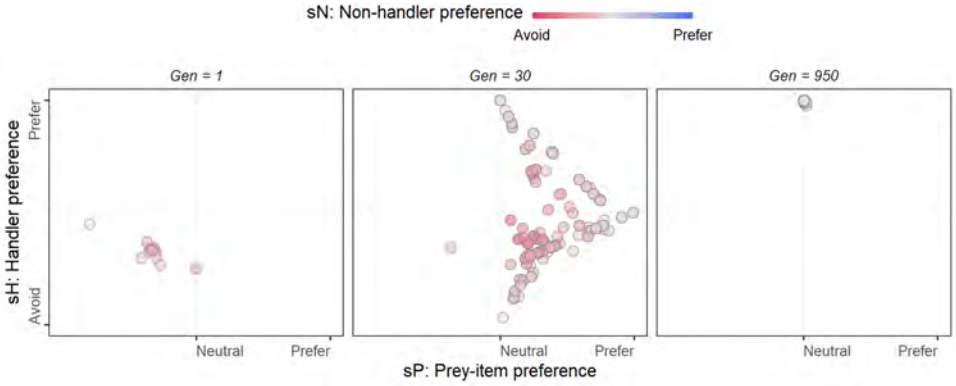

Figure 3.A17 | Evolution of movement strategies upon initializing all movement and competition preferences at -0.001. Each panel shows 2,500 individuals from a single replicate.

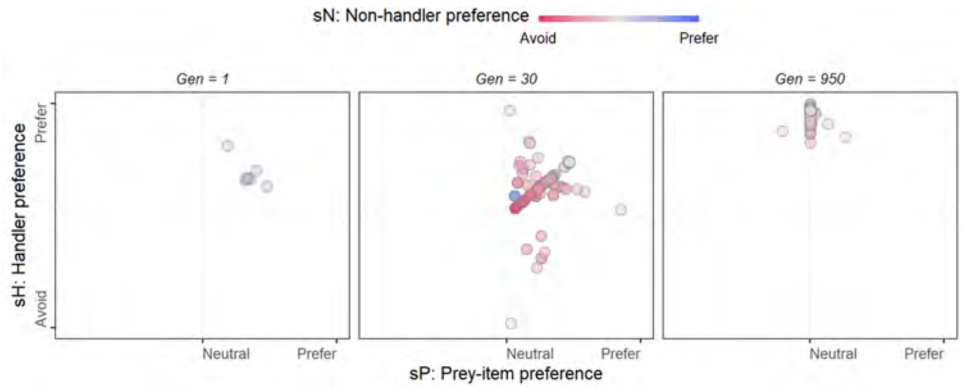

Figure 3.A18 | Evolution of movement strategies upon initializing all movement and competition preferences at 0.001. Each panel shows 2,500 individuals from a single replicate.

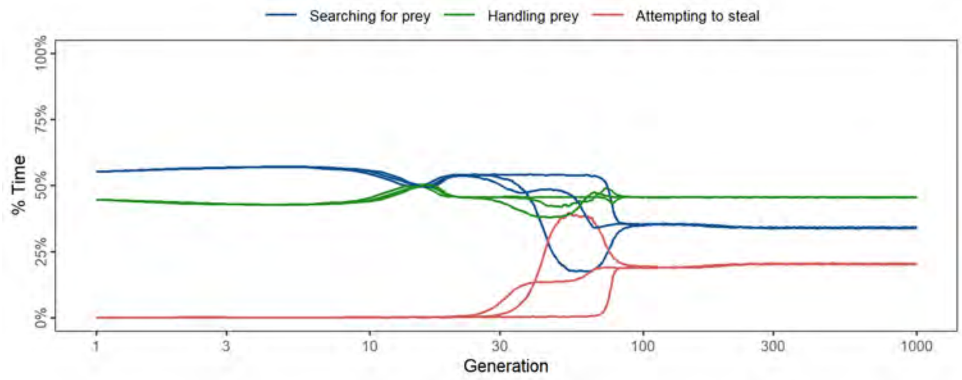

Figure 3.A19 | Ecological equilibria in population activity budget upon initializing all movement and competition preferences at 0.0. Shown are three replicate simulations.

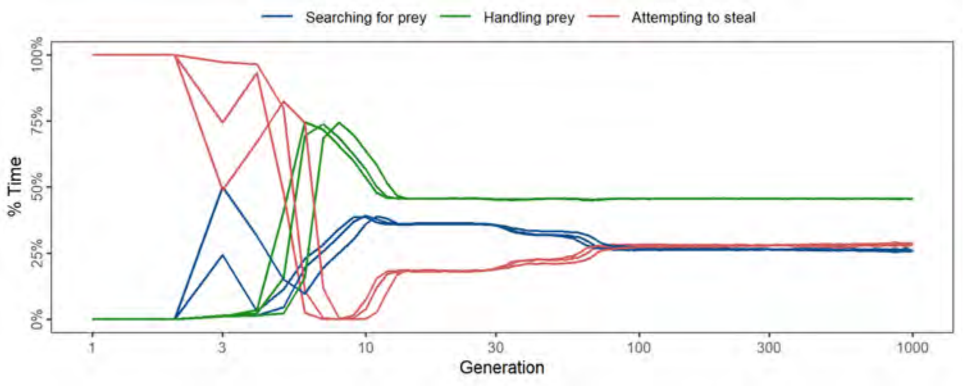

Figure 3.A20 | Ecological equilibria in population activity budget upon initializing all movement and competition preferences at -0.001. Shown are three replicate simulations.

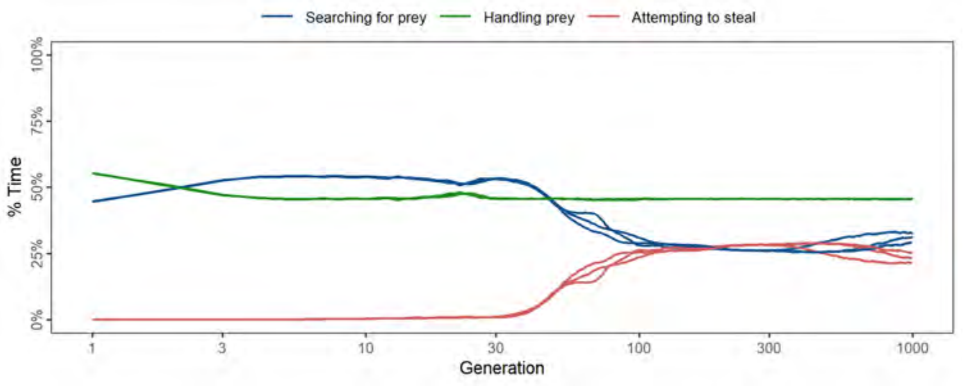

Figure 3.A21 | Ecological equilibria in population activity budget upon initializing all movement and competition preferences at 0.001. Shown are three replicate simulations.

4

IDEAL FREE DISTRIBUTION OF UNEQUAL COMPETITORS: SPATIAL ASSORTMENT AND EVOLUTIONARY DIVERSIFICATION OF COMPETITIVE ABILITY

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ABSTRACT

Ideal free distribution theory attempts to predict the distribution of well-informed (‘ideal’) and unconstrained (‘free’) foragers in space based on adaptive individual decisions. When individuals differ in competitive ability, a whole array of equilibrium distributions is possible, and it is unclear which of these distributions are most likely. In the first part of our study, we show that strong competitors have an intrinsically stronger preference for highly productive habitat patches than poor competitors. This leads to an equilibrium distribution where the average competitive ability on a patch is strongly correlated with the productivity of the patch. In the second part of our study, we consider what happens if differences in competitive ability are heritable and, hence, subject to natural selection. Under constant environmental conditions, selection eliminates such differences: a single strategy prevails that optimally balances the costs and benefits associated with competitive ability. If the productivity of patches changes during the lifetime of individuals, the spatial assortment of competitors of equal competitive ability gives poor competitors a systematic advantage in times of environmental change, while good competitors benefit from equilibrium conditions. Using evolutionary individual-based simulations, we demonstrate that environmental change may then lead to the diversification of competitive ability.

4.1. INTRODUCTION

Animals constantly have to make decisions on movement within or between habitats, especially in variable environments. The distribution of individuals depends on these decisions, which take into account the properties of the habitat and the distribution of conspecifics. The simplest forager distribution model (Fretwell and Lucas, 1969) assumes a population of identical foragers, which are 'ideal' in that they have complete knowledge of the distributions of resources and conspecifics and are 'free' in that they are unrestricted in their movement. Foragers are then expected to distribute such that any further movement between patches does not increase the intake of any individual, yielding the so-called ideal free distribution (IFD). If foragers do not interfere with each other and share resources equally, the distribution of foragers corresponds to the distribution of resources, termed 'input matching' (Parker, 1978). Although the IFD serves as a useful null model, in reality, individuals are neither 'ideal' nor 'free', and there is increasing evidence that consistent individual differences influence habitat choice and spatial distributions (Ehlinger, 1990; Holtmann et al., 2017a; Bonnot et al., 2018; Schirmer et al., 2019, 2020). This development is both a challenge and an opportunity for the theoretical framework of the ideal free distribution.

Several models have studied the distribution of foragers by relaxing key assumptions of the IFD, for example considering individuals that behave idiosyncratically and in non-optimal ways (Jackson et al., 2004; Matsumura et al., 2010) or incorporating individual differences that affect optimal decision making (Holt and Barfield, 2008; Edelaar et al., 2008), specific examples including body size (Price, 1983; Railsback and Harvey, 2002), gizzard size (Van Gils et al., 2005) or competitive ability (Sutherland and Parker, 1985; Houston and McNamara, 1988; Sutherland and Parker, 1992; Van de Pol et al., 2007; Smallegange and van der Meer, 2009). In particular, individual variation in competitive ability has been the focus of several modelling studies. Such variation is incorporated into IFD models in two different ways. In interference competition models, competitive ability affects the impact of interference on individual intake rates (Sutherland and Parker, 1992; Smallegange and van der Meer, 2009). In this case, IFD theory predicts the segregation of unequal competitors over resource patches, where the most competitive types accumulate on patches with the highest resource levels, while weaker competitors occur at the lower resource levels. In exploitation competition models, the competitive ability of an individual determines the individual's share in the local resources, for example via the capacity to defend territories (Huxley, 1934). In this case, IFD theory predicts that, at equilibrium, the competition intensity on each patch (= the sum of the competitive abilities of the occupants of the patch) is proportional to the resource abundance on that patch (Sutherland and

Parker, 1985, 1992). Such an equilibrium distribution can be realized in many different ways, and in principle, it is possible that weak and strong competitors co-occur on all patches or that weak competitors accumulate on patches with the highest productivity. Sutherland and Parker (1985) hypothesised that the most likely distribution of foragers converges on the IFD with equal competitors, which corresponds to the situation where, at equilibrium, the distribution of competitive types is roughly the same for all occupied patches. In contrast, Houston and McNamara (1988) argued that strong competitors should be slightly overrepresented on resource-rich patches, simply as a consequence of the number of ways in which the equilibrium distribution can be realized. Further work showed that the sequence and mechanism, by which foragers distribute across both patches, can have a significant impact on the equilibrium distributions that are reached (Houston and McNamara, 1988; Spencer et al., 1995).

Virtually all theoretical work on the distribution of unequal competitors has only considered the choice between two patches. The first goal of this study is to extend the theory to a more fine-grained environment with multiple patches. In addition, we consider a whole spectrum of competitive abilities. We show that stronger and weaker competitors differ in their patch preferences and that stronger competitors have, in comparison to weaker competitors, a systematic bias in favour of resource-rich patches. One would therefore expect competitor assortment, where strong competitors accumulate on resource-rich patches, while weak competitors typically occur on resource-poor patches. By means of individual-based simulations, we will show that such assortment does indeed take place under exploitation competition and that the effect is much stronger than the ‘statistical mechanics’ approach of Houston and McNamara (1988) suggests.

Most studies on the distribution of unequal competitors assume that differences in competitive ability are fixed and externally given. In many situations, it is likely that such differences are at least partly heritable (Baldauf et al., 2014). This implies that competitive ability is an evolvable trait. Therefore, we can ask not only how individual variation in competitive ability influences habitat choice and spatial distributions but also how (variation in) competitive ability is shaped by natural selection. Addressing this question is the second goal of this study.

One might expect that natural selection has the tendency to eliminate all variation in competitive ability, thus leading to a single strategy that optimally balances the costs and benefits associated with a given level of competitive ability. With a simple argument and some evolutionary simulations, we will show that this is indeed the case if the environment is stable, that is, if the resource level per patch remains constant. Making use of the assortment result derived in the first part of our study, we then argue that the situation may be different in case of a changing environment. With a simulation study, we will demonstrate that, under changing conditions, selection can lead to the diversification of competitive ability.

Our twofold purpose is therefore to first investigate the equilibrium distributions emerging from individual-based patch choice decisions, and secondly to study the evolutionary dynamics that this scenario implicates. We present a) an analytical description of how habitat preferences depend on individuals' competitive abilities, and b) a simulation model of how spatial assortment can lead to the diversification of competitive ability. We thus show that spatial distributions are not only determined by the interactions between unequal competitors but that the process of repeated redistribution can by itself propel the evolution of several competitive morphs.

4.2. MODELS AND RESULTS

We consider a population distributed across a number of patches, each of which provides a constant influx of resources that is shared among the foragers present on the patch. This situation is commonly known as a 'continuous input' model (Tregenza, 1995). Individuals differ in their competitive ability, that is, their ability to defend resource shares against competitors. The intake rate of an individual on a habitat patch with resource influx R depends on the relation of the individual's competitive ability to the 'competition intensity' C on this patch, which is defined as the sum of the competitive abilities of all individuals present. In line with earlier work (Houston and McNamara, 1988; Sutherland and Parker, 1992; Tregenza, 1995), we assume that the individual can consume a fraction c_i/C of the local resources, yielding the intake rate:

$$F(c_i, R, C) = \frac{c_i}{C}.R = c_i.\frac{R}{C} \tag{1}$$

The ratio R/C may be viewed as the 'resource availability' on a given patch (per unit of competitive ability). As long as patches differ in their resource availability, at least some individuals have an incentive to move to a patch with higher resource availability. This will continue until an 'ideal free distribution (IFD)' is reached where all occupied patches have the same resource availability R/C (Sutherland and Parker, 1985; Tregenza, 1995; Houston and Lang, 1998).

4.2.1. SPATIAL ASSORTMENT: GOOD COMPETITORS PREFER RESOURCE-RICH PATCHES

At the ideal free distribution, the ratio R/C is equalized across all patches. Hence, the ideal free distribution depends on the distribution of competition intensity over patches and not directly on the distribution of individuals. In fact, many different distributions of foragers may lead to the same competition intensity on a given patch. For example, the same value $C = 10$ occurs when a patch is occupied by 10 individuals with competitive ability 1.0 or by 100 individuals with competitive ability 0.1. This implies that the IFD criterion (equality of the ratio R/C) can be satisfied by many different distributions of competitors over the patches. The question is whether some of these distributions are more likely than others. Sutherland and Parker (1985) predicted that the most likely distribution should correspond to the ideal free distribution with equal competitors since such a distribution corresponds to a random mixture of competitors over patches. Houston and Lang (1998) noticed that among the many possible ways by which the IFD criterion can be satisfied those options where stronger competitors tend to occur on resource-rich patches are somewhat overrepresented. In analogy with statistical mechanics, they argue that it is, therefore, likely that at least some assortment of competitors over patches will occur. Although this argument is elegant, it is not immediately obvious whether principles of statistical mechanics can be applied to agents that do not move at random but by choosing the most suitable patch. Spencer et al. (1995) and Houston and Lang (1998) expanded on these results and showed that the sequence in which individuals move may have considerable influence on the resulting equilibrium distributions. Further, Houston & Lang showed that the movements of strong competitors may cause the subsequent movement of inferior competitors, providing a plausible mechanism by which spatial assortment may occur across patches. We here show that, more generally, the patch preferences of weaker competitors differ systematically from those of stronger competitors.

Consider an individual that compares two patches as to their suitability: patch 1 with resource influx R_1 and current competitive intensity C_1 and patch 2 with resource influx R_2 and current competitive intensity C_2. Assume further that patch 1 is the resource-richer patch, $R_1 > R_2$. An ideal and free individual with competitive ability c_i should prefer the resource-richer patch 1 if this patch, after the arrival of the individual, yields a higher intake rate:

$$c_i . \frac{R_1}{C_1 + c_i} > c_i . \frac{R_2}{C_2 + c_i} \tag{2}$$

Notice that the denominators in (2) take account of the fact that the competition intensity of each patch would increase by, should our individual move to that patch. Inequality (2) is equivalent to:

$$c_i > \frac{C_1 C_2}{R_1 - R_2} . \left(\frac{R_2}{C_2} - \frac{R_1}{C_1} \right) \tag{3}$$

The sign of the right-hand side of (3) is determined by the right multiplier, as the left one is qua assumption positive. If the resource-rich patch 1 has a higher resource availability ($R_1/C_1 > R_2/C_2$), the right-hand side of (3) is negative, implying that all individuals prefer this patch, regardless of their competitive ability. This changes when the resource-rich patch 1 gets crowded to such an extent that the resource-poor patch 2 has a higher resource availability ($R_2/C_2 > R_1/C_1$). In this case, (3) is a threshold criterion: only those individuals with a sufficiently large competitive ability (larger than the right-hand side of (3)) will prefer the resource-rich patch 1, while individuals with lower competitive ability will prefer the resource-poor patch 2.

The above argument shows that individuals with a large competitive ability have a higher likelihood to prefer resource-rich patches than individuals with a smaller competitive ability. We therefore expect the assortment of competitive abilities along a resource gradient. To investigate the strength of this effect, we ran some individual-based simulations. We consider 100 patches with resource levels running from 0.01 to 1.0 at increments of 0.01. A population of 10,000 individuals containing the five different competitive types (0.1, 0.2, 0.4, 0.8, 1.6) in equal proportions is initially distributed randomly over the patches. Individual foragers are chosen in random order to compare intake rates among patches and move to the patch offering the highest intake rate. The individuals redistribute until no single individual can improve their intake rate any further, at which point a stable distribution is reached. As shown in figure 4.1, the ensuing distributions are characterized by spatial assortment, where individuals of high competitive ability consistently occur more frequently on high resource patches, while individuals of low competitive ability occur on low resource patches. The degree of spatial assortment is surprisingly strong considering the relatively small influence of competitive ability on the comparison of potential intake rates between different patches ($C \gg c_i$; eqn 2). As the IFD is approached, the difference between the R/C ratio of different patches becomes successively smaller, such that many patches offer relatively similar intake rates. In this case, the influence of individual competitive ability becomes temporarily decisive, producing the observed spatial correlations. As the differences between the R/C ratios decrease yet further, the threshold approaches zero and becomes irrelevant again.

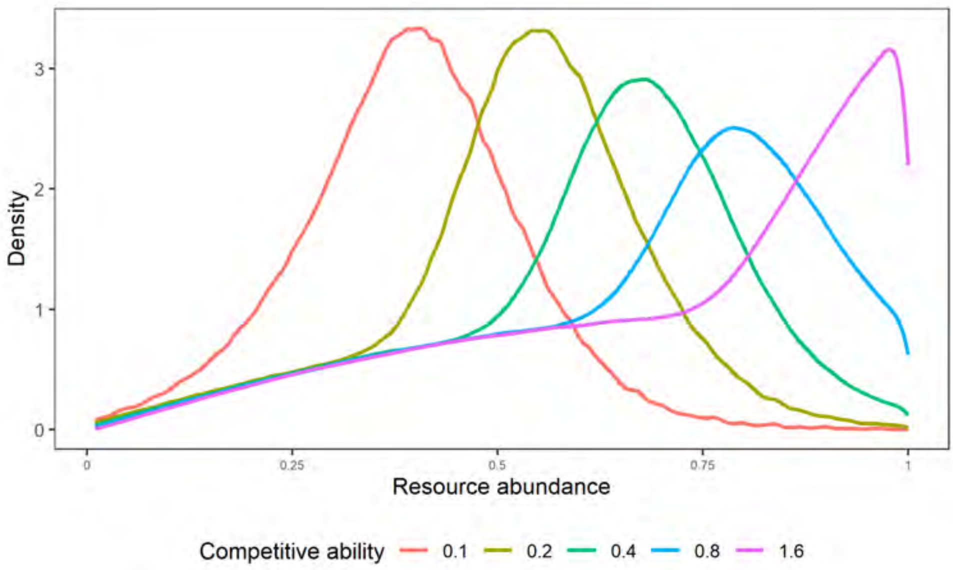

Figure 4.1 | Ideal free distribution of unequal competitors over habitat patches differing in resource abundance. 10,000 individuals were initially distributed randomly over 100 patches with resource abundance values running from 0.01 to 1.00 at intervals of 0.01. One of five competitive ability values was randomly assigned to each individual. Then individuals moved sequentially (in random order) to the best-suited patch, until an ideal free distribution was reached. The graph shows the distribution of each competitive type at the IFD by combining the results of 100 replicate simulations.

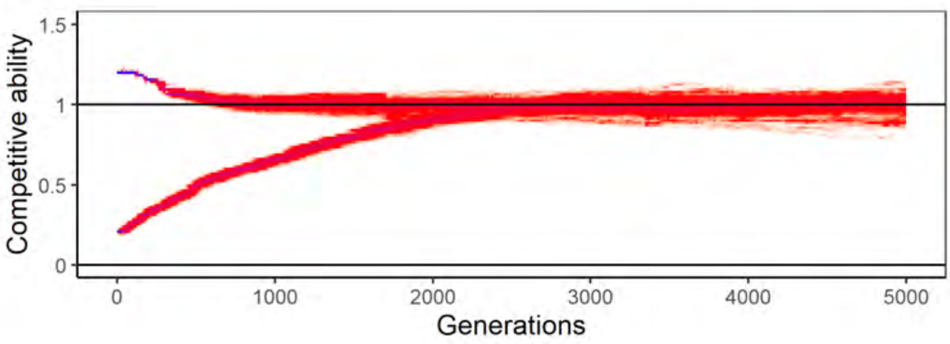

Figure 4.2 | Evolution of competitive ability under IFD conditions. Two simulations, starting at different initial conditions, for the evolution of competitive ability in a system where 10,000 individuals distribute over 100 patches with resource abundances varying between 0 and 1. The cost parameter k had the value 0.005. Both simulations converge to the value $c^* = 1.0$ the value of competitive ability predicted by equation (5). The relative frequencies of trait values within each generation are encoded by a colour gradient from 0.0 (= white) to 0.3 (= red) and 1.0 (= blue).

4.2.2. EVOLUTION OF COMPETITIVE ABILITY

Differences in individual competitive ability may arise at all levels from genetics to development and environmental effects during adulthood. From an evolutionary perspective, the presence of different types of competitors in a population poses the question of how multiple competitive types can coexist in a population. In the following we will consider how competitive abilities evolve in a patchy environment, first for a population that is permanently at the ideal free distribution (within generations) and second for a population where the IFD is repeatedly perturbed by changes in the environment.

In an evolutionary model, we have to specify how differences in intake rates translate into differences in survival and reproduction (Darwinian fitness). In optimal foraging models, either average food intake rate or lifetime resource consumption is typically taken as a proxy for fitness. When considering the evolution of competitive ability, this would not make much sense: according to equation (1), the intake rate on each patch is proportional to an individual's competitive ability. Hence, the highest possible competitive ability would evolve if it could be realized without costs. Here, we assume that a higher competitive ability is metabolically costly, and that the per-time-unit costs for a competitive ability c_i amount to kc_i resource units, where k is a constant of proportionality. Our fitness proxy is therefore based on the net intake rate:

$$W(c_i) = c_i.\frac{R}{C} - c_i.k = c_i.\left(\frac{R}{C} - k\right) \tag{4}$$

which, accumulated over the lifetime of an individual, is our measure of lifetime reproductive success. At the IFD, the resource availabilities R/C are equal across all patches and given by $R/C = \sum R_j / \sum c_i = \sum R_j/(N\bar{c})$ where N is the number of individuals and $\bar{c}$ is their average competitive ability. If we insert this expression into (4), we can conclude that the net intake rate W increases with c_i if $\sum R_j/(N\bar{c}) > k$ and decreases with c_i if $\sum R_j/(N\bar{c}) < k$. This implies that competitive ability will converge to a level c^* at which $\sum R_j/(N\bar{c}) = k$. As the corresponding population is monomorphic, the value c^* is equal to the average competitive ability ($c^* = \bar{c}$). This yields:

$$c^* = \bar{c} = \sum \frac{R_j}{N.k} \tag{5}$$

To check this expectation, we ran individual-based evolutionary simulations. Each individual is endowed with a heritable competitive ability. Within generations, individuals move to a patch yielding the maximal intake rate (given their competitive ability); movement will stop once the ideal free distribution is reached. Between generations, individuals produce offspring that inherit the competitive ability of their parent (subject to rare mutations). As the number of offspring is proportional to the net intake, accumulated over lifetime, those competitive abilities will increase in frequency that realize the highest net foraging success. A more detailed description of the model is provided in the appendix. Figure 4.2 shows that, irrespective of the initial conditions, the simulations evolve to the value of c^* predicted by equation (5) and therefore confirm our analytical expectations.

4.2.3. CHANGING ENVIRONMENTS: EVOLUTION OF COMPETITIVE DIVERSITY

If environmental conditions remain constant within a generation, a population of foragers will rapidly converge to the IFD. Accordingly, the population will converge to a monomorphic state where all individuals have the same competitive ability c^*. Some limited variation around c^* remains due to the ongoing influx of mutations (selection close to the evolutionary equilibrium is weak and not very efficient in eliminating mutations that are close to c^*), but larger-scale variation in competitive ability is eliminated. Resource environments are rarely static, however, and the ideal free distribution is therefore often a fleeting target. If

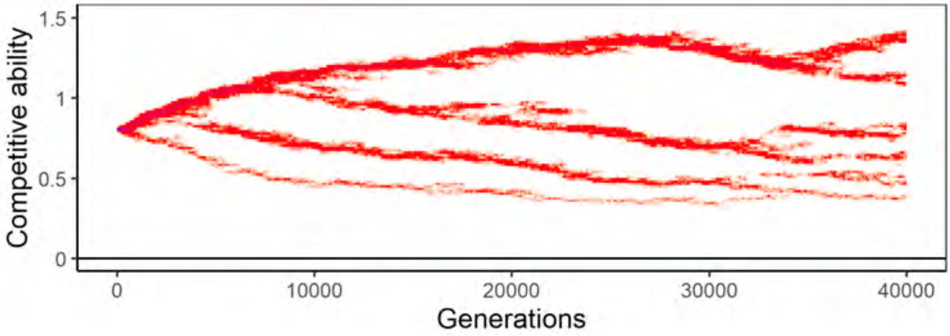

Figure 4.3 | Evolutionary diversification of competitive abilities under changing environmental conditions. The graph shows one representative simulation for the same parameter settings as in fig. 4.2. Now, however, the resource influx per habitat patch does not remain constant throughout a generation but randomly changes on average once every four time units. In the course of evolution, the population 'branches' into distinct competitive types.

the environment changes repeatedly within a generation and if it takes time to re-establish the IFD after each change, it is no longer obvious that only a single competitive ability will persist.

To see this, consider a population with variation in competitive abilities. As we have seen above, strong competitors will, under IFD conditions, accumulate on resource-rich patches, while weak competitors will mainly occur on resource-poor patches. If the environment (i.e., the resource influx per patch) changes at random, previously resource-rich patches will, on average, deteriorate while previously resource-poor patches will, on average, improve. This implies that changing conditions will, on average, be detrimental for strong competitors (that have accumulated on the previously resource-rich patches) and beneficial for weak competitors (that mainly occur on the previously resource-poor patches). It is conceivable that this principle will facilitate the coexistence of different competitive types, where in times of stasis (under IFD conditions), strong competitors have a higher net intake rate, while in times of change, weak competitors have a higher net intake rate.

To test this idea, we ran our evolutionary simulations under a stochastic regime of change, where the patch-specific resource levels changed at a rate of 0.25 (i.e., on average every 4 time units). In this variant of the model (see the appendix for details), foragers scan their environment at a rate of 0.5, thus noticing on average every 2 time units whether changes have occurred that may induce them to move to a patch with a higher net intake rate. Figure 4.3 shows that, under these

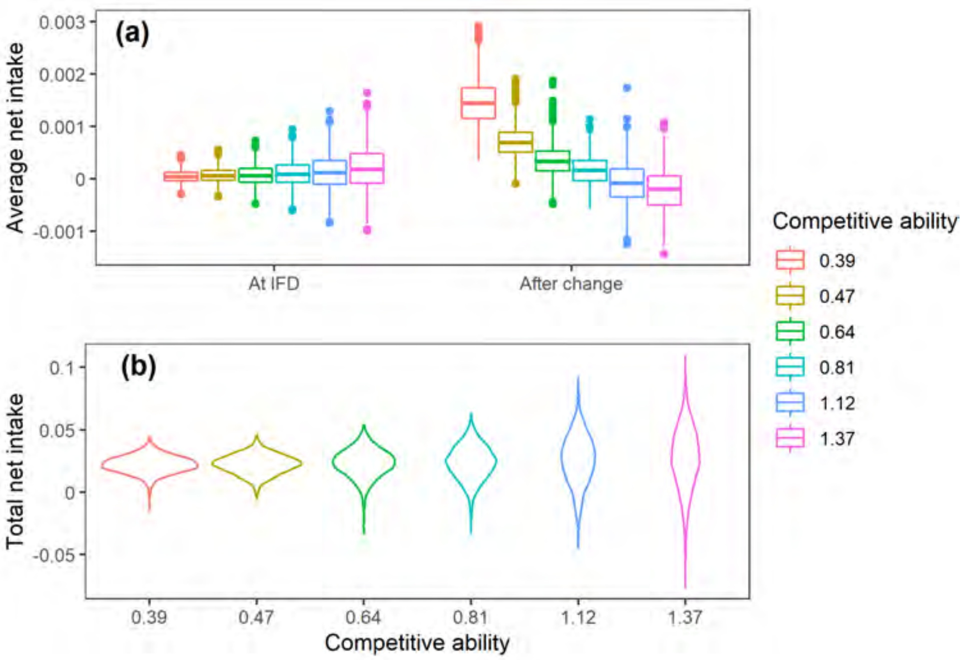

Figure 4.4 | Net intake rates under changing environmental conditions. For the simulation in fig. 4.3, we binned the six competitive types in generation 40,000 and **(A)** averaged their momentary net intake rates under IFD conditions (left part of the graph) and immediately after a change of the environment (right part of the graph). Net intake rate increases with competitive ability under stable conditions (at IFD), while it decreases with competitive ability under changing conditions. **(B)** The total net intake over individual lifetime is roughly the same for all six morphs.

changing conditions, evolution does indeed not lead to a monomorphic state. Instead, the population diversifies into a large number of coexisting competitive types.

Figure 4.4 demonstrates that, as predicted, the coexisting competitive types receive a differential net intake at equilibrium and after a change. Under stable conditions (when the population is close to the IFD), the net intake rates increases with competitive ability, while under changing conditions the weakest competitors have the highest net intake rate. The spatial assortment of less competitive individuals on poor patches and more competitive individuals on rich patches produces a transient benefit of spatiotemporal variation for the former.

4.3. DISCUSSION

Competition is a central motive in ecology and evolution and may determine forager distributions as well as the course of natural selection. We here considered the patch choice decisions of individuals, the equilibrium distributions emerging from these decisions, and the evolutionary dynamics of competitive abilities under stable and changing environmental conditions. We arrived at two key insights. First, the ranking of habitat patches as to their suitability (= net intake rate) is systematically affected by the competitive ability of the decision-making individual. Quite generally, strong competitors have a higher tendency to prefer resource-rich patches than weak competitors. Although this bias is relatively small, it can result in strong spatial assortment, where stronger competitors accumulate on resource-rich patches, while weaker competitors mainly occur on resource-poor patches. Second, this spatial assortment has important implications for the evolution of competitive ability. Under constant environmental conditions, variation in (heritable) competitive abilities cannot persist, and the population will converge to a monomorphic state with one type of competitor. If, however, environmental conditions change within generations, spatial assortment leads to a situation where strong competitors have an advantage under stable conditions (at IFD), while weak competitors have an advantage in periods of environmental change. As a consequence, foragers differing in competitive ability can have the same fitness (= net intake rate, summed or averaged over lifetime), allowing coexistence. We have shown that such polymorphism does indeed evolve: through repeated 'evolutionary branching' (Geritz et al., 1998; Baldauf et al., 2014), a large number of competitive types emerges and stably coexists.

In contrast to interference models, continuous input models, such as the one considered here, do not predict the segregation of unequal competitors, as the IFD condition (equality of resource abundance R/C across patches) can be satisfied in a multitude of ways. Sutherland and Parker (1985) and Parker and Sutherland (1986) speculated that unequal competitors will typically occur in roughly equal proportions at all patches, which would lead to the same IFD as predicted in the absence of differences in competitive ability. This is not the case in our model implementation, where at the IFD strong competitors are over-represented on the resource-rich patches. For the special case of two patches, other studies (e.g., Houston and McNamara 1988; Spencer et al. 1995; Houston and Lang 1998) arrived at a similar conclusion, but based on different arguments. In Appendix B, we investigate in some detail how our findings relate to the results of these earlier studies. We confirm the findings of Spencer et al. (1995) and Houston and Lang (1998) that the degree of competitor assortment strongly depends on the way how individuals make their patch choice decisions, and we add one insight to those discussed in these papers. Both Spencer et al. (1995) and Houston and Lang (1998) consider foragers moving into the patches from the outside (a mechanism we call ‘external initialisation’): two initially empty patches fill up due to the sequential arrival of individuals, each newly arriving individual choosing the patch offering the highest intake rate. In contrast, our study considers an ‘internal initialisation’ scenario, where the individuals are initially distributed randomly over the patches and subsequently sequentially relocate themselves if another patch offers a higher intake rate. In case of two patches, we show (fig. 4.A1) that external initialisation leads to strong assortment, while internal initialisation does not lead to assortment at all. In other words, the distribution of ideal and free competitors over patches strongly depends on whether the competitors make their choices when entering the system from the outside (external initialisation) or from within (internal initialisation).

The no-assortment result of figure 4.A1 points at an interesting discrepancy between the two-patch scenario typically considered in the literature and the multi-patch scenario considered in our study. Why does one of our key findings, assortment of competitors at a multi-patch IFD, break down for the special case of two patches? In Appendix B, we provide an explanation. We show that our threshold criterion (3) is generally (i.e., also for the case of two patches) applicable to the external initialisation scenario, and that it therefore explains the assortment results of Spencer et al. (1995) and Houston and Lang (1998). However, the criterion ceases to hold in the special case of two patches and internal initialisation, where it needs to be replaced by an alternative criterion (see Appendix B), which no longer predicts assortment. Interestingly, assortment is re-established if the two patches are split into sub-patches that have the same properties as their ‘mother patch’ (fig. 4.A2). This implies that the distribution of competitors over space may depend strongly on the ‘graininess’ of the environment. If, for example, the habitat choice situation is framed in a coarse-grained manner, such as a decision between deciduous and coniferous forest, our model would not predict assortment. In contrast, the same model would predict the accumulation of strong competitors in productive habitats if the otherwise identical situation is framed in a more fine-grained way, such as a decision between a multitude of deciduous and coniferous forest plots.

The existing models on the distribution of unequal competitors assume that differences in competitive ability are externally given. Such an analysis is incomplete if competitive differences have a heritable component. If this is the case, ideal free distribution theory, which is rooted in evolutionary optimality thinking (Netz et al., 2022), should pose the question whether unequal competitors can stably coexist in the course of evolution and, if so, how the distribution of competitive types is shaped by natural selection. We have shown that the evolutionary coexistence of unequal competitors is unlikely if the population is at an ideal free distribution all the time. This conclusion may change, however, if deviations from IFD conditions occur regularly. Such deviations are, for example, to be expected if sensory and/or locomotory constraints are taken into account (i.e., if the individuals are less 'ideal' and 'free' than IFD theory assumes). Here, we considered an alternative scenario, where IFD conditions are frequently perturbed due to environmental change. By means of a simple model, we demonstrated that distinct competitive types can emerge and stably coexist in the course of evolution. Consistent individual differences may therefore be as much a consequence as they are a cause of spatial distribution of individuals within the population (see also Wolf and Weissing 2010). As the evolved differences in phenotype (= competitive ability) lead to consistent differences in behavioural dispositions (= patch preferences; see (3)), we can conclude that spatiotemporal variation of the environment paves the way to the evolution of 'personality' differences.

Environmental variation is well-known to facilitate species coexistence via the storage effect (Chesson and Warner, 1981; Johnson and Hastings, 2022), and can also play a role in explaining intraspecific polymorphism (Chesson, 1985; Ellner and Sasaki, 1996). In our model, spatial assortment and environmental variation produce environmental niche differences between weak and strong competitors, where the former reap higher intake immediately after environmental change, whereas the latter gain higher resource shares at the ideal free distribution. This may be regarded as analogous to the storage effect acting within discrete generations. Also in animal personality research, different authors have argued environmental variation to be a key driver of individual differences (e.g., Dingemanse and Wolf 2010; Wolf and Weissing 2010; Dall et al. 2012). How spatiotemporal variation influences the occurrence of personality differences is hard to assess in wild populations, but emergent spatial patterns have been studied in a number of taxa. In great tits (*Parus major*), spatiotemporal variation in resources (here, nest boxes) within and between populations and study plots have been implicated in the coexistence of different exploratory tendencies (Nicolaus et al., 2016; Mouchet et al., 2021). Similarly, dispersal syndromes have been reported to be present in heterogeneous environments with fluctuations in habitat quality, risks and competition leading to spatial structuring of a population (Duckworth, 2006; Cote et al., 2010), much like in our simulations. Taborsky et al. (2014) found that habitat competition between cichlids of different body sizes leads to assortment and ultimately assortative mating, which is another potent factor by which spatial distributions can affect the course of evolution in sexually reproducing species. There is also empirical evidence for habitat choice based on personality, leading to a biased spatial distribution of behavioural types and behaviour-environment correlations (Edelaar et al., 2008; Pearish et al., 2013; Holtmann et al., 2017b). However, in these cases, the mechanisms underlying such spatial structuring of personality types are often in the dark.

Our two key results, the emergence of spatial assortment in a continuous input model of the IFD with unequal competitors, and the occurrence of polymorphism under spatiotemporal variation in an evolutionary model incorporating the very same, are both derived from an extension of a simple analytical model with certain mechanistic assumptions. We suggest that this is a constructive approach to study the robustness of these analytical models, and to uncover phenomena that would be otherwise overlooked. This model also acts as a useful starting point to relax further assumptions of IFD and extend to other dimensions of biologically relevant traits such as responsiveness to environmental change or limits to perception.

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APPENDIX

A. DESCRIPTION OF THE EVOLUTIONARY SIMULATION MODEL

ECOLOGICAL SETTING

We consider 100 patches, with resource densities drawn from a uniform distribution between 0 and 1 at initialization and during every change of the environment.

Individual movements and environmental change occur in an event-based approach, where each event occurs at a constant rate. Individual foragers scan their environment at a rate of 0.5, compare the potential intake across all patches and move to the patch providing the highest intake rate. Environmental change occurs at a rate of 0.25, and therefore on average every four time units. For computational convenience, foragers consume resources at discrete intervals of one time unit.

REPRODUCTION AND INHERITANCE

We consider discrete, non-overlapping generations of 100 time units, at the end of which reproduction occurs. For simplicity, reproduction is asexual. Individuals are haploid and have a single gene locus encoding for competitive ability that is inherited from parent to offspring. For each individual, the cumulative lifetime net intake W_{cum} is calculated. To prevent negative fitness values, a baseline value W_0 is added to W_{cum}, which can be interpreted as food intake that is unaffected by competitive interactions. The number of offspring produced per parent is determined by a weighted lottery that ensures that the expected number of offspring of an individual is proportional to $W_{cum} + W_0$ and that population size remains constant at 10,000 individuals. Offspring inherit the competitive ability from their parent, subject to rare mutations of small effect size. Mutations occur at a rate of 0.01 per reproduction event. When a mutation occurs, a random number, drawn from a normal distribution with mean zero and standard deviation $\sigma = 0.01$, is added to the parental value. At the beginning of the new generation, offspring are randomly distributed over the patches.

B. COMPARISON WITH TWO-PATCH MODELS

For the special case of two habitat patches, Houston and McNamara (1988) showed that the distribution of competitors over patches at the IFD is biased in such a way that strong competitors are more likely to occur on the resource-rich patch. This result reflects the fact that among the many possible distributions satisfying the IFD condition, those with an accumulation of strong competitors

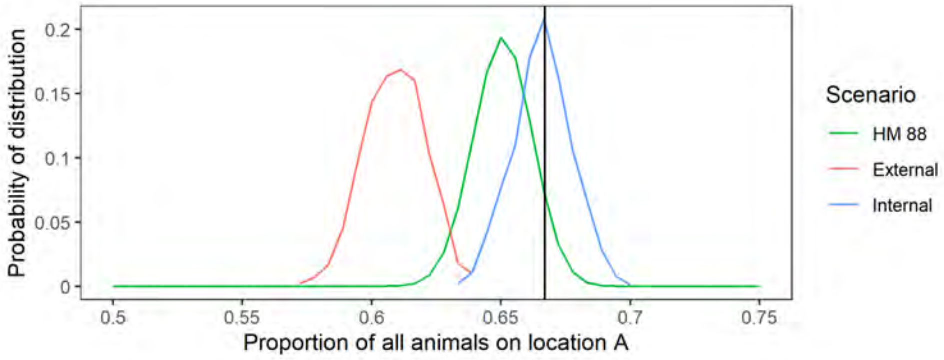

Figure 4.A1 | Implications of three habitat choice scenarios for the assortment of competitors. Following Houston and McNamara (1988), we consider a population of 180 individuals that distribute over two patches differing in quality. Resource abundance on patch A is twice the resource abundance on patch B. If all individuals were equal, 2/3 would occur on patch A at the IFD (vertical black line). Assume now that individuals differ in competitive ability: there are 90 good competitors that are twice as strong $c_1 = 2c_2$ as the 90 bad competitors. The green curve shows the probability distribution of the proportion of individuals on the resource-rich patch A, as derived from the 'statistical mechanics' analysis of Houston and McNamara (1988). The major part of this distribution is to the left of the value 2/3, indicating that, on average, strong competitors accumulate on the resource-rich patch. The **red curve** shows the probability distribution resulting from the 'external initialisation' scenario, where two initially empty patches fill up due to the sequential arrival of individuals, each newly arriving individual choosing the patch offering the highest intake rate. This choice scenario leads to an even stronger assortment of competitors to patches. The **blue curve** shows the probability distribution resulting from the 'internal initialisation' scenario, where the individuals are initially distributed randomly over the patches and subsequently sequentially relocate themselves if the other patch offers a higher intake rate. No assortment does occur in this scenario. The distributions shown are based on 1,000 replicate simulations per scenario.

on the resource-rich patch are over-represented. To see this, consider two patches A and B, of which A is twice as resource-rich as B ($R_A = 2R_B$). If all competitors are equal, 2/3 of all individuals would therefore occur in patch A in the ideal free distribution. Consider now two types of competitors, of which type 1 is twice as strong as type 2 ($c_1 = 2c_2$); both types are equally frequent ($N_1 = N_2 = N/2$). In figure 4.A2, the green curve shows the frequency distribution of the number of individuals in patch A for all realisations of the IFD condition. In the majority of cases, the number of individuals on patch A is smaller than $2N/3$, implying that the strong competitors are over-represented on this resource-rich patch. The green distribution in figure 4.A1 represents the complete set of IFD realisations, and the validity of Houston and McNamara's 'statistical mechanics' argument relies on the assumption that the IFD that is actually realised is an unbiased sample of all IFD realisations.

A subsequent investigation by Houston and Lang (1998) showed that the distribution of actual IFD realisations strongly depends on the way the equilibrium distribution of competitors over patches is achieved. If, for example, the good competitors make their habitat choice decisions before the bad competitors, the number of individuals on the resource-rich patch will be $2/3N$ at the IFD, as in the case of equal competitors. If, in contrast, competitors make their decisions sequentially, in a random order, good competitors accumulate even more strongly on the resource-rich patch A than predicted by Houston and McNamara (1988). In either case, the solution set calculated by Houston and McNamara (1988) is not representative for the realized distribution of competitors over patches.

An important detail of Houston and Lang (1998) treatment is that their individuals sequentially enter the two patches from the outside, whereas in our model we assume that the foragers are already distributed across the patches and subsequently redistribute until an IFD is reached. Figure 4.A1 shows that the initialisation has a clear effect on the outcome. While ‘outside initialisation’ (red) leads to a pronounced assortment (i.e. the accumulation of strong competitors on the resource-rich patch A), this is not the case for the scenario where the individuals were first distributed randomly over the two patches (blue). In both cases, the realized distributions of competitors over patches are considerably different from the one predicted by Houston and McNamara (1988).

In view of our threshold criterion (inequality (3) in the main text), it is understandable that ‘outside initialisation’ leads to pronounced assortment: strong competitors have a higher tendency to choose the research-rich patch than weak competitors. But why does this argument break down in the case of ‘random initialisation’? We see two reasons for this. First, strong and weak competitors only differ in their patch preferences if the difference in resource availabilities (= the difference in R/C-values) is such that the right-hand side of (3) is larger than the lowest competitive ability c_{min} and smaller than the highest competitive ability c_{max}. If the patches fill up sequentially (‘outside initialisation’), the resource availabilities R_A/C_A and R_B/C_B will, due to the choices of the newly arriving individuals, remain similar to each other, implying that the threshold criterion (3) will often lead to different outcomes for weak and strong competitors. If, in contrast, the patches are initialised at random, the resource availabilities will initially differ a lot, implying that the threshold criterion (3) leads to the same outcome for different competitors. This, however, cannot be the whole story, as we showed in the main text that random initialisation does lead to pronounced competitor assortment in a multi-patch scenario.

Our second reason highlights a difference between the two-patch scenario (which is the standard scenario considered in the literature) and a multi-patch scenario (as the one considered in our study). Threshold criterion (3) is based on inequality (2), which implicitly assumes that the decision-making individual compares two patches that it does not occupy. This is the case if individuals enter the system from the outside, and it is typically the case if many patches are compared with each other (as an individual can only occupy one of the patches, most patch comparisons involve patches not occupied by the individual). The situation is different in the two-patch scenario: if an individual makes a choice 'from within', it must already occupy one of the two patches under comparison. Let us call the occupied patch P_{occ} and the other patch P_{other}. The individual should switch to the other patch if that other patch yields a higher intake rate:

$$c_i.\frac{R_{other}}{C_{other}+c_i} > c_i.\frac{R_{own}}{C_{own}} \tag{A.1}$$

or, equivalently, if:

$$c_i < \frac{C_{own}C_{other}}{R_{own}}.\left(\frac{R_{other}}{C_{other}} - \frac{R_{own}}{C_{own}}\right) \tag{A.2}$$

If the own patch has a higher resource availability $R_{own}/C_{own} > R_{other}/C_{other}$, the right-hand side of (S2) is negative, implying that individuals should never switch to the other patch, irrespective of their competitive ability. However, strong and weak competitors may differ in their patch preferences if the resource availability is higher on the other patch. Now, (S2) is a threshold criterion which is most likely satisfied for weaker competitors. This is in line with the findings of Houston and Lang (1998), who noticed that weak (but not strong) competitors may revise their earlier patch choice decisions once a strong competitor has moved into their patch. Notice that the 2-patch criterion (S2) does no longer contain the difference in resource richness $R_{own} - R_{other}$ in the denominator of the right-hand side. This means that the bias between strong and weak competitors is not based on differences in resource richness per se, but on differences in resource availability. Accordingly, one should not expect the assortment of strong competitors to resource-rich patches, in line with figure 4.A1 (blue line).

This is where the difference between a two-patch scenario and a multi-patch scenario becomes decisive. In a multi-patch scenario, relevant patch comparisons occur predominantly between patches not currently occupied, and therefore threshold (3) applies rather than (S2). Likewise, the increased number of patches makes diverging patch choice decisions between individuals of different competitive ability more likely. Extending the figure 4.A1 to multiple patches, we observe that some spatial assortment indeed occurs when individuals (fig. 4.A2, blue curves in the left panels), even if these patches are down-scaled versions of patches A and B in the two-patch scenario. Previous theoretical treatments have predominantly focused on the two-patch scenario, and this qualitative difference between two and multiple patches is therefore of some significance. We also observe a substantial increase of spatial assortment between two- and ten-patch scenarios if foragers are initialized outside of the patches (fig. 4.A2, red curves in the left panels).

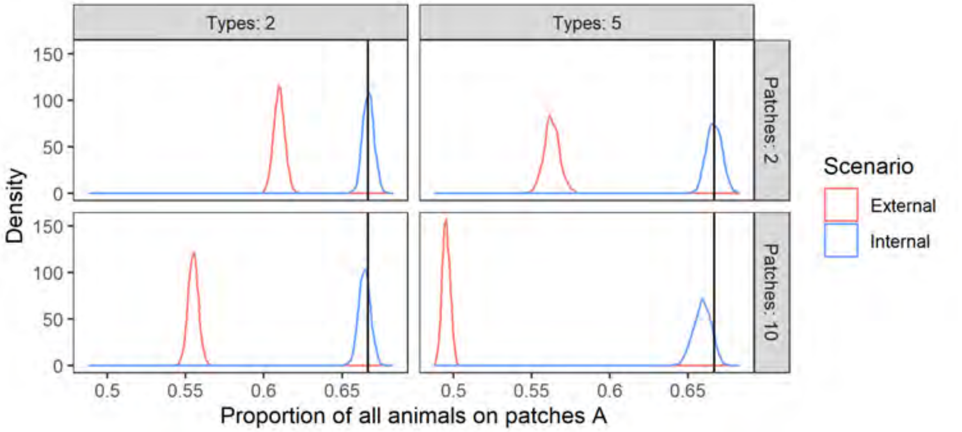

Figure 4.A2 | Effect of the number of patches and the number of competitive types on spatial assortment in two habitat choice scenarios. As in fig. 4.A1, the panels show the distribution of competitors over patches, based on 1,000 simulations for the external initialisation scenario (red) and the internal initialisation scenario (blue). The population now consists of 2,000 individuals, which can either be of two types (as in fig. 4.A1) or of five types, with competitive abilities $c_i = c_1 / i$. There are either two patches A and B (as in fig. 4.A1) or ten patches, where five are resource rich, while the other five are resource poor. As before, the resource influx in the resource-rich patches is twice as large as in the resource-poor patches.

By the same token, we can extend our simulations to consider the effect of more than two competitive types. Intuitively, the threshold criterion should become more relevant for a broader range of competitive types. Considering five instead of two competitive types, where competitive ability is given by $c_i = c_1 / i$, we observe strengthened spatial assortment for external initialization (fig. 4.A2, red curves in right panels). At random initialization (fig. 4.A2, blue curves in right panels) an increased number of types does not automatically lead to spatial assortment: On two patches, competitive types are distributed randomly independent of the number of types considered. Only when 10 patches are considered, does an increased number of types lead to some reinforcement of spatial assortment.

Again, this is explained by the difference between equations (3) and (S2). For the simulations shown in figure 4.A2, we used a population size of 2,000, but this parameter only affects the spread of the probability distributions and not their locations.

5

EFFECTS OF DEVELOPMENT AND PARENTAL CARE ON HAMILTON'S FORCE OF SELECTION

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ABSTRACT

The force of selection describes the sensitivity of population growth to changes in life history parameters, with a focus usually on the survival probabilities from one age class to the next. Importantly, according to Hamilton the force of selection generally decreases after the onset of reproduction, thereby providing a possible explanation for patterns of senescence. A second characteristic feature is that the force of selection remains constant up to the age of first reproduction. This latter observation, however, rests on the assumption that offspring become independent from their parents right after birth. I show here in a minimal model that if offspring are reliant on their parents, either during early embryonal development or via parental care at later stages, the force of selection on offspring survival generally increases up until the age at which offspring become independent. This provides a possible explanation for the commonly observed pattern of decreasing mortality during early ontogeny. Further, genes acting during recurrent life stages are observed to experience a heightened force of selection compared to genes that act strictly age-specifically, demonstrating the need to develop a mechanistic understanding of gene activation patterns through which to consider life history evolution.

5.1. INTRODUCTION

The patterns of mortality observed in natural populations can be understood from an evolutionary point of view either as the product of optimization under constraints or through the balance between selection and mutation. These competing approaches are exemplified by the two major evolutionary theories of ageing, the Antagonistic Pleiotropy theory (Williams, 1957) and the Mutation Accumulation theory (Medawar, 1952). Under Antagonistic Pleiotropy, patterns of mortality are determined by functional trade-offs between early and later stages of life, whereas Mutation Accumulation considers mortality at a given stage of life to be determined by the balance between deleterious mutations and the strength, by which such mutations are selected against. Trade-offs and mutation regimes are very difficult to determine empirically, but as long as trade-offs are absent, the force of selection acting on life history parameters can be derived straightforwardly from the observed survival and reproduction rates themselves: Hamilton (1966) defined the force of selection as the differential of the growth rate over the logarithm of survival probability:

$$F(p_i) = \frac{dr}{d\log p_i} \tag{1}$$

This expression has some interesting properties. First, the force of selection remains constant through the early stages of life before the onset of reproduction, where decreasing cohort sizes are balanced by an increase in prospective reproduction. Second, after reproduction commences, the force of selection is bound to decrease with age. These conclusions however hinge upon the scale, at which variation in survival probabilities occurs (Baudisch, 2005). Hamilton assumed that variation occurs relative to the magnitude of survival probabilities, which would for example be the case if the probability to survive from one stage to the next is the product of a number of probabilities to survive different risk factors, and one of these, a risk factor constant across different life stages, is subject to deleterious mutations. If survival probabilities instead vary by a constant amount independently of their magnitude, or relative to mortality rates, the force of selection comes to depend on the age-specific survival parameters and therefore does not need to remain constant during infancy and may also rise at later stages of life (Baudisch, 2005). The question at which scale variation typically occurs will likely not be met with a definitive answer, and these measures should therefore be considered as equally relevant. Depending on mutation regime and life history parameters, the force of selection therefore does not need to stay constant before maturity, and also need not always decline after maturity is reached (e.g. negative senescence, Vaupel et al. 2004; Jones and Vaupel 2017).

Hamilton's force of selection is hence not as general as once thought. We still may wish to develop an understanding for how selection pressures behave across different life-histories, irrespective of the exact parameterization. If survival probabilities are assumed to be age-independent, and therefore constant across different age classes, the two features of constancy before maturity and monotonous decline beyond are retained, regardless of the scale of variation considered or indeed the patterns of fertility observed. The decline of the force of selection may then still serve as a model explanation for widely observed patterns of functional decline and increased mortality with age, even though exceptions may occur. The supposed constant force of selection during infancy however contrasts with extensive evidence that mortality decreases towards maturity ('ontogenescence', Levitis 2011; Levitis and Martínez 2013). Age-structured models generally assume offspring to become independent the moment they are born, and thereby ignore dependencies between parents and offspring (although see Lee 2003; Kahn et al. 2015; Roper et al. 2022). Indeed, offspring of many taxa crucially depend on their parents during substantial parts of ontogeny, and parents are often prevented from beginning a new reproductive cycle while taking care of their young. Hamilton himself already suggested a mechanism termed 'sibling replacement', by which the force of selection might increase during successive juvenile stages, but he never expressed these ideas in the form of a rigorous model. In 2003, Lee presented a model incorporating energy transfers between family members that demonstrated the potential for the force of selection to increase during successive juvenile stages. Roper et al. (2022), who considered a spatial model with an explicit focus on kin selection, under certain conditions also observed an increasing force of selection at the juvenile stage. Both models incorporate a large amount of mechanistic detail regarding the interactions between family members, and the generality of these findings with respect to the force of selection is presently unclear. In the following, I will develop a much simpler conceptual model that demonstrates the general tendency of the force of selection to increase during dependent juvenile stages.

5.2. THE MODEL

Consider a population, in which the offspring develop over consecutive stages J_1 to J_n while being fully dependent on their parent. These stages could be successive gestational stages from fertilization to birth, or juvenile stages during which offspring strictly rely on their parent for food and shelter. For simplicity, assume that adults always only cater to a single offspring at a time. We then denote adult reproductive stages A_1 to A_n that run in parallel to the juvenile stages J_1 to J_n. Adults survive from stage A_i to A_{i+1} with probability p_i, and if the adult dies, so does the offspring. Juveniles survive from J_i to J_{i+1} with probability s_i, and die with probability $1-s_i$. If the offspring dies, the adult returns to stage A_1 and begins a new reproductive cycle. If juveniles pass stage J_n, the juvenile becomes an independent adult and joins the adults at stage A_1 to begin a new cycle of reproduction. Parameters p_i and s_i thus denote adult and juvenile survival. Since juveniles of a given stage are bound to be accompanied by adults of a corresponding stage, we only need to keep track of adult individuals. For $n=4$ stages, this results in the life cycle shown in figure 5.1, yielding the following class-structured model $\vec{A}(t+1)=\boldsymbol{M}\vec{A}(t)$:

$$\begin{pmatrix} A_1(t+1) \\ A_2(t+1) \\ A_3(t+1) \\ A_4(t+1) \end{pmatrix} = \begin{pmatrix} p_1(1-s_1) & p_2(1-s_2) & p_3(1-s_3) & p_4(1+s_4) \\ p_1 s_1 & 0 & 0 & 0 \\ 0 & p_2 s_2 & 0 & 0 \\ 0 & 0 & p_3 s_3 & 0 \end{pmatrix} \begin{pmatrix} A_1(t) \\ A_2(t) \\ A_3(t) \\ A_4(t) \end{pmatrix} \tag{2}$$

Reproduction is thus finalized only at the end of stage A_4, when juveniles become independent of their parent and join the pool of adults in stage A_1. While the model represents true age classes for juveniles, which can only advance between stages in one direction, for adults the model instead considers different stages of a reproduction cycle that can be undergone multiple times. This also means that for the purposes of this model, vital rates do not depend on parental age.

A matrix such as the one above with non-negative entries, and where all classes are connected, is guaranteed to have a single positive leading eigenvalue λ_1 (Charlesworth, 1994). Thus, in the long run, populations will end up growing at a constant rate λ_1, and if $\lambda_1 > 1$, such a population grows geometrically. Associated with the leading eigenvalue are a right and left eigenvector. The right eigenvector $\vec{u}$ represents the stable class distribution of individuals, which is approached by the population during growth. The left eigenvector $\vec{v}$ represents reproductive values, indicating the expected future reproduction of an individual in a given stage, relative to the other stages. The force of selection for adult and juvenile survival p_i and s_i may then be calculated using the left and right eigenvectors (see appendix, Caswell 1978; Otto and Day 2012):

$$F(x) = \frac{dr}{d\ln x} = \frac{x}{\lambda} \frac{\vec{v}^T \left(\left. \frac{d\boldsymbol{M}}{dx} \right|_{x=x*} \right) \vec{u}}{\vec{v}^T \vec{u}} \tag{3}$$

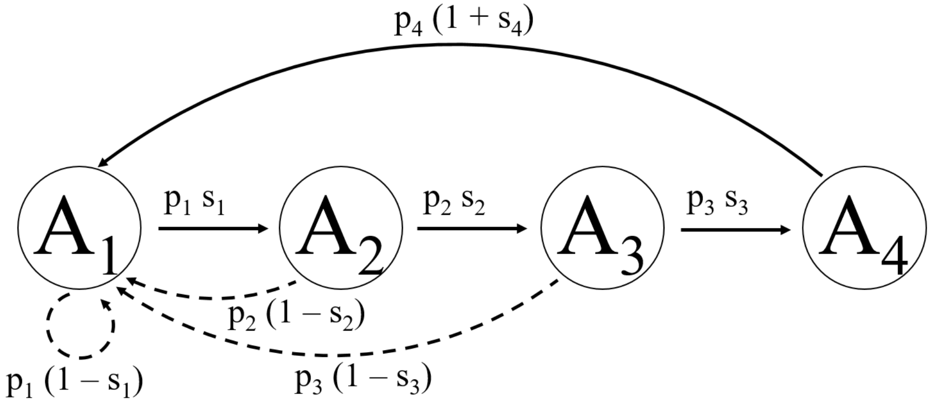

Figure 5.1 | Life-cycle with parent-offspring dependence. Adult age classes run from A_1 to A_4, each tracking the number of adults with dependent offspring. and express the survival probabilities of the parent and offspring from one stage to the next. At the end of A_4, offspring join their parents in the pool of mature adults.

The force of selection on juvenile survival s_i for all stages $i < n$ then has the pleasingly simple form

$$F(s_i) = \frac{u_{i+1}(v_{i+1} - v_1)}{\vec{v}^T \vec{u}} \tag{4}$$

and the force of selection on adult survival p_i for all stages $i < n$ is

$$F(p_i) = \frac{u_i v_i}{\vec{v}^T \vec{u}} \tag{5}$$

Using the formulas for left and right eigenvectors, $\vec{v}^T \boldsymbol{M} = \lambda \vec{v}^T$ and $\boldsymbol{M}\vec{u} = \lambda \vec{u}$ respectively, we first inspect the general behaviour of these functions over consecutive life stages, before turning to a specific example where survival rates are the same across all stages.

5.2.1. GENERAL RESULTS

The force of selection on the survival of offspring over the first three stages is

$$
\begin{aligned}
F(s_1) &= \left(1-\frac{p_1}{\lambda}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}\\
F(s_2) &= \left(1-\frac{p_1}{\lambda}+\frac{p_1 s_1}{\lambda}-\frac{p_1 s_1 p2}{\lambda^2}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}\\
F(s_3) &= \left(1-\frac{p_1}{\lambda}+\frac{p_1 s_1}{\lambda}-\frac{p_1 s_1 p_2}{\lambda^2}+\frac{p_1 s_1 p_2 s_2}{\lambda^2}-\frac{p_1 s_1 p_2 s_2 p_3}{\lambda^3}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}
\end{aligned}
\tag{6}
$$

Thus, from stage i to stage $i+1$ the force of selection on juvenile survival changes by

$$
F(s_{i+1}) - F(s_i) = \frac{\prod p_j s_j}{\lambda^{i-1}}\left(1-\frac{p_i}{\lambda}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}
\tag{7}
$$

, which is positive for all values $p_i < \lambda$. The force of selection therefore increases for all biologically realistic values of p_i, as long as population growth is positive.

5

The force of selection on adult survival over the first three stages is

$$
\begin{aligned}
F(p_1) &= \frac{u_1 v_1}{\vec{v}^T\vec{u}}\\
F(p_2) &= \left(1+\frac{p_1 s_1 - p_1}{\lambda}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}\\
F(p_3) &= \left(1+\frac{p_1 s_1 - p_1}{\lambda}+\frac{p_1 s_1 p_2 s_2 - p_1 s_1 p_2}{\lambda^2}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}
\end{aligned}
\tag{8}
$$

The force of selection on adult survival therefore changes from stage i to stage $i+1$ by

$$
F(p_{i+1}) - F(p_i) = \frac{\prod p_j s_j}{\lambda^{i}}\left(1-\frac{1}{s_i}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}}
\tag{9}
$$

, which is equal to or smaller than zero for all biologically realistic values of s_i. The force of selection on adult survival therefore always decreases over successive adult reproductive stages.

We thus observe that when offspring depend on their parents, the force of selection does not stay constant during infancy, but instead always increases. From the beginning of maturity onwards, the force of selection decreases over successive adult stages. Here it should be noted however that the classes represent reproductive stages rather than age classes, which we will turn to at a later point. These results are derived from Hamilton's classical formula for the force of selection, and hence assume variation in parameters relative to their magnitude.

5.2.2. STAGE-INDEPENDENT ADULT AND JUVENILE SURVIVAL RATES

In the following, I will present an example in which juvenile and adult survival rates are assumed to be constant. This provides an intuitive understanding for the behaviour of the force of selection and allows for the derivation of a general solution. Assuming age-independent juvenile and adult survival rates ($s_1 = s_2 = s_3 = s_4$; $p_1 = p_2 = p_3 = p_4$), the force of selection experiences a decelerating increase in the juvenile age classes and a decelerating decrease in the adult reproductive stages that follow (fig. 5.2, for $s = p = 0.9$). Notably, the force of selection on adult survival is much higher than for juvenile survival, because the reproductive stages can reoccur multiple times during the lifetime of an adult.

The constant juvenile and adult survival rates permit us to derive general expressions for the force of selection on juvenile and adult survival:

$$F(s_i) = \frac{\delta - 1}{\delta - s}\left(1 - \left(\frac{s}{\delta}\right)^i\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}} \tag{10}$$

$$F(p_i) = \left(\left(\frac{1}{s} - \frac{\delta - 1}{\delta - s}\right)\left(\frac{s}{\delta}\right)^i + \frac{\delta - 1}{\delta - s}\right)\frac{u_1 v_1}{\vec{v}^T\vec{u}} \tag{11}$$

, where δ is the leading eigenvalue of the matrix $\boldsymbol{M}/p$ (see appendix). The force of selection on juvenile and adult survival is therefore independent of adult survival p, and depends on stage i only through the term $(s/\delta)^{i-1}$. Since s/δ is always smaller than 1 (see appendix), this term approaches zero with increasing i. Multiplied with a negative factor in the case of the force of selection on juvenile survival, and with a positive factor in the force of selection on adult survival, the force of selection on juvenile and adult survival are increasing and decreasing saturating functions of i (fig. 5.2). Following Hamilton, equations 10 and 11 consider the force of selection as the derivative of population growth rate over the logarithm of survival probability. If the derivative is taken over the untransformed survival parameter, mortality rates etc., the force of selection is considered on a different scale and scaling factors that depend on stage-specific survival enter the equation (Baudisch 2005, eqn 5). If parameters are constant across all stages, however, as assumed above, this scaling factor is a constant and the overall shape of the derived functions is preserved. While not universal, we can therefore still speak of a general tendency of the force of selection to increase during infancy even if alternatives to Hamilton's formulation of the force of selection are considered and mutations affect survival probabilities in a variety of ways.

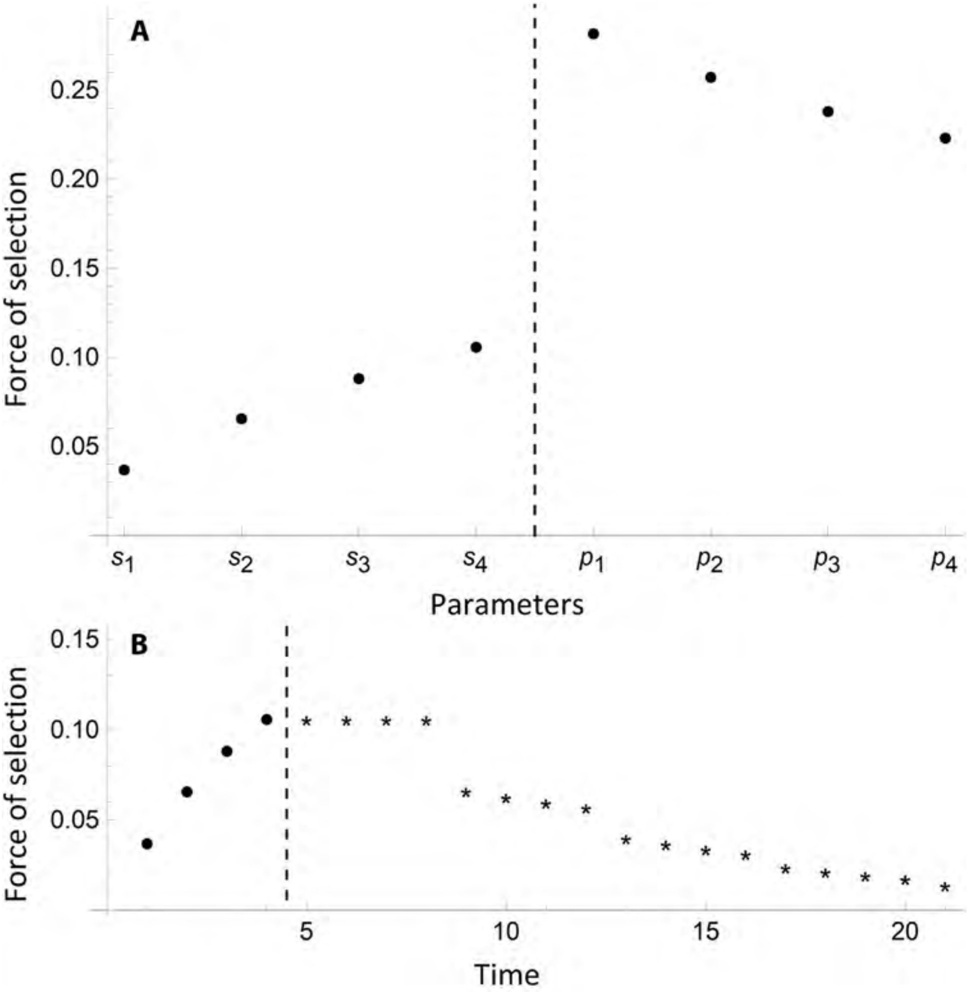

Figure 5.2 | The force of selection during infancy and adulthood. **(A)** During infancy, the force of selection increases in a slowly saturating manner. The force of selection on adult reproductive stages decreases over consecutive stages, but is much higher than in juvenile age classes. **(B)** The force of selection on age-specific survival is equal to the force of selection on s_1 to s_4) for the first 4 age classes (•), and from thereon needs to be calculated for adult age classes through eq. 13 (*). Until the first offspring become independent at age 8, the force of selection on adults is equal to the last juvenile stage, and thereafter decreases. The broken line marks the onset of maturity.

5.2.3. FORCE OF SELECTION ON ADULT AGE CLASSES

So far, we considered the force of selection on juvenile and adult survival parameters. Juveniles progress through stages in one direction, and therefore stages represent true age classes. Adult survival however occurs in the context of a reproductive cycle, as shown in figure 5.1, and the force of selection on adult survival thus relates to reoccurring life stages. The force of selection on adult ages classes can then be calculated as follows.

Consider a modified transition matrix $\boldsymbol{M}^{\circ}$ with $\boldsymbol{M}^{\circ}_{1,4} = p_4$, whereby offspring release at the end of stage 4 is excluded. This matrix can then be used to track a single cohort of individuals over different stages and multiple time steps. Adjusting for growth rate, we can calculate the fraction of the stable age distribution due to a cohort of a certain age:

$$\vec{u}^{\circ}(t) = \boldsymbol{M}^{\circ t} \begin{pmatrix} u_4 p_4 s_4 \\ 0 \\ 0 \\ 0 \end{pmatrix} \lambda^{-t} \tag{12}$$

Using the same reproductive values as before, and differentiating over all p_i, we can calculate the force of selection acting on the survival of adults at a given age.

$$F(t) = \frac{dr}{d\log p}(t) = \frac{\sum_{i=1}^{4} \frac{p_i}{\lambda} \vec{v}^T \left(\left. \frac{d\boldsymbol{M}}{dp_i} \right|_{p_i = p_i *} \right) \vec{u}^{\circ}(t)}{\vec{v}^T \vec{u}} \tag{13}$$

In this case, and in keeping with standard theory, the force of selection remains constant up until first reproduction at the age of 8, and decreases thereafter (fig. 5.2, stars).

5.3. DISCUSSION

I have demonstrated here that the selection force generally increases over successive juvenile stages in which offspring depend on their parent. Intuitively, offspring death during early developmental stages is much less costly to parents than during later stages, because the parental investment of time and mortality risk increases over consecutive stages of the reproductive cycle. For example, if offspring die after two time steps, parents lose twice as much time, and experienced twice the mortality risk, than if offspring die after one time step. The mechanism of 'sibling replacement' proposed by Hamilton therefore delivers a possible explanation for diminishing mortality rates during early ontogeny. Particularly if matings are easy to come by, the force of selection on offspring survival may thus be initially quite low, and from there increases along with the time/mortality risk invested by parents, until offspring become independent.

Patterns of mortality are determined by the force of selection in mutation-selection balance, or when mutations occur that have opposing fitness effects at different age classes. The model then suggests that mortality rates should decrease from conception until offspring gain independence, remain stable while juveniles are independent but have not begun reproduction, and begin to increase from the time of first reproduction. This seems to be supported by empirical evidence that reports falling mortality rates during ontogeny in a wide range of taxa ('ontogenescence', Levitis 2011). In humans, mortality rates continue to fall from birth until the age of 10 to 13 (Barclay, 1954; Comfort, 1964; Mace, 2000). Further, fetal death rates appear to decrease dramatically over the first trimester of pregnancy, where overall miscarriage risk is reported to drop from 9.4% at 6 weeks of gestation to 4.2% at 7 weeks, 1.5% at 8 weeks, 0.5% at 9 weeks and 0.7% at 10 weeks (Tong et al., 2008). The preclinical rate of pregnancy loss may be yet higher, with 30% of pregnancies lost after successful implantation (as indicated by hCG-testing, Wilcox et al. 1988; Zinaman et al. 1996). These empirical findings can be plausibly explained by the model presented here, but it is important to keep in mind the limitations of a simple measure such as Hamilton's force of selection; if selection is so strong as to completely deplete any occurring variation, or if drift dominates over selection, the force of selection has no influence on observed rates of mortality. Additionally, if the force of selection is calculated from simple life history data on survival and reproduction, functional trade-offs or evolutionary conflicts that may exist between parents and offspring are ignored. So how much of the observed patterns of ontogenescence could be due to the diminished force of selection in early life?

Extrinsic mortality risks that are common during youth, e.g. due to starvation or predation, may be to a large part unavoidable and not subject to genetic variation or selection. On the other hand, the high rates of failure during the first trimester of pregnancy may easily be under such weak selection that deleterious mutations can accumulate. Medical research indeed seems to indicate a broad variety of causes for early pregnancy failures, e.g. failure of gene activation, chromosomal abnormalities and errors of cytokinesis and karyokinesis (Braude et al., 1991; Michels and Tiu, 2007), and such a pattern of heterogeneity is more consistent with mutation accumulation than selection under trade-offs (Austad and Hoffman, 2018). If there was a trade-off between mortality in early stages and developmental robustness in later stages, equation [10] would indicate that alleles increasing early-life mortality in favor of developmental robustness later on should be favored. Another important aside is the assumption that genes act age-specifically, the effect of which is observed in the contrast between the force of selection on adult reproductive stages and adult age classes. Developmental stages occur but once in the lifetime of individual organisms, but reproductive cycles can be undergone multiple times, and this alone increases the force of selection on recurrent or persistently active genes. From a mechanistic point of view, it seems plausible that developmental stages entail a greater number of age-specific genes than age classes during adulthood.

The model I presented here is highly conceptual in nature, and some clear limitations should be highlighted. Individuals have only a single offspring at a time, thus there is no resource competition between siblings (Kahn et al., 2015), and offspring is either dead or alive. The dependency of offspring on their parent is either absolute or non-existent, such that offspring do not optionally rely on their parents for improved survival, as observed in species with facultative parental care (e.g. dung beetles, Capodeanu-Nägler et al. 2016. Such extensions are feasible, but the specification of costs and benefits of parental care becomes nontrivial, with different modelling options to be explored. The models that so far have observed an increasing force of selection before the age of first reproduction were in fact mechanistic models that considered interactions between relatives in greater detail (Lee, 2003; Roper et al., 2022). And finally, because the model considers adult reproductive stages rather than age classes, vital rates are independent of parental age. As we have seen, this still permits the calculation of an age-dependent force of selection, but it prevents the incorporation of age-dependent adult survival rates as well as offspring survival rates that depend on the age of the parent (maternal effect senescence, Moorad and Nussey 2016; Hernández et al. 2020; Ivimey-Cook and Moorad 2020). Further work also remains to be done on the force of selection before maturity with regards to potential parent-offspring conflicts (Ronce and Promislow, 2010; Kramer et al., 2016) and the effect of density dependence (Mylius and Diekmann, 1995; Pen and Weissing, 2000; Kokko, 2021).

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APPENDIX

To determine the force of selection acting on juvenile and adult survival at any given life stage, the right and left eigenvectors are used. The elements of the right eigenvector are given by the following equations:

$$\begin{aligned}\lambda u_1 &= p_1(1-s_1)u_1 + p_2(1-s_2)u_2 + p_3(1-s_3)u_3 + p_4(1+s_4)u_4\\ \lambda u_2 &= p_1 s_1 u_1\\ \lambda u_3 &= p_2 s_2 u_2\\ \lambda u_4 &= p_3 s_3 u_3\end{aligned} \tag{A.1}$$

Assuming that p_i and s_i are constant over all stages, we obtain a general expression for the elements of the right eigenvector:

$$u_i = \left(\frac{ps}{\lambda}\right) u_1 \tag{A.2}$$

The left eigenvector is determined by the following equations.

$$\begin{aligned}\lambda v_1 &= p_1(1-s_1)v_1 + p_1 s_1 v_2\\ \lambda v_2 &= p_2(1-s_2)v_1 + p_2 s_2 v_3\\ \lambda v_3 &= p_3(1-s_3)v_1 + p_3 s_3 v_4\\ \lambda v_4 &= p_4(1-s_4)v_1 + 2p_4 s_4 v_1\end{aligned} \tag{A.3}$$

Again assuming that p and s are constant over all stages, the first term on the right-hand-side is constant. The difference between consecutive elements of the left eigenvector is then

$$\begin{aligned}v_2 - v_1 &= \frac{\lambda - p}{ps} v_1\\ v_3 - v_2 &= \frac{\lambda}{ps}(v_2 - v_1)\\ v_4 - v_3 &= \frac{\lambda}{ps}(v_3 - v_2)\end{aligned} \tag{A.4}$$

which can be generalized to

$$\Delta_i = \left(\frac{\lambda}{ps}\right)^{i-1} \frac{\lambda - p}{ps} v_1 \tag{A.5}$$

Taking the sum over stages i and simplifying, a general expression is obtained for the elements of the left eigenvector:

$$v_i = \left(\frac{\lambda - p}{ps} \frac{1 - \left(\frac{\lambda}{ps}\right)^{i-1}}{1 - \frac{\lambda}{ps}} + 1 \right) v_1 \tag{A.6}$$

Further, p can be factored out of matrix $\boldsymbol{M}$, such that $\boldsymbol{M} = p\boldsymbol{M_0}$, where M_0 only depends on variable s. The leading eigenvalues of and are then related through p: $\lambda_1 = p\delta_1$, where δ_1 is the leading eigenvalue of M_0, given by the characteristic polynomial:

$$\delta^4 + (s-1)\delta^3 + (s^2 - s)\delta^2 + (s^3 - s^2)\delta - s^3 - s^4 = 0 \tag{A.7}$$

This eigenvalue will always be equal to or larger than one, such that, if no offspring survives ($s = 0$), the population is bound to shrink at a rate $\lambda = p$. Plugging A.2 and A.6 into equations 4 and 5 and replacing $\lambda = p\delta$, one obtains the equations 10 and 11 for the force of selection on juvenile and adult survival.

6

DETAILS MATTER WHEN MODELLING THE EFFECTS OF ANIMAL PERSONALITY ON THE SPATIAL DISTRIBUTION OF FORAGERS

A comment to DiNuzzo and Griffen (2020)

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Aparajitha Ramesh
Jakob Gismann
Pratik R. Gupte
Franz J. Weissing

Nullius in verba

Motto of the Royal Society
of the United Kingdom

Proceedings of the Royal Society B (2022), 289(1970), 20210903.

By means of a simulation study, DiNuzzo and Griffen (2020) investigate whether individual variation in a personality trait can explain ‘undermatching’, an often-observed deviation from the ideal free distribution (IFD). Here, we raise five points of concern about this study, regarding (i) the interpretation of the results in terms of personality variation; (ii) deficiencies in the technical implementation of the model, leading to wrong conclusions; (iii) the effects of population size on deviations from the IFD; (iv) the measure used for quantifying deviations from the IFD and (v) the analysis of the mud crab data. Finally, we provide an overview of the evolutionary ramifications of the relation between animal personality and the IFD.

6.1. PERSONALITY VARIATION AND THE IFD

The individuals in DiNuzzo and Griffen’s model tend to maximize their intake rate. At each point in time, they are perfectly informed about the distribution of resources (which remains constant) and the distribution of foragers (which can change due to movement). Individuals differ in ‘activity’, that is the rate at which they recognize that their current intake rate is sub-optimal; once they observe a discrepancy, they move instantaneously to the habitat patch yielding a maximal intake rate. In this model, each individual has to move at most once: if all individuals have moved (or stayed at their initial position, as this already yielded a maximal intake rate), the IFD is reached. It is therefore obvious that less active individuals that, by definition, take on average more time steps for making a movement decision, retard the approach of the population to the IFD. Hence, it is also obvious that the ‘time to reach IFD’ increases with an increase of the proportion of inactive individuals. In other words, it is not personality variation per se that retards the approach to the IFD but rather the presence of inefficient movers.

6.2. PROBLEMS WITH THE TECHNICAL IMPLEMENTATION OF THE MODEL

Above we argued that it is obvious that the ‘time to reach IFD’ increases with the proportion of inactive individuals. In view of this, it is surprising that DiNuzzo and Griffen report a hump-shaped relationship in one of their simulation scenarios (their fig. 4e) and even a monotonic decline in the time to reach IFD with increasing proportions of inactive individuals in case of a type II functional response (their electronic supplementary material, fig. S1, reproduced here in figure 6.1A). We think both results are artefacts. The pattern in their electronic supplementary material fig. S1 is caused by a comparison between intake rates calculated with two different formulas. As a consequence, individuals can 'believe' that they are already in a habitat maximizing their intake rate, while really they are not.

In addition, an incorrect formula of a ratio-dependent functional response type II is used (following Abrams and Ginzburg 2000). A detailed explanation of these mistakes can be found in our electronic supplementary material (Netz et al., 2021). If these mistakes are corrected, the time to reach IFD shows the expected increasing trend with the proportion of inactive individuals (fig. 6.1B), rather than the decreasing trend reported by DiNuzzo and Griffen. Hence, a saturating type II functional response leads to a similar relationship between the proportion of active consumers and time-to-IFD as an unlimited linear (type I) functional response. Special explanations for discrepancies between type I and type II models (the 'domino effect' explanation in electronic supplementary material, 1.4 of DiNuzzo and Griffen 2020) are not needed and are actually misleading.

We can further show by a simple mathematical argument that the correspondence between the two model variants considered by DiNuzzo and Griffen should be even stronger: the special version of the type II functional response used by DiNuzzo and Griffen (following Abrams and Ginzburg 2000) should lead to exactly the same time-to-IFD and the same consumer distribution over patches as their type I functional response (see part 3 of our electronic supplementary material Netz et al. 2021). We were therefore surprised that our figure 6.1B does not exactly match with figure 3 in DiNuzzo and Griffen (2020): it generally takes 100 time steps longer to reach the IFD. Re-running the scenario underlying figure 3 in DiNuzzo and Griffen 2020 with their own published NetLogo code, we did obtain an exact replicate of our figure 6.1B. We conclude that DiNuzzo and Griffen must have used a different version of their simulation program to produce their figure 3.

In addition, the simulation program in DiNuzzo and Griffen (2020) produces a substantial bias in reported time to reach the IFD. Each simulation run stops once movement has ceased for 50 time steps, assuming that this is a clear indication that the IFD has been reached. The problem is that movement can cease for 50 time steps even in situations where the population is still far from an IFD (fig. 6.2a). This easily happens in populations with a large proportion of highly inactive individuals. the lack of movement may just reflect the reluctance of these individuals to move (rather than having reached a habitat with maximal intake rate, where movement is no longer necessary). Figure 6.2 shows two replications of figure 4E in DiNuzzo and Griffen (2020), one with the published NetLogo code (fig. 6.2B) and a second with an improved version (see our electronic supplemen-

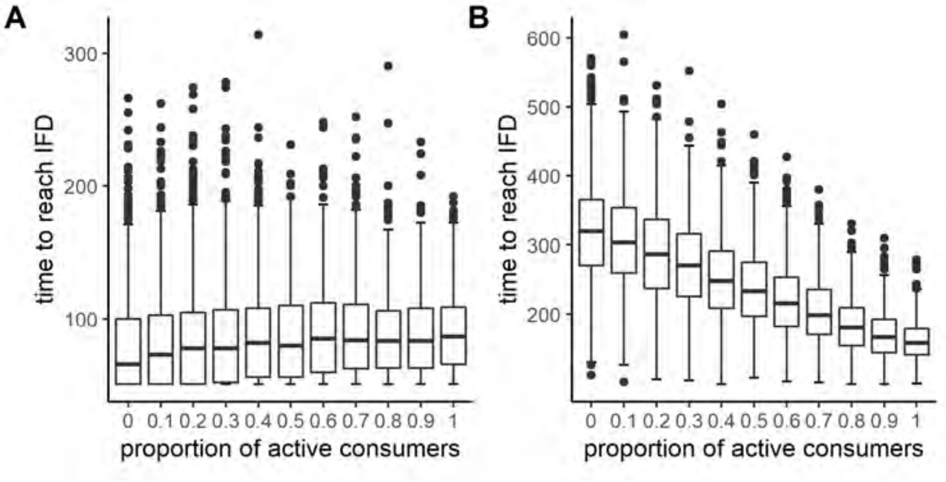

Figure 6.1 | Replication of DiNuzzo and Griffen's electronic supplementary material fig. S1 (A) using their original NetLogo code and (B) using a corrected version of their code. Both panels show the time to reach the ideal free distribution (IFD) for various proportions of'active'(80% activity) and'inactive'(20% activity) consumers with a type II functional response in 1000 replicate simulations. According to DiNuzzo and Griffen's NetLogo code, the time-to-IFD increases with the proportion of active consumers. A corrected version of the code (see our electronic supplementary material, Netz et al. (2022) for details) yields the expected pattern of decreasing waiting times with increasing proportions of active consumers.

tary material; Netz et al. 2022) where DiNuzzo and Griffen's stopping criterion is replaced by a check whether the IFD has indeed been reached (fig. 6.2C). It is obvious that the stopping criterion has a large effect on the simulation outcome. Notice that neither outcome shows the puzzling 'hump' of figure 4E in DiNuzzo and Griffen (2020). As we produced figure 6.2B with DiNuzzo and Griffen's published NetLogo code, we have to conclude again that a different version of their simulation program was used to derive their figure 4E.

A more detailed account of the technical issues reported above (and some additional issues) and corrected versions of the NetLogo program can be found in our electronic supplementary material (Netz et al., 2021).

6.3. EFFECTS OF POPULATION SIZE

DiNuzzo and Griffen investigated the effect of population size on the time to reach the IFD. However, the timescale of their model implementation is quite different from a 'natural' timescale. In their simulation program, individuals make decisions sequentially, and only one individual can make a decision in each time step. As in a larger population more individuals have to take decisions, this automatically increases the time to reach a certain target distribution. Moreover, the time to reach the IFD is inflated by the fact that active individuals are restricted in their movement because they have to 'wait' for inactive individuals. For these reasons, it is more natural to use a continuous timescale, where individuals take movement decisions independently of each other, at a rate that is proportional to their activity level. This can be done in a straightforward manner, by translating the discrete-time model of DiNuzzo and Griffen into an otherwise equivalent event-based model (making use of the Gillespie algorithm, Gillespie 1976; a description and implementation of such a model can be found in Netz et al. (2021). Figure 6.3 shows how in the event-based version of the model the time to reach the IFD depends on the population size N and the proportion of active individuals. For each population size, the time to reach the IFD is, as expected,positively related to the proportion of inactive individuals. However, the event-based version of the model does not support DiNuzzo and Griffen's conclusion that the time to reach the IFD increases with population size. This only occurs for very low population densities ($N = 8$ and $N = 40$ in figure 6.3),and even in these cases, the effect is small. At higher population sizes, the time to reach the IFD decreases with population size: as shown in figure 6.3, the IFD is reached much faster in a population with N=1000 individuals than in any of the smaller populations. This can be explained as follows. In the case of the low population sizes considered by DiNuzzo and Griffen, the initial density of individuals is very low (typically only one individual per patch). In such a case, an individual can only improve its intake rate by moving to a more profitable patch. In case of a large population size (and a higher initial density per patch), there is an additional option: if an individual on a patch decides to leave in order to improve its intake rate elsewhere, all remaining individuals on that patch profit as their intake rate increases due to alleviated within-patch competition (see Wolf et al. 2008). This effect is not addressed by the study of DiNuzzo and Griffen, although the authors state, 'in most natural systems, there are many more consumers than patches'.

6.4. QUANTIFYING THE APPROACH TO THE IFD

DiNuzzo and Griffen conducted their study in order to investigate whether personality differences can explain'undermatching', the commonly observed phenomenon that high-resource patches tend to be relatively under-exploited, while low-resource patches are relatively over-exploited. Yet, they devote only one figure (their fig. 2) to this phenomenon. In general, they quantify deviations from the IFD by measuring the time to reach the IFD. This measure has at least three disadvantages. First, 'time-to-IFD' is determined by the last individual that moves

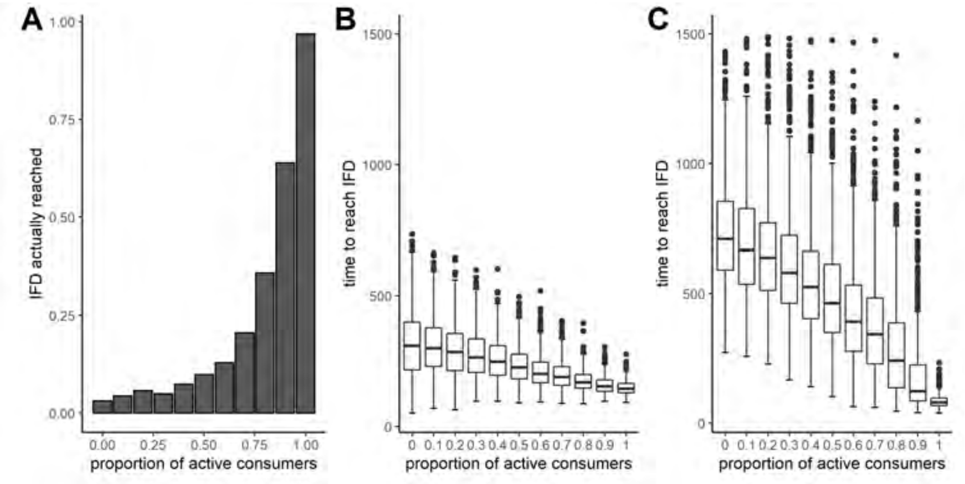

Figure 6.2 | Systematic bias in outcomes due to premature termination of simulations. The NetLogo code underlying the simulations in [1] assumes that the IFD is reached after 50 time steps of inactivity. **(A)** The proportion of simulations that have actually reached the IFD after 50 time steps of inactivity in the scenario underlying fig. 4E in DiNuzzo and Griffen (2020). **(B)** Replication of fig. 4E, using DiNuzzo and Griffen's NetLogo code. **(C)** The same set of simulations for an improved version of the NetLogo code, where a simulation now stops when the IFD is actually reached. In all simulations, 'active' consumers have an activity level of 90% while 'inactive' consumers have an activity level of 10%.

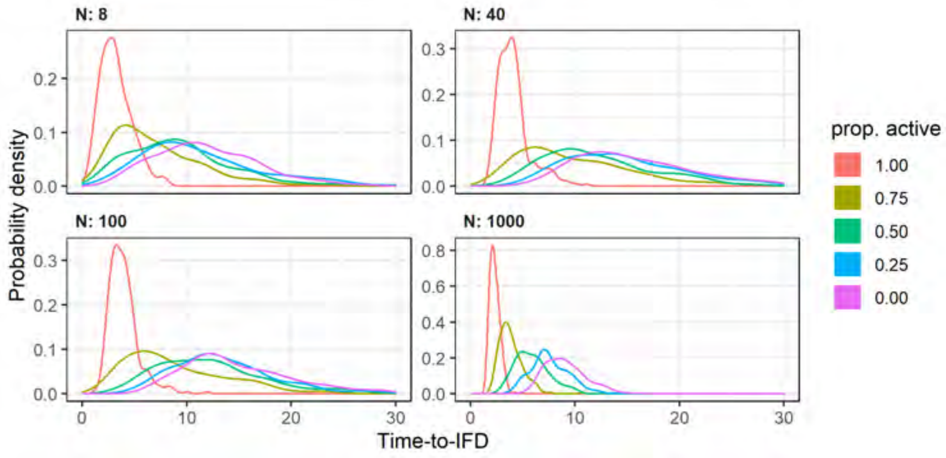

Figure 6.3 | Probability distributions of the time until the ideal-free distribution is reached, based on 1000 replicate simulations per setting. In a system with 49 habitat patches, the panels show how the time to reach IFD depends on the proportion of 'active'(movement rate 0.8) and 'inactive'(movement rate 0.2) individuals for four population sizes, N.

to a patch with an optimal intake rate. In other words, a single individual with very low activity can have a very large effect on the time-to-IFD. Second, 'time-to-IFD' depends on the initial conditions; it takes longer to reach the IFD if the initial spatial distribution of individuals differs a lot from the IFD. Third, 'time-to-IFD' is only a sensible measure when the IFD is actually reached. This, however, will only be the case in highly standardized simulation models with a fixed resource distribution. As stated by DiNuzzo and Griffen: 'In most systems, the IFD is a moving target owing to temporal environmental variation and directional change (i.e. habitat degradation)'. In section 1.5 of their electronic supplementary material, DiNuzzo and Griffen show some simulation results for a scenario with temporally varying patch quality. Surprisingly, 'time-to-IFD' is also used for this scenario (their electronic supplementary material fig. S2), where it is difficult for us to understand how the IFD can ever be reached in the case of rapid environmental change. How can movement cease for 50 time steps (the criterion for reaching the IFD) if the distribution of patch qualities changes completely every 10 or 20 time steps? Under such changing conditions, we would advocate using a more robust, population-level measure for deviations from the IFD, such as the variance in intake rates across patches.

6.5. ANALYSIS OF THE MUD CRAB SYSTEM

We are puzzled by the fact that DiNuzzo and Griffen revert to a simple calculation of activity ratios in their analysis of the refuge use data on the mud crab, *Panopeus herbstii* (Toscano et al., 2014), instead of taking advantage of their individual-based model. The model becomes necessary because such a simple calculation does not suffice, as it ignores the distribution of personality in the population. Hence, their figure 5 illustrates the influence of personality on the IFD only in the sense that no single crab is 'ideal' in immediately leaving its refuge and moving to the patch with highest profitability, but not the implications of the distribution of activity levels in the population. Additionally, the data come from a special (predation cue) treatment, not from standard conditions, and the crabs differ substantially in size (actually body size is used as a proxy for activity level) and accordingly also in their resource needs and competitive abilities.

6.6. OUTLOOK

We have the impression that DiNuzzo and Griffen view 'personalities' mainly as (maladaptive) deviations from optimal or efficient behaviour. By contrast, many studies show that personality variation is often shaped by adaptive evolution (Dall et al., 2004; Wolf et al., 2007; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010; Luttbeg and Sih, 2010; Bergmüller and Taborsky, 2010; Wolf and Weissing, 2012). For example, Wolf et al. (2008) demonstrate that 'inactivity' (called 'unresponsiveness') may be viewed as an efficient strategy in achieving a high foraging success and approaching an IFD. An adaptive perspective on personality variation leads to novel eco-evolutionary questions regarding the interplay of individual behavioural variation and the spatial distribution of foragers. The IFD is a prototype example of a model linking ecology (the spatial distribution of foragers) to evolution (optimal or evolutionarily stable movement decisions). Future research is needed to reconcile the IFD with the eco-evolutionary causes and consequences of personality for at least two reasons: first, the IFD model presupposes that the resource intake rate is a proxy for fitness (Tregenza, 1995). But how, then, can different personality types persist at stable proportions, when inactive individuals consistently achieve a lower intake rate than their more active conspecifics? Second, a personality perspective may change what spatial distribution is optimal. In animals, differences inactivity are usually associated with (adaptive) differences in energy metabolism (Careau et al., 2008). When foraging individuals differ in energetic expenditure, they should not take maximizing the intake rate as their sole guiding principle (Campos-Candela et al., 2019). In other words, individuals differing in activity should use different decision rules, and the optimal behaviour of a polymorphic population may, even at equilibrium, deviate considerably from the IFD of a monomorphic population.

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7

RESPONSE MODE BORDERS, EVOLUTIONARY TIPPING POINTS AND EXTINCTION RISK

A comment to Botero et al. (2015)

Christoph Netz

7.1. OVERVIEW

How populations adapt to different temporal regimes of change is an important question for evolutionary biologists. Botero and colleagues (2015) used individual-based simulations to investigate the evolutionary responses of populations to different regimes of temperature change. They report 1) the consistent evolution of response modes, such as plasticity or adaptive tracking, under different regimes of environmental change, and 2) the occurrence of extinction when the borders between different response modes are crossed via a change of the environmental regime. I reimplemented their model and could replicate their overall findings. The consistent evolution of response modes can be straightforwardly explained by the measured fitness of response modes across the parameter space of environmental regimes. The second finding with regards to where extinction occurs and what role the response mode borders play deserves some closer scrutiny and clarification. We find that response mode borders do not in and of themselves present a heightened risk of extinction. If a change in environmental regime brings a population at risk of extinction, the potential for evolutionary rescue is however plausibly lowered if the nearest viable phenotype consists of a wholly different response mode rather than lying within the current response mode. Thus, if response mode border and extinction threshold are crossed simultaneously, a ‘tipping point in evolutionary rescue potential’ may occur. To determine these points, both the viability of single response mode strategies and the borders between alternative strategies need to be determined.

7.2. INTRODUCING THE MODEL

The model of Botero and colleagues considers a population of individuals living in an environment that is characterised by the frequency of environmental change and the predictability of the current environmental state. Thus, the environment can change at different rates ranging from fast to slow and can be predicted via a cue that ranges from being entirely unreliable to being strictly correlated. Individuals achieve a high fitness if their phenotype matches the environmental condition throughout their lifetime. The phenotype is determined by an evolving response strategy; these strategies can be classified into five different ’response modes’: 1) Adaptive tracking, where individuals have a fixed phenotype, and the population tracks the environment via evolutionary change, 2) Diversifying bet-hedging, where individuals have fixed phenotypes during their lifetime, but offspring are allocated stochastically across alternative phenotypes, 3) Conservative bet-hedging, where individuals have a fixed phenotype, that lies at an intermediate value of (typically fast) environmental oscillations, 4) Irreversible, or developmental plasticity, where individuals adapt their phenotype at the beginning of their lifetime in response to an environmental cue, and 5) Reversible plasticity, where individuals adapt their phenotype within their lifetime in response to a cue provided by the environment. The plastic response strategies incur a cost on the individual. Response strategies are further defined by parameters specific to each response mode, which are subject to evolution (e.g. the frequency at which the phenotype is updated based on cues in the case of reversible plasticity, or the proportion of the two morphs in the case of diversifying bet-hedging). The conceptual distinction between conservative bet-hedging and adaptive tracking lies solely in the evolutionary dynamics of the phenotype, which in the case of adaptive tracking follows the changing environment, but in the case of conservative bet-hedging remains static at an intermediate value of a rapidly oscillating environment that produces stabilizing selection. In both cases however phenotypes are simply determined through a single gene. The difference between irreversible and reversible plasticity lies in the rate, at which phenotypes are updated, and the two also differ in the cost of plasticity they incur. Broadly, we can thus distinguish between three major response modes, which are adaptive tracking, diversifying bet-hedging and plasticity.

The parameter space of environmental conditions runs from zero predictability, where cues are uninformative, to perfect predictability, where cues give a reliable indication of the environment, and from fast environmental fluctuations that occur within the lifetime of individuals, to slow change that occurs over several hundred generations. The mismatch between an individual's phenotype with its environment is measured at different timepoints during the lifetime of an individual as the absolute difference between environment and phenotype, $M_{i,t} = |E_t - I_{i,t}|$. An individual's lifetime payoff, hereafter called fitness, is then calculated as $W_i = exp\left(-\tau \sum M_{i,t}\right)$; τ is a constant determining how steeply fitness decays with mismatch. Additional costs are substracted for strategies that employ reversible and irreversible phenotypic plasticity, respectively. The next generation is then generated in a weighted lottery based on these values (for details see Botero et al. 2015).

7.3. RESPONSE MODE EVOLUTION

Botero and colleagues could show that response modes evolve with remarkable consistency in different parts of the environmental parameter space (fig. 2 in the original paper). Adaptive tracking is observed to evolve at the lowest rates of change, independent of cue predictability, whereas developmental and reversible plasticity occur in intermediate and rapidly changing environments when pre-

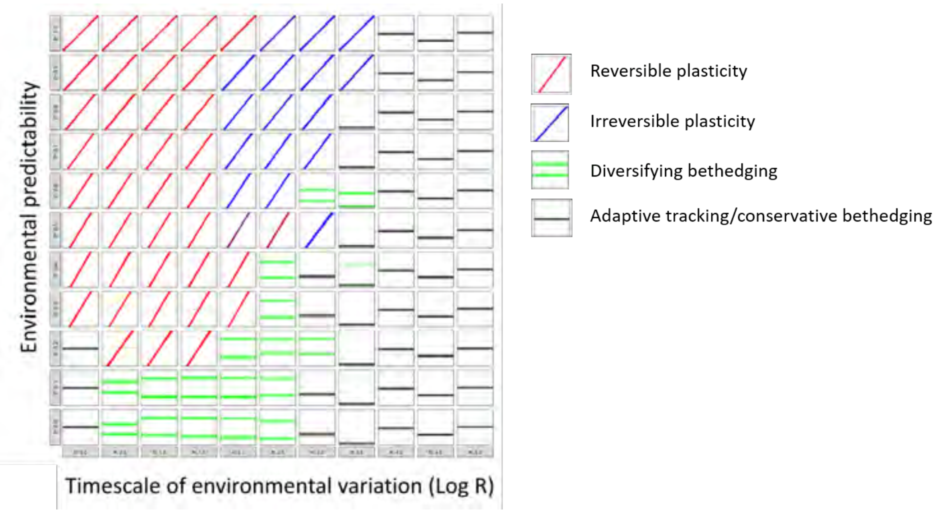

Figure 7.1 | Evolution of adaptive response modes. Evolved response modes occur in clearly delineated regions in the parameter space of environmental predictability and the timescale of environmental variation. Shown are the results of a single simulation of our reimplementation. Each population was allowed to evolve for 5,000 generations at a fixed size, under environmental regimes as defined by environmental predictability and the timescale of environmental variation.

dictability is high. Conservative bet-hedging occurs where changes are rapid and unpredictable, and diversifying bet-hedging covers the middle ground between fast and slow-changing environments when predictability is low.

Based on the model description of Botero et al. (2015) alone, I reimplemented their model and could confirm these results (fig. 7.1). What causes this pattern of distinctive adaptive response modes? Evolution is not frequency-dependent in these simulations, and reproduction is asexual. If sufficient phenotypic variation is introduced by mutations, it may therefore be suggested that populations evolve to the adaptive response mode that in the long term yields the highest fitness. This hypothesis was checked by running further simulations in which the response strategies were restricted to a single of the major three response modes, adaptive tracking, diversified bethedging and plasticity. The plastic strategies were restricted to update their phenotype at every timestep; this choice was made because the additional costs incurred by such a strategy compared to a irreversible plasticity strategy are quite low (=0.05). All other response-mode specific parameters were allowed to evolve for 50,000 generations, after which the fitness was recorded over a time frame of 1,000 generations. Such an extended timeframe was used to ensure that populations experience a sufficient range of environmental conditions, and are not performing well just because phenotype

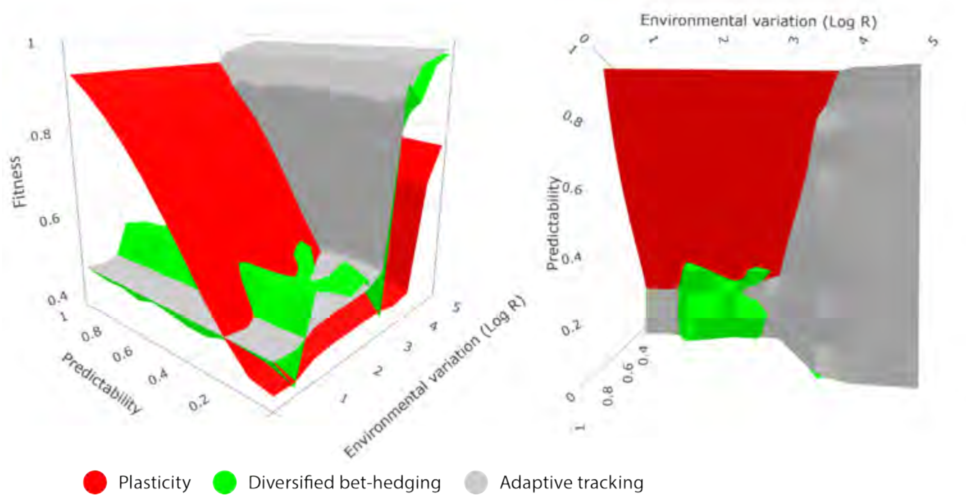

Figure 7.2 | Performance of the three main response modes under different combinations of environmental variation and predictability. Plasticity is shown in red, adaptive tracking in grey and diversifying bet-hedging in green. Simulations were run for each response mode over 50,000 generations for predictability between values of 0 and 1 in increments of 0.1 and for the timescale of environmental variation ($\log_{10}(R)$) between values of 0 and 5 in increments of 0.5. Fitness was subsequently measured and averaged over 1,000 generations.

and environment happen to coincide. Each adaptive response mode can thus be assigned a level of average fitness under a given environmental setting (fig. 7.2). If populations indeed evolve to the response mode that yields the highest fitness, the freely evolved response strategies should coincide with the response mode that performs best at a given parameter setting. Looking from above on figure 7.2, we recover almost exactly the pattern observed in figure 7.1. The evolved adaptive response strategies observed in figure 7.1 thus by and large fall into the optimal response modes of each parameter combination in figure 7.2.

Three brief observations with regards to these results: First, because a constantly updating plasticity strategy was chosen as representative of the plastic response mode in general, the slope with regards to environmental variation at perfect predictability is zero. In the unconstrained simulations, developmentally plastic response strategies at an intermediate speed of change would enjoy a somewhat higher fitness than shown here. The intersection between plasticity and adaptive tracking would therefore lie a bit higher and to the right, and the whole red plane would fall off gently to the left. Secondly, at perfect predictability and slow change the maximum fitness of plasticity lies below the one of adaptive tracking. This difference is the sole consequence of the costs applied to plastic strategies. Such costs could be natural, but where absent, plastic response modes will be equally suitable as adaptive tracking under slow change and high predictability. Third, The frequency of environmental variation R is considered at rather large increments of $\log_{10}(R) = 0.5$, i.e. change by a factor of $10^{0.5} \approx 3.2$. Simulations performed at finer resolutions showed that the consistency of evolutionary outcomes vanishes at the borders between two response mode regions (as also noticed by Botero et al. 2015).

7.4. EXTINCTION AND EVOLUTIONARY TIPPING POINTS

In the second part of their study, Botero and colleagues consider what happens if populations are shifted from the environmental regime under which they evolved into novel environmental regimes that were never experienced before. In the new environment, and in contrast to before, population sizes are flexible and extinction becomes a possibility. The offspring number is drawn from a Poisson distribution with mean $q_i * W_i / W_{max}$, where W_i is calculated as before, W_{max} is the theoretically possible phenotypic optimum, and q is a scaling factor that translates relative fitness into expected number of offspring.

Extinction is reported to occur due to at least two different phenomena: First, extinction can occur during transitions into parameter regions that are particularly challenging for any response mode, where even resident populations may go extinct. Secondly, extinctions can occur when a population is shifted across the border between adaptive response mode regions and cannot adapt rapidly enough due to the extensive genetic changes that separate different response modes.

This second finding is discussed by Botero and colleagues in terms that might suggest that the crossing of a response mode border poses an intrinsic extinction risk. They for example write that

> “The boundaries between response mode regions in our model correspond to evolutionary tipping points, where even minor changes in environmental parameters can have dramatic and disproportionate consequences on population viability.” (Botero et al. 2015, p. 184)

The crossing of a response mode border by itself however merely signifies the presence of a better alternative phenotype, and as such cannot create a risk of extinction. The intersection of fitness planes of two alternative response modes is independent from where a response mode becomes threatened with extinction, as further illustrated below.

Let us assume that evolutionary change *within* each response mode occurs much faster than changes *between* response modes, and further that the fitness landscape of each response mode has a single global optimum. Assuming that populations always lie at the phenotypic optimum of their current response mode, we can regard each response mode as a single strategy with its performance being a function of the environmental conditions. The intersection of the fitness functions of two such strategies constitutes the response mode border. In contrast, and assuming that evolutionary rescue via a change in response mode is not possible, the extinction threshold lies where the expected number of offspring of the response strategy drops below one. This is shown conceptually in figure 7.3 at the example of adaptive tracking and developmental plasticity. Response mode borders and extinction thresholds will coincide, wherever the fitness of one strategy descends steeply, crossing both extinction threshold and alternative response mode, or if the fitness function of one strategy runs in parallel and close to the extinction threshold. Importantly, however, there is no direct causal link between response mode borders and extinction thresholds. The extinction threshold in Botero et al.'s model is determined by a parameter q, which turns a relative fitness measure into expected number of offspring. The extinction threshold can therefore be varied at liberty, which is also demonstrated in figure S6 of the original study by Botero and colleagues. Any coincidence of response mode border and extinction threshold is thus a matter of how q is chosen, and there is no reason to believe that populations might be more sensitive to environmental changes close to the response mode borders than anywhere else.

The independence of response mode border and extinction risk can also be seen from the patterns of extinction observed when populations of different origin are dislocated across the parameter space. In contrast to Botero et al. (2015), who shifted populations only between neighbouring parameter conditions, I shifted evolved populations across the whole parameter range. We observe that, while extinction may locally coincide with the borders of response mode regions, e.g. between adaptive tracking and plasticity ($R = 3.5, P = 0.7, 0.8$), the pattern of extinction for a given response mode does not follow the response mode borders, but rather the shape of the performance planes in figure 7.2: Where the response mode border between adaptive tracking and plasticity turns right with increasing predictability, the extinction threshold for all populations following an adaptive tracking strategy runs strictly parallel to the y-axis (fig. 7.4). This makes sense: Adaptive tracking, in the absence of any influence of the response mode border, is left unaffected by predictability values and only depends on the rate of change.

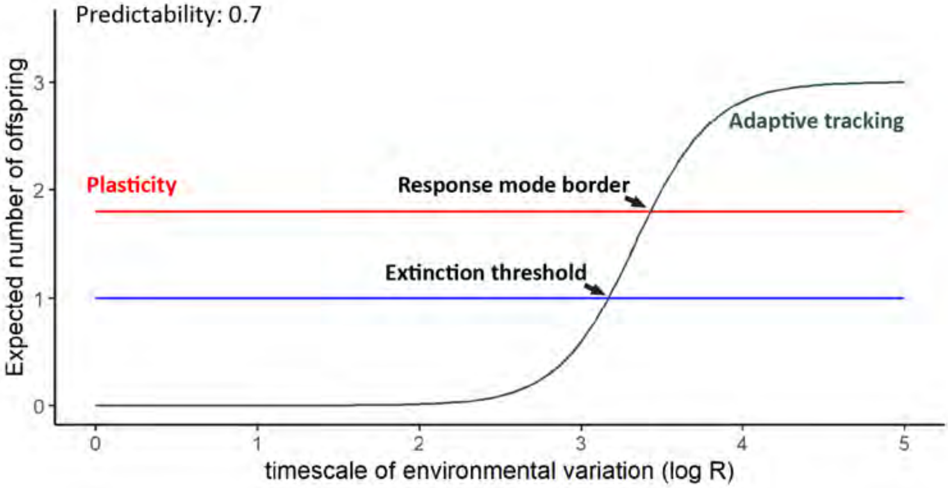

Figure 7.3 | Schematic fitness functions of plasticity (red) and adaptive tracking (grey). Extinction occurs below the blue line, when reproduction drops below 1. The extinction threshold therefore constitutes the intersection of adaptive tracking with the blue line, whereas the response mode border lies at the intersection of plasticity and adaptive tracking. Each of the three lines can be altered independently through corresponding parameters. The shown functions roughly correspond to a transect of fig. 7.2. at predictability $P = 0.7$.

7.5. TIPPING POINTS IN EVOLUTIONARY RESCUE POTENTIAL

Response mode borders by themselves therefore do not pose an extinction risk. The point that Botero et al. drive at may however be a subtler one. If a population is dislocated into a new environment, and now is under threat of extinction, the potential for evolutionary rescue is much higher if the next viable phenotype lies within the same response mode than if it lies in a different response mode that can only be reached through substantial genetic modifications. In other words, if response mode border and extinction threshold are both crossed at the same time, there may be a tipping point in evolutionary rescue potential. In contrast, if a population temporarily crosses the extinction threshold, but evolutionary rescue within the current response mode is possible, there is no such tipping point, and extinction is ultimately much less likely. This latter scenario is not visible in figure 7.3, because it only shows the optimal strategy of each response mode, and thereby assumes evolutionary rescue within response modes. If we substitute the term ‘tipping point in evolutionary rescue potential’ for ‘evolutionary tipping point’, the interpretation of what Botero et al. (2015) wrote becomes much clearer. Response mode borders correspond to tipping points in evolutionary rescue potential if and only if an extinction threshold is crossed at the same time.

7.6. CONCLUSIONS

To anticipate the consequences of environmental change on population viability, it is of primary importance to focus on individual response modes and where their expected reproduction drops below one. It is not possible to determine extinction risks from response mode borders alone. However, if response mode borders and extinction thresholds coincide with each other, the potential for evolutionary rescue may be considerably reduced, and determining where these ‘tipping points in evolutionary rescue potential’ lie may be important to predict the capacity of different populations to adapt to environmental change.

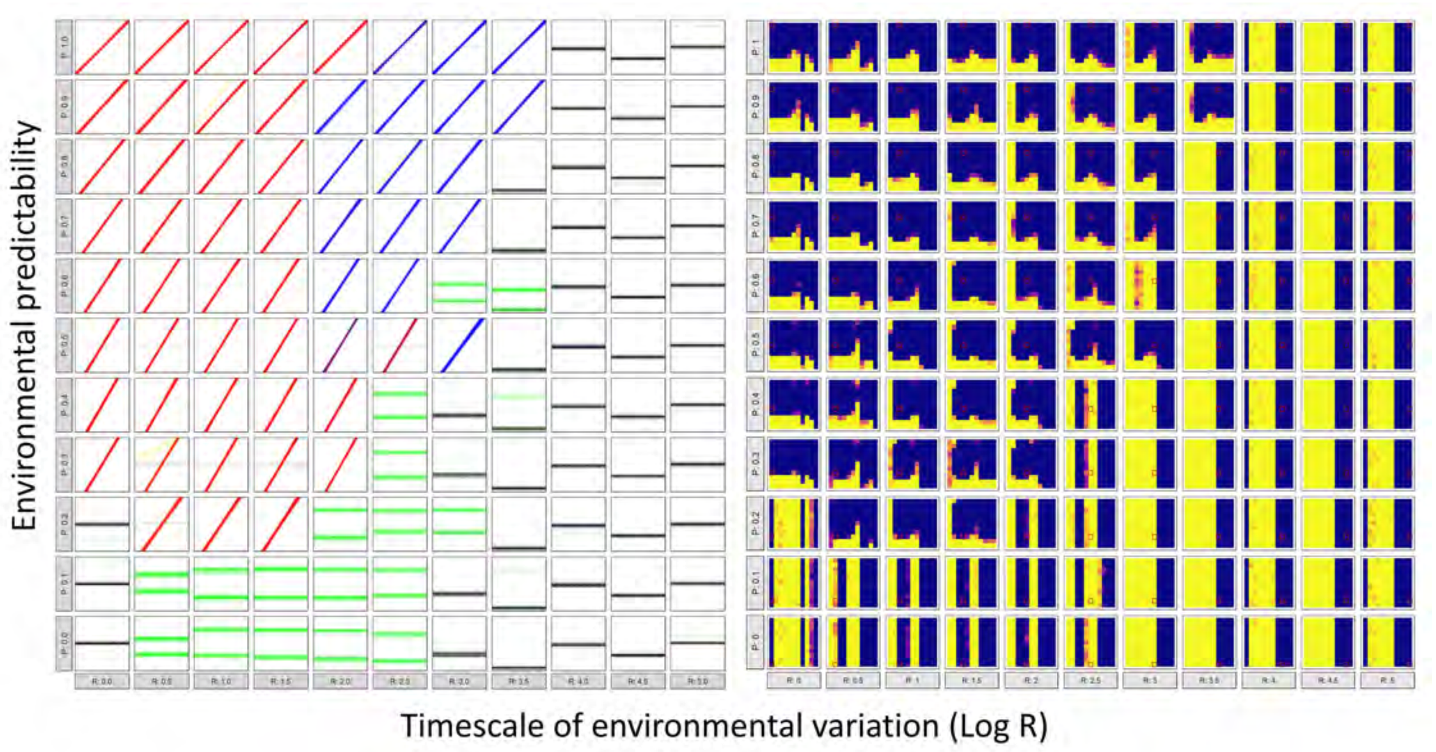

Figure 7.4 | Response modes (left) and patterns of extinction (right) as simulated by Botero et al. (2015). Response modes follow the same colour code as in the original plot: Adaptive tracking/conservative bet-hedging (black), phenotypic plasticity (red), developmental plasticity (blue), and diversifying bet-hedging (green). The right plot shows each of the evolved populations on the left transferred to all other parameter regimes, extinction frequency is indicated by colour running from zero (blue) to one (yellow), measured over 10 replicate translocations. The original parameter combination is marked with the red square. Response mode borders on the left do not coincide with patterns of extinction on the right: The extinction boundary for adaptive tracking runs strictly parallel to the x-axis, rather than showing any kind of slope as the adaptive response mode borders. At high predictabilities, the response mode border does not coincide with the extinction threshold.

CODE AVAILABILITY

Simulation model code and data analysis is available on Github:

`https://github.com/christophnetz/ann_tipping_points`

ACKNOWLEDGEMENTS

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8

GENERAL DISCUSSION

The Indian subcontinent used to be home to one of the largest vulture populations worldwide. In the 1990s, however, a mysterious collapse occurred, reducing one of the most abundant birds of prey, the white-bellied vulture, to the brink of extinction (Prakash et al., 2003). Populations decreased by 99 %, and the sudden collapse had rippling effects: Stray dog populations increased, and so did the prevalence of rabies. Black kites rose dramatically in number and today are India's most common raptor. In 2003, scientists could finally identify the culprit: Diclofenac, an anti-inflammatory agent used in veterinary medicine, proved to be extremely toxic to vultures of the genus *Gyps* (Oaks et al., 2004; Shultz et al., 2004). In 2006, India, Nepal and Pakistan banned the use of Diclofenac, and nowadays the populations of vultures have begun a slow recovery (Galligan et al., 2020).

The fate of India's vulture population shows how much our understanding of nature can hinge on minute organismic details of different species. In such cases, evolutionary theory often has preciously little to contribute. We might have expected the vultures to evolve resistance against Diclofenac due to the strong selection pressure during the population collapse. However, no such resistance has emerged, presumably because vultures do not vary much in their susceptibility to Diclofenac. Likewise, there is no recognizable evolutionary rationale for why vultures should be so incredibly susceptible to Diclofenac in the first place, since related raptors and new world vultures are largely unaffected. Without venturing into the molecular mechanisms, the vultures' susceptibility to Diclofenac thus seems entirely idiosyncratic. Ecology and evolution are full of such details at various levels of organization, and this makes the development of strong predictive models very difficult, if not impossible. The role of models in ecology and evolution is therefore often to explore select scenarios that may give us a sense of what is possible in nature.

One of the main motives of my PhD was that models should be simple, but not too simple, and that many models in evolutionary biology might fall into the latter category. Mechanistic details can be greatly influential towards natural processes, as the story of the vultures exemplifies. I thus tried over different instances to develop more comprehensive models by including certain details that are usually left out. If details matter, they must do so in a non-generalizable way, and thus no global pattern emerges from these efforts except maybe in that model behaviour becomes more varied, and certain concepts become increasingly ambiguous. In the following, I will first discuss the chapters of this thesis individually, followed by some thoughts on the methodology of individual-based models in evolutionary biology. I close with some considerations of a general nature with respect to the relation between evolutionary theory and biological mechanism.

EVOLUTION OF MOVEMENT BEHAVIOUR

In the first two chapters, I explored the evolution of movement strategies. The spatial extent of populations is frequently ignored in theoretical models but can be shown to have wide-ranging effects on ecological and evolutionary processes. The spatial distribution of individuals is however also shaped by their movement behaviour, a product of evolution. In the tradition of eco-evolutionary dynamics, we can thus jointly consider the spatial distribution of individuals and the evolution of movement strategies.

Chapter 2 considered the coevolution of movement strategies in predators and prey. Here, we could show that evolution does not assume a stable equilibrium, but repeatedly gives rise to novel, innovative movement strategies that spread and take over the population. This not only changes population dynamics, but also the spatial distributions of resources, prey and predators. Distinctive ecological patterns that emerge are spiral waves, static spots of different sizes, and intermittent periods of homogeneously mixed populations. Working on chapter 2 was particularly interesting and challenging. Due to the enhanced degrees of freedom along which ecological and evolutionary dynamics occur, this model almost develops a life of its own. The rich internal dynamics has the potential to provide genuine surprises, such as the sit-and-wait predation strategies that were observed or the herbivores following behind the predators in their every step. These examples express the creative quality that is so characteristic of evolution by natural selection (Lehman et al., 2020). Models like these probably resemble the reality of nature much better than simple models that focus on certain phenomena in isolation. At the same time, analysing such a model, teasing apart the different components and identifying the key mechanisms is tremendously challenging, and a comprehensive account of possible behaviours is near-impossible. I think models of this kind hold important lessons on how to piece together the simpler models that guide our understanding, but there is also a risk to get lost in them and arrive at unwarranted conclusions.

The second project of this kind, presented in chapter 3, investigates a producer-scrounger system, where some individuals forage for items, and others attempt to steal from them. This occurrence of so-called kleptoparasitism influences the movement strategies, spatial distributions and resource consumption of the population. The comparison between simulations, where kleptoparasitism can be either obligate or facultative, is particularly instructive: Resource intake is overall much lower under obligate kleptoparasitism, but obligate kleptoparasites are only viable in a small parameter range of resource growth, compared to facultative kleptoparasites that occur under a broader set of conditions. The former also tends to produce spatial dynamics akin to a reaction-diffusion system, when local dispersal is incorporated, while the latter does not. Expanding these simulations to also include population dynamics as in chapter 2 would be a very interesting direction of future research.

The way movement strategies were implemented in these models resembles the method of step-selection analysis that is used on empirical datasets in movement ecology (Fortin et al. 2005, see Gupte 2022 for a more extensive discussion). Our models of movement strategy evolution could therefore be of some interest to movement ecologists who might wish to explore the evolutionary processes giving rise to different movement strategies and individual variation observed in nature. Indeed, the ability to model individual variation without any assumptions with regards to its distribution is one of the major strong suits of the evolutionary individual-based modelling approach applied in these two chapters.

Both projects give us insights into the evolution of movement strategies and the eco-evolutionary dynamics of the spatial distribution between predators and prey, and competitors of different strategies, respectively. It should be pointed out however, that while our models specify the genetic basis of movement strategies, these assumptions are not based on currently available knowledge of any particular organism. One of the conclusions from these models is that mechanisms matter, but as long as the genetic, developmental and cognitive basis of movement and foraging behaviour is in the dark, such models have to be interpreted with care and recognition of their preliminary character.

COMPETITIVE ABILITY

Foragers may often differ in their ability to compete over limited resource shares, and these interactions can influence their spatial distribution on a resource landscape. The question of how they will be distributed if all foragers maximize their intake has been the subject of extensive treatments in the ideal free distribution literature (Tregenza, 1995). If foragers earn resource shares as weighted by their competitive ability, the equilibrium condition allows for a range of equilibrium configurations, where individuals of different competitive ability may freely intermingle. In chapter 4 I could show however that the patch choice decisions made by individuals in approach to the equilibrium distribution differ markedly as a function of their own competitive ability, and thereby leads to spatial assortment. The larger the number of patches between which individuals choose, the stronger this effect of spatial assortment becomes. Further, if foragers move onto the patches from the outside, spatial assortment is stronger than if foragers are initially distributed randomly over the patches.

Spatial assortment also has implications for the original presence of unequal competitors. We incorporated the habitat choice model into an evolutionary simulation, where competitive abilities are allowed to evolve. Under static environmental conditions, the population evolves towards a single equilibrium, but when spatiotemporal variation is incorporated, a large number of disparate morphs emerge via successive branching events. This is because weak competitors come to occur on resource-poor patches with less intense competition. As the environment changes, the good patches on average become worse, and the bad patches on average improve. This produces a temporary advantage for weak competitors, while the foragers redistribute, and is what causes the repeated branching events. Thus we show that 1) spatial assortment occurs where it is not predicted based on equilibrium conditions, and 2) spatial assortment together with environmental variation drive the differentiation into a number of competitive morphs, where weak competitors can coexist with strong competitors, despite being consistently disadvantaged at equilibrium distribution.

The model is an idealization in two important respects. First, we assumed that all patches have an equal chance to be of a certain quality, and that the resource levels prior to an environmental change are independent of the resource levels thereafter. If there are intrinsic differences between patches which are stronger than the temporal variation within patches, the advantage of weak competitors would be considerably reduced. Second, just as in the two previous models, we considered only asexual reproduction. There is no doubt that the details of sexual reproduction could affect the conclusions drawn from any of these models. The reason to primarily consider asexual reproduction is twofold. First, introducing sexual reproduction would force us to make a host of additional assumptions of uncertain validity. We simply do not know how competitive ability or movement strategies are encoded at the level of the genome, or whether not maternal effects and cultural transmission could prevail over genetic factors. Secondly, asexual reproduction is arguably the simplest reproductive system to consider, and this simplicity allows us to study the mechanism of interest in relative isolation without immediately superimposing other layers of considerable complexity. The understanding of each process in isolation may then also enable the prediction of how they intersect. In principle, a mechanism of spatial assortment such as the one described in this chapter could also contribute to assortative mating.

THE FORCE OF SELECTION DURING EARLY LIFE

A central concept in the evolutionary theory of ageing is Hamilton's force of selection. The important insight of Hamilton was that the strength of evolution over different age classes does not act on reproductive values, but on the growth rate (Hamilton, 1966). The force of selection thus consists of the selection gradients on survival probability across different age classes. In the typical age-structured models, the force of selection remains constant until individuals reach the age of maturity, and thereafter monotonically decreases. If individuals however depend on each other, e.g. via energy transfers and helping behaviour, the force of selection may behave rather differently, as was first demonstrated by Lee (2003). In chapter 5 I could show by means of a simple analytical model, that the force of selection always increases for as long as offspring depend on their parents. When offspring become independent, the force of selection remains constant until the age of first reproduction is reached. These results have to be seen in the context of the work of Baudisch (2005), who showed that the force of selection can plausibly be considered at different scales of phenotypic variation, depending on the mechanisms that underlie the latter.

An increase in the force of selection during periods, in which offspring depend on their parents, may explain the commonly observed pattern of decreasing mortality rates during early life in two different ways. First, deleterious mutations can accumulate more easily during early life stages, when the force of selection is weak, than at later life stages, when the force of selection has increased. This is the mutation accumulation hypothesis of ageing, even though it here occurs during the first life stages. Secondly, mutations that negotiate a mortality trade-off between different life stages are selected for when they shift mortality to earlier life stages. This is analogous to the antagonistic pleiotropy theory of ageing, which is based on the same mechanism operating in the opposite direction post-maturity, when the force of selection decreases over consecutive age classes.

The simple analytical framework used in this chapter assumes that adults only have a single offspring at a time. This will of course not be true in species with many offspring in a single clutch, or where consecutive offspring generations overlap with each other. In this case, a more complicated set of assumptions may need to be employed. Siblings can compete, but also provide help and shelter for each other, and the nature of these interactions will have effects on the force of selection. A case in which the simple model fits nature arguably quite well is human gestation, and indeed here mortality rates fall off steeply as time progresses (Levitis, 2011).

SOME COMMENTS ON METHODOLOGY

With the exception of chapter 5, all chapters of this thesis use individual-based models in one way or another. Individual-based models have a very mixed reputation in the scientific community, however, and thus an evaluation of the advantages and drawbacks seems in order. I will start with the drawbacks.

Individual-based models are studied through simulation and often entail a great number of parameters. This means that a systematic search of the parameter space is computationally expensive, and some model behaviour can be missed simply because the corresponding parameter values were not explored, or the runtime was too short. Further, individual-based models usually come in the form of expansive programs, which can be tremendously messy, opaque and prone to errors, further aggravated by the fact that many such models are produced by relative beginners to both programming and theory. For peer review, individual-based models form a particular challenge: While analytical work is usually reviewed by mathematically-literate referees, the structure and code of individual-based models can be highly idiosyncratic, and scrutiny therefore much more difficult and time-consuming (although analytical treatments may also get similarly contrived). Thus, journals and referees sometimes appear to either reject or accept complicated simulation models primarily based on the story told, and less so with regards to the validity of the model described. A lot of time could be spent on the review of already-published individual-based models. The experience of the one comment I published on this however leads me to doubt whether such work has an impact for any but the most high-profile articles.

Despite these challenges, individual-based models also have significant advantages. Individual-based models give the researcher a great amount of creative freedom, which may be used to start from conceptual ground zero and question the commonly-made assumptions of other approaches. Working with individual-based models from the beginning has taught me to persistently go back and forth between the mechanisms of nature and their representation in different models. There may be tremendous advantage in individual-based models to a) check analytical models against (Dieckmann and Doebeli, 1999; van Doorn and Weissing, 2002; Van den Berg and Weissing, 2015; Long and Weissing, 2020), b) uncover phenomena not described through analytical means (Hildenbrandt et al. 2010, chapter 2), and c) help guide our intuition and provide inspiration (Pen and Flatt 2021, the analytical work of chapter 4 was developed off the results of the simulation model, and the same is true for Qvarnström et al. 2023).

As indicated before, however, the efficient communication of such models and their connection to existing bodies of theory can be challenging. Existing theory is in large parts analytical, and it is therefore incumbent on the modeller of individual-based models to always seek the comparison with analytical work, and otherwise to reduce the presented simulation models to their minimal form, the only way in which they qualify for communication purposes.

GENERAL REFLECTIONS

At the start of this PhD, my idea was to study the coevolution of behaviours in predators and prey by means of mechanistic individual-based models. This was done first in chapter 2, where I showed that the coevolution of movement strategies leads to rapid transitions between different ecological patterns. Likewise, chapter 3 shows how kleptoparasitism within a population can affect the resource landscape and the movements of conspecifics. The weakness of these two models is the uncertainty of the mechanisms considered. Not much is known about what guides movement or foraging behaviours, and even less information exists about the genetic basis at which heritable variation may occur. These models therefore certainly give an impression of what is possible in nature, and in doing so may provide a valuable counterweight to the austere simplicity of some analytical formulations, but they do not have much claim to realism. The mechanistic details matter, but if they are unknown, models cannot get much further than exploring possibilities.

In my other two studies, I orientated myself at the simplifying assumptions commonly used in the literature, for example that individuals have an ideal perception of their environment (optimal foraging theory, chapter 4), or that genes have an age-specific effect (life-history theory, chapter 5). Assumptions of this kind will be outright false in almost any case, but they can nevertheless be constructive. First of all, by making an assumption shared with many other models, our results become more easily comparable to the existing literature. Secondly, the conscious creation of a caricature hopefully facilitates our understanding of the more complicated cases encountered in nature. By superimposing different such caricatures, we can hope to approximate nature (Levins, 1966). Four years ago, I would have argued that a) an assumption is not a good one just because it is made by many others, and indeed the risk of being wrong in a significant way thereby increases, and b) it is by no means guaranteed that we can reduce processes in nature in such a way, the whole may well be more than the sum of its parts. Today I would give the following pragmatic response. Firstly, the danger of uncritically adopting certain assumptions is admittedly a real one, particularly if one never looks beyond one's own field of research. The ubiquity of George Box's quote ('All models are wrong'; Box 1976) may give an indication that most theoreticians are aware of the fundamental problem, if not of the specific instances. We can ultimately do no better than search for the most suitable model setup for a given purpose, both through incremental improvements of existing models and the search for entirely novel perspectives. In doing so, we always need to be vigilant of the relation between assumptions made and conclusions drawn. Secondly, the whole may not be reducible to its components, but where this is the case, i.e. where efforts of reduction fail and every last detail is relevant to the behaviour of the whole, theory simply has no power.

On a more general level, the fundamental challenge of evolutionary theory seems in my eyes to be that it considers a simple process in a very complicated world. Natural selection itself is rather straightforward, but the mechanisms that underlie variation, inheritance and selection can be very intricate. Evolutionary biologists therefore need to conceptualize and simplify nature in different ways, and this works well in some cases and fails in a lot of others. Different currents in evolutionary biology specialize on select mechanisms, the importance of which they consequentially highlight, and this makes it difficult to occupy a balanced point of view. Evolutionary theory, it is fair to say, has in the past overwhelmingly focused on what is selected for, and much less on how variation occurs. This is partly because the theory of natural selection predates the knowledge of genetic and developmental mechanisms (still only known in the broadest terms beyond select model systems!), and partly because models struggle to incorporate such details while remaining analytically tractable. The lesser-known second part of the popular quote by George Box goes to says that ‘It is inappropriate to be concerned about mice when there are tigers abroad’ (Box, 1976). One has to wonder whether the pursuit of increasingly intricate frameworks in which selection operates, e.g. with regards to the evolution of eusociality, ageing or sexual ornamentation, is not turning a mouse into a tiger, while not giving sufficient due to the mechanisms under which phenotypic variation occurs. The result of a theory only built on considerations of selection, and not also on faithful representations of genetic and developmental mechanisms inevitably leads to a myopic view of evolution (Gould and Lewontin 1979; Saunders 1989; Stoltzfus 1999; Lynch 2007; see also Nijhout 1990; Newman 2002 for the related issue between genes and development). Ultimately evolutionary theory can only benefit from integrating theoretical considerations of development and genetics. A brief illustration follows.

Consider how the coat pattern of zebras might have evolved, and how it might evolve further. A slightly caricatured evolutionary theoretician might start out with the simplest conceivable genotype-phenotype encoding, a lattice, in which the colour of each cell is encoded by a single gene. The zebra is perfectly free to evolve whichever phenotype is optimal for its survival, as long as variation occurs in the right amount and selection is strong. Maybe stripes evolved to deter predators or because they serve best the purpose of deterring parasites

(Caro et al., 2014). The choice of this particular genotype-phenotype mapping has significant implications for the variation we expect to observe in populations of zebras. Namely, there should be gradual differences between zebras, some noise in the coat pattern, but nothing extraordinary. This is surely an example of so-called inappropriate atomization as referenced by D'Arcy Thompson (1942). Another scientist that emphasises mechanisms would draw from a much larger field of theory and might get the idea that stripes can easily arise in reaction-diffusion systems as discovered by Turing (1952). Reaction-diffusion systems consist of two interacting components, one of which is an activator, the other an inhibitor (Kondo and Miura, 2010). Depending on the diffusion coefficients, such systems can produce stripes, spots or some other dynamical patterns (see also the ecological patterns occurring in chapter 2). We can then still introduce considerations of selective advantages for one or the other phenotype, but the variation we are expected to observe is shaped by the identified mechanism. In a reaction-diffusion system, small parameter changes can change the occurring pattern very rapidly, for instance turning stripes into spots. As it happens, just such a spotted zebra foal was recently photographed along with its striped mother in the Masai Mara (fig. 8.1), an occurrence that would be deemed impossible under the atomic genotype-phenotype encoding.

Figure 8.1 | A baby zebra with spots in the Masai Mara National Reserve in Kenya. Patterns such as stripes and spots occur naturally in reaction-diffusion systems, and transitions between the two may be due to changes in developmental timing or altered diffusion rates of involved molecules. ©Lori Labrecque/AdobeStock.

While in some cases a focus on selection can greatly simplify our understanding of evolution, in others the same is true for considerations of the developmental mechanisms, as the example of the zebra shows. The logic of natural selection cannot replace knowledge of the mechanisms guiding development and mutation, or indeed the interactions that produce selection in the first place. Evolutionary theory thus needs to play an integrative role and draw on many different fields of research as required, even if that puts its status as a seemingly sovereign discipline at risk. In this thesis, I have primarily focused on developing individual-based models that consider interactions and environmental scenarios beyond what is ordinarily be considered by theory. Simulation-based approaches more generally provide the liberty to do the same with genetic and developmental mechanisms, and the combination of the two might be our best chance to give a comprehensive and natural model representation of evolution. To understand the evolution of organisms, we should opportunistically exploit pattern and simplicity where it emerges across the tree of life, and simulation-based approaches form an indispensable part of such a strategy.

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AFTERTHOUGHTS

Jonathan Pruitt was discovered as a fraud in January 2020,[1] and this incident became a formative moment for me as a young researcher. After the first suspicions about one of his papers became public, I started looking myself at the data of some of his other papers. But I did not discover any irregularities, for much of the same reasons that such irregularities are usually not discovered. The spreadsheets were a bit messy, and I was very unsure of my own judgement. Pruitt had already published in all the journals of rank and name and was cited over 4,000 times, generally being considered a rising star in Behavioural Ecology. I did not necessarily trust him but rather confided in my broader social and professional environment. As it turns out, scientists in groups are not as fail-proof as one might think, and rigorous scientists cannot blindly rely on the assurance of the collective. Like so many frauds, Pruitt was successful because he gave his audience exactly what they wanted. In doing so, he skilfully pandered to the preconceptions and epistemic desires of his field. The aftermath of his fraud was revealing: The most widely shared concern was that researchers would now have to spend time correcting old work, rather than publishing new papers, as they apparently are intended to. Comparatively little regret was expressed over the loss of insight, or indeed the need to re-evaluate the direction of the field. Even though highly cited, Pruitt's work seemed all of a sudden fairly insubstantial. The response by established academic institutions was disappointing. Journals took forever to retract obviously fraudulent papers and generally operated with a complete lack of transparency. The major investigative work was performed on PubPeer by a few anonymous accounts,[2] and only to a lesser extent by Pruitt's co-authors or the journals. McMaster University took over two years before severing ties with Pruitt.[3] The maintenance and review of the public record of knowledge seems to be largely abandoned by official institutions, and is now left to outsiders. Everybody else is busy cultivating their citation scores and social relations.

Consequentially, I replaced my attitude of trust for published work with a stance of general scepticism, at least within the scope of my own expertise. But of course, the extent to which one can practice such scrutiny as an individual is extremely limited, and at the end we all have to fall back onto our peers. What forces shape our current academic environment, and why is it so hard for scientists to pursue knowledge in the best way they see fit?

The first reason is that success is tremendously hard to assess in science without engaging deeply with the materials at hand. Achievements that are unambiguously valuable due to their simplicity or immediate application are rare, and particularly so in theoretical biology. Thus, scientists depend almost entirely on the evaluations of other scientists, and the sole path to influence and job security is via the endorsement of the community. Under these circumstances, people try to do science in a way that is most agreeable to the many, and conformity is legion.

The second reason is the way that competition is structured in academia. PhD students and Postdocs compete for permanent positions, and once a permanent position is acquired, supervision of such PhD students and postdocs takes up a sizeable portion of time next other tasks such as admin, teaching and fundraising. A large portion of academic output is therefore produced by relatively inexperienced researchers whose professional existence is under question. The work produced under such circumstances naturally aims first and foremost at the insurance of ones' continued professional existence, and not at making a constructive contribution or becoming a better scientist. Thus, the literature abounds with papers that regurgitate all the right catchphrases, but otherwise provide very little novel insight. The more intense the competition gets, the more scientists focus on the production of great quantities of such papers. As scientists have less time to read an increasing amount of papers, and spend less scrutiny on the papers they review or cite, the indicators of scientific quality become more superficial and unreliable, the individual scientists more disoriented, and good work less rewarding.

The third reason is that PhD students are cheap labour, and universities are politically incentivized to educate as many of them as possible. The rationale is that highly-skilled labour is in high demand, but the policy covers disciplines where industry demand as such does not exist. As a result, the professional hierarchy in academia is very steep, and has gotten steeper over the last years and decades.[4] The relatively inexperienced PhD students experience great pressure to be as productive as possible, while the professors at the top have so many students to supervise, administer and apply to grants for that the best qualified do little research of their own.

The solution I would like to propose is to restructure the professional hierarchy and the competition acting within. My suggestion would be to educate far fewer PhD students while increasing the number of permanent researcher positions below the level of the professor. PhD students would thus face less competition and better supervision, and professors could afford more time to do research themselves. The selection at each level of the professional hierarchy should largely ignore citation scores and publication lists, and instead focus on methodological competence as relevant to the respective position. Beyond the PhD level, scrutiny should go into depth of single 'best piece' papers, to be able to address issues of scientific depth and to determine what a candidate's work looks like at its best.

Under the current conditions, scientists are made to hurry and run fast in the same direction. This would make sense if we collectively knew where we are going, but in research that is usually not the case. Scientists should be given the freedom to pursue risky projects, form stable productive work relations, and generally be able to follow their own vision of what good science is. This would automatically open the door for reforms that most scientists desire, but fail to coordinate around, including greater transparency and the abolition of the 'triple-pay' publishing system.[5] After all, the people who pursue a scientific career are despite all uniquely motivated by idealism, and this is a resource not to be wasted.

NOTES

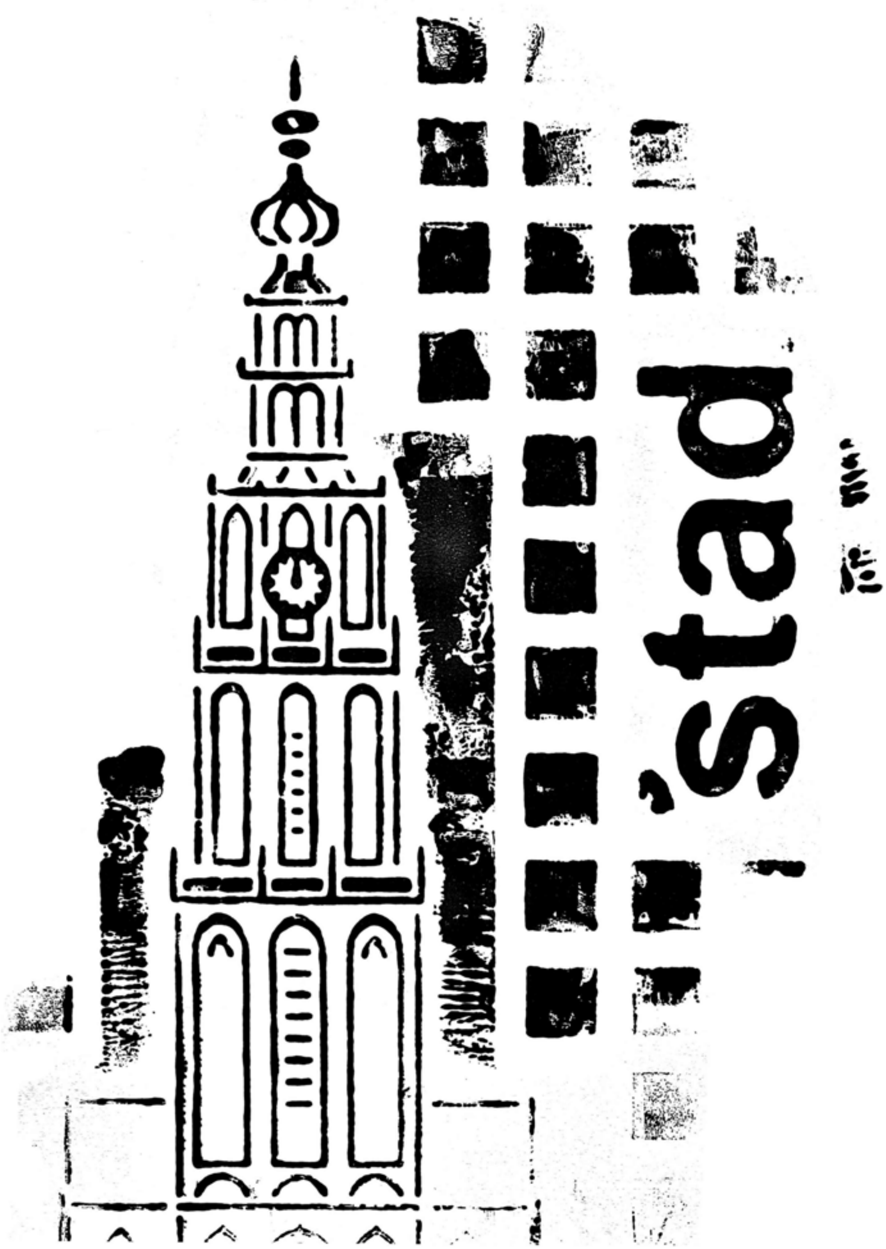
[1] *Prominent spider biologist spun a web of questionable data.* E. Pennisi, February 2020, *Science.*

[2] E.g. PubPeer user *Helianthus winteri* on Sweeney et al. (2013), *Behav Ecol* 24(5):1205-1210.

[3] *Embattled spider biologist resigns university post.* E. Pennisi, July 2022, *Science Insider.*

[4] *Tijdelijke contracten bij universiteiten in perspectief,* Rathenau Instituut 2023.

[5] *Turning the Supertanker,* a Deutsche Bank investment advisory report on Reed Elsevier (2005): "The industry structure can only be described as bizarre - the state funds most research, pays the salaries of most of those checking the quality of research (in peer review processes), and then buys most of the published product. This has been rather elegantly described as the "triple-pay" model." And further: "bluntly, we believe that the professional publishers add little value to the research process. (...) How happy are you, as taxpayers, that your governments are enabling private sector operators, with very little invested capital, to earn 40% operating margins?"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ABOUT THE AUTHOR

I was born in Hamburg, on the 4th of April, 1994. Nature and wilderness have been my life's themes from very early on, and I spent my childhood watching birds, raising tree saplings and collecting mushrooms. In 2012, I started my bachelor studies in Biology at the Philipps-Universität Marburg, towards the end of which I discovered my fascination for evolution as a unifying theme in nature. In 2015 I moved to Munich for the master course 'Evolution, Ecology and Systematics', where I studied the phylogenetic relationship between Darwin's Star Orchid and Morgan's Sphinx moth under the tutelage of Susanne Renner. At the time, I grew frustrated with the difficulties to generalise from the specific circumstances of empirical studies, and also with the dependence on the tools, thoughts and concepts developed by others. This was unacceptable to me, and I therefore decided to look behind the curtain of theory, which brought me to the lab of Franjo Weissing and the beautiful city of Groningen. Here I found a home for my master thesis and, after a gap year spent in South Africa, Colombia and a lonely German forest, the place where I began my PhD project in September 2018, the final product of which you now hold in your hands. I am now set to begin a postdoc position in Bern on the division of labour in cooperatively breeding cichlids.

LIST OF PUBLICATIONS

1. **Netz, C.**, Hildenbrandt, H. and Weissing, F. J. (2022). Complex eco-evolutionary dynamics induced by the coevolution of predator–prey movement strategies. *Evolutionary Ecology*, 36(1):1-17.
2. **Netz, C.**, Ramesh, A., Gismann, J., Gupte, P. R. and Weissing, F. J. (2022). Details matter when modelling the effects of animal personality on the spatial distribution of foragers. *Proceedings of the Royal Society B*, 289(1970):20210903.
3. Gupte, P. R., **Netz, C.** and Weissing, F. J. (2023). The joint evolution of animal movement and competition strategies. *The American Naturalist*, Just Accepted.
4. **Netz, C.**, Ramesh, A. and Weissing, F. J. (2023). Ideal free distribution of unequal competitors: spatial assortment and evolutionary diversification of competitive ability. *Animal Behaviour*, 201:13-21.
5. **Netz, C.** (2022). Effects of development and parental care on Hamilton's force of selection. *bioRxiv*, 2022-10.