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Introduction

1.1 Why species?

This book is about species. Indeed, every ecology and evolutionary biology book is about species, because all life is classified into units of diversity that we call species. But this book is about the units themselves—what species are, how they form, the consequences of species boundaries and diversity for evolution, and patterns of species accumulation over time. Finding a title was hard because 'species' is used as a catch-all term for organisms and life. This is not a book about the whole of evolutionary biology and I was painfully aware that an earlier author had first dibs on a similar title for a more general account of the evolution of life. Underline the word species on the front cover and I hope the aim of the book is clear.

Species are central for understanding the origin and dynamics of biological diversity. Explaining why lineages split into multiple distinct species is one of the main goals of evolutionary biology. Yet, we often take the existence of species and their properties for granted. Precisely what we mean by species and whether they really exist as a property of nature has been widely discussed, but rarely modelled or tested critically with data. Approaches for understanding the origins of diversity differ markedly within species (the realm of microevolution) versus between species (the realm of macroevolution). Does this reflect a true discontinuity in biological processes or simply an artefact of how different scientific fields developed? In turn, genetic and ecological interactions between species should play a dominant role in structuring evolutionary dynamics. Yet, most studies of contemporary evolution focus on single populations, and do not consider explicitly the effects of multiple coexisting species.

The time is ripe to revisit the concept of species and its consequences for how organisms evolve. Description of the diversity of life has been revolutionized by the use of molecular markers and increasingly by whole-genome sequencing. With the power to reconstruct the tree (or web) of life for all organisms, do we still need species? Maybe it would be better to abandon them altogether and portray diversity as a branching (sometimes fusing) hierarchy?

The central thesis of this book is that species represent more than just a unit of taxonomy; they are a model of how diversity is structured and how groups of related organisms evolve. The 'species hypothesis' is that natural processes act in a way that generates units of diversity, called species, which then determine evolutionary dynamics: organisms interact in a qualitatively different way within species than between

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species. In theory, diversity could be structured in other ways; for example, organisms might interact with each other via reproduction, sharing of genes, competition, and so on in ways that just decline gradually with increasing evolutionary divergence. What is exciting is that tools are now available to test alternative models for the structure of diversity and to estimate the role of alternative processes such as selection and gene flow. Species are no longer the focus of philosophical debate, but they represent a theory amenable to empirical tests and estimation. The answer is important both for understanding where diversity comes from and for predicting contemporary evolution.

1.2 The evolutionary dynamics of species

The scope of the book can be summarized as follows. Try to visualize all life on earth tracing back over time to its origins and forward into a hazy future (Fig. 1.1). Myriad strands are visible that constitute lineages of genes, which come together in individual organisms visible as dots on the plane of the present. In some parts of life, these strands shuffle each generation through sexual reproduction; in others they associate over longer periods through clonal inheritance and only rarely transfer genes. Zooming out a little, dots of contemporary individuals do not form a starry sky on the plane of the present, but group in clusters that share similar genetic composition and biological characteristics (Fig. 1.1). Tracking backwards and forwards in time, it can be seen that the strands of gene lineages group within these clusters, whereas there are few exchanges between them. These clusters are our hypothetical species units. They are evolutionarily independent, because interactions such as gene exchange and competition are stronger within species, and weaker, rare, or absent between them. We draw ellipses round them to highlight our hypothesis that this is the structure of diversity.

What then describes the evolutionary dynamics of these species entities? And what processes control those dynamics and cause them to vary among different types of organisms? Species originate by speciation. Tubes formed by the time-integration of species circles occasionally split and diverge into two separate species (Fig. 1.1). Biological attributes of individuals and environmental conditions around these divergence events reveal the causes of speciation, such as geographical isolation and the availability of new ecological niches. In turn, species are lost through extinction, when the final individual from a species dies with no descendants.

Speciation operates over long timescales and most of our understanding comes from retrospective studies. The snapshot of time since pioneering naturalists of the 1700s and 1800s until the present has seen few species origins across the tree of multicellular life (although plenty of extinctions). But over these contemporary timescales (Fig. 1.1), species continue to evolve as they encounter new conditions and shift their geographical locations. A great deal is known about the genetic and environmental determinants of evolution within species and populations. Often these accounts focus on a single species at a time. Yet, species can still interact with each other either ecologically or by occasional exchange of genes through hybridization or other

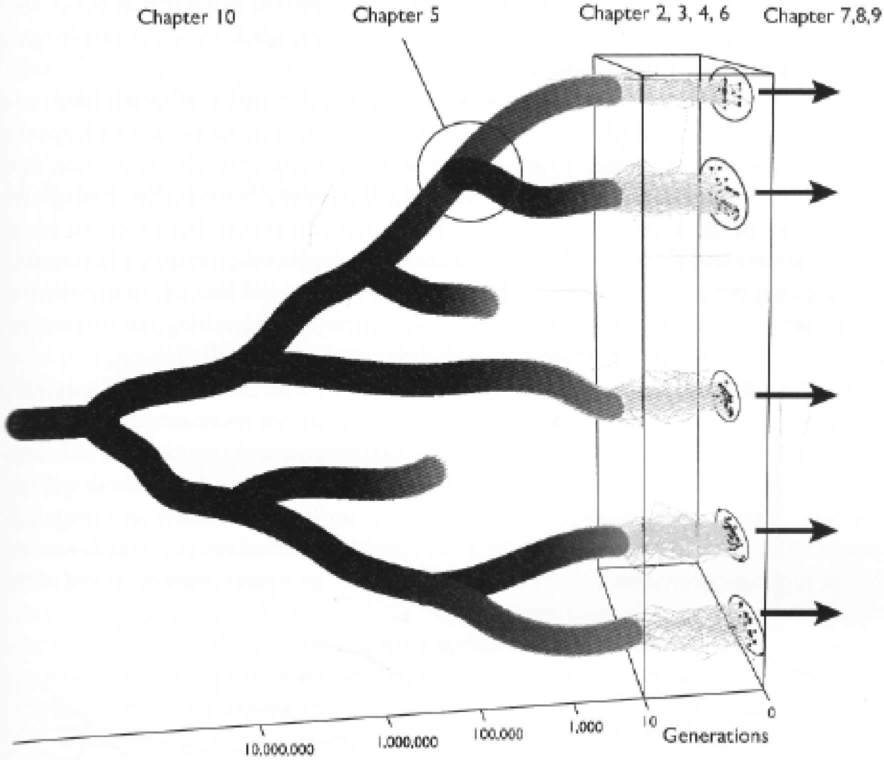

Fig. 1.1 An illustration of the evolutionary dynamics of species. Individual organisms in the present are shown as black dots on a plane representing genetic and phenotypic variation. Shared ancestry is represented by grey lines showing parent–offspring links such that vertices represent individuals during previous generations. Individuals are grouped in genetic clusters that exchange genes but with limited gene exchange between them. These are hypothetical species units denoted by ellipses. Zooming out to longer timescales, tubes representing these species units originate by speciation and are lost by extinction. Species units are important to understand not only the origin of diversity patterns in the wider clade but also how the clade will respond to future changes (represented by arrows).

mechanisms of gene transfer. The degree of ecological similarity or strength of reproductive barriers between species—which depend on the history and forces behind their initial divergence and how long they have been in contact or isolated from each other—will affect how sets of species evolve in changing conditions. The nature of species and their interactions is therefore a vital component for predicting contemporary and future evolution.

As an extra layer of complexity, contemporary evolution in turn feeds back to affect the likelihood of both speciation—that is, whether divergence occurs and the resulting new species survive long enough to leave a new 'tube' visible on the species tree—and extinction. Full specification of the dynamics of speciation, evolution of those species, and extinction requires these feedbacks to be included, which is challenging because of the wide span of timescales.

These processes together shape the large-scale dynamics of branching and expansion across the whole tree of life. Zooming out to a distance at which species themselves appear as points, whole groups of species rise and fall via chance, new innovations, or as conditions change (Fig. 1.2). We normally view this through the murky glass of the fossil record or phylogenetic reconstruction, but from our idealized viewpoint we can see the detailed dynamics of species origination and extinction as branching patterns on the tree. The pattern of growth and decline in numbers of species is not independent between groups, but can depend on ecological interactions between species making up those major clades.

This describes the scope of this book. What is the structure of diversity? Does it fall into species units and how do we delimit them? What causes diversification into multiple species? How does the nature of species boundaries and interactions influence ongoing evolution in diverse assemblages? And how do all these processes shape biodiversity? The focus is intentionally broad. Much work on the nature and origins of species has focused in detail on genetic and ecological mechanisms behind the evolution of reproductive isolation. My aim is to step back and present an overview of the

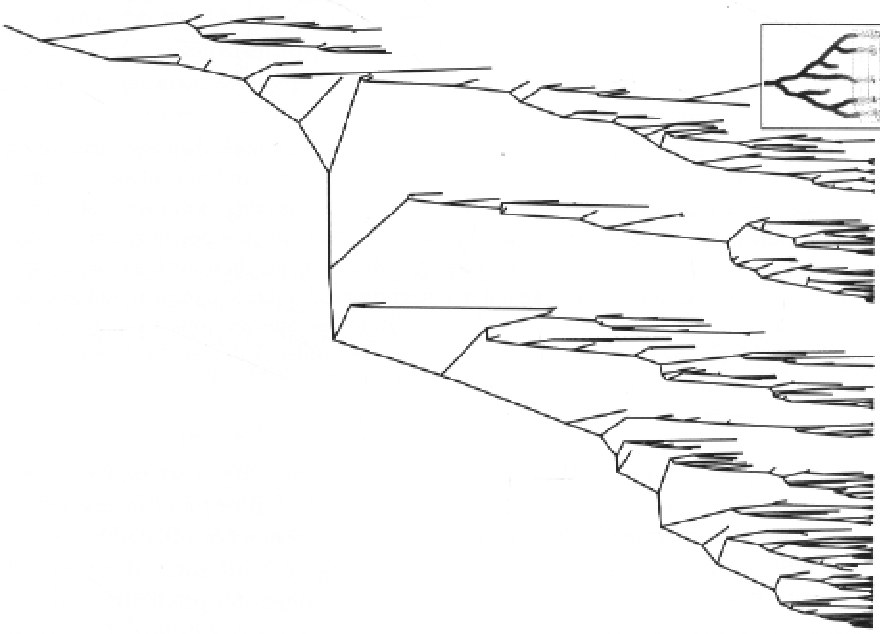

Fig. 1.2 Proliferation of species lineages over long timescales. Zooming out on the clade represented in Fig. 1.1, indicated by the rectangular inset, reveals the growth and decline of species richness through differential levels of speciation and extinction across clades.

evolutionary biology of species, incorporating their nature, origins, proliferation, and consequences. I have attempted to go back to basics. What is the pattern of nature that we are trying to explain? What are the potential processes that explain this pattern? And what are the consequences for other evolutionary phenomena?

1.3 Structure of the book

The book chapters follow the order described in section 1.2. Chapters 2 to 4 look at what species are and how to delimit them. Chapter 2 first considers the forces that cause lineages to diversify into multiple distinct and independently evolving groups and presents definitions of key concepts. I discuss whether forces of diversification act to generate discrete units, that is, species, rather than alternative diversity patterns such as a continuum of forms. The chapter aims to develop concrete theory that makes testable predictions for distinguishing alternative models of the structure of diversity.

The next two chapters test these ideas by considering empirical evidence for the existence of species versus alternative hypotheses for the structure of diversity. Focusing first on evidence for genetic and phenotypic clustering, chapter 3 outlines the theory and practice of species delimitation. Is there statistical evidence that discrete species are real and constitute the major unit of diversity in many taxa? Chapter 4 then describes methods for delimiting species based on the action of reproductive isolation and divergent selection. Prospects for using whole-genome data for interrogating diversity patterns and processes across whole clades—only recently feasible for microbes, and not yet easy for eukaryotes at such scales, but rapidly approaching—are discussed.

Chapter 5 shifts the focus to consider what causes a single species to split into multiple descendants, namely the process of speciation. Understanding speciation requires knowledge of when and why scenarios arise that promote splitting of a previously cohesive species, as well as genetic mechanisms operating once such conditions arise. I review evidence for causes of speciation from analysis of speciation patterns across clades. Dispersal and gene flow are identified as key parameters explaining speciation rates in different organisms. I ask whether speciation rates and patterns depend mainly on ecological opportunity or on intrinsic genetic properties of organisms.

Chapter 6 concludes the discussion of the nature and origins of species with an in-depth look at the consequences of sex, recombination, and alternative lifestyles for species and speciation. Many authors argue that species are only found in sexual organisms and define species by reference to recombination. Others have hesitated over the reality of species in microbes, because they do not reproduce sexually (although recombination by other means is common). I evaluate the theory and evidence for the importance of recombination in generating diversity patterns, by comparing sexual and asexual clades, and microbes with alternative modes of reproduction.

The next three chapters investigate the consequences of species for contemporary evolution. Chapter 7 explores the effects of different types of species boundaries on how organisms evolve in new environments. Many studies of contemporary evolution assume that evolution can be predicted from understanding selection and genetics on a species-by-species basis. I describe examples where this assumption does not apply. For example, will a gene for antibiotic resistance spread across species boundaries? That depends in part on genetic barriers to exchange and in part on the ecological consequences of transferring a trait that affects competitive interactions.

Continuing this line of reasoning, chapter 8 explores the effects of ecological interactions among species on evolution. Species diversity evolves because lineages diversify to use distinct resources and habitats. The standing diversity of traits and resource use will therefore have a great impact on how each species evolves when faced with a change in the environment. I present simple models showing how interactions affect evolution and discuss results from experiments evolving communities of co-occurring microbial species. Evolutionary dynamics are greatly altered by the presence of multiple co-occurring species in ways that will depend on the forces behind the origin and coexistence of those species.

Spurred on by theories and results in the previous chapters, chapter 9 outlines challenges and possible solutions for predicting evolutionary dynamics of whole communities in the wild. The advantages of adopting a synthetic approach are illustrated through discussion of real-world cases, including managing gut bacteria for human health and ecosystem responses to climate change. Research questions and broad approaches are outlined to extend current work to whole communities of microbes and longer-lived eukaryotes. I argue that understanding and prediction of evolutionary dynamics will only be possible by considering whole systems of interacting species. A key challenge is to track evolution over intermediate timescales of around 100–10,000 generations that are too long to follow observationally for long-lived organisms, but too short to be resolved by fossil and phylogenetic approaches.

Chapter 10 expands to consider how the above processes influence species diversity over long timescales and broad spatial scales. Diversity patterns result in part from speciation and in part from dispersal, evolution, and extinction. Classical studies looked for traits that speed up rates of diversification. Although these studies found interesting patterns, ecological opportunity and limits seem to be more important in shaping diversity than fast diversification per se. The effect of a given trait depends on the environment. I conclude the chapter by discussing how patterns of selection and isolation shape higher-level diversity patterns. The same processes that shape genetic variation within species also shape diversity patterns above the level of species, but playing out over longer timescales across sets of interacting species.

Chapter 11 aims to synthesize these theories of species origins and consequences. An approach that incorporates the nature of species, the forces behind their origin and coexistence, and their genetic and ecological interactions is essential to tackle these questions. We are now in a position to embrace the complexity of the diversity of life.